Plant Physiol. (1978) 62, 185–190

A Comparison of Photosynthetic Characteristics of *Encelia* Species Possessing Glabrous and Pubescent Leaves[1]

Received for publication December 5, 1977 and in revised form March 8, 1978

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ABSTRACT

Measurements of the dependence of photosynthesis on light, CO_2, and temperature are reported for two species of *Encelia* (Compositae) which differ in leaf pubescence and in geographical distribution. *Encelia californica* is glabrous and occurs in relatively mild, but arid habitats and *Encelia farinosa* is heavily pubescent and occurs in hot, arid habitats. Both species possess the C_3 photosynthetic pathway. Under high irradiances and normal atmospheric conditions the two species have high photosynthetic rates, exceeding 3 nanomoles of CO_2 per square centimeter per second (48 milligrams of CO_2 per square decimeter per hour) and complete light saturation does not occur by full noon sunlight. The high photosynthetic capacity is related to a high efficiency of utilization of intercellular CO_2 combined with high stomatal conductance. Leaf estimates of total soluble protein and fraction I protein are higher in these species than in most plants, although the proportion of fraction I protein is not higher. Both *E. californica* and *E. farinosa* attain a maximum rate of photosynthesis between 25 and 30 C, despite the fact that the two species grow in very different thermal habitats. Neither *E. californica* nor *E. farinosa* shows significant acclimation in the temperature dependence of photosynthesis when grown under different temperature regimes. The presence of leaf hairs which reduce leaf absorptance and consequently leaf temperature plays an important part in the ability of *E. farinosa* to survive in its native high temperature environment. When the effects of pubescence are taken into account, there are few if any significant differences in the photosynthetic characteristics of the two species.

Growing in the arid regions of southwestern North America are several species of the genus *Encelia* of the Heliantheae tribe of the family Compositae (20). Most *Encelia* species are distributed allopatrically and occur in habitats of contrasting temperature regimes. For instance, mean daily maximum air temperature for Blythe, Calif. (interior desert), where *Encelia farinosa* occurs, is 35.2 C in May, whereas in Santa Barbara, Calif. (coastal sage vegetation), where *Encelia californica* occurs, the mean daily maximum air temperature in May is 20.6 C, almost 15 C lower (22).

Leaves of species within *Encelia* are distinguished by the presence or absence of leaf hairs (pubescence) (20). These multicellular hairs form thick mats on both the upper and lower leaf surfaces. The pubescence can reduce leaf absorptance to as low as 29% of the incident photosynthetically active solar radiation (400–700 nm) in *E. farinosa* (8). In comparison, leaf absorptance to photosynthetically active radiation is 84% in the glabrous leaves of *E. californica* (8).

There are two major effects of this leaf pubescence in *E. farinosa*. Since leaf pubescence reflects solar radiation, it reduces the heat load of the leaf and, thus, reduces leaf temperature (7, 9). However, it also reduces the absorption of photosynthetically active solar radiation, thus reducing the rate of photosynthesis (8, 9). These hairs appear to have a minimal effect on the leaf boundary layer resistance (9).

Given that *E. californica* and *E. farinosa* grow in habitats which differ greatly in air temperatures, the question asked in this study was whether the photosynthetic characteristics of the two species differ when light reflectance by pubescence is taken into account. A second and closely related question posed concerned the ability of each species to acclimate when grown in the temperature regime of the other species.

MATERIALS AND METHODS

For laboratory measurements, plants were grown from seed in 10-cm pots containing Perlite. These were watered twice daily with nutrient solution (14). The plants were grown with natural lighting during the summer months in phytocells (environmental growth facilities capable of precise control of the temperature, CO_2, and water vapor levels) under either a 35 C day and 25 C night regime (phytocell A) or a 20 C day and a 15 C night regime (phytocell B). Attenuation of the solar beam by the phytocell glass and structural support was about 20%. A more complete description of the phytocells has been provided by Björkman *et al.* (4). The two temperature regimes were chosen so as to be similar to the spring growing conditions for these plants in their native habitats. To compare the responses of plants grown under these controlled conditions and in the field, photosynthetic characteristics of *E. farinosa* were measured in a field experimental garden (4) on the floor of Death Valley, Calif. Plants in the Death Valley garden were irrigated daily.

Leaf Absorptance Measurements. Leaf absorptances to incident quantum flux were measured with an Ulbricht integrating sphere (23-cm diameter), coated on the inside with a thin layer of magnesium oxide. The theory and description of the Ulbricht integrating sphere have been discussed by Rabideau *et al.* (18). Absorptances for the 400 to 700 nm band were measured by directing light from a xenon lamp or sunlight into the integrating sphere (for sunlight using a mirror attached to a heliostat) through an opening in the sphere. A quantum sensor (model 190-SR, Lambda Instruments, Lincoln, Nebr.), attached to the integrating sphere, was used to measure light reflected from the leaves and the magnesium dioxide standard in the 400 to 700 nm band.

