Photosynthesis in *Encelia farinosa* Gray in Response to Decreasing Leaf Water Potential[1]

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ABSTRACT

Photosynthetic responses of intact leaves of the desert shrub *Encelia farinosa* were measured during a long term drought cycle in order to understand the responses of stomatal and nonstomatal components to water stress. Photosynthetic rate at high irradiance and leaf conductance to water vapor both decreased linearly with declining leaf water potential. The intercellular CO_2 concentration (c_i) remained fairly constant as a function of leaf water potential in plants subjected to a slow drought cycle of 25 days, but decreased in plants exposed to a 12-day drought cycle. With increasing water stress, the slope of the dependence of photosynthesis on c_i (carboxylation efficiency) decreased, the maximum photosynthetic rates at high c_i became saturated at lower values, and water use efficiency increased. Both the carboxylation efficiency and photosynthetic rates were positively correlated with leaf nitrogen content. Associated with lower leaf conductances, the calculated stomatal limitation to photosynthesis increased with water stress. However, because of simultaneous changes in the dependence of photosynthesis on c_i with water stress, increased leaf conductance alone in water-stressed leaves would not result in an increase in photosynthetic rates to prestressed levels. Both active osmotic adjustment and changes in specific leaf mass occurred during the drought cycle. In response to increased water stress, leaf specific mass increased. However, the increases in specific leaf mass were associated with the production of a reflective pubescence and there were no changes in specific mass of the photosynthetic tissues. The significance of these responses for carbon gain and water loss under arid conditions are discussed.

Net photosynthetic rate decreases as leaf water stress increases (13, 14). The decline in photosynthesis (A)[2] with decreasing leaf water potential (ψ_l) is often linear (1, 2, 7, 12, 15–19). Both stomatal and nonstomatal components are thought to be responsible for the decreased photosynthetic rate, and several investigators (2, 3, 7, 12, 20) have measured the change in the dependence of net photosynthesis on c_i as an estimate of the extent of the change in nonstomatal components during drought stress. In

[2] Abbreviations: A, photosynthetic rate; A_{max}, photosynthetic rate at high irradiance and ambient CO_2 levels; A_o, photosynthetic rate at high irradiance and intercellular CO_2 concentration of 330 $\mu l \ l^{-1}$; g, leaf conductance to water vapor; g', leaf conductance to carbon dioxide; c_i, intercellular CO_2 concentration, c_a, ambient CO_2 concentration; l_s, relative stomatal limitation on photosynthetic rate; Δw, leaf to air water vapor gradient; ψ_l, leaf water potential; SLM, specific leaf mass; SPM, specific pubescence mass; WUE, water use efficiency; RWC, relative water content; HID, high intensity discharge.

these studies, there was a decline in the initial slope of the CO_2 dependence curve ($\partial A/\partial c_i$, often called the carboxylation efficiency) and also a decrease in A at high c_i. Not all studies of photosynthesis during water stress have shown a decrease in the carboxylation efficiency, and in those studies it may be that the stress development was too rapid for a decrease in carboxylation efficiency to occur (13).

Recently, attention has been focused on quantitatively assessing the extent to which photosynthesis is colimited by stomatal and nonstomatal components (11). The different limitations can be analyzed evaluating what has been called the 'supply' function (stomatal or diffusion component) and the 'demand' function (nonstomatal component). The demand function is the A versus c_i response curve, and the supply function is a line with an x-axis intercept equal to the c_a and a negative slope equal to a specified g'. Since the supply function defines the photosynthetic rate permitted by diffusional limitation, the intersection of the demand function with the supply function gives the values of A and c_i which would be realized for those conditions.

The extent of relative stomatal limitation of the photosynthetic rate, l_s, is then defined as the percentage reduction in photosynthesis below the rate which would occur if stomatal conductance were infinite. Thus,

$$l_s = \frac{(A - A_o)}{A_o} \times 100$$

where A_o is the photosynthetic rate to be expected when $c_i = c_a$.

