

Photosynthetic responses to slowly decreasing leaf water potentials in *Encelia frutescens*

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Abstract. The importance of reduced leaf conductance (stomatal and boundary layer) in limiting photosynthetic rates during water stress was studied in *Encelia frutescens*, a drought-deciduous leaved subshrub of the Mohave and Sonoran Deserts. Light-saturated CO_2 assimilation rates of greenhouse grown plants decreased from $42.6 \pm 1.6 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ ($\bar{x} \pm \text{s.e.}$) to $1.7 \pm 1.7 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ as leaf water potential decreased from -1.5 MPa to -4.0 MPa . The dependence of light saturated CO_2 assimilation rate on leaf intercellular CO_2 concentrations between 60 and $335 \mu\text{l l}^{-1}$ was also determined as leaf water potential declined. This enabled us to compare the effects of leaf water potentials on limitations to carbon assimilation imposed by leaf conductance and by intrinsic photosynthetic capacity. Both leaf conductance and intrinsic photosynthetic capacity decreased with decreasing leaf water potential, but the decrease in leaf conductance was proportionately greater. The relative stomatal limitation, defined as the percent limitation in photosynthetic rate due to the presence of gas-phase diffusional barriers, increased from 11 ± 2 ($\bar{x} \pm \text{s.e.}$) to $41 \pm 3\%$ as water potentials became more negative. Since both leaf conductance and intrinsic photosynthetic capacity were severely reduced in an absolute sense, however, high photosynthetic rates could not have been restored at low leaf water potentials without simultaneous increases in both components.

Introduction

Encelia frutescens (Gray) is a drought-deciduous leaved subshrub of the Mohave and Sonoran Deserts. Over its distribution, the amount and timing of precipitation are highly unpredictable on both a seasonal and annual basis. In response, *E. frutescens* is opportunistic, exploiting periods of high soil moisture whenever they occur. Under favorable soil moisture conditions, *E. frutescens* is characterized by high growth rates and copious flowering. While the exhaustion of soil water reserves eventually leads to leaf abscission and dormancy, leaves of *E. frutescens* may also experience varying degrees of intermittent water stress during the time that the plants bear leaves, because of the unpredictable nature of additional rainfall. The effect of decreasing leaf water potentials on the photosynthetic behavior of *E. frutescens* should, therefore, be of great impor-

tance in understanding how net carbon gain is regulated over the growing season.

A reduction in photosynthetic rate with decreasing leaf water potential has been observed in virtually all plants (Hsiao and Acevedo 1974). The rate at which photosynthesis declines as leaf water potential (ψ_l) becomes more negative, however, differs widely (Odening et al. 1974; Lawlor 1976; Ludlow 1976; Mooney et al. 1976; O'Toole et al. 1977; Björkman et al. 1979; Ehleringer 1983; Forseth and Ehleringer 1983). Similarly, leaf conductance (stomatal + boundary layer) to water vapor (g) also decreases with decreasing ψ_l , but as with photosynthetic rates there is considerable variation in the rate of decline depending on species and pretreatment (Hsiao and Acevedo 1974; Ludlow 1980). If the intrinsic photosynthetic capacity of the leaf is unaffected by decreasing ψ_l , then the decreases in photosynthetic rate with decreasing ψ_l will be due to decreases in g . However, proportional decreases in g and intrinsic photosynthetic capacities would mean that stomatal behavior is only partially responsible for decreased photosynthetic rate at low ψ_l . The relative decreases in g and intrinsic photosynthetic capacities seem to vary between plants (Boyer 1970; Redshaw and Meidner 1972; Osonubi and Davies 1980; Forseth and Ehleringer 1983).

Farquhar and Sharkey (1982) suggest that stomatal limitations to photosynthesis during water stress have generally been overestimated. This can result from comparing g to a residual CO_2 conductance, often referred to as the mesophyll or carboxylation efficiency conductance (Ku and Edwards 1977), which describes the efficiency with which CO_2 in the leaf intercellular air spaces diffuses to and is incorporated in carboxylation reactions. The error lies in assuming that, if the intercellular CO_2 concentration (c_i) were to increase due to increases in stomatal conductance, then photosynthetic rate (A) would also increase in a linear manner. If the relationship between A and c_i deviates greatly from linearity becoming concave at high c_i , then comparisons of g and carboxylation efficiency determined at low c_i become difficult to interpret.

The purpose of this study was to determine the stomatal and non-stomatal limitations to photosynthesis as plants were subjected to progressively lower soil water potentials over a period of several weeks. To do this, we measured the dependence of photosynthesis on c_i for leaves of *Encelia frutescens*. Stomatal and non-stomatal limitations to photosynthesis will be discussed relative to one another at specific water potentials and absolutely in respect to the overall

decline in photosynthetic rate with decreasing ψ_l . The resulting photosynthetic behavior is discussed relative to plant performance and potential adaptive value in the native habitat.

Methods

Field collected seeds of *Encelia frutescens* were planted and grown in the greenhouse at the University of Utah, Salt Lake City, Utah. When the plants were six months old, and two months prior to beginning measurements, the plants were transplanted into 40 liter peat pots. The relatively large soil volume was desirable for controlling soil and plant water potential during the drought phase of the experiment. Plants were grown in a naturally lit greenhouse supplemented with HID lamps to create daily photon irradiance totals of 40–50 mol m⁻² (400–700 nm). Daily temperature ranges were approximately 35/25°C and midday relative humidity was approximately 10%. At the time photosynthetic measurements were taken, the study plants were 0.4–0.5 m in height and 0.5–0.6 m in diameter.

The potting soil consisted of two parts vermiculite, two parts perlite, two parts peat moss, four parts redwood compost, one part sand, and four parts autoclaved soil. Phosphate was available in the form of superphosphate present in the potting soil. Nitrogen was administered as potassium nitrate, calcium nitrate and urea (2%) dissolved in the water supply once a week at a total concentration of 150 ppm. Plants undergoing a drought treatment were watered with deionized water supplemented every 4–6 days with Hoagland's solution.

