Photosynthesis and Microclimate of Camissonia Claviformis, A Desert Winter Annual

J. Ehleringer, H. A. Mooney, J. A. Berry

PHOTOSYNTHESIS AND MICROCLIMATE
OF *CAMISSONIA CLAVIFORMIS,*
A DESERT WINTER ANNUAL[1,3]

J. Ehleringer,[2] H. A. Mooney and J. A. Berry
Department of Biological Sciences, Stanford University,
Stanford, California 94305 USA

AND

Department of Plant Biology, Carnegie Institution of Washington,
Stanford, California 94305 USA

Abstract. The photosynthetic characteristics of the C_3 desert winter annual *Camissonia claviformis* and the microclimate of the *Camissonia* habitat in Death Valley, California on 21 March 1976 are presented. This species has one of the highest photosynthetic capacities of any higher plant, with rates exceeding 6 nmole CO_2 cm^{-2} sec^{-1} at midday irradiances and optimum leaf temperatures. The photosynthetic temperature optimum is at 20°C, in concert with the prevailing cool winter temperatures of this desert habitat. The daily totals of primary production and water loss for *Camissonia* on 21 March are calculated using leaf energy budget and CO_2 diffusion photosynthetic equations. Measured and predicted leaf temperatures were 2–4°C below air temperatures during the day. The rate of primary production is predicted to be 68.1 g CO_2 m^{-2} day^{-1} under high stomatal conductances, while daily transpiration at these stomatal conductances will be 5.54 kg m^{-2} day^{-1}. The effects of decreases in stomatal conductance on daily primary production, transpiration, and water-use efficiency are calculated and show that the values of these 3 parameters diminish rapidly with decreasing stomatal conductance.

Key words: California; Camissonia; Death Valley; desert; desert annuals; microclimate; photosynthesis; primary production; water use efficiency.

INTRODUCTION

The warm deserts of southwestern North America are characterized by having 2 distinct groups of ephemeral annual vegetation (Went 1948, Shreve 1951, Mulroy and Rundel 1977). These are the winter and the summer annuals. Each group germinates and completes its entire life cycle over the brief period of 6 weeks to several months when soil moisture is abundant in these habitats.

Many winter annuals possess germination regulation mechanisms which prevent the seeds from germinating in the hot summer months and allow germination to occur only during periods of sufficient soil moisture and favorably low temperatures (Went 1948, Juhren et al. 1956, Beatley 1974). In general, the winter annuals possess a vegetative rosette growth form (Beatley 1969, Mulroy and Rundel 1977) which places the leaves in a relatively warm microclimate during the cool winter months.

Mulroy and Rundel (1977) have shown that winter annuals of the Mojave and Sonoran Deserts possess the C_3 photosynthetic pathway, whereas the C_4 photosynthetic pathway is more common in the summer annual flora. An identical trend is also evident in the species lists of winter and summer ephemeral vegetation produced for the Sonoran Desert by Shreve (1951).

Mooney et al. (1976) measured photosynthetic rates of the annual *Camissonia claviformis* and observed extraordinarily high rates at noon irradiances. That study, which was concerned with the efficiency of photosynthesis in *Camissonia*, revealed that over most irradiances the leaves could operate at or near maximal quantum yields. The leaves of *C. claviformis* form a basal rosette (Fig. 1). The leaves are flat, variably dissected, and relatively large in size. There is very little overlap in leaves, and thus little if any mutual shading.

Little additional information, however, is available on the photosynthetic capacities of winter annuals and about the relationships between plant microclimate and primary productivity. This study examines the photosynthetic characteristics of *Camissonia claviformis,* a winter annual common to the deserts of southwestern North America and relates these to habitat conditions in Death Valley, California.

