High Photosynthetic Capacity of a Winter Annual in Death Valley

Abstract. Camissonia claviformis, *a winter annual of Death Valley, California, that fixes carbon dioxide by the C_3 mechanism, has an in situ photosynthetic rate at midday in spring of nearly 6 nanomoles of carbon dioxide per square centimeter per second—an exceptionally high rate.* Camissonia *fixes absorbed noon sunlight in the 400- to 700-nanometer region into chemical energy with an efficiency of 8.5 percent, which is 80 percent of that theoretically possible for intact leaves. This performance is primarily due to an unusual capacity to utilize high irradiances. Factors associated with this include a high stomatal conductance to carbon dioxide and high levels of soluble protein and ribulose-1,5-diphosphate carboxylase.*

The deserts of the southwestern United States are periodically covered with diminutive annual plants which germinate after infrequent rains. If moisture is available for prolonged periods, or at favorable microsites, the annuals may attain relatively large stature in a matter of several weeks and produce large quantities of seed. If the rains come late, these plants can complete their entire life in 6 to 10 weeks before the onset of summer drought and high temperatures (*1*). The question we ask here is whether the rapid growth and development of a desert annual is associated with an unusual photosynthetic capacity.

Using a mobile laboratory (*2*), we investigated the photosynthetic performance of the desert annual *Camissonia claviformis*, an evening primrose, in mid-March in Death Valley, California. The measurements were made in situ on plants which had germinated after a storm that had produced more than 60 mm of rain 6 weeks previously. All measurements were made on an intact attached leaf (13.2 cm^2) in a cuvette in which temperature and the concentrations of water vapor and CO_2 of the atmosphere could be controlled and varied (*3*). Artificial illumination was provided by a metal-arc lamp positioned above the cuvette. Measurements of the exchange of water vapor and CO_2 by the leaf were made by using a ventilated open gas exchange system essentially as described in (*4*), except that HM-111 relative humidity sensors (Weather Measure Corp., Sacramento, Calif.) were used to measure water vapor exchange. Previous studies indicated that sources of error are small (± 2 percent). Variability between leaves was not measured. The quantum yield was determined in white light. Absorptance of the leaves to photosynthetically active quanta from the light source used was determined by utilizing an Ulbricht integrating sphere and a quantum sensor (model LI 190-SB, Lambda Instruments, Lincoln, Neb.). Leaf samples were analyzed for total and soluble protein and ribulose-1,5-diphosphate (RuDP) carboxylase activity. Total protein was determined by the Kjeldahl method (*5*), soluble protein by the Lowry method (*6*), and RuDP carboxylase was activated and assayed as described in (*7*).

Net photosynthesis of *Camissonia* is essentially linearly related to irradiance to levels exceeding 100 nanoeinsteins per square centimeter per second, and only slight curvature occurs in the light response above that level to full noon irradiances (Fig. 1). Under midday spring irradiances, the net photosynthetic rate of *Camissonia* exceeded 5.9 nmole of CO_2 per square centimeter per second (93.5 mg dm^{-2} $hour^{-1}$). By contrast, such highly productive cultivated plants as sunflower, a dicotyledon with C_3 metabolism, and maize, a monocotyledon with C_4 metabolism, have maximum net photosynthetic rates of 44 and 85 mg dm^{-2} $hour^{-1}$ (*8*, p. 244). High photosynthetic rates for wild herbaceous species are normally less than 60 mg dm^{-2} $hour^{-1}$ and for wild woody species less than 25 mg dm^{-2} $hour^{-1}$ (*9*). Based on the dry weight of leaves the rate for *Camissonia* under these light conditions was 179 mg of CO_2 per gram per hour.