Leaf water potentials were measured with a Scholander pressure chamber. The leaf water potential (ψ_l) was assumed to be equal to the xylem pressure potential of whole twigs including the uppermost 4 to 6 leaves. Reported values are averages of three replicates taken at midday when leaf water potentials were most negative. The leaf water potential is a function of both the predawn leaf water potential and the transpiration rate, and should be expected to fluctuate diurnally. However, in our experiments the midday leaf water potential was effectively constant throughout most of the day, because of the constant environmental conditions in the glasshouse. At high ψ_l , the maximum diurnal variation was about 1.0 MPa, and at low ψ_l about 0.3 MPa.

Water stress was induced by decreasing the frequency of and amount given in watering. ψ_l of experimental plants was monitored on a daily basis and study plants were watered as necessary to maintain desired soil water potential values. This meant that the extent of watering ranged from saturating the entire soil volume every other day, in order to maintain the highest soil water potentials, to providing only 1.4 l water every two to three days in order to maintain the lowest soil water potentials. At least three to four days elapsed between decreases in the amount of water provided and measurements of photosynthetic parameters at the resultant, lowered ψ_l . ψ_l decreased from -1.5 to -4.0 MPa over a period of several weeks under the stepwise decreasing watering regime used during the drought cycle. The maximum difference between predawn and midday ψ_l was about 1.0 MPa. Diurnal fluctuations in ψ_l of up to 1.0 MPa also occurred immediately after watering when plants were at low ψ_l , but decreased to about 0.3 MPa within 1–2 days thereafter. Photosynthetic measurements of water stressed

plants were not taken until several days after the plants received supplemental watering. Plants at high ψ_l exhibited no increase in ψ_l following watering.

Gas exchange measurements were conducted on an open gas-exchange system as described by Ehleringer (1983). Due to the small size of individual leaves (100–250 mm²), whole twigs with the uppermost four or five attached leaves were used for gas exchange measurements. Gas exchange by stem tissues was negligible compared to that of the leaves and was ignored in all calculations.

To observe the effect of growth temperature on the temperature dependence of photosynthesis, plants were grown in controlled environments with 14 h/10 h day/night temperature regimes of 20/15°C and 35/25°C. Plants grown in the two different temperature regimes, unfortunately, experienced somewhat different light intensities during growth and this effected the absolute photosynthetic rates. Therefore, these data are presented as relative photosynthetic rates. The procedures followed for measurements of the temperature dependence of photosynthesis were similar to those of Forseth and Ehleringer (1983).

For simultaneous measurement of photosynthetic rate (A_{\max}), leaf conductance (stomatal + boundary layer) (g), and intercellular CO₂ concentration (c_i), attached leaves were sealed into a cuvette with an irradiance of 1.8 mmol photons m⁻² s⁻¹ (400–700 nm), ambient CO₂ concentration of 335 µl l⁻¹, 21% O₂, leaf temperature at 30°C (the thermal optimum), and a Δw of 21 mbar bar⁻¹. Measurements of A_{\max} , g , and c_i were taken as the values obtained following a one to two hour period of adjustment by the leaf to the cuvette conditions.

The dependence of photosynthesis on c_i was determined on the same leaves after measurements of A_{\max} . The same light level, Δw , and leaf temperature were used as during measurement of A_{\max} . The c_i was controlled by altering the ambient CO₂ concentration in the cuvette. A_{\max} was the first point on this response curve. Ambient CO₂ concentration was then increased in steps of 100–200 µl l⁻¹. High c_i values were difficult to obtain at very low ψ_l because of stomatal closure. After measuring rates of photosynthesis at high c_i , ambient CO₂ concentration was returned to 335 µl l⁻¹ and the leaves were given 0.5–1.0 h to recover before proceeding with measurements. There was a decrease in g at high ambient CO₂ concentrations, which often failed to fully recover when ambient CO₂ concentrations were reduced. The leaves were considered to have recovered sufficiently if photosynthetic rates were the same at the same c_i previously measured for A_{\max} . Ambient CO₂ concentrations were then decreased in steps of 100 µl l⁻¹ to measure photosynthetic rates at low c_i . The initial slope of A vs c_i was calculated from points with c_i between 60 and 150 µl l⁻¹.

In calculating Δw , the partial pressure of water vapor in the intercellular airspaces of the leaf was assumed to be in equilibrium with the leaf water potential. This resulted in an intercellular relative humidity of 97% rather than 100% at leaf water potentials of -4.0 MPa (Nobel 1974). The calculation of c_i included a correction for the effect of transpiration rate on the diffusion of CO₂ into the leaf (von Caemmerer and Farquhar 1981).

All of the work reported here was done at the University of Utah at an elevation of 1,460 m. Total ambient pressure averages 86 kPa compared to 101.3 kPa at sea level. When

presenting the dependence of photosynthetic rate on c_i , CO_2 concentrations may be expressed either as absolute partial pressures in pascals or as fractions of the total atmosphere in $\mu\text{l l}^{-1}$. As total atmospheric pressure declines, both the partial pressures of CO_2 and O_2 decline proportionately. Decreases in the CO_2 partial pressure cause decreases in photosynthetic rates by substrate limitation, but these are partially compensated for by decreased competitive inhibition by oxygen in RuBP carboxylase. Because of these simultaneous and opposing effects of decreasing total atmospheric pressure on photosynthetic rates, neither measurements of CO_2 in pascals nor $\mu\text{l l}^{-1}$ provides perfectly comparable results when measurements are made at different atmospheric pressures. The model of Farquhar et al. (1980) was said to estimate the effect of low atmospheric pressure on the reported relationships between net photosynthesis and c_i , assuming constant RuBP saturation and a constant RuBP carboxylase activity. This model enabled us to compare the photosynthetic rate at a particular c_i for measurements made at an atmospheric pressure of 101.3 kPa and those made on the same leaf at an atmospheric pressure of 86 kPa while holding all other parameters constant. The initial slope of A vs c_i measured at 86 kPa atmospheric pressure will appear to be either about 4% greater or 11% less than those made at sea level depending on whether c_i is expressed in pascals or $\mu\text{l l}^{-1}$, respectively. Neither unit avoids slight problems in comparing data sets measured at different elevations and atmospheric pressures. We have chosen to express c_i in $\mu\text{l l}^{-1}$ because 1) it is advantageous for graphical manipulations and 2) the initial slope of the response curve relating photosynthesis as a function of c_i ($\partial A/\partial c_i$ in this paper, and the mesophyll conductance of many authors) then has the same units as leaf conductance ($\text{mol m}^{-2} \text{s}^{-1}$). The $\partial A/\partial c_i$ values reported here are therefore expected to be slightly less than those of a comparable data set measured at sea level and expressed in the same units.