METHODS AND MATERIALS

The photosynthetic characteristics of and the microclimatic parameters adjacent to leaves of *Camissonia claviformis* were measured on 21 March 1976 on the floor of Death Valley, California. The study site is located approximately 200 m north of the United States National Park Service headquarters at an elevation of 60 m below sea level. Both photosynthetic
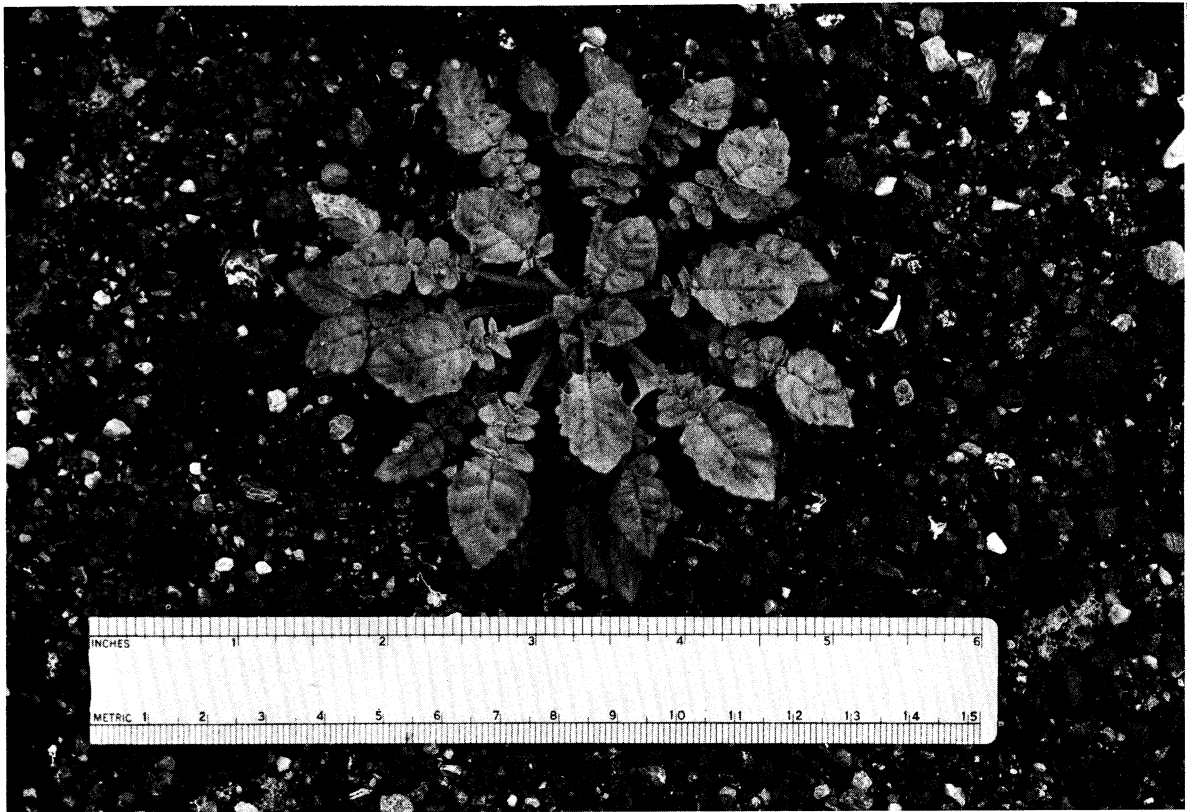
FIG. 1. Canopy architecture for *Camissonia claviformis* on the floor of Death Valley, California, showing the large, flat leaves with minimal leaf overlap.

and leaf water potential measurements were made on mature plants that had germinated 6 weeks previously following a 60 mm rain.

Photosynthesis and transpiration were measured using a mobile laboratory (Mooney et al. 1971, Björkman et al. 1973). All measurements were made *in situ* on an intact attached leaf (13.2 cm²) in a cuvette (Björkman and Holmgran 1963) in which leaf temperature and the atmospheric concentrations of water vapor and carbon dioxide could be controlled and varied. The measurements of the exchange of water vapor and carbon dioxide by the leaf were made using a ventilated open gas exchange system as described earlier by Ehleringer and Björkman (1977). Artificial illumination of the leaves was provided by a metal-arc lamp positioned above the cuvette. Irradiance was varied using neutral density filters. Previous studies had indicated that sources of error within the system are small (±2%). Variability between leaves in the field was not measured. However, light saturated photosynthetic rates were measured on leaves of plants grown under laboratory conditions and found not to differ significantly from the field measurements.

Absorptances of the leaves to photosynthetically active quanta (400 to 700 nm) from the light source

and from the sun were determined by utilizing an Ulbricht integrating sphere (Rabideau et al. 1946) and a quantum sensor (model 190-SR, Lambda Instruments, Lincoln, Nebraska). Leaf absorptances to total solar radiation (400 to 3000 nm) were determined using an integrating sphere similar to the one described by Birkebak and Birkebak (1964).