Gas Exchange Measurements. For gas exchange measurements on an incident light basis, a single attached leaf was inserted into a ventilated open system leaf chamber (total volume 150 ml) similar to that described by Björkman and Holmgren (3). Light

[1] Supported by National Science Foundation Grant BMS 75-03933 and a Carnegie Institution Predoctoral Fellowship to J. E. C. I. W.-D. P. B. Publication No. 614.

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was provided from a 2.5-kw short arc xenon lamp (Christie Electric Corp., Los Angeles) in conjunction with appropriate lenses, heat filters, and neutral density filters. Quantum flux incident on the leaves was continuously monitored with silicon cells that had been calibrated against a quantum sensor. For field measurements of photosynthesis, light was provided by a Sylvania 1,000-w metal arc lamp together with appropriate housing and power supply (Hubbell Lighting Division, Oakland, Calif.).

Leaf temperature was measured with very fine copper-constantan thermocouples attached to the lower surface and was adjusted by controlling the temperature of the leaf chamber water jackets. Gas from a cylinder containing 21% O_2 in N_2 (CO_2-free air) was continuously and precisely mixed with 1% CO_2 in N_2 by a high capacity gas mixing pump (model G-27/3-F, Wösthoff OHG, Bochum, Germany). The resulting gas stream was humidified by passing through a vessel, maintained at 5 C above the desired dew point. The vessel contained a large area of Miracloth, which was wetted by capillary uptake of water that had been slightly acidified with H_2SO_4. The gas stream was then passed through a dual coil water jacketed condenser whose temperature was kept at the desired dew point. A small portion of this humidified gas stream was passed at a constant rate (250 ml min^{-1}) through a humidity sensor (hygrometer HM-111, Weathermeasure Corp., Sacramento, Calif.) and then through the reference cell of a differential CO_2 analyzer (model 865, Beckman Instruments, Fullerton, Calif.). Another portion (300- to 800-ml min^{-1}) was passed via an electronic flow meter (model DP45, Validyne Corp., Northridge, Calif.) to the leaf chamber. A portion (250 ml min^{-1}) of the gas returning from the chamber was passed through another humidity sensor, the sample cell of the differential CO_2 analyzer, and then through an O_2 analyzer (model 209, Westinghouse Electric Corp., Pittsburgh, Pa.). All sensor inputs were connected to a real time computer based data acquisition system (model S-9, Non-Linear Systems, Del Mar, Calif.) described earlier by Björkman *et al.* (4). The system was programmed to make appropriate linearizations, corrections, and conversions, and to compute rates of CO_2 and water vapor exchange, stomatal conductance to gaseous diffusion, and intercellular CO_2 pressure. It also provided a record of the incident quantum flux, leaf temperature, and of the O_2, CO_2, and water vapor partial pressures in the leaf chamber. Several parameters were continuously displayed on analog recorders, providing a backup record and permitting a qualitative assessment of the experimental manipulations. The gas exchange system was housed in a mobile laboratory which allowed use of the same system for both field and laboratory measurements.

Light absorptance values for individual leaves used in the experiments were determined with the apparatus described above.

In the photosynthesis-light response experiments, leaves were first exposed to light at an intensity of about 200 nE cm^{-2} sec^{-1} (400–700 nm). After a constant photosynthetic rate had been obtained, the light was lowered in steps to total darkness, at each step attaining a constant photosynthetic rate before advancing to the next lower light level. Leaf temperature was held constant during each experiment at 30 C. The CO_2 partial pressure was that of normal air (310–330 μbar) and the water vapor pressure deficit was kept at about 10 mbar.

In a series of experiments in which atmospheric CO_2 partial pressure were varied, the results are expressed as a function of the intercellular CO_2 partial pressure. This expression allows for the removal of CO_2 gradients associated with low stomatal conductances. The intercellular CO_2 concentration is calculated as

$$CO_{2_{int}} = CO_{2_{amb}} - P/C$$

where $CO_{2\ int}$ and $CO_{2\ amb}$ are the intercellular and ambient CO_2 partial pressures, P is the net photosynthetic rate, and C is the leaf conductance to CO_2 (determined indirectly as the leaf conductance to water loss divided by 1.56). Light intensity during these experiments was constant at an incident irradiance of 170 nE cm^{-2} sec^{-1}. Leaf temperature was kept at 30 C and the water vapor pressure deficit was approximately 10 mbar.

