The carbon gain benefits of solar tracking in a desert annual

H. A. MOONEY & J. R. EHLERINGER, Department of Biological Sciences, Stanford University, Stanford, California 94305 U.S.A., and Department of Biology, University of Utah, Salt Lake City, Utah 84112 U.S.A.

Abstract. A comparison between two sympatric winter desert annuals, *Camissonia claviformis* and *Malvastrum rotundifolium* showed that both gained similar amounts of carbon during a spring day, although by very different means. *Camissonia* has horizontally fixed leaves which have a very high photosynthetic capacity. The temperature optimum of photosynthesis for this species is near 20°C. *Malvastrum* has leaves with a lower photosynthetic capacity and a photosynthetic temperature optimum near 30°C. Leaves of the latter species remain normal to the sun throughout the course of the day. The tracking response and high temperature optimum for photosynthesis of *Malvastrum* result in a high daily carbon gain and also a high water-use efficiency.

Introduction

Leaves from a number of plant species have been reported to track the sun, so that their leaf surfaces remain perpendicular to the sun's rays throughout the day (Yin, 1938; Begg & Torsell, 1974; Bonhomme, Varlet Grancher & Artis, 1974; Shell, Lang & Sale, 1974; Shell & Lang, 1976; Wainwright, 1977). Included among these solar trackers are such herbaceous species as *Malva neglecta* (Yin, 1938) and *Lupinus arizonica* (Wainwright, 1977) as well as cultivated plants such as *Helianthus annuus* (Shell & Lang, 1976), *Stylosanthes humilis* (Begg & Torsell, 1974), and *Vigna sinensis* (Bonhomme *et al.*, 1974). Previous studies with these species have been concerned with the physiological mechanisms for tracking and except for the *Vigna* study have not considered the photosynthetic benefits that might be derived from tracking the sun.

This study is aimed at a preliminary assessment of the possible carbon balance benefits to a plant that could be derived by having leaves that track the sun. We approached this question by comparing two sympatric C_3 winter annuals native to the warm deserts of southwestern North America. *Malvastrum rotundifolium* is a

solar tracker, whereas *Camissonia claviformis* is not (Fig. 1). Both species germinate following fall and winter rains and complete their life cycles before the onset of high summer temperatures.

We experimentally determined the CO_2 and water vapour exchange characteristics of leaves of both species. These data were incorporated into a photosynthesis-leaf energy budget model (Ehleringer & Miller, 1975) which simulated their daily carbon gain and water loss for a typical spring day in their native habitat. Further simulations examined stomatal conductance effects on carbon gain and water use efficiency.
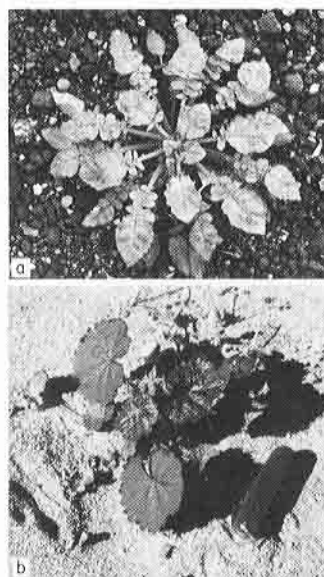

Figure 1. (a) *Camissonia claviformis* and (b) *Malvastrum rotundifolium*.

Materials and methods

Photosynthetic measurements

Measurements of photosynthesis and transpiration were made with an open gas exchange system (Björkman *et al.*, 1973; Ehleringer & Björkman, 1977). A ventilated

Correspondence: Dr H. A. Mooney, Department of Biological Sciences, Stanford University, Stanford, California 94305 U.S.A.

leaf cuvette similar to that of Björkman & Holmgren (1963) was used. Light was provided by a metal halide lamp in conjunction with appropriate housing, heat filters, and neutral density filters. Quantum flux incident on the leaves was continuously measured with silicon cells calibrated against a quantum sensor (Model LI 190-SR, Lambda Instruments, Lincoln, Nebraska). Leaf temperature was controlled by means of water jackets and measured with very fine copper-constantan thermocouples attached to the lower surfaces. Gas from a cylinder containing 21% oxygen in nitrogen (CO_2-free air) was continuously and precisely mixed with 1.00% CO_2 in nitrogen by a high capacity gas mixing pump (Model G-27/3-F, Wöstoff OHG, Bochum, Germany). The resulting gas stream was humidified by passing it through a vessel, maintained at 5°C above the desired dew point temperature, containing a large area of Miracloth wetted by capillary uptake of water slightly acidified with sulphuric acid. The gas stream was then passed through a dual coil water-jacketed condenser kept at the desired dew point. A small portion of this humidified gas stream was passed at a constant rate (250 cm^3 min^{-1}) through a humidity sensor (hygrometer HM-111, Weathermeasure Corp., Sacramento, Calif.) and then through the reference cell of a differential CO_2 analyzer (Model 865, Beckman Instruments, Fullerton, Calif.). Another portion (300–800 cm^3 min^{-1}) was passed, via an electric flowmeter (Model DP45, Validyne Corp., Northridge, Calif.) to the leaf chamber. A portion (250 cm^3 min^{-1}) of the gas returning from the chamber was passed through another humidity sensor, the sample cell of the differential CO_2 analyser, and then through an oxygen analyser (Model 209, Westinghouse Electric Corp., Pittsburgh, Pa.).