All regressions discussed in the text were significant at the 0.005 level or better. Regression equations, r^2 values and significance levels for the slopes are given in figure legends. Confidence intervals given in the text are ± 1 standard error.

Results

Before analyzing the response to drought, the temperature dependence of photosynthesis was determined at leaf temperatures ranging between 15 and 48°C. To assess the ability of *E. frutescens* to acclimate to changing environmental temperatures, plants were grown in growth chambers with contrasting temperature regimes, and the effect of growth conditions was then measured by comparing the photosynthetic performance of plants from both treatments under common conditions. Leaves of *E. frutescens* showed a pattern consistent with observations in other *Encelia* species; there was no change in either the temperature optimum or the relative rates at which photosynthesis declined at temperatures above or below the optimum in response to different thermal growth conditions (Fig. 1). The thermal optimum for plants from both high and low temperature treatments was approximately 30°C. Photosynthetic rates remained in excess of 80% of maximum between 18 and 41°C, but declined steeply outside this range. All subsequent work during the drought experiments was done using

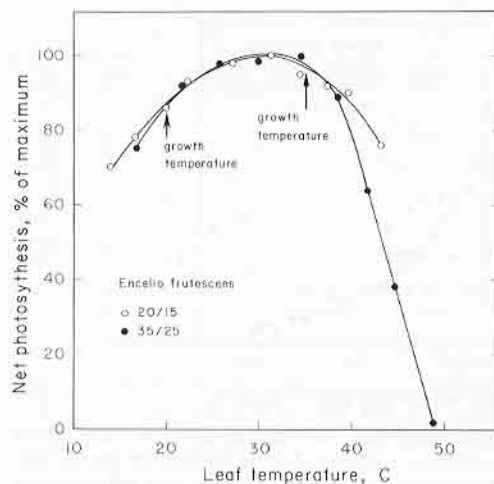


Fig. 1. The effect of growth temperature on the temperature dependence of photosynthesis in *Encelia frutescens*. Plants were grown in controlled environments at day/night temperature regimes of 20/15°C and 35/25°C. Curves are relativized for comparison of temperature optima. Arrows indicate ambient temperatures during growth.

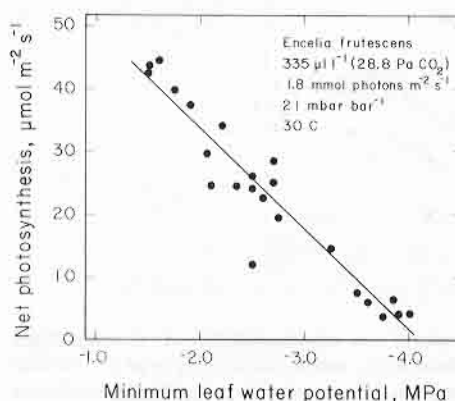


Fig. 2. The effect of decreasing minimum daily leaf water potential (ψ_l) on net photosynthesis (A_{\max}) in $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ measured at an irradiance of $1.8 \text{ mmol photons m}^{-2} \text{ s}^{-1}$ (400–700 nm), leaf-air vapor pressure difference (Δw) of 21 mbar bar^{-1} , leaf temperature of 30°C , ambient CO_2 concentration of $335 \mu\text{l l}^{-1}$ ($= 28.8 \text{ Pa}$), and an oxygen concentration of 21% ($= 18 \text{ kPa}$). The equation of the regression line is $A_{\max} = 15.9 * \psi_l + 65.5$ ($r^2 = 0.905$, $P < 0.001$).

leaf temperatures within $\pm 0.2^\circ \text{C}$ of the 30°C thermal optimum.

Photosynthetic characteristics were very responsive to changes in leaf water potential (ψ_l) measured at its midday minimum. The net photosynthetic rate (A_{\max}) under favorable conditions of high irradiance, moderate leaf-air vapor pressure gradients (Δw), and optimal leaf temperature, was measured on leaves of plants subjected to decreasing soil water availability over a period of several weeks. A_{\max} decreased linearly with decreasing ψ_l with a slope of $15.9 \pm 1.1 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1} \text{ MPa}^{-1}$ ($P < 0.001$) (Fig. 2). Photosynthetic rates decreased from 41.6 ± 1.6 to $1.7 \pm 1.7 \mu\text{mol m}^{-2} \text{ s}^{-1}$ as ψ_l decreased from -1.5 to -4.0 MPa . Midday ψ_l remained at -1.5 MPa in potted plants that received watering every other day and were subjected to an environment with high irradiance and high

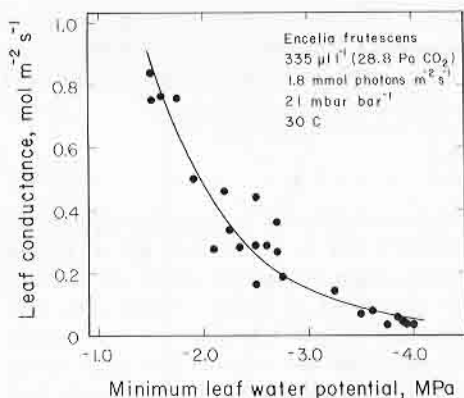


Fig. 3. The effect of minimum daily leaf water potential (ψ_l) on leaf conductance (g) under the conditions defined in Fig. 2. The equation of the regression line is $\log(g) = 0.517 * \psi_l + 0.724$ ($r^2 = 0.928$, $P < 0.001$)

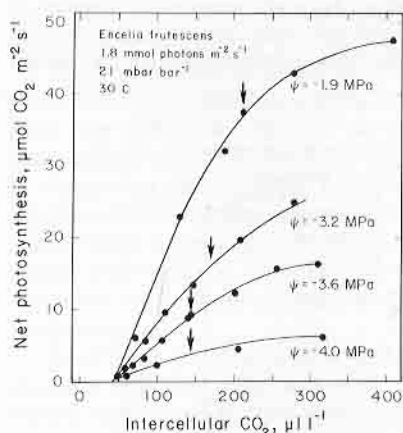


Fig. 4. The dependence of net photosynthesis (A) in $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$, on intercellular CO_2 concentration (c_i) in $\mu\text{l l}^{-1}$ at four different values of leaf water potential (ψ_l). Ambient conditions in the cuvette were the same as those defined for Fig. 2, only ambient CO_2 was varied to control c_i . Arrows indicate the c_i measured simultaneously with A_{max} when plants were at the four respective values of ψ_l

evaporative demand during growth. Field observations (Ehleringer unpublished data) suggest that midday ψ_l for *E. frutescens* are rarely higher than -1.5 MPa at any time of the year.