For measurements of the temperature dependence of photosynthesis, the rates of photosynthesis and transpiration were initially measured with leaf temperature equal to 30 C. Incident light level was 170 nE cm^{-2} sec^{-1}, ambient CO_2 pressure 325 μbar, and water vapor deficit less than 10 mbar. After photosynthetic equilibrium had been reached, the leaf temperature was lowered in several steps (about 5 C each), again a new steady-state rate was achieved before the next temperature change. When photosynthesis at the lowest temperature had been measured, leaf temperature was increased to 30 C. After the photosynthetic rate at 30 C had achieved a rate equal to the original value, the leaf temperature was increased in steps of 5 C each.

In each laboratory gas exchange experiment sample size was two to three shrubs. From each shrub mature leaves varying from 10 to 20 cm^2 in area were used. The experimental data presented are typical results from individual experiments and not means of all experiments. For the laboratory measurements of photosynthesis the variation in rate between leaves was less than 10%. The field observations of photosynthesis in *E. farinosa* are the results of single observations only. Previous analysis of the gas exchange system had indicated that sources of error are small (± 2%) (16).

Chl and Protein Determinations. Leaf Chl content and Chl *a*/*b* ratios were determined in 80% acetone as described by Arnon (1). Soluble protein was determined with the Lowry method (13) and total protein as measured by percent nitrogen by the Kjeldahl method (12).

For the determination of fraction I protein, a 1.5-ml sample of ground *Encelia* leaves in extraction buffer was placed on a 38-ml 10 to 30% sucrose gradient according to the procedure of Björkman *et al.* (2). These samples were placed in a centrifuge and spun at 84,000*g* for 60 hr at 2 C. The gradient was then fractioned into 1-ml samples and soluble protein content for each fraction was determined.

RESULTS

Light Dependence of Photosynthesis. There were substantial differences at high irradiances in the light response curves of *E. californica* when this plant grown under the two different temperature regimes in the phytocells and measured at a common temperature of 30 C (Fig. 1). Peak photosynthetic rates at incident

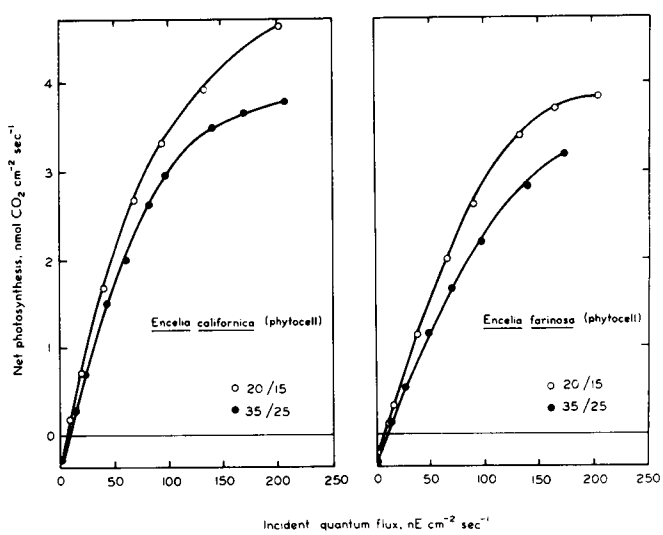

FIG. 1. Photosynthesis *versus* light response curves for intact leaves of *E. farinosa* and *E. californica* grown in phytocells at two different temperature regimes. Measurements were made at a leaf temperature of 30 C, 325 μbar CO_2, 21% O_2, and a water vapor pressure deficit of less than 10 mbar.

quantum flux densities of about 200 nE cm^{-2} sec^{-1} were 4.6 and 3.8 mol of CO_2 cm^{-2} sec^{-1} for plants grown in 20/15 C and 35/25 C growth conditions, respectively. The differences in photosynthetic rates diminished as the quantum flux density was reduced. Values for the incident quantum yields were similar for the two growth regimes. Under both growth conditions, the net photosynthetic rates were high in comparison with reported values for many other C_3 plants at high quantum flux densities and normal CO_2 and O_2 levels. Additionally, unlike the situation in most C_3 species, the photosynthetic rate did not saturate at quantum flux densities approaching full noon sunlight, which on a horizontal surface at the summer solstice is just slightly greater than 200 nE cm^{-1}.

Net photosynthetic rates for *E. farinosa* grown under the two different temperature regimes in the phytocells differed both in maximum rates and incident quantum yields when measured at 30 C leaf temperature (Fig. 1). Maximum photosynthetic rates were 3.2 and 3.8 nmol of CO_2 cm^{-2} sec^{-1} for the 35/25 C and 20/15 C temperature grown plants, respectively, while quantum yields on the basis of light incident on the leaves were 0.033 and 0.041 nmol of CO_2 fixed per einstein. These differences can be attributed to the differences in leaf absorptance measured using the Ulbricht integrating sphere. Leaf absorptances measured were 80 and 65% for 20/15 C and 35/25 C growth conditions, respectively. When the photosynthetic rates are plotted on the basis of light absorbed by the leaves (incident quantum flux × leaf absorptance), there are no differences between the curves. Plotting the data on an absorbed quantum basis also removed most of the observed differences between the rates for *E. californica* and *E. farinosa* at low and intermediate light levels. This suggests that there may have been some small differences in the photosynthetic rates at the highest quantum flux densities between the two species when grown in the same regime, as well as within each species grown under different regimes. However, almost all of the measured differences in photosynthetic rates between species and growth conditions were due to leaf absorptance differences.