Leaf water potentials were measured on individual leaves using a Scholander type pressure bomb (Scholander et al. 1965).

Microclimate parameters adjacent to *C. claviformis* plants were monitored at hourly intervals through the daylight hours. Net radiation over the plant-soil surface was measured with a net radiometer (Micromet Instruments, Bothell, Washington). Total and diffuse solar radiation fluxes were measured with a pyranometer (model LI 200-S, Lambda Instruments, Lincoln, Nebraska). The wet and dry bulb temperatures were measured with 36 gauge copper-constantan thermocouples. The tip of the thermocouple for wet bulb measurements was in the shape of a small ring with the thermocouple junction at the center of the ring. This thermocouple was then dipped into deionized water. The thin film of water on this ring quickly approached the wet bulb temperature even at low wind
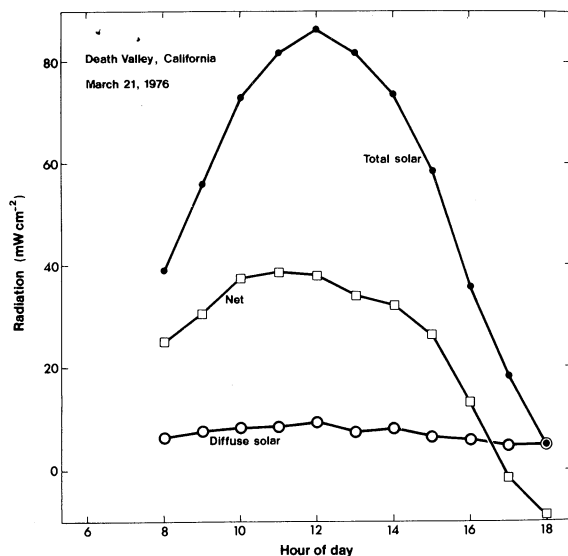
FIG. 2. Daily courses of total and diffuse solar radiation and of net radiation measured on the floor of Death Valley, California on 21 March 1976.

speeds. The temperature difference between leaf and air temperatures was measured with two 36 gauge copper-constantan thermocouples arranged in series and ≈1 cm apart. One thermocouple of this pair touched the underside of the leaf. This short distance between thermocouples provided an accurate estimate of the difference between leaf temperature and the air temperature adjacent to the leaf.

RESULTS

Microclimate

21 March 1976 was a clear, cloudless day on the floor of Death Valley with total solar radiation varying sinusoidally through the day (Fig. 2). Most of this solar radiation was the direct beam component, the diffuse beam component being generally 12% through the day. Peak solar radiation on a horizontal surface at midday reached 86 mW cm^{-2}, indicating that the atmospheric transmission coefficient was ≈80% on this date. Net radiation over the plant-soil surface varied in a manner similar to that of total solar radiation, but was of lower magnitude (Fig. 2). The net radiation at midday was

TABLE 1. Predicted and measured leaf temperatures for *Camissonia claviformis* and air temperatures on 21 March 1976 on the floor of Death Valley, California. Measured leaf temperatures are the means of 16 leaves. Predicted leaf temperatures assume a stomatal conductance of 2.5 cm sec^{-1}. Temperatures are in °C

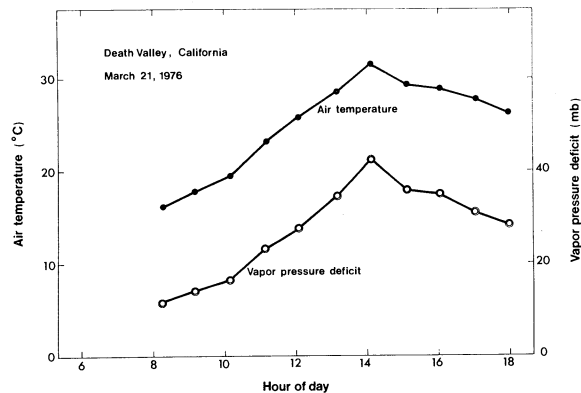| Hour	Air temperature	Measured leaf temperature	Predicted leaf temperature
1030	20.3	18.4	19.0
1230	25.7	22.7	22.9
1430	28.7	25.8	24.3

FIG. 3. Daily courses of air temperature and water vapor pressure deficit measured on the floor of Death Valley, California on 21 March 1976.