Decreases in A_{max} were associated with decreases in leaf conductance to water vapor (g). Values of g measured simultaneously with A_{max} declined in a curvilinear fashion as ψ_l decreased (Fig. 3). g decreased rapidly with decreases in ψ_l when ψ_l was high, but approached zero asymptotically as ψ_l became very negative.

The relationship between net photosynthesis (A) and the intercellular CO_2 concentration (c_i) was determined at different values of ψ_l (representative curves in Fig. 4). As ψ_l became more negative, there was a decrease in both the initial slope at low c_i ($\partial A / \partial c_i$) (often referred to as the carboxylation efficiency) (Fig. 5) and the maximum photosynthetic rate at high c_i (Fig. 6). Using linear regressions from the data in Figs. 5 and 6, we estimated that $\partial A / \partial c_i$ and the photosynthetic rate at a c_i of $335 \mu\text{l l}^{-1}$ decreased by 78% and 86%, respectively, from their original values as ψ_l decreased from -1.5 to -4.0 MPa.

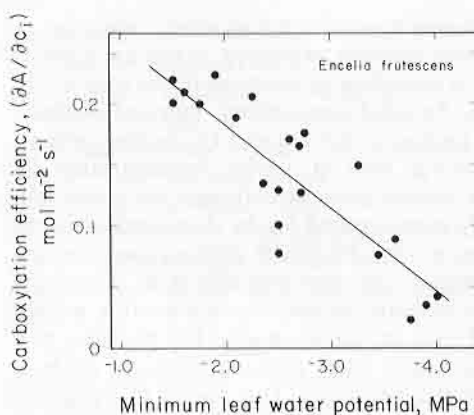


Fig. 5. The carboxylation efficiency or slope of the initial, linear region of the c_i dependence curve for net photosynthesis ($\partial A / \partial c_i$) in $\text{mol m}^{-2} \text{ s}^{-1}$ as a function of decreasing minimum daily leaf water potential (ψ_l). The equation of the regression line is $\partial A / \partial c_i = 0.679 * \psi_l + 0.320$ ($r^2 = 0.733$, $P < 0.001$)

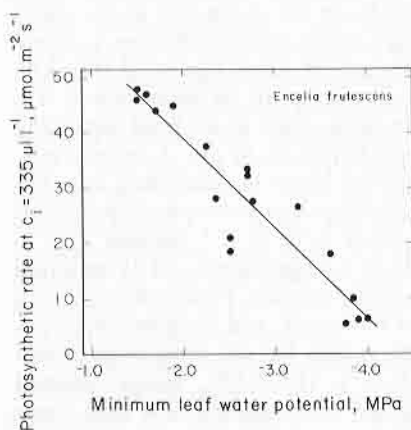


Fig. 6. The net photosynthetic rate (A_0) when c_i equals the ambient CO_2 concentration ($335 \mu\text{l l}^{-1}$) used during the measurement of A_{max} . A_0 is shown as a function of decreasing minimum daily leaf water potential (ψ_l). A_0 was taken from c_i dependence curves of photosynthesis such as those shown in Fig. 4. The equation of the regression line is $A_0 = 16.18 * \psi_l + 71.46$ ($r^2 = 0.863$, $P < 0.001$)

Kjeldahl nitrogen was determined in all experimental leaves immediately following photosynthetic measurements. A linear relationship ($r^2 = 0.38$; $P < 0.005$) was observed between $\partial A / \partial c_i$ and Kjeldahl nitrogen (Fig. 7). If diffusional limitations to CO_2 movement between the intercellular spaces and the sites of carboxylation are small relative to the limitation to photosynthesis imposed by the carboxylation step itself (which appears to be the case, Farquhar and Sharkey 1982), then $\partial A / \partial c_i$ should be directly proportional to the activity of RuBP carboxylase in the leaf (Collatz 1977; Farquhar et al. 1980; von Caemmerer and Farquhar 1981). Since RuBP carboxylase has been found to be a large and consistent fraction of total leaf protein (Jensen and Bahr 1977), and since both total leaf protein and RuBP carboxylase have been found to be well correlated with Kjeldahl nitrogen in many species (Seemann et al. 1980b), the relationship between Kjeldahl nitrogen and $\partial A / \partial c_i$ is consistent with the interpretation that the decrease in $\partial A / \partial c_i$ was associated with a linear decrease in RuBP carboxylase.

The c_i observed in leaves of *E. frutescens* at the time

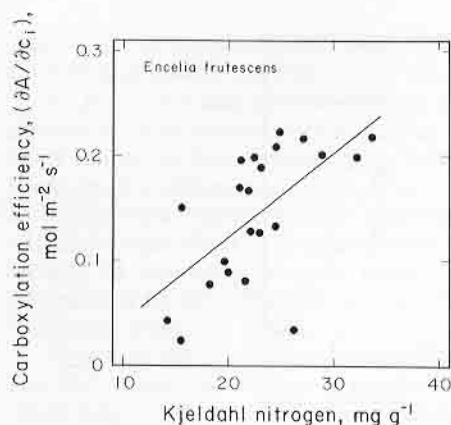


Fig. 7. The carboxylation efficiency or slope of the linear portion of the c_i dependence curve ($\partial A/\partial c_i$) in $\text{mol m}^{-2} \text{s}^{-1}$ as a function of Kjeldahl nitrogen in mg g^{-1} . The equation of the regression line is $\partial A/\partial c_i = 0.00813 * (\text{Kjeldahl Nitrogen}) - 0.0405$ ($r^2 = 0.385$, $P < 0.005$)