As a part of our efforts to understand the photosynthetic responses of warm desert plants to their native environment, we were interested in evaluating the extent to which stomatal and nonstomatal components affected photosynthetic rates, particularly as soil moisture levels decreased. The current investigation utilized *Encelia farinosa*, a common, drought-deciduous leaved shrub, found throughout much of the Sonoran Desert. Gas exchange characteristics of this species with respect to irradiance, temperature, and intercellular CO_2 have been characterized from both field grown and laboratory grown materials (9, 10). The objective of this study was to determine the stomatal and nonstomatal limitations to photosynthesis as plants were subjected to progressively lower soil water potentials over a period of several weeks, such as might occur periodically under natural field conditions.

MATERIALS AND METHODS

E. farinosa were germinated from seed and initially grown under well watered conditions in a greenhouse which had supplemented HID lighting. In early summer, plants were transplanted to 40-L pots and placed outdoors, where they continued to receive abundant water and frequent fertilization with Hoagland solution. The large soil volume was desirable for controlling soil and leaf water potential later during the drought phase of

the experiments. Approximately 6 weeks after being transferred outdoors, the photosynthetic measurements were begun. All plants were grown and measured at the University of Utah, Salt Lake City, Utah (elevation = 1460 m). Average diurnal air temperature fluctuations during the time plants were growing outside ranged from a 32.1°C daytime maximum to a 17.7°C nighttime minimum.

Water stress was induced by allowing soil water in the pots to be depleted. The water stress treatments were further subdivided into two types: 'fast' drought and 'slow' drought. If the fast drought treatment, soils were initially charged with water and then no further soil water was added. Soil water depletion was due almost exclusively to plant transpiration, since the soil surface was covered with plastic sheets to reduce evaporation. The time necessary for plants to decrease soil water contents such that midday leaf water potentials decreased from −1.5 MPa to −4.5 MPa was approximately 12 d. The slow drought treatment differed in that at various stages of the drought cycle, small amounts of water were added to the soil to slow down the rate at which leaf water potentials decreased. In this treatment, the time it took for leaf water potentials to decline from −1.5 MPa to −4.5 MPa was approximately 25 d.

Leaf water potentials were measured on single leaves using a pressure chamber. All measurements reported in this study are from the same leaves that were used in the gas exchange measurements. In addition to total leaf water potential measurements, the osmotic water potentials were obtained by measuring pressure-volume curves on single leaves. Methodology for the osmotic water potential and osmotic adjustment determinations followed Wilson et al. (22).

Gas exchange measurements were conducted using an open gas exchange system as described by Ehleringer (7). For A_{max}, g, and c_i, attached leaves were sealed into a cuvette with an incident irradiance of 1.8 mmol photons m^{-2} s^{-1} (400–700 nm), an ambient CO_2 concentration of 330 μl l^{-1}, 21% O_2, a leaf temperature of 30°C, and a Δw of 17 mbar bar^{-1}. Measurements of A_{max}, g, and c_i were taken as the steady state values after a period of a 1 to 2 h adjustment by the leaf to the cuvette conditions.

The dependence of photosynthesis on incident irradiance levels was determined on the same leaves after measurements of A_{max}. The incident photon flux was increased to approximately 2.1 mmol photon m^{-2} s^{-1}, but otherwise cuvette parameters were kept the same as for the measurement of A_{max}. Photosynthetic rates were recorded after steady state values had been obtained. Light was lowered in steps to approximately 0.2 mmol photon m^{-2} s^{-1}, at each point waiting for steady state values before recording and then proceeding to the next lower light level. Individual representative curves are presented to illustrate the responses.

Following the photosynthetic light response curve, the incident irradiance was increased to 1.8 mmol photon m^{-2} s^{-1} in order to then measure the dependence of photosynthesis on c_i. Leaf temperature and Δw in these measurements were kept the same as in the photosynthetic light dependence curves. The c_i was controlled by varying the ambient CO_2 concentrations within the cuvette. Again, individual representative curves are presented to illustrate the responses.

Following the set of gas exchange measurements on each leaf, the leaf absorptance in the 400- to 700-nm waveband was determined using an Ulbricht integrating sphere (5) and then the Kjeldahl nitrogen content of that same leaf was also determined.