38 mW cm^{-2}, ≈45% of the downward solar radiation flux.

Air temperatures near the soil surface ranged from 16.1° to 31.3°C during the daylight hours (Fig. 3). Peak air temperatures occurred in the mid-afternoon (1400), lagging 2 hours behind the peak in the diurnal flux of solar radiation.

Water vapor pressure deficit ranged from 12 to 42 mb (Fig. 3). As the measured water vapor pressure of the air remained essentially constant at 5.4 mb, changes in the water vapor pressure deficit were essentially due only to changes in air temperature.

Temperatures of *C. claviformis* leaves were measured at 3 times during the day (Table 1). These measured leaf temperatures average consistently 2° to 3°C below air temperature. In comparison, most of the adjacent perennial shrubs had leaf temperatures at or above air temperature. This strong leaf under-temperature is perhaps surprising given that these plants had large, horizontal leaves (as is discussed later) which would lead to high heat loads under midday irradiances. The leaves are green in color and have a mean total solar absorptance (400 to 3000 nm) of 49.8%, a typical value for green leaves (Birkebak and Birkebak 1964). Leaf temperatures predicted by inserting the measured leaf characteristics and microclimate values into an energy budget equation (Gates 1968) were quite similar to those measured in the field (Table 1). The energy budget analysis suggests that the strong leaf under-temperatures of *Camissonia* were maintained in the leaves of these plants despite the high leaf absorptance, large leaf size, and low leaf angle, because of a high stomatal conductance to water loss and the resulting high transpiration rates.

Leaf water potential

Leaf water potentials ranged from −0.5 to −0.9 MPa during the daylight hours (Fig. 4). Through most of the day leaf water potentials were in the range of −0.8 to −0.9 MPa. Predawn leaf water potentials averaged −0.4 MPa.
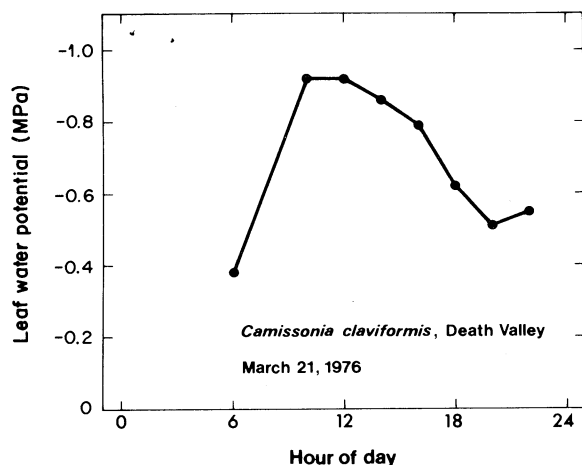
FIG. 4. Daily course of leaf water potentials for *Camissonia claviformis* on the floor of Death Valley, California.
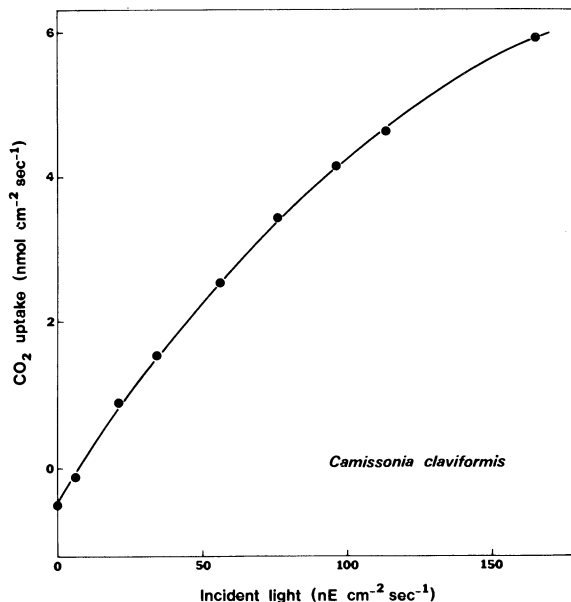

FIG. 5. Light dependence of photosynthesis for *Camissonia claviformis* on the floor of Death Valley, California under spring conditions. Leaf temperature was held constant at 30°C. The atmospheric conditions were 325 μbar CO_2, 21% O_2, and a water vapor pressure deficit of <10 mbar.