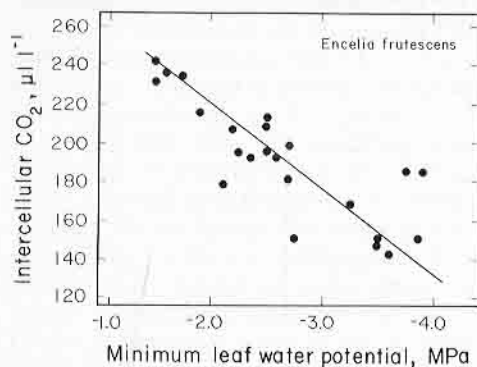


Fig. 8. The interstitial CO_2 concentration (c_i) measured under the conditions defined in Fig. 2. c_i is shown as a function of minimum daily leaf water potential (ψ_l). The equation of the regression line is $c_i = 3.12 * \psi_l + 274.8$ ($r^2 = 0.683$, $P < 0.001$)

of measuring A_{\max} (Fig. 8) depends on both the conductance to CO_2 diffusion ($g_{\text{CO}_2} = g/1.6$) into the leaf and the capacity of the leaf to utilize internally available CO_2 for photosynthetic carboxylations. The arrows on Fig. 4 indicate the observed c_i under the ambient conditions of A_{\max} at four ψ_l values. It is evident that c_i measured at A_{\max} is on or just slightly above the linear region described by $\partial A/\partial c_i$. This meant that the most important factors responsible for determining c_i were g and $\partial A/\partial c_i$. If the inherent capacity of the leaf for CO_2 assimilation and the conductance to CO_2 diffusion decreased in a perfectly proportional manner as ψ_l decreased, then c_i should have remained constant (Farquhar and Sharkey 1982). Instead of a balanced decrease in these parameters and a constant c_i , we observed that in leaves of *E. frutescens*, c_i decreased as ψ_l became more negative. This indicated that g decreased relatively more than $\partial A/\partial c_i$.

Water Use Efficiency (WUE) was calculated as the ratio of $\mu\text{mol CO}_2$ fixed/ $\text{mmol H}_2\text{O}$ transpired during measurement of A_{\max} . Although leaf temperature and Δw were held constant throughout the experiment, WUE increased from

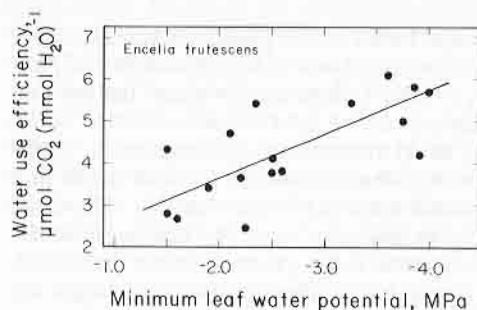


Fig. 9. Water use efficiency (WUE), measured under cuvette conditions of constant leaf temperature and vpd as defined in Fig. 2. WUE is shown as a function of decreasing minimum daily leaf water potential (ψ_l). WUE is calculated as the ratio of the photosynthetic and transpiration rates, $\mu\text{mol CO}_2/\text{mmol H}_2\text{O}$. The equation of the regression line is $\text{WUE} = -0.899 * \psi_l + 1.87$ ($r^2 = 0.475$, $P < 0.005$)

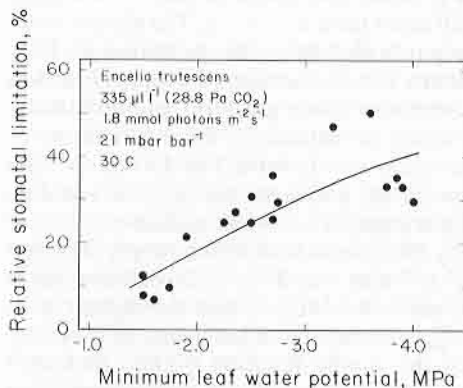


Fig. 10. Relative stomatal limitation as a function of minimum daily leaf water potential (ψ_l). Values are calculated as the percent difference between net photosynthesis with infinite conductance, A_0 , and the actual rate measured as A_{\max} . The equation of the regression line is $\arcsin(l_s/100) = -0.848 * \log(\psi_l) + 0.184$ ($r^2 = 0.742$, $P < 0.001$)

3.2 ± 0.32 to $5.4 \pm 0.35 \mu\text{mol mmol}^{-1}$ as ψ_l decreased from -1.5 to -4.0 MPa (Fig. 9). The observed 59% increase in WUE was a consequence of the decrease in c_i and was caused by the disproportionately large decreases in g compared to $\partial A/\partial c_i$.

Farquhar and Sharkey (1982) proposed a measure of relative stomatal limitation, l_s , defined as the percent reduction in photosynthesis below the rate which would occur if stomatal conductance were infinite.

$$l_s = \left[\frac{A_0 - A_{\max}}{A_0} \right] * 100.$$

The photosynthetic rate at infinite stomatal conductance (A_0) is the photosynthetic rate when c_i is equal to ambient CO_2 concentration ($335 \mu\text{l l}^{-1}$, 28.8 Pa) on the A vs. c_i dependence curve, if we ignore boundary layer conductance, which for a small leaved shrub like *E. frutescens* will be quite large. Calculating l_s for leaves of *E. frutescens* under increasing water stress (Fig. 10), revealed an increase in l_s from 10.7 ± 2.2 to $40.9 \pm 3.2\%$ as ψ_l decreased from -1.5 to -4.0 MPa.

Discussion

The relative stomatal limitation to photosynthesis, l_s , takes into account the changing nature of the dependence of photosynthesis on c_i . Thus, l_s depends on many factors and increases in l_s can be caused by 1) decreases in g , 2) decreases in $\partial A/\partial c_i$, or 3) increases in A_0 (increases in RuBP regeneration capacity). An increase in l_s could mean that $\partial A/\partial c_i$ has decreased relatively more than A_0 . However, our data (Figs. 5, 6) indicated that A_0 has actually decreased more rapidly than $\partial A/\partial c_i$ as water stress developed. The decrease in l_s was due to disproportionately larger decreases in g rather than a change in the shape of the A vs. c_i dependence curve as ψ_l became more negative.