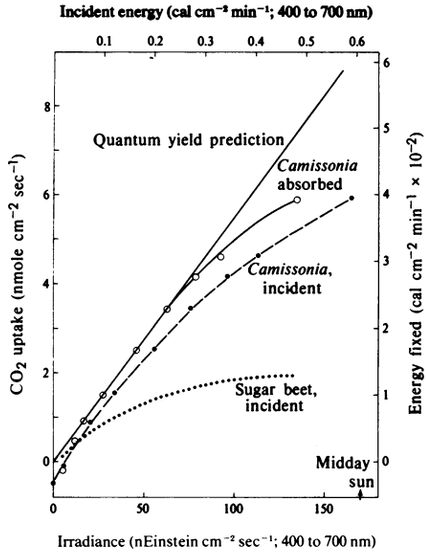

Fig. 1. Photosynthetic light response of *Camissonia claviformis* and sugar beet (*Beta vulgaris*). The observed photosynthetic values on *Camissonia* were determined at 30°C and 320 μbar of CO_2, and are those indicated for incident radiation. For the curve for *Camissonia* labeled "absorbed" the incident radiation was multiplied by 0.814, the fraction of sunlight in the region 400 to 700 nm that is absorbed by a *Camissonia* leaf, as determined by measurements in an integrating sphere. The sugar beet data are from Hall (*13*). Incident quanta are converted to incident calories as described in Loomis and Williams (*24*) and absorbed CO_2 to chemical energy fixed by the relation $CO_2 + H_2O + 112.3$ kcal → $(CH_2O) + O_2$.

The absorbed quantum yield (slope of a plot of absorbed quanta against net photosynthesis at low light levels) of *Camissonia* is 0.055 mole of CO_2 per einstein, at ambient CO_2 and O_2 concentrations and the measurement temperature of 30°C, a value similar to those obtained for many C_3 and C_4 species of higher plants (*10, 11*). This indicates that maximum efficiency of the photosynthetic reaction of *Camissonia* is similar to that of other plants, but the maximum rate achieved at high irradiance is higher. Errors in our measurements which might result in overestimates of the rate of photosynthesis would also result in an overestimate of the quantum yield. The normal quantum yield obtained in these studies provides a control on the accuracy of our photosynthetic rate measurements.

Camissonia leaves absorb 81 percent of the photosynthetically active wavelengths (400 to 700 nm) from sunlight, a value similar to that for other nonpubescent leaves (*12*). An estimate of the maximum potential photosynthetic rate at any particular irradiance can be obtained from the absorptance of the leaf and its quantum yield. The rates of photosynthesis of *Camissonia* observed at an irradiance corresponding to full noon sun were in excess of 80 percent of the maximum potential value at that irradiance. In contrast the photosynthetic rate of sugar beet (*13*), a C_3 crop plant that has been previously used in describing the photosynthetic efficiency of leaves (*14*), is less than 30 percent of this maximum potential rate at the same irradiance. These values correspond to an efficiency of energy conversion (photosynthetically active energy received divided by energy converted) of 8.5 and 3 percent, respectively, for *Camissonia* and sugar beet. Efficiencies based on the total solar spectrum would be approximately one-half of those given. It is clear from Fig. 1 that this difference between species in photosynthetic efficiency at high light intensity is due to the fact that sugar beet becomes light-saturated at irradiances below full sun while *Camissonia* does not.

The response of photosynthesis to changes in the intercellular CO_2 concentration (Fig. 2) is approximately linearly dependent on CO_2 concentration at all CO_2 concentrations below 300 μbar and is not saturated at intercellular concentrations of 700 μbar of CO_2. The rate of photosynthesis measured under ambient conditions corresponds to an intercellular CO_2 concentration of approximately 250 μbar. The high CO_2 concentration required for saturation and the CO_2 compensation point of about 50 μbar indicate that *C. claviformis* is most likely a C_3 plant. The steep initial slope of the CO_2 dependence curve and the very high rate achieved at high CO_2 concentrations are suggestive that high levels of the photosynthetic carboxylating enzyme RuDP carboxylase and of other enzymes may be present.

