

Ecophysiology of *Amaranthus palmeri*, a sonoran desert summer annual

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Summary. Basic photosynthetic and water relations characteristics in relation to soil water availability were investigated in *Amaranthus palmeri*, a common C_4 summer annual of the Sonoran Desert. Under conditions of high soil water availability, photosynthetic capacity exceeded $70 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ at a leaf temperature optimum of 42°C , and photosynthesis was not light saturated at an irradiance of $2.0 \text{ mmol m}^{-2} \text{ s}^{-1}$ (400–700 nm). Leaves of *A. palmeri* exhibited diheliotropic movements, allowing them to take advantage of their high photosynthetic capacity. In response to a long term drought cycle, both photosynthetic rate and leaf conductance to water vapor decreased, reaching minima at an approximate leaf water potential of -2.9 MPa . Active leaf osmotic adjustment appeared to play an important role in allowing leaves to maintain gas exchange activities down to these low leaf water potentials. The photosynthetic rate became light saturated at the lower leaf water potentials. Although the two parameters decreased in concert, the decreased photosynthetic rate was not due to increased stomatal diffusion limitations, since intercellular CO_2 concentrations remained constant over the range of leaf water potentials. Instead it appeared that during the drought cycle, both intrinsic photosynthetic capacity and leaf protein content decreased as well. These results suggested a coordination of gas exchange parameters during long term drought such that the intercellular CO_2 concentration remained constant.

Introduction

Following infrequent rains in the Sonoran Desert of North America, the slopes and washes are often carpeted to various degrees by an annual flora. Two distinct groups of ephemerals are recognized, winter and summer annuals, each being associated with a major precipitation period (Shreve and Wiggins 1964; Mulroy and Rundel 1977). Since the precipitation in these habitats is often low and the seasonal pattern unpredictable, there may be considerable selective pressure on these annuals to complete their life cycle during the brief window in which water is available. This may be achieved by flowering at a smaller size, accelerated growth rates, or both.

Recently, attention has been focused on the physiological and morphological characteristics of winter desert annuals that may contribute to high growth and photosynthetic rates at times when soil water is readily available and to

the maintenance of these activities into the drought period (Mooney et al. 1976; Monson and Szarek 1979; Mooney and Ehleringer 1978; Ehleringer and Forseth 1980; Forseth and Ehleringer 1982a, b, 1983; Ehleringer 1983). Five components are thought to contribute: 1) unusually high photosynthetic capacities (Mooney et al. 1976; Armond and Mooney 1978; Forseth and Ehleringer 1982a; Werk et al. 1982), 2) leaf solar tracking to insure high incident quantum flux (PAR) levels (Ehleringer and Forseth 1980; Forseth and Ehleringer 1982b), 3) photosynthetic acclimation to high leaf temperatures (Seemann et al. 1979; Forseth and Ehleringer 1982a), 4) leaf osmotic adjustment to keep stomata open as soil water potentials decline (Forseth and Ehleringer 1982b), and 5) a high above ground relative to below ground allocation pattern (Monson and Szarek 1981; Clark and Burk 1980; Bell et al. 1979).

Very little attention has been focused on the characteristics of summer Sonoran Desert annuals. It is known that many summer desert annuals possess the C_4 photosynthetic pathway (Mulroy and Rundel 1977), but other physiological characteristics are unknown. This paper describes the basic photosynthetic characteristics of *Amaranthus palmeri*, a common C_4 summer annual occurring in the Sonoran Desert. As drought is a significant part of the life cycle of these ephemerals, plants were examined under watered short term atmospheric drought and long term soil drought conditions.

Materials and methods

For laboratory measurements, plants were grown from seed in 40 l pots. They were watered daily and fertilized weekly. The plants were grown outdoors during the summer months in Salt Lake City, Utah. The physical environment in Salt Lake City during the summer is approximately 5°C cooler than the typical *Amaranthus palmeri* habitat within the Sonoran Desert, but in other respects is quite similar. For the drought experiments, water was withheld and the pots dried out over a 3–4 week period. This time frame is similar to the soil water depletion period seen under field conditions.