Measurements were also collected on leaves produced under different leaf water potentials in order to determine if there were direct effects of a change in SLM on photosynthesis. For each sample, the leaf absorptance was first measured on a 2.1 cm^2 central part of the leaf away from the leaf midvein. The pubescence was then scraped away and the weights of the pubescence

and the remainder of the leaf were determined after drying for 48 h at 80°C. The SPM was calculated as the mass of leaf pubescence (top and bottom) per unit projected area.

RESULTS

Before beginning the gas exchange measurments of the plant response to long term soil water depletion, preliminary photosynthetic measurements were made on well watered plants (midday leaf water potentials of approximately −1.6 MPa). A_{max}, g, and c_i were all very similar to the values reported earlier by Ehleringer and Björkman (9).

Water was then withheld from the potted *E. farinosa* and the plant response to progressive soil water depletion was monitored. A_{max} decreased in a linear manner from 55 μmol m^{-2} s^{-1} to 0 μmol m^{-2} s^{-1} as leaf water potential declined from −1.6 MPa to −5.2 MPa (Fig. 1). The slope of the relationship was significant (A_{max} = 14.17 ψ_l + 73.0, r^2 = 0.864, P < 0.001), although there were no apparent differences between the fast drought and slow drought responses. From this regression, the calculated zero intercept for net photosynthesis was −5.2 MPa.

When the response of net photosynthesis to photon flux was measured on individual leaves exposed to long term drought, it was evident that associated with the overall decline in photosynthetic rates light saturation occurred at progressively lower irradiances (Fig. 2). Under well watered conditions (leaf water potential of −1.7 MPa), net photosynthesis was not light saturated at maximum midday irradiances (2 mmol photons m^{-2} s^{-1}). However, by the time leaf water potentials had declined to −3.2 MPa, photosynthetic light saturation was evident under maximum midday irradiances. At leaf water potentials of −4.0 MPa, photosynthesis was light saturated by 1.0 mmol photons m^{-2} s^{-1}. The incident quantum yield of photosynthesis (initial slope of the curves in Fig. 2) declined as leaf water potential decreased. However, this apparent decrease in quantum yield was the result of leaf absorptance changes caused by increased amounts of a reflective leaf pubescence (9, 10), and not to any intrinsic decrease in absorbed quantum yield with increasing leaf water stress.

Leaf conductance to water vapor measured at the same time as A_{max} also declined linearly with decreasing leaf water potential
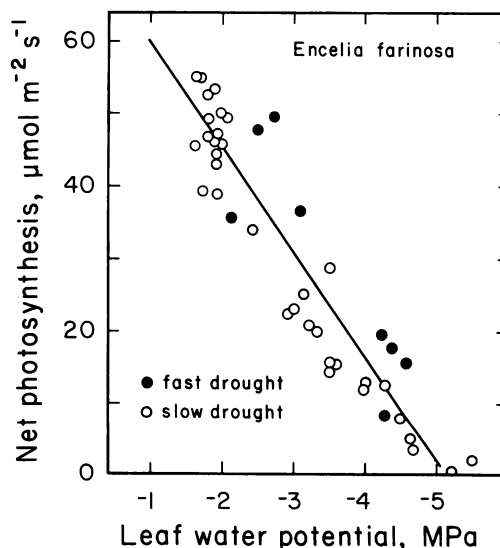

FIG. 1. The effect of ψ_l on net photosynthesis (A_{max}) measured at an irradiance of 1.8 mmol photons m^{-2} s^{-1} (400–700 nm), leaf temperature of 30°C, Δw of 17 mbar bar^{-1}, ambient CO_2 concentration of 330 μl l^{-1}, and an O_2 concentration of 21%. The equation of the regression line is A_{max} = 14.17 ψ_l + 73.0 (r^2 = 0.864, P < 0.01).
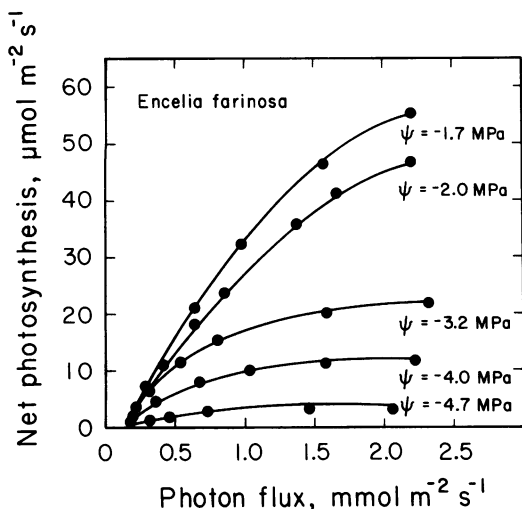
FIG. 2. The effect of photon flux (400–700 nm) on net photosynthesis for leaves at different leaf water potentials. Measurement conditions were a leaf temperature of 30°C, Δw of 17 mbar bar^{-1}, ambient CO_2 concentration of 330 $\mu l\ l^{-1}$, and an O_2 concentration of 21%.