The soluble protein content of *Camissonia* leaves was 776 μg cm^{-2}, and total nitrogen, on a dry weight basis, 4.3 percent. The RuDP carboxylase activity in vitro was 7.13 nmole cm^{-2} sec^{-1}, one of the highest measured in natural leaves. This in part accounts for the very high photosynthetic rates observed. Soluble leaf protein was extracted after grinding in liquid nitrogen according to Loomis and Battaile (*15*). Actual levels of soluble protein and enzyme activity may be higher, as *Camissonia* leaves contain a protein-precipitating agent.

In *Camissonia*, stomatal conductances to CO_2 exceeded 1.6 cm sec^{-1} at high irradiances. This value exceeds the typical maximal conductance for many species (*16*) and, in view of the high rates of photosynthetic CO_2 fixation observed, is required to permit rapid diffusive transport of CO_2 into the leaf.

The temperature dependence of photosynthesis in *Camissonia* was relatively flat between 15° and 30°C, varying less than 0.8 nmole cm^{-2} sec^{-1}. The optimum is at approximately 20°C, which is in concert with the prevailing cool temperatures of its winter and spring growing seasons. Leaf temperatures of *Camissonia* were often 4° to 8°C below air temperatures because of high rates of transpiration. This means that under typical midday air temperatures (25° to 35°C), leaf temperatures were very close to the temperature optimum. In comparison, shrubs growing in the same environment have leaf temperatures close to air temperature and correspondingly higher temperature optima of photosynthesis (*17, 18*).

The very high photosynthetic rates observed in this study and also the high rates (4 nmole cm^{-2} sec^{-1}) recently observed in the C_3 desert species *Encelia farinosa* (*12*) bring a renewed interest in the intrinsic photosynthetic capacities of C_3 compared with C_4 species. Since the relatively recent discovery of the C_4 photosynthetic pathway, gas exchange studies have indicated that the C_4 species performed at photosynthetic rates far superior to those of C_3 species (*19*). While this may be true in general, it is clear that some C_3 plants can have photosynthetic rates at least as high as those of most C_4 plants.

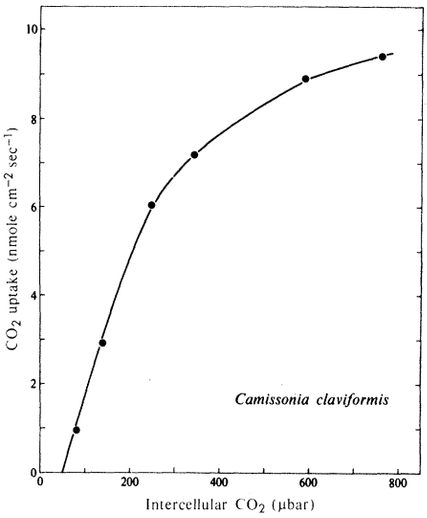

Fig. 2. Photosynthetic CO_2 response of *Camissonia claviformis* determined at a leaf temperature of 30°C and an irradiance of 170 nanoeinsteins per square centimeter per second (400 to 700 nm).

Energy conversion by photosynthetic processes is generally considered to be less than 2.5 percent of the incident solar energy (*14*); however, the intrinsic efficiency of the photosynthetic process at limiting irradiances for individual leaves is much higher. Measurements of the quantum yield of CO_2 fixation with intact leaves of species from a number of families (*10*) indicate an average of 0.054 mole of CO_2 fixed per einstein of absorbed light (400 to 700 nm). This suggests that the maximum biological efficiency of solar energy conversion should approach 10.6 percent of the photosynthetically active radiation, or 5.3 percent of the total solar spectrum. This potential efficiency is not typically realized in part because the photosynthetic processes in most plants saturate at moderate light intensities. Thus at high light levels (above that required to saturate photosynthesis) the apparent efficiency is lower. The significant point to be made here is that while leaves of plants may have the same photosynthetic efficiency at low light levels, their efficiencies may differ greatly at high light levels. The fact that *Camissonia* can utilize full solar radiation incident on the leaf without saturation permits it to approach the potential efficiency. As for the rate of carbon fixation per unit of ground surface, it would appear that a single *Camissonia* leaf [leaf area index = 1 (*20*)] may fix carbon at a rate similar to that of an entire productive corn canopy [leaf area index = 4.3 (*21*)] and greater than that of a cotton canopy [leaf area index = 5.7 (*22*)].