Measurements were made on *Camissonia* plants growing under natural conditions in Death Valley, California

during the spring. *Malvastrum* were grown from seed i environmentally controlled glasshouses called phytocells (Björkman *et al.*, 1973) with natural irradiation and a day/night temperature regime of 20°/15°C.

Measurements of photosynthesis at high irradiances were made on phytocell-grown *Camissonia* and yielded rates comparable to those measured on field plants.

Simulation of daily carbon gain

To simulate the daily gain in photosynthesis and water loss a photosynthesis-leaf energy budget model, described by Ehleringer & Miller (1975) was used. The microclimatic parameters necessary for the simulations were taken from measurements previously made by us in Death Valley. These include long and short wave radiation fluxes, temperatures, and water vapour pressures. Leaf structural characteristics and microclimatic parameters used in the simulations have been summarized in Table 1. The simulation proceeded on an hourly basis, and output from the model included leaf temperature, photosynthesis and transpiration rates.

Measurements of leaf movements

Hourly measurements of leaf angle and leaf azimuth were made on *Malvastrum* and *Camissonia* through the daylight hours. Leaf angles (in degrees) were measured from the horizontal, and azimuth was expressed a degrees deviation from south (0°), with east as −90° and west 90°. These data were collected on plants growing on the floor of Death Valley, California. Sample size was three leaves from each of three different plants.

Results

Solar tracking

Over the course of the day, leaves of *Malvastrum* closely tracked the sun's movements (Fig. 2). As a result of

Table 1. Principal input variables for the photosynthesis-leaf energy budget simulations of Figure 4

Parameter	Value	Units
Input		
Malvastrum		
Leaf width	2	cm
Leaf absorptance (400–700 nm)	90	%
Leaf absorptance (400–3000 nm)	50	%
Leaf angle	variable	
Minimum stomatal resistance	0.5	s cm^{-1}
Camissonia		
Leaf width	3	cm
Leaf absorptance (400–700 nm)	85	%
Leaf absorptance (400–3000 nm)	50	%
Leaf angle	0	degrees
Minimum stomatal resistance	0.5	s cm^{-1}
Microclimate		
Wind speed	100	cm s^{-1}
Water vapour pressure	0.6	KPa
Sky infrared radiation	350	Wm^{-2}
Maximum solar radiation	900	Wm^{-2}
Maximum air temperature	30	°C
Minimum air temperature	15	°C
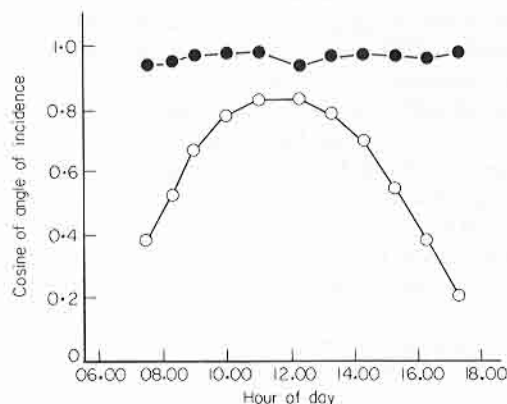
Figure 2. Cosine of the angle of direct beam short-wave radiation on leaves of (o) *Camissonia claviformis* and (•) *Malvastrum rotundifolium* through the day in Death Valley, California, 17 March.
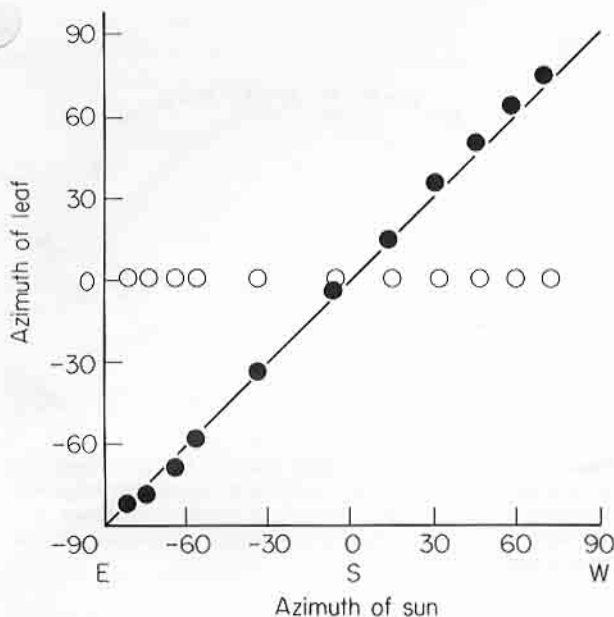
Figure 3. Leaf azimuths of leaves of (o) *Camissonia claviformis* and (•) *Malvastrum rotundifolium* as related to the sun's azimuth, 17 March. The daily path of the sun proceeds east (−90°) to west (90°) or left to right along the abscissa. The line represents the situation where leaf azimuth is identical to solar azimuth.