Photosynthesis

Net photosynthesis of *C. claviformis* measured under normal atmospheric conditions (325 μbar CO_2, 21% O_2) is essentially linearly related to irradiance between 0 and 100 nE cm^{-2} sec^{-1} (Fig. 5). Above 100 nE cm^{-2} sec^{-1} and up to full noon sunlight conditions (170 nE cm^{-2} sec^{-1}), only a slight curvature occurs in response to changes in irradiance. At typical spring midday irradiances, the measured net photosynthetic rate exceeded 5.9 nmole CO_2 cm^{-2} sec^{-1} (93.5 mg CO_2 dm^{-2} hr^{-1}). The absorbed quantum yield (slope of a plot of net photosynthesis against absorbed quanta) for *Camissonia* is 0.055 mole CO_2 per einstein at the measurement temperature of 30°C, a value similar to those obtained for many C_3 plants (Ehleringer and Björkman 1977). Stomatal conductances to CO_2 were >1.6 cm sec^{-1} at the highest irradiances.

The temperature dependence of net photosynthesis was measured under typical midday irradiances (Fig. 6). Between 15° and 30°C, the temperature dependence was relatively flat, varying less than 0.8 nmole CO_2 cm^{-2} sec^{-1}. The optimum leaf temperature for photosynthesis occurred at 20°C. Below 15°C and above 30°C, the net photosynthetic rate dropped precipitously.

Daily primary production and transpiration estimates

Using the observed microclimate values, leaf parameters, and photosynthetic characteristics, the daily courses of photosynthesis and transpiration were calculated at hourly intervals for 21 March. For these calculations a combined leaf energy budget-photosynthesis model similar to Ehleringer and Miller (1975) was used.

The energy budget equation used to calculate the temperature of a single side of individual leaves was

$$\frac{a}{2}S + \frac{\epsilon}{2}IR = \epsilon\sigma(T_l + 273)^4 + h_c(T_l - T_a)$$
$$+ L(\rho_l - \rho_a)/(r_l + r_a) \qquad (1)$$

where a is the absorptance of the leaf to solar radiation, S is the direct, diffuse and reflected solar radiation incident on the leaf, IR is the upward and downward infrared radiation fluxes incident on the leaf, ϵ is the emissivity, σ is the Stephan-Boltzman constant, T_l and T_a are leaf and air temperatures, h_c is the convection coefficient, L is the latent heat of vaporization, ρ_l and ρ_a are the water vapor densities of the leaf and the air, and r_l and r_a are the stomatal and boundary layer resistances to water vapor. A linear solution to the energy budget equation as presented by Miller (1972) was used to calculate leaf temperatures.

Transpiration rate was calculated as

$$E = \frac{\rho_l - \rho_a}{r_l + r_a} \qquad (2)$$

where E is the transpiration rate and other variables are the same as described earlier.