For gas exchange measurements on an incident light basis, a single attached leaf was inserted into a ventilated open system leaf cuvette (total volume 150 ml). The cuvette was made of nickel plated brass with a glass top. The cuvette sides and glass top were waterjacketed for control of cuvette temperature. Light was provided by a 1,000 W sodium vapor HID lamp in conjunction with neutral

density filters. Quantum flux incident on the leaf was continuously monitored with silicon cells that had been calibrated against a quantum sensor.

Leaf temperature was measured with 36 gauge copper-constantan thermocouples attached to the lower surface and was adjusted by controlling the temperature of the leaf cuvette water jackets. Line air was scrubbed of CO_2 by bubbling through KOH and then dried by passing the air stream over indicating silica gel. This air was continuously mixed with gas from a cylinder containing 1% CO_2 in N_2 . The gas mixture was controlled using rotameters. A small portion of the resulting gas was passed through an infrared gas analyzer (Analytical Development Corp., Hoddesdon, England) for absolute CO_2 concentration determination. (For lower flow rates the CO_2 free gas was continuously and precisely mixed with the 1% CO_2 gas using a high capacity gas mixing pump (Wösthoff OHG, Bochum, West Germany).) The resulting gas stream was humidified by passing through a bubbling vessel maintained at 5°C above the desired dew point. 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 (4 ml s^{-1}) through a relative humidity sensor (Vaisala, Helsinki, Finland) and then through a magnesium perchlorate desiccant before entering the reference cell of a differential gas analyzer (Beckman Instruments, Fullerton, CA). Flow rates to the cuvette were measured with a differential pressure transducer (Validyne Corp., Northridge, CA). A portion of the returning gas passed through another relative humidity sensor, magnesium perchlorate desiccant, and then entered the sample cell of the differential gas analyzer. All gas lines consisted of stainless steel tubing and were heated to approximately 50°C to prevent condensation. All sensor inputs were connected to a digital millivolt meter. Voltages from the millivolt meter were typed into a micro-computer 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 concentration. It also provided a record of the incident quantum flux, leaf temperature, and CO_2 and water vapor concentrations within the cuvette. Outgoing humidity and differential CO_2 concentrations were continuously displayed on an analog recorder, providing a qualitative assessment of the experimental manipulations.

In the photosynthesis-light response experiments, leaves were first exposed to light at an intensity of about $2\text{ mmol m}^{-2}\text{ s}^{-1}$ (400–700 nm). After a constant photosynthetic rate had been achieved, the light was lowered in steps to total darkness. Photosynthesis was allowed to stabilize at each step before advancing to the next lower light level. Leaf temperature was held constant during each experiment at $40 \pm 1^\circ\text{C}$. The CO_2 concentration in the cuvette (equal to outgoing CO_2 concentration) was $320\text{--}330\text{ }\mu\text{l l}^{-1}$ CO_2 and the water vapor pressure deficit was kept at about 10 mbar.

In the experiments in which atmospheric CO_2 concentrations were varied, the results were expressed as a function of the intercellular CO_2 concentration calculated as

$$C_i = C_a - 1.6 A/g$$

where C_i and C_a are the intercellular and ambient CO_2 concentrations, A is the net photosynthetic rate, and g is

the leaf conductance to water loss. Light intensity during these experiments was constant at $1.9\text{--}2.0\text{ mmol m}^{-2}\text{ s}^{-1}$. Leaf temperature was kept at 40°C and the water vapor pressure deficit was approximately 10 mbar.

For measurements of the temperature dependence of photosynthesis, the rates were initially measured at 30°C . Incident light levels were $1.9\text{--}2.0\text{ mmol m}^{-2}\text{ s}^{-1}$, C_a was $325\text{ }\mu\text{l l}^{-1}$, and the water vapor pressure deficit of 10 mbar. After photosynthetic equilibrium had been obtained, the leaf temperature was lowered in several steps (about 5°C each). Photosynthesis was allowed to stabilize at each step 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.