Figure 4. The temperature dependence of photosynthesis at high irradiances and normal atmospheric conditions for individual leaves of (o) *Camissonia claviformis* and (•) *Malvastrum rotunifolium.*

these leaf movements, the cosine of the angle of incidence of the sun's direct rays to the leaves remained near unity throughout the day. Both leaf angles and leaf azimuths of *Malvastrum* changed during the day in response to solar altitude changes. However, leaf azimuth movements followed the sun's path more closely than did leaf angle changes (Fig. 3). On the other hand, the leaf angles of *Camissonia* remained constant throughout the day. As a result, the cosine of the angle of incidence of solar radiation fluctuated from 0.21 at low solar altitudes to 0.83 at solar noon.

Photosynthetic characteristics

Malvastrum rotundifolium is capable of moderately high photosynthetic rates. At incident irradiances of 2 mmol m^{-2} s^{-1} (400–700 nm), normal atmospheric conditions and a leaf temperature of 30°C, *Malvastrum* fixes carbon at a rate of 43 μmol CO_2 m^{-2} s^{-1}. Photosynthesis is not saturated at 2 mmol m^{-2} s^{-1}, which is well above midday irradiances (1.8 mmol m^{-2} s^{-1}) during the growing season. In contrast, *Camissonia claviformis* has an exceptionally high photosynthetic capacity. Under normal atmospheric conditions and at 1.6 mmol m^{-2} s^{-1} the photosynthetic rate is 59 μmol CO_2 m^{-2} s^{-1}. The higher rate of photosynthesis in *Camissonia* is probably related to unusually high enzyme levels (Mooney *et al.*, 1976). Total leaf nitrogen content of *Camissonia* was 4.3% versus 3.6% for *Malvastrum*.

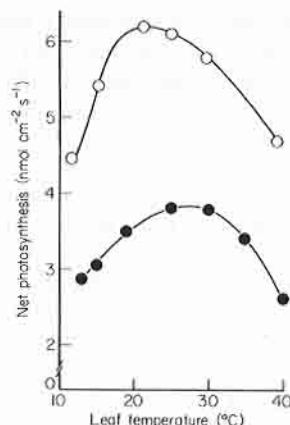The temperature dependence of photosynthesis at high irradiances differs greatly between the two species (Fig. 4). Photosynthesis in both species is strongly de-pendent on leaf temperature, with the optimum temperature occurring near 20°C in *Camissonia* and close to 30°C in *Malvastrum*.

Daily simulations

The predicted daily course of net photosynthesis on a unit leaf area basis for both *Camissonia* and *Malvastrum* is presented in Fig. 5. Rates of photosynthesis are presented for two types of *Malvastrum* leaves: those typically seen that maintain their surfaces perpendicular to the sun ('tracking') and a hypothetical type that hold a fixed horizontal position ('nontracking'), analogous to leaves of *Camissonia*. These simulations were conducted using a minimum leaf resistance of 0.5 s cm^{-1} for water vapor, which is characteristic of both species under optimal growth conditions.
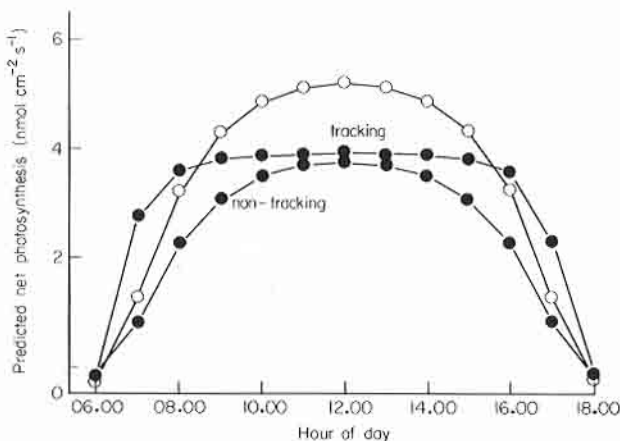