FIG. 4. The dependence of net photosynthesis on intercellular CO_2 concentration for leaves at different leaf water potentials. Measurement conditions were 1.8 mmol photons $m^{-2}\ s^{-1}$ (400–700 nm), a leaf temperature of 30°C, leaf-water vapor concentration gradient of 17 mbar bar^{-1}, and an O_2 concentration of 21%.
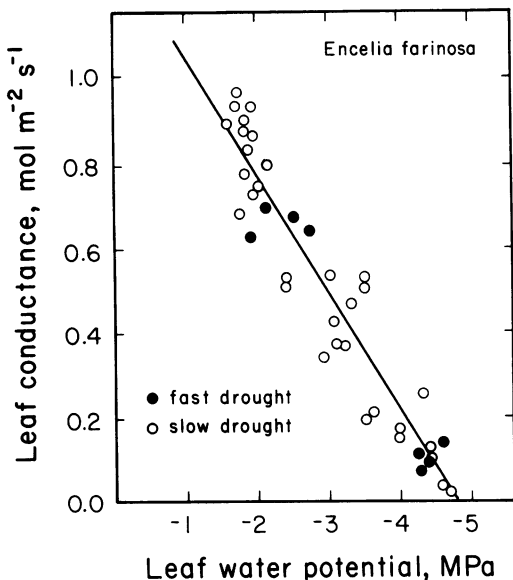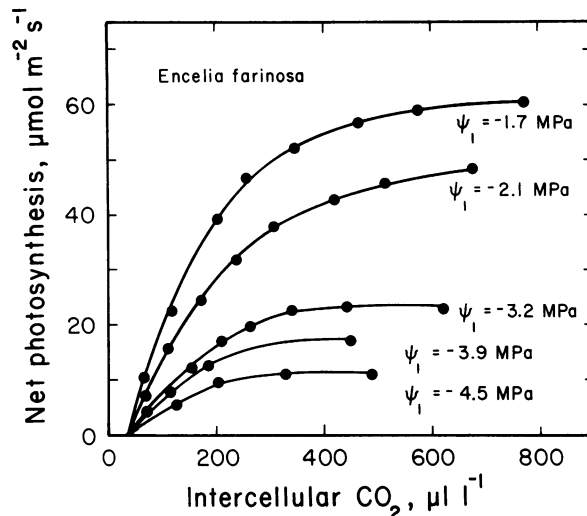

FIG. 3. The effect of ψ_1 on g under the conditions defined in Figure 1. The equation of the regression line is g = $-0.277\ \psi_1$ + 1.32 (r^2 = 0.894, P < 0.01).
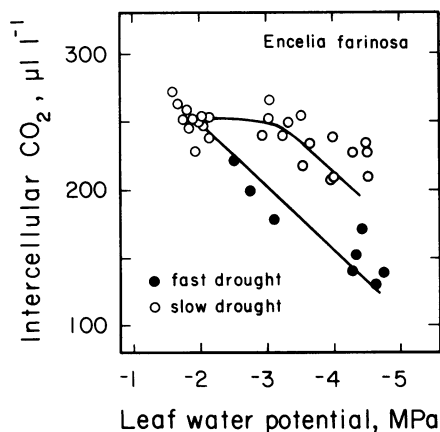

FIG. 5. The dependence of intercellular CO_2 concentration at A_{max} on leaf water potential (for the same plants as measured in Fig. 1). (O), represents plants droughted over a 25-d period; (●) represents plants droughted over a 12-d period.