The sample size for photosynthetic experiments was 3–6 leaves from different plants. Leaf absorptances were measured with an integrating sphere as described by Ehleringer (1981). Total leaf nitrogen was determined on the same samples used in the photosynthetic measurements using the micro-Kjeldahl method.

The measurements of leaf water potential and osmotic adjustment were collected using a Scholander pressure chamber. Methodology for the osmotic adjustment determinations followed Wilson et al. (1980). Data presented are averages of 4–7 leaves.

Results

Net photosynthetic rate in leaves of *Amaranthus palmeri* was strongly temperature dependent. Under ambient CO_2 levels and high incident irradiances, the temperature optimum was at 42°C (Fig. 1). The photosynthetic rate (A) at 42°C was $81\text{ }\mu\text{mol m}^{-2}\text{ s}^{-1}$. At the thermal optimum, the leaf conductance to water loss (g) was 20.3 mm s^{-1} and the intercellular CO_2 concentration was $135\text{ }\mu\text{l l}^{-1}$. Ninety percent of peak photosynthetic rate occurred between 36 and 46°C . The decrease in photosynthetic rate was relatively steep on both sides of the temperature optimum. The rate at 25°C was only 50% of the rate at the temperature optimum and unstable photosynthetic rates occurred above approximately 52°C .

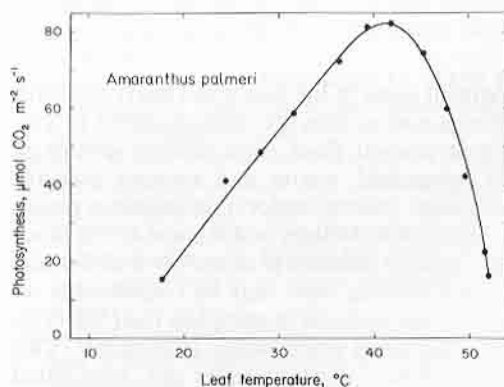


Fig. 1. The temperature dependence of net photosynthesis in leaves of *Amaranthus palmeri*. Experimental conditions were an incident quantum flux of $2\text{ mmol m}^{-2}\text{ s}^{-1}$, ambient CO_2 levels of $325\text{ }\mu\text{l l}^{-1}$, and a water vapor pressure deficit of 10 mbar. Midday leaf water potentials were approximately -0.5 MPa .

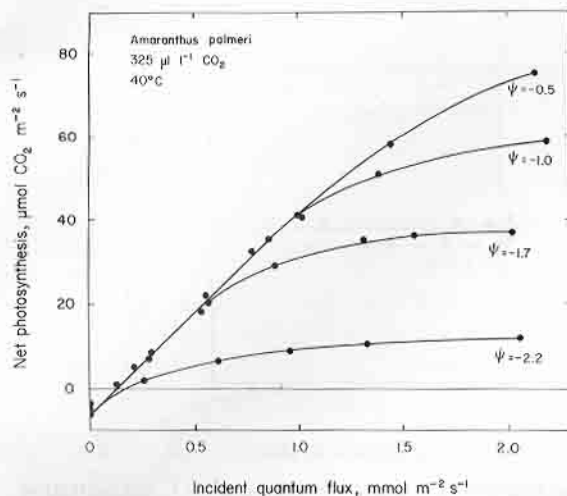


Fig. 2. The response of net photosynthesis to changes in incident quantum flux for leaves of *Amaranthus palmeri* experiencing different leaf water potentials. The decreased leaf water potentials were imposed during a long term drought cycle. Experimental conditions were a leaf temperature of 40°C , ambient CO_2 levels of $325 \mu\text{l l}^{-1}$, and a water vapor pressure deficit of 10 mbar

Having determined the temperature optimum for photosynthesis, photosynthesis-light response curves were conducted at a leaf temperature of 40°C . On well watered plants ($\psi_{\text{leaf}} = -0.5 \text{ MPa}$) the peak photosynthetic rate was near $80 \mu\text{mol m}^{-2} \text{ s}^{-1}$ (Fig. 2). Leaves were not light saturated, even at a peak irradiance of $2 \text{ mmol m}^{-2} \text{ s}^{-1}$. Up to irradiances of about $1.0 \text{ mmol m}^{-2} \text{ s}^{-1}$, the response of photosynthesis to irradiance was linear. The absorbed quantum yield for light intensities below $0.5 \text{ mmol m}^{-2} \text{ s}^{-1}$ was 0.053.