Photosynthesis was calculated in an Ohm's Law analogy as

$$P = \frac{[CO_2]_a - [CO_2]_i}{1.56(r_l + r_a) + r_m} - R \qquad (3)$$

where P is the photosynthetic rate, $[CO_2]_a$ and $[CO_2]_i$ are the CO_2 concentrations in the outside air and at the site of carboxylation, r_m is the mesophyll resistance, and R is the respiration rate. Mesophyll con-
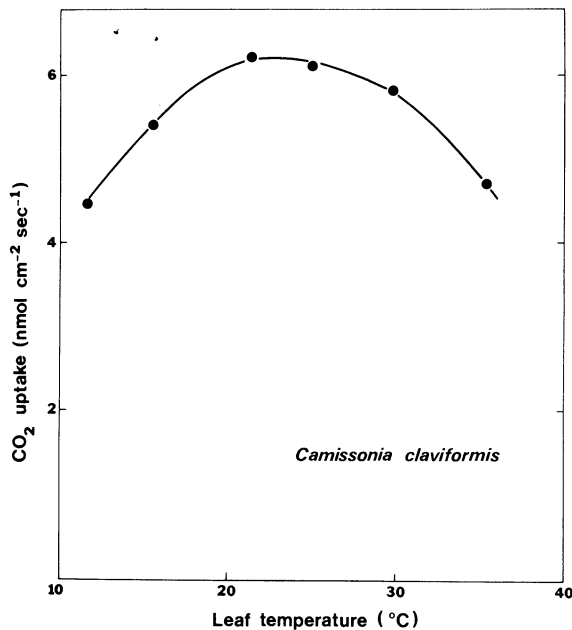
FIG. 6. Temperature dependence of photosynthesis for *Camissonia claviformis* on the floor of Death Valley, California under spring conditions. Incident light intensity was 170 nE cm^{-2} s^{-1}. The atmospheric conditions were 325 μbar CO_2, 21% O_2, and a water vapor pressure deficit of <10 mbar.
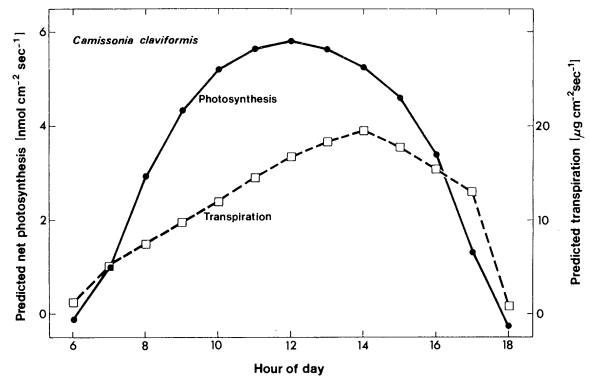

FIG. 7. Predicted rates of net photosynthesis and transpiration for leaves of *Camissonia claviformis* using the microclimatic conditions for 21 March 1976.

ductance was calculated from the net photosynthesis–light curves and then inverted to yield mesophyll resistance. For our calculations, this method of calculating mesophyll resistance from a mesophyll conductance-light intensity curve provided the necessary sensitivity at very low and high light intensities.

The predicted rate of net photosynthesis for *Camissonia* varied in a sine-like manner during the daylight hours (Fig. 7). At 1200, a peak photosynthetic rate of 5.8 nmole CO_2 cm^{-2} sec^{-1} was predicted. Since air and consequently leaf temperatures were near the optimum photosynthetic temperature during the day, the

temperature effect on photosynthesis was minimal and the photosynthetic rate changed primarily in response to changes in solar irradiance. On the other hand, the transpiration rate is strongly temperature dependent. Peak air and leaf temperatures are reached 2 h after the midday solar irradiance. Consequently, there was a 2 h phase shift in the peaks in rates for photosynthesis and transpiration. Photosynthetic rates for *Camissonia* leaves on this day were predicted to be 68.1 g CO_2 m^{-2} day^{-1} and water loss to be 5.54 kg m^{-2} day^{-1} (Table 2). The high daily rate of primary production resulted in a predicted transpiration/photosynthesis (T/P) ratio of 81. To estimate the impact of the high stomatal conductances in *Camissonia* on daily primary production and the T/P ratio, daily simulations for 21 March were performed using different maximum midday stomatal conductance estimates (Table 2). As midday stomatal conductances decreased, total daily carbon gain and transpiration dropped asymptotically, but not in parallel. At a maximum midday stomatal conductance of 0.2 cm sec^{-1} (perhaps not uncommon at dry periods during the growing season), the daily carbon gain fell to 8.4 g CO_2 m^{-2} day^{-1}. This value is just 12% of the estimate for the maximum midday stomatal conductance of 2.5 cm sec^{-1}. Since the decline in carbon gain and water loss as stomatal conductance decreases is not parallel, the T/P ratio does not remain constant. Rather as stomatal conductance decreases the T/P ratio is predicted to increase. That is to say, these leaves have lower water use efficiencies as stomatal conductance decreases. This ratio more than doubles in going from a midday stomatal conductance of 2.5 cm sec^{-1} to 0.2 cm sec^{-1}. The reason why this T/P ratio increases is because leaf temperatures during the day are above the photosynthetic temperature optimum. Any decrease in stomatal conductance will drive up the leaf temperature further and necessarily result in a lower photosynthetic rate.