Leaf conductances to water loss at moderate and high light levels were high in both species under both growth regimes. Estimates of leaf conductances were 1.4 and 2 for *E. californica* and 1.7 and 2 cm sec^{-1} for *E. farinosa* under 35/25 and 20/15 C growth conditions, respectively. Intercellular CO_2 pressures for *E. californica* and *E. farinosa* leaves calculated using these leaf conductance estimates ranged from 217 to 232 μbar.

Field observations in both winter and summer of the photosynthesis *versus* light response curves of *E. farinosa* leaves were very similar to those observed in the high temperature phytocell-grown individuals (Fig. 2). The photosynthetic rate at full noon sunlight was 3.7 nmol of CO_2 cm^{-2} sec^{-1}, but this rate was not a light-saturated value. There appeared to be little change in the light response curves through the year. Leaf conductance to water loss in both winter and summer leaves was high, averaging approximately 1.7 cm sec^{-1} at high quantum flux densities. As a consequence intercellular CO_2 pressures ranged from 208 to 213 μbar at moderate and high quantum flux densities.

CO_2 Dependence of Photosynthesis. The dependence of the net photosynthetic rate on intracellular CO_2 pressure was quite steep in leaves of *E. californica,* irrespective of the growing condition (Fig. 3). The CO_2 dependence curves did not reach saturating levels at CO_2 pressures exceeding 600 μbar. At intracellular pressures of approximately 600 μbar and 21% O_2, the net photosynthetic rates of the *E. californica* leaves are 8.4 nmol of CO_2 cm^{-2} sec^{-1}, a high rate for any plant. When the intercellular CO_2 pressure is expressed as nmol cm^{-3} rather than μbar, the calculated initial slopes of the CO_2 dependence curves ($\Delta P/\Delta C_i$, where ΔP is the change in photosynthesis and ΔC_i is the change in intercellular CO_2 concentration) are 0.55 and 0.58 cm sec^{-1} for growth conditions of 20/15 C and 35/25 C, respectively.

The leaves of *E. farinosa* also possessed a high capacity for photosynthesis, but the absolute values plateaued at much lower rates and at lower CO_2 pressures suggesting that light intensity has become limiting (Fig. 3). Again, as with the *E. californica* measurements, these rates were measured at a leaf temperature of 30 C and an incident quantum flux density of 170 nE cm^{-2} sec^{-1}. Although the initial slopes are the same for plants grown under the two temperature regimes ($\Delta P/\Delta C_i$ of 0.53 cm sec^{-1}), the peak rates were quite different. Both *E. farinosa* response curves plateaued near 700 μbar. At intracellular CO_2 concentrations slightly greater than 700 μbar, the photosynthetic rates were 7.3 and 5.1 nmol of CO_2 cm^{-2} sec^{-1} for growth regimes of 20/15 C and 35/25 C, respectively. Most likely, the differences between the two *E. farinosa* curves result from leaf absorptance differences. Leaf absorptances for the cooler growth regime were 80%, whereas in the warmer growth environment the leaf absorptances were 65%. Since the incident quantum flux density was held constant in both experiments, the light intensities absorbed by the leaves will differ and light levels would become limiting at a lower intercellular CO_2 pressure in those leaves having a lower absorptance even if the photosynthetic capacities were the same.

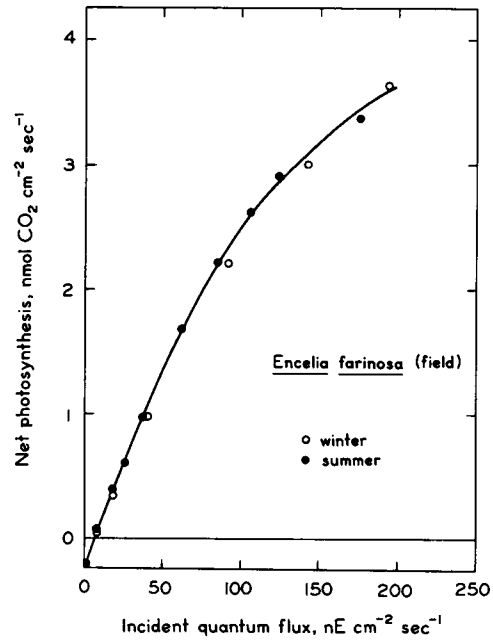

FIG. 2. Photosynthesis *versus* light response curve for intact leaves of *E. farinosa* grown in the Death Valley garden in the winter and the summer. Measurements were made under the same conditions as Figure 1. These measurements were made on leaves developed under summer conditions of midday air temperatures of approximately 43 C and winter conditions of midday air temperatures of approximately 18 C.