We may further ask to what degree the absolute decline in photosynthesis with decreasing ψ_l is attributable to changes in g vs. changes in intrinsic capacities. This may be seen by examining A vs. c_i curves at high and low ψ_l , and using the notion of supply functions (Farquhar and Sharkey 1982; Jones 1973; Raschke 1979) (Fig. 11). The slope of a supply function is equal to a specified leaf conductance to gaseous CO_2 diffusion ($\text{mol m}^{-2} \text{s}^{-1}$). The supply functions describe the photosynthetic rates permitted by CO_2 diffusional limitations. The intersection of a supply function with an A vs. c_i response curve gives the photosynthetic rate and c_i which would be realized for those conditions.

Two supply functions are shown in Fig. 11 representing the highest and lowest leaf conductances (g) observed during the drought experiment. The lowest measured value of A_{\max} is indicated by the intersection of the supply function $g=0.041 \text{ mol m}^{-2} \text{s}^{-1}$ with the A vs. c_i dependence curve measured when ψ_l was -4.0 MPa . One of the highest measured values of A_{\max} during the experiments is given by the intersection of the supply function $g=0.82 \text{ mol m}^{-2} \text{s}^{-1}$ with the A vs. c_i dependence curve determined when ψ_l was -1.9 MPa . If the intrinsic photosynthetic capacity had decreased (as was observed) with decreasing leaf water potential, but leaf conductance had remained the same (as in unstressed plants), then the photosynthetic rate which would have occurred is found by taking the intersection of supply function $g=0.82 \text{ mol m}^{-2} \text{s}^{-1}$ and the A vs. c_i dependence curve determined at a ψ_l of -4.0 MPa . From this analysis, only 6% of the absolute decrease in photosynthetic rate associated with decreased ψ_l could have been prevented by maintaining a high g while the intrinsic photosynthetic capacity declined. Similarly, we can ascertain what the photosynthetic rate would have been if values of A_0 and $\partial A/\partial c_i$ had remained high, but g had decreased (as observed). Taking the intersection of supply function $g=0.041 \text{ mol m}^{-2} \text{s}^{-1}$ with the A vs. c_i dependence curve determined when ψ_l was -1.9 MPa and comparing this hypothetical value with the same minimum and maximum observed rates described above, we calculate that only 4% of the total decrease in photosynthesis associated with water stress could have been prevented by retaining high values of A_0 and $\partial A/\partial c_i$ while g declined. Thus, while the relative limitation imposed by stomates increases substantially at low ψ_l , the absolute decrease in photosynthesis can be attributed almost equally to both stomatal closure and decreased intrinsic photosynthetic capacity. Under water stress conditions, high photosynthetic rates cannot be achieved by increasing either component alone.

Unlike many desert species, leaves of *E. frutescens* show no increase in photosynthetic stability at high temperatures

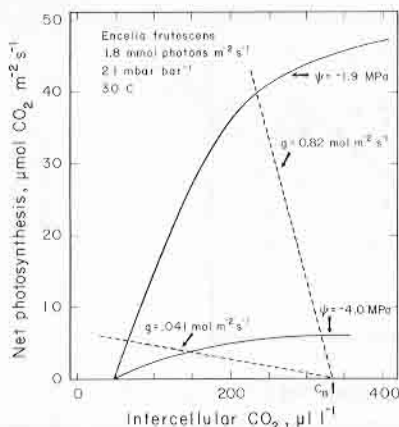


Fig. 11. Representative photosynthesis – c_i dependence curves (solid lines) for the highest and lowest leaf water potentials and supply functions (dashed lines) with slopes proportional to the highest and lowest conductances ($\text{mol m}^{-2} \text{s}^{-1}$) (g) observed during the drought cycle. The intersection of a supply function and a photosynthesis – c_i response curve predicts the photosynthetic rate which would be observed for a leaf with specified value of g and photosynthesis vs. c_i response curve.

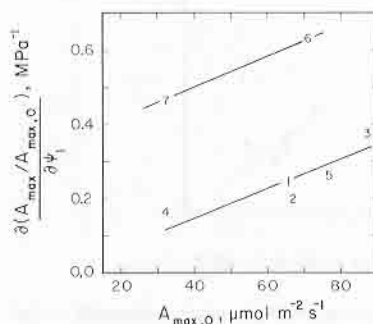


Fig. 12. The relative rate of decline in photosynthesis with decreasing leaf water potential as a function of the calculated photosynthetic rate under optimal conditions of a leaf water potential of 0 MPa for desert species grown under high irradiances. Data are from several sources: 1 *Encelia frutescens* (this study), 2 *Encelia farinosa* (Ehleringer and Cook 1983), 3 *Amaranthus palmeri* (Ehleringer 1983), 4 *Larrea divaricata* (Mooney 1980), 5 *Malvastrum rotundifolium* (Forseth and Ehleringer 1983), 6 *Lupinus arizonicus* (Forseth and Ehleringer 1983), 7 *Nerium oleander* (Björkman et al. 1980).

in response to higher growth temperatures. This trend, however is consistent with what has been observed in other *Encelia* species (Ehleringer and Björkman 1978). Photosynthetic rate reached 50% of maximum at about 43°C and decreased precipitously with further increases in temperature. This is comparable to the upper limit of thermal stability observed in most winter annual species growing under early spring conditions (Seeman et al. 1980a; Forseth and Ehleringer 1982a). It is below the range of maximum temperatures tolerated by desert evergreen perennials or summer annuals (Downton et al. 1980), and it is below the range of many desert winter annuals when acclimated to end of season conditions (Forseth and Ehleringer 1982a). This observed photosynthetic temperature dependence suggests that leaves of *E. frutescens* must utilize periods of moderate temperatures for photosynthesis and growth or,

under high air temperatures, utilize high g to achieve high rates of evaporative cooling.

E. frutescens had an intermediate ability to maintain positive photosynthetic rates at low ψ_l when compared to other sympatric desert species. A_{\max} in annual species from these deserts decreases to zero at ψ_l ranging from -1.6 to -3.85 MPa (Mooney 1980; Ehleringer 1983; Forseth and Ehleringer 1983). For other desert perennials A_{\max} decreased to zero at ψ_l ranging from -2.1 to -8.0 MPa (Odenev et al. 1974; Björkman et al. 1980; Mooney 1980; Ehleringer and Cook 1983).