TABLE 2. Predicted daily rates of carbon gain and water loss and water use efficiencies (T/P ratio) for *Camissonia claviformis* on 21 March as a function of the midday stomatal conductance. Units for stomatal conductance are cm sec^{-1}, for carbon gain are g CO_2 m^{-2} day^{-1}, for transpiration are kg m^{-2} day^{-1}, and the water use efficiency g H_2O/g CO_2

Stomatal Conductance	Carbon Gain	Transpiration	T/P
2.5	68.1	5.54	81
2.0	63.4	5.25	83
1.0	45.8	4.15	91
0.5	27.3	2.92	107
0.2	8.4	1.57	185

DISCUSSION

The net photosynthetic rate of *Camissonia claviformis* is among the highest known for higher plants and certainly among the highest known for C_3 plants. Under midday irradiances and at the temperature optimum, the photosynthetic rate was greater than 6 nmole CO_2 cm^{-2} sec^{-1} (96 mg CO_2 dm^{-2} hr^{-1}). For comparison, highly productive agricultural species generally have rates between 40 and 85 mg CO_2 dm^{-2} hr^{-1} (Sestak et al. 1971, Zelitch 1971) and the desert shrub species on the floor of Death Valley have rates between 10 and 35 mg CO_2 dm^{-2} hr^{-1} (Mooney et al. 1976). The maximum photosynthetic efficiency (quantum yield) of *C. claviformis* is similar to that of other C_3 plants (Ehleringer and Björkman 1977). The high photosynthetic capacity in this species is thus not because of an increase in the efficiency of the photosynthetic process, but rather because of an ability to utilize the higher irradiances common to its native desert habitat.

With a basal rosette arrangement of leaves, the utilization of the high photosynthetic capacity of individual leaves under midday conditions is assured. In terms of the carbon gaining capacity on a ground surface area basis, the single layer of prostrate leaves forming the canopy is able to fix carbon at a rate at least equivalent to the adjacent higher leaf area index shrub species, and higher than many of our productive annual crop systems such as corn, cotton, soybean, and wheat (Baker and Musgrave 1964, Jeffers and Shibles 1969, Zelitch 1971). By possessing a canopy which consists of a single leaf layer and with leaves that are able to fix carbon at near quantum yield capacities at all light intensities, this species has built a canopy structure with less construction costs than adjacent shrub species, but one which can fix carbon at a rate equal to, if not exceeding, that of the adjacent shrubs. This is highly advantageous to *Camissonia* since the species must complete its life cycle in a period as short as several months before the surface soil moisture which it utilizes is depleted. Additionally, the rate of water loss on a ground surface area basis should be less than for other plants having more extensive canopies. Therefore, on a canopy basis, transpiration/photosynthesis ratios should be more favorable in *Camissonia*. The horizontal leaf arrangement at the ground surface also allows *Camissonia* to take advantage of the higher temperatures in this zone during the cool winter months.

The reproductive structures of *C. claviformis* are on a long peduncle arising from the center of the basal rosette. While this arrangement of the reproductive structure is not unique to *Camissonia*, it does however mean that there is very little shading of the leaves by the flowers, which might otherwise reduce the carbon gaining capacity of the canopy.

The carbon gaining capacity of this annual is very much dependent on water availability. Under conditions of abundant soil moisture, high leaf conductances can be maintained. This in turn allows for a high rate of carbon gain and a high water-use efficiency (low T/P ratio). Increased leaf resistances and/or high leaf temperatures result in a lower water use efficiency in *Camissonia*. The T/P ratio predicted by the simulations for *Camissonia* was 81–107 for moderate to high stomatal conductances. It is interesting that our estimated T/P ratio for *Camissonia* is similar to the estimate of 82 (converting his data to weight) of Johnson (1975), which he thought should be typical for C_3 desert winter annuals. Two significant differences, however, are that Johnson's estimates were based on a temperature of 20°C whereas our estimates are for 30°C and that he estimated maximum photosynthetic rates to be much lower than for *Camissonia* near 18 mg CO_2 dm^{-2} hr^{-1}.

Winter annuals are a variable component of desert ecosystems. The abundance of winter annuals is dependent on when the initial rains occur, temperatures, and continued water availability (Beatley 1969, 1974). This study has shown that the desert winter annual *Camissonia claviformis* has an extremely high photosynthetic capacity. Given sufficient soil moisture and high stomatal conductances, leaves of *Camissonia* are able to utilize this capacity to achieve high rates of carbon fixation and large biomasses. Future studies should determine if high photosynthetic rates are typical of desert annuals and what factors are responsible for maintaining this extraordinary high photosynthetic rate.