Field estimates of the CO_2 dependence of net photosynthesis in *E. farinosa* were in agreement with the laboratory measurements (Fig. 4). Leaf absorptances were quite similar to those found in the 35/25 C phytocell-grown plants. The CO_2 dependence curve saturated at about 600 μbar. At this intercellular CO_2 pressure, the peak rate was 5.6 nmol of CO_2 cm^{-2} sec^{-1}. The initial slope of the CO_2 dependence curve was 0.58 cm sec^{-1}, quite similar to the estimates for phytocell-grown plants.

The measurements of the CO_2 dependence of net photosynthesis for *E. farinosa* and *E. californica* suggested that the initial slopes of these response curves were the same although the rates at higher intercellular CO_2 pressures differed. To test whether or not this difference at high intercellular CO_2 pressures was due to a difference in the number of quanta absorbed, an experiment was conducted in which the absorbed quantum flux densities were made approximately the same for *E. farinosa* and *E. californica* leaves. It is difficult to achieve identical absorbed quantum flux densities because actual leaf absorptances cannot be determined

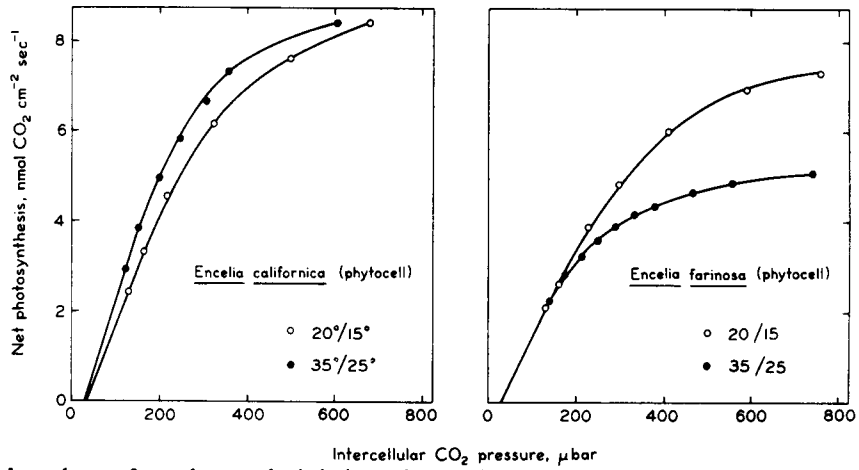

FIG. 3. Intercellular CO_2 dependence of net photosynthesis in intact leaves of *E. farinosa* and *E. californica* grown in phytocells at two different temperature regimes. Measurements were made at a leaf temperature of 30 C, 170 nE cm^{-2} sec^{-1}, 21% O_2, and a water vapor pressure deficit of less than 10 mbar.

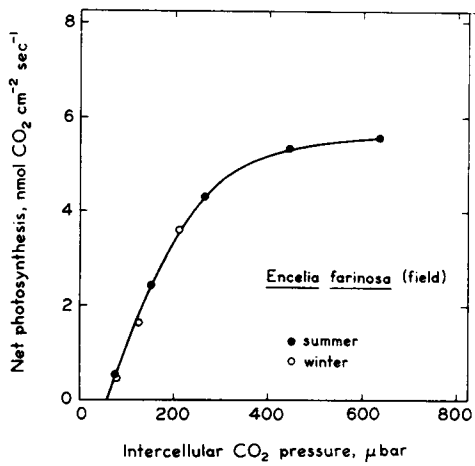

FIG. 4. Intercellular CO_2 dependence of net photosynthesis in intact leaves of *E. farinosa* measured in the Death Valley garden in the winter and the summer. Measurements were made under the same conditions as Figure 3. Growth conditions are the same as in Figure 2.