Factors that contribute to this high capacity in *Camissonia* include a high stomatal conductance to CO_2 and high levels of soluble proteins, including RuDP carboxylase and presumably other potentially rate-limiting enzymes, per unit leaf area. It is not clear why C_3 plants, be they crop plants or plants from mesic habitats in general, lack such a capacity. It appears, however, that environmental selection in the desert ecosystem has produced species with unusual capacities to capture light and fix CO_2. There is also a trend toward increased photosynthetic capacity with a decrease in leaf longevity in arid regions (*23*). Selective pressures for rapid development and the reduced competition for light in the desert environment may be related to these trends.

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27 May 1976; revised 23 July 1976

Bounds on "Bound Water": Transverse Nuclear Magnetic Resonance Relaxation in Barnacle Muscle

Abstract. *Relatively mobile protons that do not exchange with D_2O exist in barnacle muscle cells. These are not part of the nonfreezing "bound water" that does exchange. Ninety-seven percent of the muscle water exhibits a single transverse relaxation time of 35 milliseconds: one water molecule per thousand, which is briefly and irrotationally bound, will produce the observed relaxation properties.*

Most of the water in muscle tissue has a nuclear magnetic resonance (NMR) transverse relaxation time (T_2) of about 1/50 that of the pure liquid, an effect known for 20 years (*1*) without an interpretation of consensus (*2*, *3*), despite the proposed use of NMR relaxation measurements for cancer diagnosis (*4*, *5*). Nuclear magnetic resonance data in rat (*3*) and frog (*6*) skeletal muscle suggest that a small observed proton fraction with a T_2 of about 1 msec exchanges at an intermediate rate (*7*, *8*) with the major portion of cell water, and thus lowers the relaxation time of this major fraction below that of pure water. We report here that single muscle cells from the giant barnacle, *Balanus nubilus*, also exhibit a small proton fraction with a millisecond T_2. However, within experimental limits, these protons do not exchange with D_2O in times as long as 24 hours, and cannot be the cause of the proton relaxation in the major portion of tissue water. On the other hand, our proton and deuteron T_2 values for the major portion of the muscle water do fit an intermediate exchange rate model that requires only 0.1 percent of the water molecules to be in an "irrotationally bound" state at room temperature. The nonfreezing water protons that we observe at −34°C [attributed to "bound water" in studies of protein solutions and tissues (*9*, *10*)], do exchange with D_2O and are clearly different from the nonexchanging protons that we observe in these cells.

In this study, single muscle cells were dissected from the depressor muscles of the barnacle, blotted on filter paper, and gently placed into an NMR sample tube. Some specimens were partially deuterated by immersion for 2 to 3 minutes in artificial seawater (Instant Ocean) made from pure D_2O (*11*), or by placing an ani-