(Fig. 3). Over the leaf water potential range of -1.6 MPa to -4.7 MPa, the relationship between these two parameters was g = $0.277\ \psi_1$ + 1.32 (r^2 = 0.894, P < 0.001). The calculated zero leaf conductance intercept was -4.77 MPa, some 0.38 MPa higher than the calculated zero intercept for net photosynthesis.

Maximum photosynthetic capacity under high c_i and the initial slope of the A versus c_i response curve (carboxylation efficiency) both declined with decreasing leaf water potential (Fig. 4). The projected CO_2 compensation point was approximately 40 $\mu l\ l^{-1}$, and did not change with leaf water potential. It appeared that at high c_i, the shape of the A versus c_i response curve became saturated under low leaf water potentials, whereas there were still slight increases in A at high c_i when leaf water potentials were high.

Leaf Kjeldahl nitrogen content decreased as leaf water potentials declined. As a consequence, there was a strong positive relationship between A_{max} and Kjeldahl nitrogen content (A_{max} = 1.36N − 5.38, r^2 = 0.74, P < 0.01). The calculated Kjeldahl

nitrogen content at an A_{max} of zero was 4.0 mg g^{-1}, surprisingly close to the 4- to 5.5-mg g^{-1} range of values commonly measured on abscised dead leaf tissues in the field (Ehleringer, unpublished data). Carboxylation efficiency as measured by the initial slope of the A versus c_i dependence curve was also tightly correlated with Kjeldahl nitrogen content ($\partial A/\partial c_i$ = 0.018 + 0.0048N, r^2 = 0.60, P < 0.02).

The intercellular CO_2 concentration associated with each A_{max} value during the drought cycle decreased with decreasing leaf water potential. c_i decreased from a maximum of approximately 260 $\mu l\ l^{-1}$ to 130 $\mu l\ l^{-1}$ over the entire leaf water potential range. However, the value of c_i depended on whether or not the plants were exposed to a fast drought cycle or a slow drought cycle (Fig. 5). At any specific leaf water potential during the drought cycle, c_i was always lower in the leaves of the fast drought cycle plants than in those of the slow drought cycle plants.

The decrease in both A_{max} and c_i with declining ψ_1 and the corresponding decrease in g could suggest that stomates were imposing a greater limitation on photosynthesis under water stress conditions. Decreases in A_{max}, c_i, and g with ψ_1 are mandatory for such a hypothesis, but not sufficient. It is also necessary

to demonstrate that the percentage of l_s increased as ψ_l declined.

From measurements of the A *versus* c_i dependence curve and knowing c_i at A_{max} as ψ_l declined, the percentage of l_s was calculated. The stomatal limitation on photosynthesis increased from 8 to 34% as leaf water potential declined from -1.7 MPa to -4.5 MPa (Fig. 6). The magnitude of l_s depended on the rate at which water stress was induced. The trend was similar to that previously shown for the change in c_i with ψ_l. At any specific ψ_l stomates on leaves of the fast drought cycle plants imposed a greater diffusion barrier than those on the slow drought cycle plants.

WUE, molar ratio of photosynthesis to transpiration, has frequently been used as a measure of plant performance under water stress. If Δw is held constant, then WUE is inversely proportional to c_i. The gas exchange data presented showed that WUE increased by a factor of two as leaf water potentials declined, but that WUE was higher in leaves of fast drought cycle plants than in those of slow drought cycle plants.

In response to decreased leaf water potentials in *E. farinosa*, it has been suggested that there are adaptive changes in leaf morphology (other than leaf pubescence) that result in an enhanced photosynthetic rate. Specifically, Cunningham and Strain (4) and Odening *et al.* (18) have shown that photosynthesis under low soil water availability was strongly correlated with specific leaf mass (based on entire leaf tissue). Ehleringer (6) has shown that the new *E. farinosa* leaves produced under lower leaf water potentials have increased amounts of a reflective pubescence on both upper and lower surfaces, and Ehleringer and Mooney (10) concluded that the changes in photosynthetic rate with changes in leaf pubescence could be accounted for by considering only the effects of pubescence on absorption. To resolve this apparent difference, measurements were made to separate the effects of a change in specific mass of the photosynthetic tissue from those