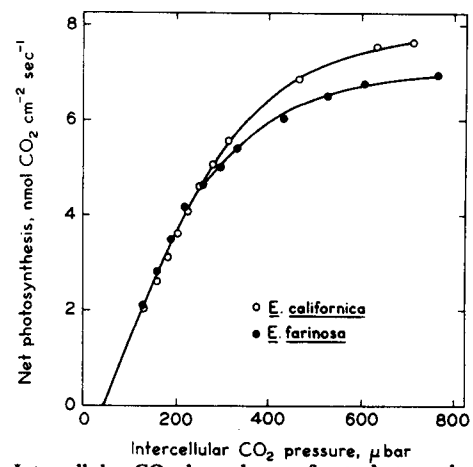

FIG. 5. Intercellular CO_2 dependence of net photosynthesis in intact leaves of *E. farinosa* and *E. californica* under conditions of similar absorbed quantum flux densities. Measurements were made at a leaf temperature of 30 C, 21% O_2, and a water vapor pressure deficit of less than 10 mbar.

until after the experiment has been completed. Figure 5 shows the CO_2 dependence of photosynthesis for these leaves under conditions of more similar absorbed quantum flux densities. The quantum flux densities absorbed were 135 and 170 nE cm^{-2} sec^{-1} for leaves of *E. farinosa* and *E. californica,* respectively. These data indicate that if the amounts of light absorbed by the photosynthetic tissues were the same, then the CO_2 dependence curves should be almost identical. Both species have $\Delta P/\Delta C_i$ values of 0.58 cm sec^{-1} and saturate at about 700 μbar with rates of 7 and 7.5 nmol of CO_2 cm^{-2} sec^{-1}. The results of this experiment and the previous experiments on the light dependence of photosynthesis in the two species suggest that there may be few if any intrinsic differences in the photosynthetic light dependence characteristics of *E. farinosa* and *E. californica.*

Temperature Dependence of Photosynthesis. In view of the great differences in air temperature between their respective native habitats it might be expected that these two species should differ in the temperature dependence of light-saturated photosynthesis. Measurements of the photosynthetic temperature responses showed that *E. californica* exhibited a pronounced dependence on leaf temperature (Fig. 6). Under both growth conditions, the rate of net photosynthesis declined sharply both below and above the temperature optimum. The temperature optimum for photosynthesis in *E. californica* was unaffected by growth conditions, remaining at 30 C. The photosynthetic rate at the temperature

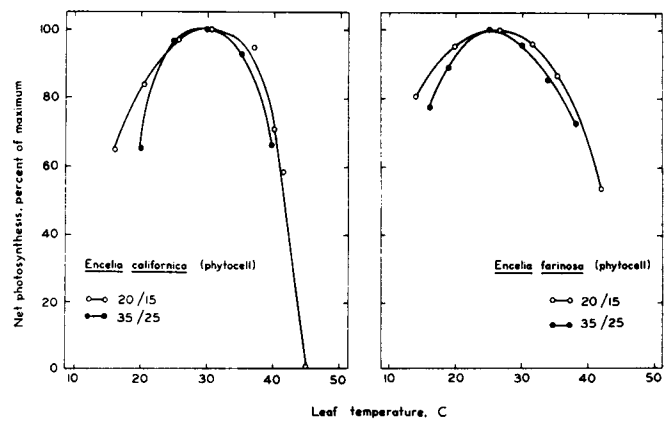

FIG. 6. Temperature dependence of net photosynthesis in intact leaves of *E. farinosa* and *E. californica* grown in phytocells at two different temperature regimes. Measurements were made at 170 nE cm^{-2} sec^{-1}, 325 μbar CO_2, 21% O_2, and a water vapor pressure deficit of less than 10 mbar.

optimum was similar in plants from the two growth conditions. Measured peak values were 4.1 and 3.9 nmol of CO_2 cm^{-2} sec^{-1} for plants grown at 20/15 C and 35/25 C, respectively. Leaves of *E. californica* grown at 20/15 C were unable to sustain photosynthesis at high leaf temperatures and compensation was reached at

46 C. Leaf temperatures approaching this value, however, do not occur in *E. californica* habitats.

In a response similar to that of *E. californica,* the temperature dependence of photosynthesis in *E. farinosa* remained unchanged between the two phytocell-growth conditions (Fig. 6). As with *E. californica* leaves, the temperature optimum remained constant. The optimum temperature for photosynthesis in *E. farinosa* was 25 C, 5 C below that for *E. californica.* This is contraty to what had been expected, since during the spring and summer, air temperatures are much higher in *E. farinosa* habitats than in *E. californica* habitats. The photosynthetic rates at the temperature optima are 4.4 and 3.8 nmol of CO_2 cm^{-2} sec^{-1} for *E. farinosa* plants grown in the phytocells at 20/15 C and 35/25 C, respectively. The temperature dependence of photosynthesis is steep although less pronounced in *E. farinosa* than in *E. californica.* At a leaf temperature of 42 C, net photosynthesis was only 54% of the rate at the temperature optimum.

The field measurements of the temperature dependence of net photosynthesis for *E. farinosa* show optima at 25 and 28 C for winter and summer conditions, respectively (Fig. 7). As with the phytocell-grown plants, the photosynthetic rate of the field plants was found to be strongly dependent on leaf temperature. Absolute rates of net photosynthesis at the temperature optimum were 3.2 and 3.4 nmol of CO_2 cm^{-2} sec^{-1} for winter- and summer-grown *E. farinosa* leaves.