Water was withheld from these plants for three weeks and the plants experienced a progressive long term drought. As leaf water potentials declined, photosynthesis-light response curves were measured at different midday leaf water potentials. Peak photosynthetic rates declined as water stress developed (Fig. 2). The decrease in photosynthetic rate was paralleled by a decrease in the light intensity required for saturation. There was no apparent decline in the quantum yield (photosynthetic efficiency) at the lower irradiances, but deviation from this maximum efficiency occurred at progressively lower irradiances as long term water stress developed. In conjunction with decreased photosynthetic capacity, the dark respiration rate also declined.

The decrease in photosynthetic capacity (A_{max}) with decreasing leaf water potential followed a nearly linear relationship (Fig. 3). The decrease in A_{max} in this long term water stress experiment was approximately $33 \mu\text{mol m}^{-2} \text{ s}^{-1}$ per MPa change in leaf water potential and reached the compensation point at a midday leaf water potential of -2.9 MPa .

As leaf water potentials began to decline with increasing drought stress, pressure-volume curves on individual leaves were used to determine turgor and osmotic potentials (Fig. 4). Under well watered conditions, total midday leaf water potential was -0.5 MPa , and the calculated relative water content was 94%. The calculated turgor and osmotic potentials at this time were 0.83 MPa and -1.33 MPa , respectively. Zero turgor pressure (and thus a stomatal conductance near zero) was calculated to occur at -1.55 MPa .

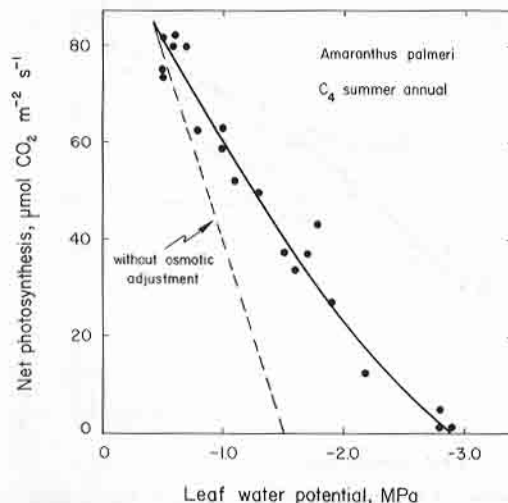


Fig. 3. The response of net photosynthesis (A_{max}) to leaf water potential in leaves of *Amaranthus palmeri* in a long term drought stress experiment. Experimental conditions were an incident quantum flux of $2 \text{ mmol m}^{-2} \text{ s}^{-1}$, ambient CO_2 levels of $325 \mu\text{l l}^{-1}$, and a water vapor pressure deficit of 10 mbar

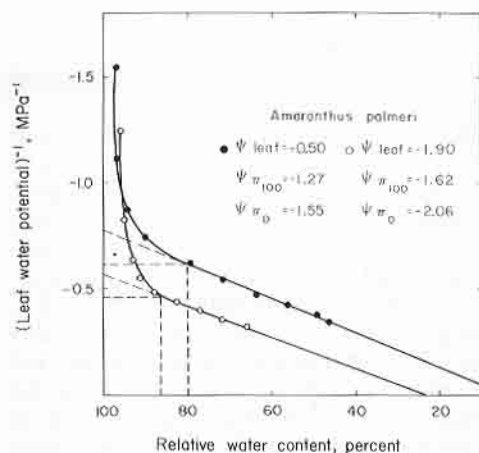


Fig. 4. Pressure-volume curves for leaves of *Amaranthus palmeri* at two midday leaf water potentials in a long term drought cycle. π_{100} and π_{20} are the osmotic potentials in MPa at 100% relative leaf water content and at zero turgor pressure, respectively

Based on these relationships, A_{max} would be expected to reach zero at a leaf water potential of approximately -1.55 MPa if osmotic adjustment were not to have occurred, and the decline in A_{max} with long-term drought stress would have been approximately $70 \mu\text{mol m}^{-2} \text{ s}^{-1}$ per MPa change in leaf water potential (shown as dashed line in Fig. 3).