LITERATURE CITED

Baker, D. N., and R. B. Musgrave. 1964. Photosynthesis under field conditions. V. Further plant chamber studies of the effects of light on corn (*Zea mays*). Crop Science. 4:127–131.

Beatley, J. C. 1969. Biomass of desert winter annual plant populations in southern Nevada. Oikos 20:261–273.

———. 1974. Phenological events and their environmental triggers in Mojave Desert ecosystems. Ecology 55:856–863.

Birkebak, R. and R. Birkebak. 1964. Solar radiation characteristics of tree leaves. Ecology 45:646–649.

Björkman, O., and P. Holmgren. 1963. Adaptability of the photosynthetic apparatus to light intensity in ecotypes from exposed and shaded habitats. Physiologia Plantarum. 16:889–914.

Björkman, O., M. Nobs, J. A. Berry, H. A. Mooney, F. Nicholson, and B. Catanzaro. 1973. Physiological adaptation to diverse environments: approaches and facilities to study plant response in contrasting thermal and water regimes. Carnegie Institute of Washington Yearbook. 72:393–403.

Ehleringer, J., and O. Björkman. 1977. Quantum yields for CO_2 uptake in C_3 and C_4 plants: dependence on temperature, CO_2, and O_2 concentration. Plant Physiology. 59:86–90.

Ehleringer, J. R. and P. C. Miller. 1975. A simulation model of plant water relations and production in the alpine tundra, Colorado. Oecologia 19:177–193.

Gates, D. M. 1968. Transpiration and leaf temperature. Annual Review of Plant Physiology 19:211–238.

Jeffers, D. L., and R. M. Shibles. 1969. Some effects of leaf area, solar radiation, air temperature, and variety on net photosynthesis in field-grown soybeans. Crop Science 9:762–764.

Johnson, H. B. 1975. Gas-exchange strategies in desert plants. Pages 105–120 in D. M. Gates, editor. Perspectives in Biophysical Ecology, Ecological Studies 12, Springer Verlag, New York, New York, USA.

Juhren, M., F. W. Went and E. A. Phillips. 1956. Ecology of desert plants. IV. Combined field and laboratory work on germination of annuals in the Joshua Tree National Monument, California. Ecology 37:318–330.

Miller, P. C. 1972. Bioclimate, leaf temperature, and primary production in red mangrove canopies in South Florida. Ecology 53:22–45.

Mooney, H. A., O. Björkman, J. Ehleringer, and J. A. Berry. 1976. Photosynthetic capacity of in situ Death Valley plants. Carnegie Institute Washington Yearbook 75:410–413.

Mooney, H. A., E. L. Dunn, A. T. Harrison, P. A. Morrow, B. Bartholomew, and R. Hays. 1971. A mobile laboratory for gas exchange measurements. Photosynthetica 5:128–132.

Mooney, H. A., J. Ehleringer, and J. A. Berry. 1976. High photosynthetic capacity of a winter annual in Death Valley. Science 194:322–324.

Mulroy, T. W., and P. W. Rundel. 1977. Annual plants: adaptations to desert environments. Bioscience 27:109–114.

Rabideau, G. S., C. S. French and A. S. Holt. 1946. The absorption and reflection spectra of leaves, chloroplast suspensions, and chloroplast fragments as measured in an Ulbricht sphere. American Journal of Botany 33:769–777.

Scholander, P. F., H. Hammel, E. Bradstreet and E. Hemmingsen. 1965. Sap pressure in vascular plants. Science 148:339–345.

Sestak, Z., J. Catsky and P. G. Jarvis. 1971. Plant Photosynthetic Production Manual of Methods. Dr. W. Junk Publications, The Hague, Netherlands.

Shreve, F. 1951. Vegetation of the Sonoran Desert. Carnegie Institution of Washington Publication 591.

Went, F. W. 1948. Ecology of desert plants. I. Observations on germination in the Joshua Tree National Monument, California. Ecology 29:242–253.

Zelitch, I. 1971. Photosynthesis, Photorespiration, and Plant Productivity. Academic Press, New York, New York, USA.