of changes in pubescence mass on the calculation of SLM. There was no significant relationship between the specific leaf tissue mass after pubescence had been removed and total specific leaf mass ($r^2 = 0.015$, NS, $n = 63$). However, the regression of SLM against SPM resulted in a significant, linear relationship (SLM $= 0.951 \times$ SPM $+ 6.87$, $r^2 = 0.876$, P < 0.001). Since the slope is nearly one, this indicated that the pubescence accounted for almost all of the observed changes in specific leaf mass. The data from Figure 7 show that there was effectively no change in the mass of the nonpubescence leaf tissue as the amount of pubescence increased.

Pressure-volume curves were measured on leaves exposed to well watered and droughted conditions. Under well watered conditions, the midday total leaf water potentials were -1.4 MPa, but under droughted conditions had declined to -4.0 MPa. The calculated osmotic leaf water potential at 100% water content declined from -1.37 to -2.07 MPa over this range, indicating an active production of solutes (osmotic adjustment) in response to decreased soil water availability (Fig. 8). The osmotic leaf water potential at zero turgor declined from -1.87 MPa to -3.97 MPa, implying that turgor pressures had decreased from 0.45 MPa to 0.03 MPa as the plants were droughted. Additionally, the calculated modulus of elasticity changed from 9.1 MPa to 24.0 MPa as plants were droughted. However, the RWC and percentage of bound water remained constant.