Midway through the drought stress experiment, total midday leaf water potentials had declined to -1.90 MPa , and the calculated relative water content was 91%. However, the calculated turgor and osmotic potentials were now 0.10 MPa and -2.00 MPa , respectively, strongly implying that osmotic adjustment had taken place. The 0.35 MPa change in osmotic potential between leaf water potentials of -0.50 and -1.90 MPa was caused by an active production of solutes, although the nature of the osmoticum was not determined. Pressure-volume curves were not measured on leaves at water potentials of -2.5 to -3 MPa . However,

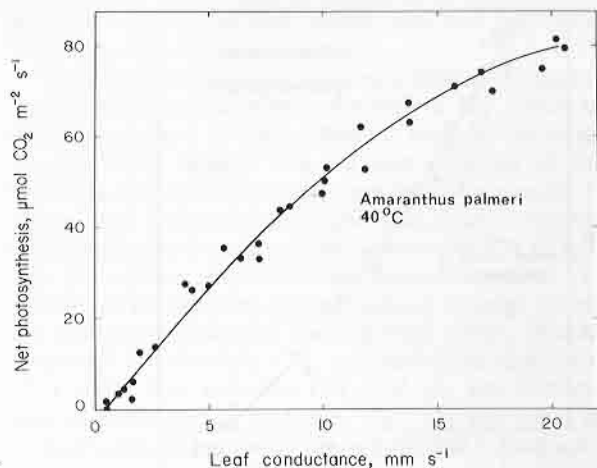


Fig. 5. The response of net photosynthesis (A_{\max}) to leaf conductance to water loss (g) in leaves of *Amaranthus palmeri*. Data are pooled from a long term drought experiment

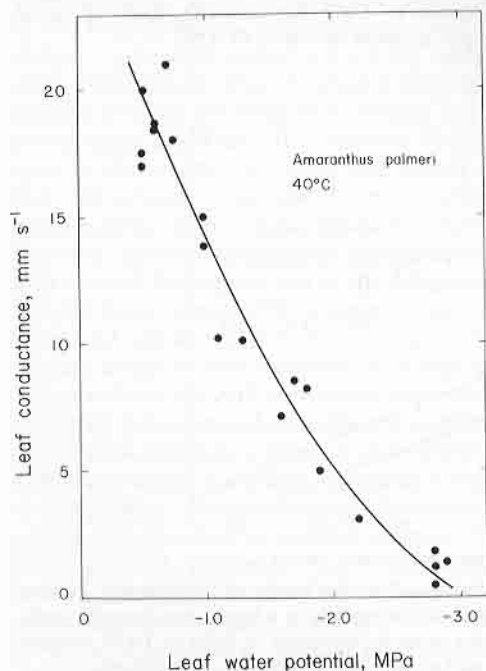


Fig. 6. The response of leaf conductance to water loss (g) to leaf water potential in leaves of *Amaranthus palmeri*. Data are pooled from a long term drought experiment

it is presumed that osmotic adjustment (though perhaps to a decreased extent) continued to occur as midday leaf water potentials declined to these values.

The correlation of A_{\max} and leaf conductance to water loss (g) at A_{\max} was compiled from measurements on plants in the long term drought stress experiment. There was a nearly linear relationship between g at A_{\max} and A_{\max} (Fig. 5). At the highest A_{\max} values, there was a slight deviation from linearity indicating that further increases in g resulted in smaller increases in A_{\max} . Based on this $A_{\max} \times g$ curve, the average C_i between A_{\max} values of 0–70 $\mu\text{mol m}^{-2} \text{s}^{-1}$ was approximately 130 $\mu\text{l l}^{-1}$. At the highest A_{\max} values, C_i was approximately 135–140 $\mu\text{l l}^{-1}$.