There are sufficient data sets now for warm desert species that we can ask whether or not the decline in photosynthesis (A_{\max}) with leaf water potential is a function of the maximum photosynthetic rate under optimal conditions or if other factors influence the rate of decline of photosynthesis. From the data cited above, we have plotted the calculated rate of decline of A_{\max} with decreasing leaf water potential as a function of $A_{\max,0}$ under optimal conditions (Fig. 12). In all of the above cited studies, the decline in A_{\max} with leaf water potential was linear, but the minimum leaf water potential in the studies was not identical. Therefore, to place the data on a common basis, we calculated what the photosynthetic rate ($A_{\max,0}$) would have been at a leaf water potential of 0 MPa, and called this the optimal condition. Although the data clearly fall into two groups, it appears that there are small, but significant increases in the rate of photosynthetic decline with decreasing leaf water potential as a function of increasing photosynthetic capacity. By far though, the major factor affecting the decline in A_{\max} with leaf water potential is whether or not the leaves are capable of active osmotic adjustment in response to decreasing soil water availability. Leaves of both species in the upper curve of Fig. 12 show no osmotic adjustment in response to declining soil water availability, whereas leaves of all five species in the lower curve of Fig. 12 exhibit active osmotic adjustment in response to decreasing soil water availability. That the decline in A_{\max} with leaf water potential in leaves which osmotically adjust is less than half the rate of those which do not osmotically adjust to decreased water availability clearly implies that osmotic adjustment confers an adaptive advantage in water limited habitats.

Another member of the genus *Encelia*, which is sympatric with *Encelia frutescens* over much of its range but occupies drier sites, is *Encelia farinosa* Gray. *E. farinosa* occurs on rocky slopes, while *E. frutescens* is generally restricted to gullies and wash habitats where soil water is more plentiful. The two species are similar in size and habit but differ in leaf morphology and in photosynthetic response to water stress (Ehleringer and Cook 1983). While *E. frutescens* leaves are small (100 – 250 mm²), essentially glabrous, and with high absorptances, *E. farinosa* leaves are larger (150 – $1,500$ mm²), pubescent, and have low absorptances.

The effect of decreasing ψ_l on the photosynthetic behavior of these two *Encelia* species helps to explain the differences in their respective ecological niches. Although the leaves of both species show very similar temperature optima (Ehleringer and Björkman 1978), and neither species is able to photosynthetically acclimate or to tolerate very high leaf temperatures, *E. farinosa* leaves exhibit features which will allow greater tolerance to hotter, drier microsites than *E. frutescens*. As ψ_l declines, A_{\max} declines more rapidly in *E. frutescens* than in *E. farinosa* reaching values of 0 at

ψ_l of -4.1 and -5.1 for *E. frutescens* and *E. farinosa*, respectively. However, the magnitude of the decline in A_{\max} with ψ_l ($\mu\text{mol m}^{-2} \text{s}^{-1} \text{MPa}^{-1}$) is 13.5% less in *E. frutescens* than in *E. farinosa*. The rate of decline in $\partial A/\partial \psi_l$ with ψ_l ($\text{mol m}^{-2} \text{s}^{-1} \text{MPa}^{-1}$) is 36% less in *E. farinosa* than in *E. frutescens*. This means that the higher photosynthetic rates in *E. farinosa* leaves at low ψ_l are due to greater stability of intrinsic photosynthetic capacity rather than maintaining higher values of g . As g decreases at lower ψ_l , the increasing reflectance of *E. farinosa* leaves helps to keep leaf temperatures from greatly exceeding the temperature optimum, and the components of intrinsic photosynthetic capacity, A_0 and $\partial A/\partial \psi_l$, are slow to decline. This allows *E. farinosa* to inhabit the drier slopes where water availability is most limited. The intrinsic photosynthetic capacity of *E. frutescens* on the other hand is more sensitive to decreasing ψ_l and this is compounded by the lack of any mechanism other than high transpiration rates to prevent excessive leaf temperatures when air temperature is above the photosynthetic optimum. Thus, *E. frutescens* is found restricted to the desert wash habitat where soil water is most abundant.

Reduced soil water potentials may develop recurrently during the periods when *E. frutescens* shrubs are active. The ability of *E. frutescens* to tolerate moderately low leaf water potentials while maintaining positive photosynthetic rates will facilitate exploitation of this intermittent rainfall regime. The increase in WUE under cuvette conditions caused by reduced g may represent a more conservative and efficient use of water as ψ_l declines. The potential value of such a conservative response in terms of increasing whole shrub seasonal carbon assimilation may be reduced or even decimated, however, by the increased Δw associated with higher air and leaf temperatures.

The decline in A_{\max} as ψ_l decreased was also accompanied by reductions in total canopy cover. These were only observed in a qualitative manner in this study, but they would be quite important to whole plant photosynthetic rates. Leaf abscission became quite pronounced at very low ψ_l . Leaf abscission commenced with the oldest leaves and became noticeably greater in stressed plants compared to well watered controls as ψ_l in the former decreased to -2.5 MPa. Total leaf area was progressively reduced as ψ_l continued to decrease, because of increased leaf abscission and reduced leaf production. These decreases in total leaf area would interact with the reported decreases in photosynthetic rate per leaf area in a multiplicative manner to reduce whole plant carbon gain. The fraction of the seasonal carbon assimilation made under conditions of low ψ_l will therefore be rather small, but will depend on the rate at which ψ_l declines under field conditions. Even reduced rates of photosynthesis late in the season may be important for crucial functions such as the completion of seed filling. Detailed phenological data are therefore needed for further evaluation of the ecological importance of the photosynthetic behavior of *E. frutescens* at low water potentials.