Figure 5. Simulated daily course of net photosynthesis of (o) *Camissonia claviformis* and (•) *Malvastrum rotundifolium.* Simulations are given for *Malvastrum* leaves that track the sun (normal condition) as well as for those held in a horizontal position. Environmental conditions are for a March day in Death Valley, California.

The 'tracking' *Malvastrum* attains a maximum photosynthetic rate early in the day and maintains this relatively high level through most of the day until late afternoon. The photosynthetic rate does not change significantly through the day, since the solar radiation received on a surface perpendicular to the sun is not changing. In contrast, the photosynthetic rate of nontracking *Malvastrum* is more or less directly proportional to the solar radiation received on a horizontal surface through the day with an expected peak rate occurring at midday. The 'tracking' *Malvastrum* leaves receive somewhat more radiation than do the nontracking leaves at midday, since at a latitude of 30°N in March the sun is not directly overhead at noon.

One striking result of these simulations is that, although *Camissonia* and *Malvastrum* have greatly differing inherent photosynthetic capacities, their total carbon gain during the day is virtually identical. The net 24 h CO_2 gained per square meter leaf surface by a tracking *Malvastrum* under the conditions illustrated in Fig. 5 would be 60.1 g, and of the *Camissonia*, 63.7 g. Thus, the tracking behaviour of *Malvastrum* can compensate to a large degree for its lower inherent photosynthetic capacity.

If leaf resistances are greater than 0.5 s cm^{-1} the daily carbon balance actually shifts in favour of *Malvastrum* (Fig. 6). This is due in part to the dissimilar photosynthetic temperature responses of the two species. As stomata close, the leaf temperatures shift upward, towards the temperature optimum of 30°C for photosynthesis in *Malvastrum* and away from the 20°C optimum of *Camissonia* (the midday air temperature for this spring simulation is 30°C).

Daily simulations were conducted with increasing minimum leaf resistances (Fig. 6). As leaf resistance increases, the total daily carbon gain declines in both species. However, while water use efficiency (as measured by the transpiration/photosynthesis ratio) is similar at low leaf resistances, water use efficiency is much greater (that is, T/P ratios are lower) in *Malvastrum* at higher leaf resistance values.

As a consequence of tracking, leaf temperatures were predicted to be generally 2–3°C higher in *Malvastrum*
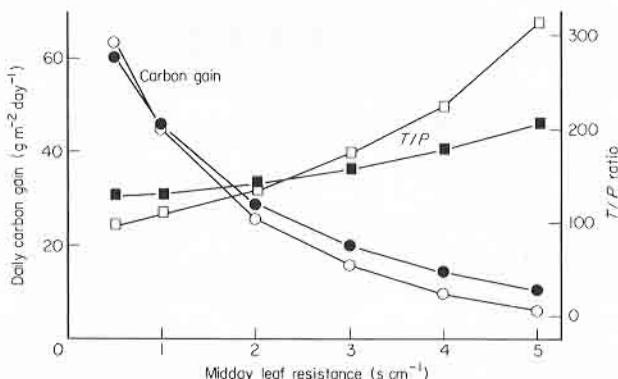
Figure 7. Simulations of the daily course of leaf-air temperature differential for *Camissonia claviformis* (open symbols) and *Malvastrum rotundifolium* (closed symbols) considering two different leaf resistances. Environmental conditions are the same as used for Fig. 5.

than in *Camissonia* (Fig. 7). The difference diminished to a minimum at midday and attained a maximum in the early morning and late afternoon hours when the solar angle was low. In a field experiment to measure the effects of tracking versus nontracking on leaf temperatures, leaves of *Malvastrum* from the same plant were either allowed to track or held in a horizontal position by a thin copper wire. The measured difference in leaf temperatures was 2.8°C at midday irradiances, which agreed well with that predicted by the leaf energy budget model.