As long term drought stress developed, g at A_{\max} declined with leaf water potential (Fig. 6). This decline in leaf

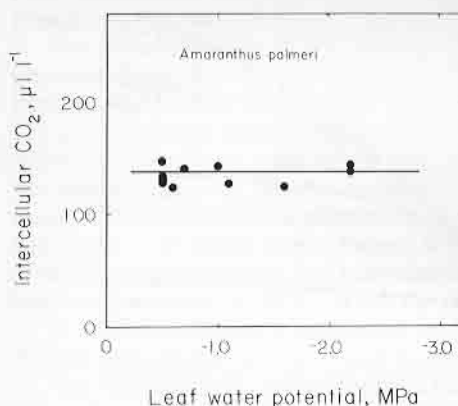


Fig. 7. The relationship between intercellular CO_2 concentration at maximum net photosynthesis (A_{\max}) and leaf water potential in leaves of *Amaranthus palmeri* during a long term drought experiment. Experimental conditions were an incident quantum flux of 2 $\text{mmol m}^{-2} \text{s}^{-1}$, a leaf temperature of 40°C, and a water vapor pressure deficit of 10 mbar

conductance with leaf water potential paralleled the observed decline in photosynthesis with leaf water potential (Fig. 3). One might initially conclude from this that the decline in A_{\max} with long term water stress was due to the decline in g . However, this is not the case because intercellular CO_2 concentrations tended to remain constant as leaf water potentials declined. As illustrated in Fig. 7, the intercellular CO_2 concentration remained at 130–140 $\mu\text{l l}^{-1}$, irrespective of midday leaf water potential. If the photosynthetic rate was strictly limited by leaf conductance, then the intercellular CO_2 concentration should have declined with decreasing leaf water potentials. That the intercellular CO_2 concentration remained constant as leaf conductance decreased with long term drought stress, implied that the intrinsic photosynthetic capacity of the leaf must have declined with decreased leaf water potential.

Photosynthetic capacity declined with water long term drought stress (Fig. 8). The photosynthetic CO_2 dependence response curve plateaued at 130–150 $\mu\text{l l}^{-1}$, typical of C_4 species. However, the photosynthetic rate at intercellular CO_2 saturation declined in concert with declining leaf water potentials. The decrease in photosynthetic capacity was associated with a decrease in leaf protein content as measured by leaf Kjeldahl nitrogen content (Fig. 9). This implied that as long term drought stress developed, protein breakdown occurred and resulted in progressively lower overall enzyme concentrations. The nitrogen was most likely transported from the leaves to the developing seeds, which normally have Kjeldahl nitrogen contents above 30 mg g^{-1} (Ehleringer, unpublished data).

The strong relationships between photosynthetic capacity, leaf conductance, and protein content with increasing water stress suggested a tight interaction of various photosynthetic components. One consequence of these interactions was that the C_i remained essentially constant as long term drought stress developed. It was clear from these experiments that the decrease in A_{\max} with long term drought stress cannot be attributed solely to decreased g or protein content. These were perhaps but two of a number of com-