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References

- Beatley JC (1974) Phenological events and their environmental triggers in Mohave desert ecosystems. *Ecology* 55:856–863
- Björkman O, Badger M, Armond PA (1978) Thermal acclimation of photosynthesis: effect of growth temperature on photosynthetic characteristics and components of the photosynthetic apparatus in *Nerium oleander*. *Carnegie Inst Wash Yb* 77:262–276
- Björkman O, Downton WJS, Mooney HA (1979) Response and adaptation to water stress in *Nerium oleander*. *Carnegie Inst Wash Yb* 79:150–157
- Björkman O, Fowler SB, Fork DC, Gunnar O (1980) Interaction between high irradiance and water stress on photosynthetic reactions in *Nerium oleander*. *Carnegie Inst Wash Yb* 80:57–59
- Boyer JS (1970) Phenological events and their environmental triggers in Mohave desert ecosystems. *Ecology* 55:856–863
- Caemmerer S von, Farquhar GD (1981) Some relationships between the biochemistry of photosynthesis and the gas exchange of leaves. *Planta* 143:376–387
- Collatz GJ (1977) Influence of certain environmental factors on photosynthesis and photorespiration in *Simmondsia chinensis*. *Planta* 134:127–132
- Downton WJS, Seemann JR, and Berry JA (1980) Thermal stability of photosynthesis in desert plants. *Carnegie Inst Wash Yb* 79:143–145
- Ehleringer JR (1982) The influence of water stress and temperature on leaf pubescence development in *Encelia farinosa*. *Amer J Bot* 69:670–675
- Ehleringer JR (1983) Ecophysiology of *Amaranthus palmeri*, a Sonoran Desert summer annual. *Oecologia* (Berlin) 57:107–112
- Ehleringer Jr, Björkman O (1978) A comparison of photosynthetic characteristics of *Encelia* species possessing glabrous and pubescent leaves. *Plant Physiol* 62:185–190
- Ehleringer J, Cook CS (1983) Photosynthesis in *Encelia farinosa* Gray in response to decreasing leaf water potential. (in prep)
- Farquhar GD, Sharkey TD (1982) Stomatal conductance and photosynthesis. *Ann Rev Plant Physiol* 33:317–334
- Farquhar GD, Caemmerer S von, Berry JA (1980) A biochemical model of photosynthetic CO₂ assimilation in leaves of C₃ species. *Planta* 149:78–90
- Forseth IN, Ehleringer JR (1982a) Ecophysiology of two solar-tracking desert winter annuals. I. Photosynthetic acclimation to growth temperature. *Aust J Plant Physiol* 9:321–332
- Forseth IN, Ehleringer JR (1982b) Ecophysiology of two solar-tracking desert winter annuals. II. Leaf movements, water relations and microclimate. *Oecologia* (Berlin) 54:41–49
- Forseth IN, Ehleringer JR (1983) Ecophysiology of two solar tracking desert winter annuals. III. Gas exchange responses to light, CO₂ and vpd in relation to long term drought. *Oecologia* (Berlin) 57:344–351
- Hsiao TC, Acevedo E (1974) Plant responses to water deficits, water use efficiency, and drought resistance. *Agr Met* 14:59–84
- Jensen RG, Bahr JT (1977) Ribulose 1,5-bisphosphate carboxylase-oxygenase. *Ann Rev Plant Physiol* 28:379–400
- Jones HG (1973) Limiting factors in photosynthesis. *New Phytol* 72:1089–1094
- Ku SB, Edwards GE (1977) Oxygen inhibition of photosynthesis. II. Kinetic characteristics as affected by temperature. *Plant Physiol* 59:991–999
- Lawlor DW (1976) Water stress induced changes in photosynthesis, photorespiration, respiration and CO₂ compensation concentration of wheat. *Photosynthetica* 10:378–387
- Ludlow MM (1980) Adaptive significance of stomatal response to water stress. In: Turner NC and Kramer PJ (eds), *Adaptations of Plants to Water and High Temperature Stress*. John Wiley and Sons, NY, p 123–138
- Ludlow MM, Ng TT (1976) Effect of water deficit on carbon dioxide exchange and leaf elongation rate of *Panicum maximum* var. *trichoglume*. *Aust J Plant Physiol* 3:401–413
- Mooney HA (1980) Seasonality and gradients in the study of stress adaptation. In: Turner NC and Kramer PJ (eds), *Adaptations of Plants to Water and High Temperature Stress*. John Wiley and Sons, NY, p 279–294
- Mooney HA, Björkman O, Collatz GJ (1976) Photosynthetic acclimation to temperature and water stress in the desert shrub *Larrea divaricata*. *Carnegie Inst Wash Yb* 76:328–335
- Mooney HA, Björkman O, Collatz GJ (1978) Photosynthetic acclimation to temperature in the desert shrub *Larrea divaricata*. I. Carbon dioxide exchange characteristics of intact leaves. *Plant Physiol* 61:406–410
- Nobel PS (1974) *Introduction to Biophysical Plant Ecology*. WH Freeman and Company, San Francisco
- Odening WR, Strain BR, Oehl WC (1974) The effect of decreasing water potential on net CO₂ exchange of intact desert shrubs. *Ecology* 55:1086–1095
- Osonubi O, Davies WJ (1980) The influence of plant water stress on stomatal control of gas exchange at different levels of atmospheric humidity. *Oecologia* (Berlin) 46:1–6
- O'Toole JC, Ozbun JL, Wallace DH (1977) Photosynthetic response to water stress in *Phaseolus vulgaris*. *Physiol Plant* 40:111–114
- Raschke K (1979) Movements of stomata. In: Harpt W, Feinleib ME (eds), *Physiology of Movements*. *Encycl Plant Physiol* (NS). Springer, Berlin pp 383–441
- Redshaw AJ, Meidner H (1972) Effects of water stress on the resistance to uptake of carbon dioxide in tobacco. *J Exp Bot* 23:229–240
- Seemann JR, Downton WJS, Berry JA (1979) Field studies of acclimation to high temperatures: winter ephemerals in Death Valley. *Carnegie Inst Wash Yb* 78:157–162
- Seemann JR, Berry JA, Downton WJS (1980a) Seasonal temperature acclimation in high temperature acclimation of desert winter annuals. *Carnegie Inst Wash Yb* 79:141–143
- Seemann JR, Tepperman JM, Berry JA (1980b) The relationship between photosynthetic performance and the levels and kinetic properties of RuBP carboxylase-oxygenase from desert winter annuals. *Carnegie Inst Wash Yb* 80:67–72
- Strain BR, Chase VC (1966) Effect of past and prevailing temperatures on the carbon dioxide exchange capacities of some woody desert perennials. *Ecology* 47:1043–1045

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