The mean maximum daily air temperatures in the field were 18 and 43 C for January, and July, respectively. Initially, it may seem remarkable that these plants have a temperature optimum for photosynthesis so different from the air temperature of their environment. The difference between the optimum temperature for photosynthesis during the summer and the mean maximum air temperature is 15 C. If the leaf temperature had been equal to the air temperature during the summer months, we would expect leaves of *E. farinosa* to be photosynthesizing at only 30% of the rate at optimum temperature during midday.

Chl and Protein Contents. Chl, soluble protein, and Kjeldahl nitrogen contents were measured on leaves of *E. farinosa* and *E. californica* grown under the two temperature regimes in phytocells (Table I). Total Chl contents were slightly higher in *E. californica* (54.5 *versus* 48.7 μg cm^{-2}), although there were no significant differences within each species grown under the two regimes. Chl *a/b* ratios were consistently higher in *E. farinosa* and differed between growth regimes. There was no change in Chl *a/b* between growth regimes in *E. californica.*

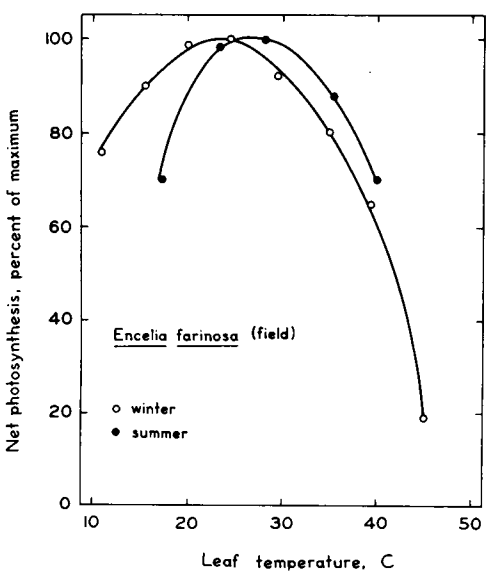

FIG. 7. Temperature dependence of net photosynthesis in intact leaves of *E. farinosa* measured in Death Valley in the winter and the summer. Measurements were made under the same conditions as in Figure 6. Growth conditions are the same as in Figure 2.

Table I. Leaf chlorophyll content, chlorophyll a/b ratios, soluble protein content, and Kjeldahl nitrogen content, and specific leaf weight for phytocell grown plants

Each value represents the average of at least four individual shrubs sampled. Procedures used are described in the Materials and Methods. Data presented are means and 1 standard deviation.

	Chlorophyll (μg cm^{-2})	Chlorophyll a/b	Soluble protein (μg cm^{-2})	Nitrogen (mg cm^{-2})	Leaf specific weight (mg cm^{-2})
Encelia farinosa					
35/25 C	49.6 ± 5.4	3.1 ± 0.1	1001 ± 62	0.43	11.78 ± 0.79
20/15 C	47.8 ± 8.7	3.6 ± 0.2	1212 ± 38	0.19	6.04 ± 0.78
Encelia californica					
35/25 C	55.3 ± 4.6	2.9 ± 0.2	-	0.28	8.88 ± 1.02
20/15 C	53.7 ± 6.1	2.9 ± 0.2	1361 ± 59	0.17	4.67 ± 0.50

Soluble protein as well as Kjeldahl nitrogen content values were high in both species (Table I). Estimates of total soluble protein exceeded 1,000 μg cm^{-2} for both species; Kjeldahl nitrogen on a leaf dry weight basis ranged from 0.17 to 0.43 mg cm^{-2}. From the data available it does not appear that differences exist between species for growth conditions. The soluble protein levels on a leaf area basis are unusually high and this is probably part of the reason why *Encelia* species are capable of high photosynthetic rates.

It is conceivable that in order to achieve high photosynthetic rates in *Encelia,* not only are high total soluble protein levels required, but perhaps a greater fraction of the protein is RuBP carboxylase than is found in most plants. To examine this possibility, the fraction I protein (RuBP carboxylase) content of *E. farinosa* and *E. californica* leaves was determined. Integration of the areas under the fraction I protein peaks in soluble protein gradients yielded estimates of 50% for both *E. californica* and *E. farinosa.* These values show that the percentage RuBP carboxylase content of the two *Encelia* species is approximately the same as in many other C_3 plants.