DISCUSSION

As leaf water potentials decreased over time in *E. farinosa*, there were decreases in A, g, and $\partial A/\partial c_i$. These data suggest a coordinated, leaf level response to long term soil water depletion. The extent to which stomatal and nonstomatal components are coupled can be assessed by measurements of l_s as drought progressed. Estimates of l_s increased from approximately 8% at -1.7 MPa to approximately 23 and 34% at -4.5 MPa for the slow and fast drought cycles, respectively. Although both data sets suggest only modest increases in l_s with drought, the rate at which leaf water potentials decrease is an important factor influencing the tightness of the coupling between stomatal and nonstomatal components. It would appear that leaf conductance adjusts quickly to increased water stress, but that nonstomatal components may respond more slowly. Thus, under the more rapidly
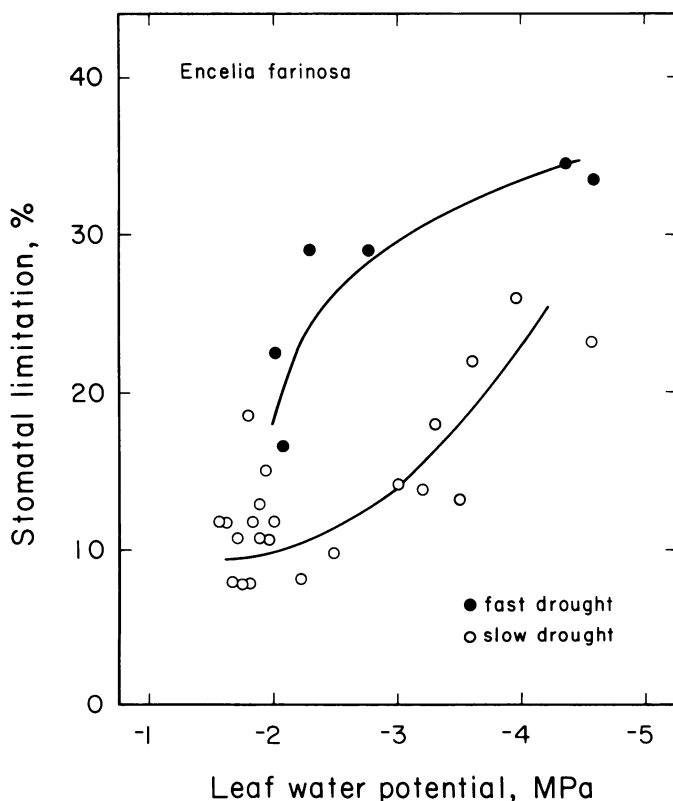
FIG. 6. The percentage stomatal limitation to photosynthesis is A_{max} as a function of leaf water potential for plants that were droughted over a 25-d period (O) and over a 12-d period (●).
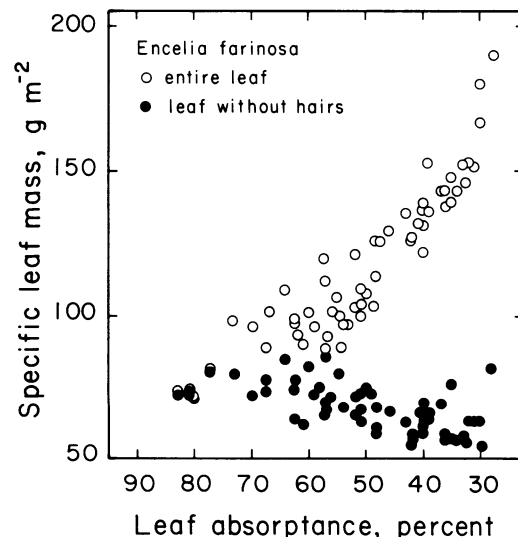
FIG. 7. The relationship between specific leaf mass and leaf absorptance (400–700 nm). Samples were collected from leaves produced at various water potentials. (O) represents total specific leaf mass, while (●) represents the specific leaf mass after the pubescence had been removed.
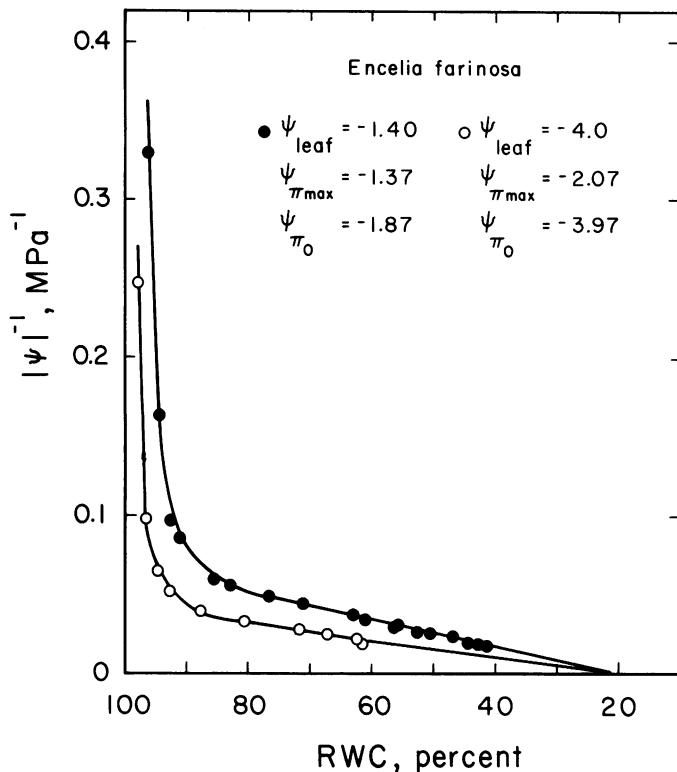
Encelia farinosa

ψ_{leaf} = -1.40	ψ_{leaf} = -4.0
$\psi_{\pi max}$ = -1.37	$\psi_{\pi max}$ = -2.07
$\psi_{\pi 0}$ = -1.87	$\psi_{\pi 0}$ = -3.97

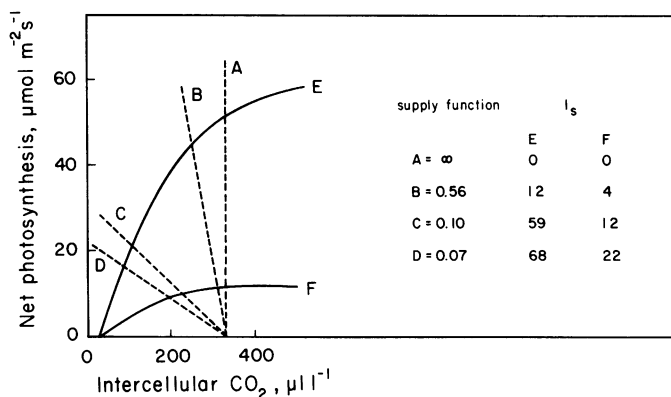FIG. 8. Pressure-volume curves for leaves under well watered and droughted conditions.