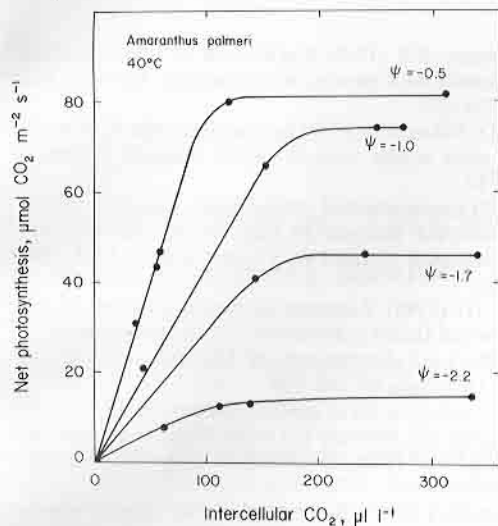


Fig. 8. The response of net photosynthesis to changes in the intercellular CO_2 concentration in leaves of *Amaranthus palmeri* at different leaf water potentials in a long term drought experiment. Experimental conditions were an incident quantum flux of $2 \text{ mmol m}^{-2} \text{ s}^{-1}$, a leaf temperature of 40°C , and a water vapor pressure deficit of 10 mbar

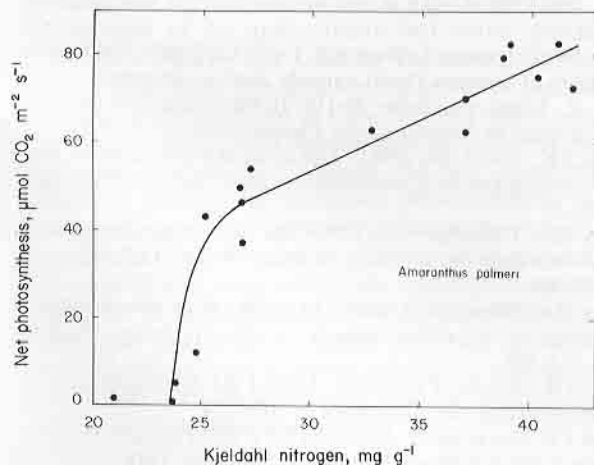


Fig. 9. The relationship of net photosynthesis (A_{max}) to Kjeldahl nitrogen content in leaves of *Amaranthus palmeri*. Data are derived from leaves in a long term drought experiment

ponents that decreased in concert with long term drought stress.

Stomatal conductance of leaves of *A. palmeri* also responded to short term atmospheric drought. In response to increasing water vapor pressure deficits (VPD), leaf conductance decreased. This resulted in decreased photosynthetic rates (Fig. 10). It was not clear whether stomata were responding directly to VPD or if leaf water potential also decreased with increasing VPD causing partial stomatal closure. Nevertheless, as VPD increased both photosynthesis and leaf conductance declined. Although the slope of the $A \times \text{VPD}$ response curve decreased with increasing soil water depletion induced drought stress, stomata remained sensitive to VPD down to the lowest leaf water potentials, implying a two stage control over water loss.

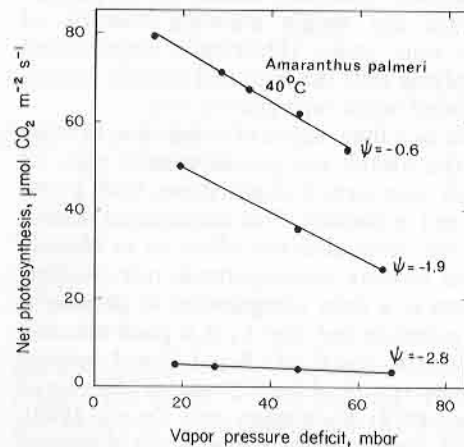


Fig. 10. The response of net photosynthesis (A_{max}) to changes in water vapor pressure deficit in leaves of *Amaranthus palmeri* at different leaf water potentials in a long term drought cycle. Experimental conditions were a quantum flux of $2 \text{ mmol m}^{-2} \text{ s}^{-1}$, a leaf temperature of 40°C , and an ambient CO_2 level of $325 \mu\text{l l}^{-1}$

Discussion

In its native Sonoran Desert habitat, *Amaranthus palmeri* is a short lived summer ephemeral. Precipitation comes from brief, but intense convection storms and is highly unpredictable. Throughout much of its distribution, it is likely that little or no further precipitation will be received during the season after the storm which induces germination. Thus, *A. palmeri* and other summer annuals must not only be able to germinate soon after a major precipitation event, but also be able to complete their life cycle based on the soil water available at the time of germination. As a consequence, we might expect to find three major types of adaptations in Sonoran Desert summer annuals. Broadly categorized, these would include 1) rapid germination characteristics, 2) rapid growth characteristics, and 3) drought tolerance mechanisms. The current investigation has demonstrated that the latter characteristic exists in *A. palmeri* and that it has a significant effect on extending the period of leaf carbon gain.