DISCUSSION

Maximum photosynthetic rates of both *Encelia* species are quite high when compared to the maximum rates of most C_3 plants (19, 23). The photosynthetic rates of C_3 species under high illumination and normal atmospheric CO_2 and O_2 levels are generally between 5 and 40 mg dm^{-2} hr^{-1}, whereas rates for *E. californica* and *E. farinosa* ranged from 50 to 72 mg dm^{-2} hr^{-1} (3.2–4.6 nmol cm^{-2} sec^{-1}). Photosynthetic rates approaching those of *Encelia* have been reported for sunflower, *Helianthus* (23). These two genera are closely related members of the subtribe Heliantheae of the family Compositae. Quantum yields for CO_2 uptake in *E. californica* and *E. farinosa* are normal for C_3 species (6). Therefore, the unusually high photosynthetic rates are not the result of an increase in quantum conversion efficiency, but must be a consequence of the ability of the plants to utilize higher light levels.

Two factors contribute to the ability of *E. californica* and *E. farinosa* to maintain high photosynthetic rates: a strong dependence of the rate of photosynthesis on CO_2 concentration, and a high stomatal conductance for CO_2 diffusion. The rate of photosynthesis can be mathematically represented in an Ohm's Law analogy as a CO_2 diffusion gradient from outside the leaf to the chloroplast divided by a series of impeding physical and "biochemical" resistances (5, 10). The slope of the photosynthesis-intercellular CO_2 pressure curve ($\Delta P/\Delta C_i$) is equivalent to the inverse of one of these resistances, namely the "internal resistance" (5, 10). Representative calculated values of this internal resistance in C_3 species vary from 6 to 33 sec cm^{-1} in sclerophylls and tree species (5, 10) and from 2.4 to 4.2 sec cm^{-1} in productive crop species (10). Estimating internal resistances for the two *Encelia* species as the inverse of $\Delta P/\Delta C_i$ yields values of 1.7 to 1.9 sec cm^{-1}, putting them in the range of some of the most productive agricultural species.

Having a high utilization of intercellular CO_2 alone is not sufficient to yield a high photosynthetic rate, since the rate of

photosynthesis also depends on diffusion of CO_2 from the outside air to the intercellular spaces. A high stomatal conductance is also necessary. In *E. californica* and *E. farinosa* stomatal conductances are high and in the same range as those reported for native annuals and crop species (10, 16). They are much higher than those reported for sclerophyllous vegetation (5).

The slope of the photosynthesis *versus* intercellular CO_2 dependence curve is presumably dependent on several components. Among these, the RuBP carboxylase concentration is likely to be prominent. RuBP carboxylase concentration is high in both *Encelia* species, but it appears that other soluble enzymes are also present in high concentration. This is indicated by the fact that while soluble protein content is higher in the two *Encelia* species than in many species, the fraction of this protein which is RuBP carboxylase is not substantially different from other C_3 species.

Intrinsic photosynthetic differences between *E. californica* and *E. farinosa* appear to be minimal. On an absorbed quantum basis, photosynthesis *versus* light response curves of *E. californica* and *E. farinosa* are similar, except at the highest quantum flux densities. The photosynthesis *versus* temperature response curves are remarkably similar with both species having an optimum temperature in the 25 to 30 C range. This may be surprising when one considers the contrast in temperature regime between the native habitats of these two species. Daytime air temperature in *E. californica* habitats are usually between 16 and 21 C during the growing season, whereas daytime air temperatures in *E. farinosa* habitats generally vary from 35 to 40 C during the summer growing season (22).

The apparent lack of temperature acclimation to changes in the growth regime was evident in both *Encelia* species. Not only did these two species share a similar temperature optimum for photosynthesis, but apparently neither species adjusts this optimum. Strain and Chase (21) observed this lack of acclimation in *E. farinosa,* but Mooney and Harrison (17) reported that acclimation did occur in *E. californica.* It is possible that there may be several factors responsible for the results obtained by Mooney and Harrison (17). In their study, both Chl content and net photosynthetic rate were quite low and the water vapor pressure deficit was permitted to increase with increasing temperature, presumably causing increases in stomatal resistance and decreases in the net photosynthetic rate.

The presence of leaf hairs (7–9) probably plays an important part in the ability of *E. farinosa* to survive in the hot, arid habitats of Mojave and Sonoran Deserts. The dead hairs surrounding both sides of the photosynthetic leaf tissue reflect light, reducing the heat load and consequently leaf temperature. The leaf undertemperature (leaf temperature below that of air) of *E. farinosa* during the spring and summer months allows the leaf to photosynthesize at or near the temperature optimum (9). The temperature dependence of net photosynthesis does not show any evidence of acclimation in *E. farinosa.* It would thus appear that for *E. farinosa,* the ability to invade desert habitats is the result of morphological adaptation and not physiological or biochemical adaptations as is the case in many desert species (11, 15, 21).

Acknowledgments—We thank H. A. Mooney and W. R. Briggs for their helpful comments and E. Ehleringer for her constant encouragement. We thank the personnel at the Death Valley National Monument for permission to conduct studies on these lands.

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