Discussion

Although knowledge of the intrinsic photosynthetic characteristics of Sonoran Desert annuals is sparse, we know that at least one species, *Camissonia claviformis*, native to the deserts of the southwestern United States, has an unusually high capacity to fix carbon (Mooney *et al.*, 1976). This is due to a low resistance to gas transfer as well as to a high concentration of the carboxylating enzyme, ribulose biphosphate carboxylase. The results presented here indicate that a plant with a lower inherent photosynthetic capacity, probably because of a lower investment in enzyme, can match the daily carbon gain of *Camissonia* by tracking the sun during the course of the day. This behavioural mechanism results in the attainment of maximal photosynthetic rates earlier in the day and for longer periods than for nontracking leaves. The tracking response also results in higher leaf temperatures than those experienced by nontracking leaves, but this is no disadvantage, because *Malvastrum* has a higher photosynthetic temperature optimum than is found in the nontracking *Camissonia* leaves. The high daily carbon gain of *Malvastrum* does not result in a proportionate decrease in water use efficiency, which is similar at low leaf resistances, and at higher leaf resistances exceeds that of *Camissonia*. Thus, it would appear that the short-lived desert annuals can achieve high

Figure 6. Simulations of the total daily carbon gain and the transpiration/photosynthesis ratio for (o) *Camissonia claviformis* and (•) *Malvastrum rotundifolium* at differing leaf resistances. Environmental conditions are the same as used for Fig. 5.
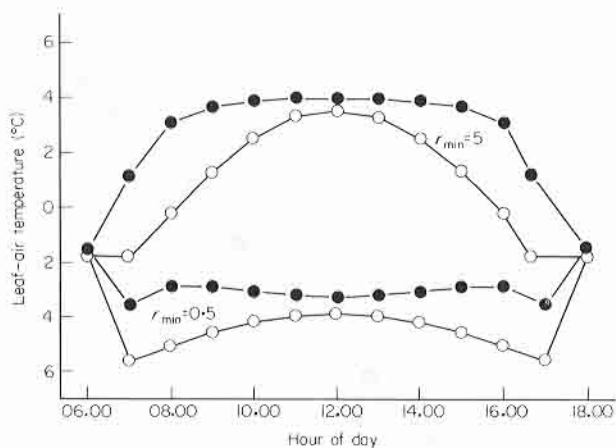
ater use efficiencies as well as large carbon gains in more than one way.

The use of a simulation model leads to several predictions of the consequences of solar tracking that can be field tested: (1) in a relative sense, solar trackers should have lower photosynthetic rates, less protein investment per leaf, and higher photosynthetic temperature optima than nontrackers; (2) solar tracking should be favourable to winter annuals both at the beginning of the season, when sun angles are low, and through the growing season, when air temperatures are moderate; (3) under conditions of high water stress, solar trackers should stop tracking because of possible excessively high leaf temperatures and the lack of sufficient carbon gain because of CO_2 diffusion restrictions; and (4) solar tracking should be a common phenomenon in annuals in high energy environments that must complete their life cycle in a relatively brief period.

Acknowledgments

eferences

Begg, J.E. & Torssell, B.W. (1974) Diaphotomastic and parahelionastic leaf movements in *Stylosanthes humilis* H. K. B. (Townsville Stylo). *Royal Society of New Zealand, Bulletin,* 12, 277–283.

Björkman, O. & Holmgren, P. (1963) Adaptability of the photosynthetic apparatus to light intensity in ecotypes from exposed and shady habitats. *Physiologia Plantarum,* 16, 889–914.

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

Bonhomme, R., Varlet Grancher, C. & Artis, P. (1974) Utilisation de l'energie solaire par une culture de *Vigna sinensis.* II. Assimilation nette et accroissement de matiere sèche, influence du phototropisme sur la photosynthèse des premières feuilles. *Annales Agronomiques,* 15, 49–60.

Ehleringer, J. & Björkman, O. (1977) Quantum yields for CO_2 uptake in C_3 and C_4 plants: dependence on temperature, carbon dioxide, and oxygen concentration. *Plant Physiology,* 56, 86–90.

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

Mooney, H.A., Ehleringer, J. & Berry, J.A. (1976) High photosynthetic capacity of a winter annual in Death Valley. *Science,* 194, 322–323.

Shell, G.S.G. & Lang, A.R.G. (1976) Movements of sunflower leaves over a 24-h period. *Agriculture Meteorology,* 16, 161–170.

Shell, G.S.G., Lang, A.R.G. & Sale, P.J.M. (1974) Quantitative measures of leaf orientation and heliotropic response in sunflower, bean, pepper and cucumber. *Agricultural Meteorology,* 13, 25–37.

Wainwright, C.M. (1977) Sun-tracking and related leaf movements in a desert lupine (*Lupinus arizonicus*). *American Journal of Botany,* 64, 1032–1041.

Yin, H.C. (1938) Diaphototropic movement of the leaves of *Malva neglecta. American Journal of Botany,* 25, 1–6.