Although growth rates of *A. palmeri* were not measured in this study, their relative magnitude can be inferred from photosynthetic rates and field biomass estimates. The photosynthetic capacity of near $80 \mu\text{mol m}^{-2} \text{ s}^{-1}$ in *A. palmeri* is extremely high, even for a C_4 species (Šesták, Čatský, and Jarvis 1971; Björkman 1975; Osmond, Björkman, and Anderson 1980). However, it is presently unknown whether or not other Sonoran Desert summer annuals, many of which are also C_4 (Mulroy and Rundel 1977), also possess such high photosynthetic capacities.

Along with a high photosynthetic capacity, leaves of *A. palmeri* have the ability to solar track (Ehleringer and Forseth 1980). That is, throughout the day the leaves move to remain perpendicular to the sun's direct rays. The result is that under low water stress conditions, leaves are able to utilize the high photosynthetic capacity and maintain high photosynthetic rates throughout the day. This should

result in a substantially higher rate of carbon gain than if the leaves maintained a constant, fixed leaf angle. At field sites in southern Arizona, stands of *A. palmeri* achieved an average dry weight standing biomass of 4,907 Kg ha⁻¹ in four weeks (Ehleringer, unpublished data), strongly implying that the high leaf carbon gaining capacity was translated into a high growth rate.

There appears to be a high degree of integration in components affecting the overall net photosynthetic rate. As A_{\max} decreased with long term drought stress, both g and protein levels changed in concert. This coordinated decline in both g and protein level does not allow us to identify any key component limiting photosynthetic rate. Rather, it suggests that there is a tight coregulation of photosynthetic component activities and that C_i is a good measure of this integrated control. The C_i of 130 $\mu\text{l l}^{-1}$ in *A. palmeri* reported in this study is typical for C_4 species (Björkman 1975; Körner et al. 1979; Robichaux and Pearcy 1980). Since a C_i of 130 $\mu\text{l l}^{-1}$ is at the breakpoint in the photosynthetic CO_2 dependence curve, it can be inferred that stomates are not limiting photosynthesis. Instead non-stomatal factors are limiting photosynthesis and the stomates are operating at a point where the water use efficiency (photosynthesis/transpiration ratio) is maximized.

In response to decreasing leaf water potentials, leaves of *A. palmeri* exhibit osmotic adjustment. The increase in solute concentration results from an active production of solutes, and is not the result of a decrease in leaf water content. This feature can be considered to be an adaptation in that it allows the stomates to remain open (positive turgor) longer into a drought period (at lower leaf water potentials). As a consequence, total daily carbon gain is enhanced. This is of particular advantage in the driest habitats where there is a low probability of additional precipitation once the drought commences. Osmotic adjustment is known to occur in other desert annuals. Leaves of the winter annual *Malvastrum rotundifolium* are capable of a 1.86 MPa reduction in osmotic potential as soil moisture decreases (Forseth and Ehleringer 1982b), and from the leaf water potential surveys of Forseth et al. (1983) one can infer that this phenomenon occurs in a number of winter and summer Sonoran Desert annuals.

The extent to which leaves of *A. palmeri* operate at these high photosynthetic capacities in the field is unknown. To date, diurnal leaf conductances have only been measured when plants were experiencing midday leaf water potentials of approximately -2.5 MPa. Under these conditions, peak leaf conductances to water vapor were approximately 5 mm s⁻¹ (Forseth et al. 1983). However, under cultivated conditions in Salt Lake City, Utah midday leaf conductances of 15-18 mm s⁻¹ are common (Ehleringer, unpublished data). Additional field work will be necessary before it is known what fractions of the life cycle are spent under different degrees of water stress.

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