FIG. 9. The dependence of photosynthesis on intercellular CO_2 concentration at high and low leaf water potentials (redrawn from Fig. 1) (———, E and F). - - -, A–D represents different supply functions, g' (mol m^{-2} s^{-1}). The table indicates the calculated stomatal limitation of photosynthesis (%) for various supply and demand functions. See text for further details.

induced water stress, the stomatal limitation appears greater because the leaf's capacity to use intercellular CO_2 has not decreased as fast as has the leaf conductance. Similar trends have been noticed by Hanson (13). Leaf water potential decreases to −4.5 MPa over a 25-d period are slow enough to be more similar to the natural drying rate under field conditions (8).

The small increase in l_s as leaf water potentials decreased from −1.7 MPa to −4.5 MPa had a minimal effect on decreasing the photosynthetic rate; it also resulted in a decreased transpiration rate and an increased water use efficiency. The decreased photosynthetic rate can be attributed to both changes in the A versus c_i response curve (nonstomatal component) and leaf conductance. This is best illustrated by calculating the effect on A of a change in g' (supply function). In Figure 9 we have replotted the

A versus c_i response curves (demand function) at ψ_i = −1.7 MPa (E) and ψ_i = −4.5 MPa (F) from Figure 4. The actually measured supply functions for curves E and F are lines B and D, respectively. As ψ_i decreased from −1.7 to −4.5 MPa, l_s increased from 12 to 22%. In order for l_s to remain at 12% for demand function F, it would require that g' have increased to 0.10 mol m^{-2} s^{-1} (supply function C). This change would have increased photosynthesis by 1 μmol m^{-2} s^{-1} (approximately 11%) to 10 μmol m^{-2} s^{-1}, but would have increased transpiration by 30%. Increasing the supply function for demand function F to the value measured for demand function E would have resulted in only a slightly higher photosynthetic rate. However, this change would have increased the transpiration rate eight fold.

E. farinosa commonly occurs throughout the Sonoran Desert in habitats with less than 250 mm annual precipitation. The shrubs are mostly deciduous during the prolonged drought periods between normal rainy seasons. However, because the precipitation pattern within the growing season is highly intermittent, these shrubs are often exposed to periodic drought stresses during the growing season. The ability of E. farinosa leaves to osmotically adjust allows stomates to remain partly open at the low leaf water potentials experienced during intermittent drought. In combination with the nonstomatal photosynthetic changes, it appears that low, but positive photosynthetic rates can be maintained during these drought periods.

In the northern portions of the Sonoran Desert, E. farinosa occasionally overlaps in distribution with Encelia frutescens. In such locations, E. farinosa occurs only on the rocky bajadas and slopes, whereas E. frutescens will occur only in the washes. These rocky slopes are drier and have much shallower soils than is found in the washes. Consistent with these microdistributional differences are the photosynthetic drought tolerances of the two species. Whereas E. farinosa is able to maintain positive photosynthesis down to leaf water potentials of −5.2 MPa, E. frutescens can maintain positive photosynthesis only down to −4.1 MPa (2).

Cunningham and Strain (4) measured seasonal photosynthetic rates and water use efficiency in E. farinosa and found a correlation with specific leaf weight. They concluded that changes in specific leaf weight were of adaptive value in allowing these shrubs to remain active into drought periods. In a similar manner, Odening et al. (18) concluded that during drought increased specific leaf weight was the factor responsible for enhanced water use efficiency. Our estimates of specific leaf mass in this study indicate that all of the increases in specific leaf mass can be attributed to increases in pubescence. While pubescence is of adaptive value in altering spectral characteristics and thus leaf temperature and water loss as has been discussed elsewhere (10, 21), it appears to play no role in the adjustment of nonstomatal photosynthetic components to low leaf water potentials. The l_s data available from this study suggest that decreased leaf conductance coupled with observed increases in leaf reflectance are the factors responsible for the increased water use efficiency under drought stress.

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