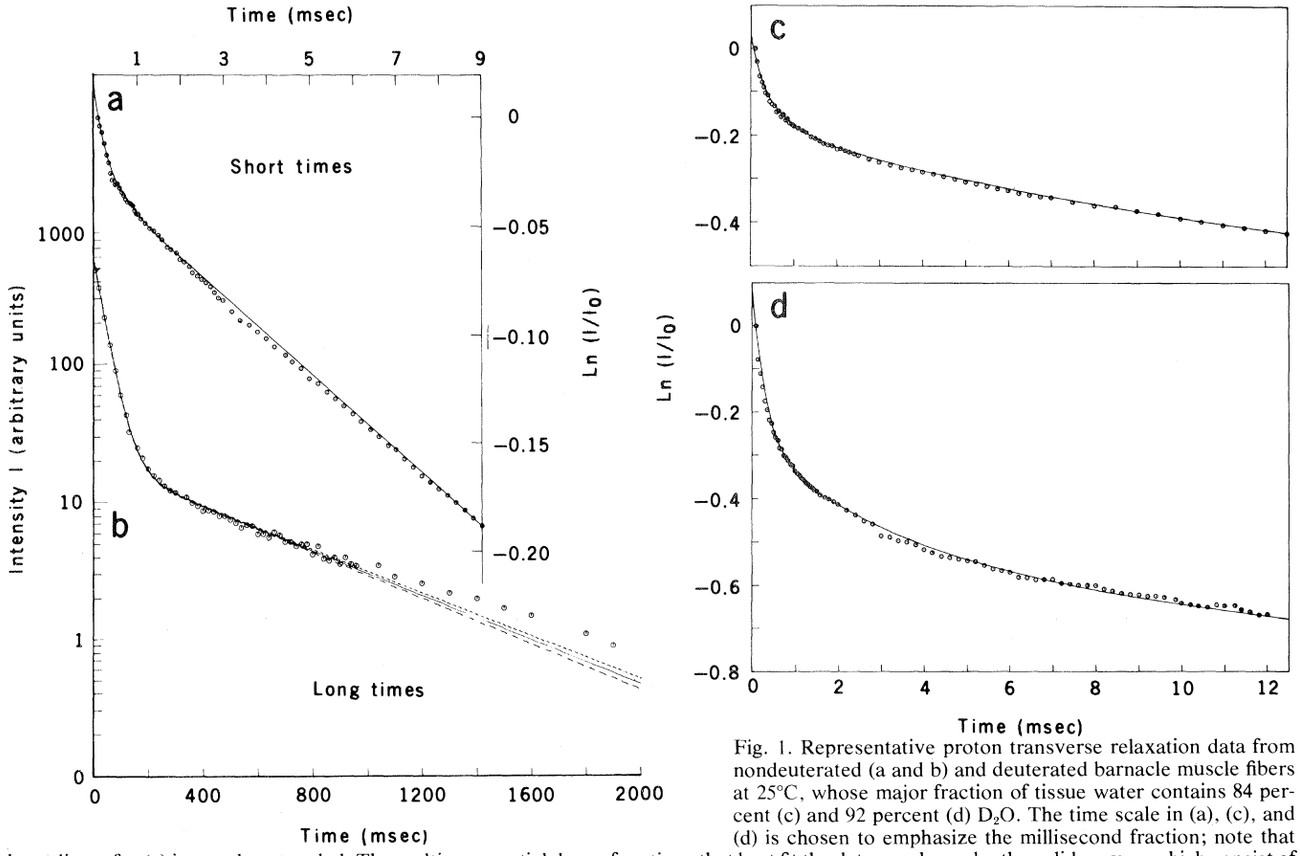

Fig. 1. Representative proton transverse relaxation data from nondeuterated (a and b) and deuterated barnacle muscle fibers at 25°C, whose major fraction of tissue water contains 84 percent (c) and 92 percent (d) D_2O. The time scale in (a), (c), and (d) is chosen to emphasize the millisecond fraction; note that the ordinate for (a) is greatly expanded. The multiexponential decay functions that best fit the data are shown by the solid curves, which consist of the sum of two (a and b) or three (c and d) exponential functions. For clarity, many of the data points are omitted. In these experiments, the CPMG pulse sequence was employed, with the pulse spacing 2τ equal to 50 μsec (a, c, and d) or 500 μsec. The fitted equations are: (a) $I/I_0 = 0.051 \exp(-t/0.80) + 0.949 \exp(-t/56.4)$; (c) $I/I_0 = 0.179 \exp(-t/0.39) + 0.099 \exp(-t/4.3) + 0.722 \exp(-t/84.5)$; and (d) $I/I_0 = 0.320 \exp(-t/0.29) + 0.184 \exp(-t/3.28) + 0.496 \exp(-t/102)$ where t is the time in milliseconds.