

Ecophysiology of two solar tracking desert winter annuals

IV. Effects of leaf orientation on calculated daily carbon gain and water use efficiency

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Summary. This paper represents an empirical study on the effect of different leaf orientations on the daily carbon gain and transpirational water loss of desert winter annuals. Laboratory physiological data on *Malvastrum rotundifolium* (Gray) and *Lupinus arizonicus* (Wats) were combined with energy budget concepts and field measurements of water relations and leaf movements to predict carbon gain patterns for horizontally oriented, diheliotropic and paraheliotropic leaf movement types. The results showed contrasting patterns of carbon gain and water loss. *L. arizonicus*, which is capable of both dia- and paraheliotropic leaf movements, had the lowest rates of daily carbon gain and water loss. But these low rates resulted in the highest water use efficiencies under early season conditions and high water availability. *M. rotundifolium*, a diheliotropic species, was predicted as having the highest rates of carbon gain and water loss on a daily basis over a wide range of environmental conditions and water availability. Despite possessing the highest rates for transpiration, its water use efficiency was higher in relation to other leaf movement types, under a variety of conditions. This result was extremely sensitive to soil water availability. The results were discussed in relation to the ecological ramifications of leaf movements in arid land annuals.

Introduction

Morphological adaptations represent a primary means for leaves to cope with environmental conditions, especially after full expansion has occurred (Begg 1980). Plants inhabiting arid lands possess a variety of morphological properties which influence their carbon gain and water use patterns (Mooney et al. 1977; Ehleringer 1980; Forseth and Ehleringer 1980). A widespread property of desert ephemerals in the southwestern United States is diheliotropism (Ehleringer and Forseth 1980). However, the basic physiological data necessary to evaluate this property in terms of carbon gain and water loss have not been available.

Earlier papers in this series described the leaf movement patterns, microclimate, field water relations and laboratory gas exchange characteristics of two desert winter annuals,

Lupinus arizonicus (Wats) and *Malvastrum rotundifolium* (Gray) (Forseth and Ehleringer 1982a, b, 1983). These papers have reported large differences between the two species in physiological and morphological responses to long-term environmental drought. Our objectives in this study were to analyze these differences in terms of carbon uptake and water loss. Our approach was to integrate empirical relationships derived from the earlier papers with an energy budget approach. Energy budget equations were used to estimate leaf temperatures and transpirational water losses for different leaf movement types. Relationships between transpiration, conductance and photosynthesis, with water potential were then utilized to calculate carbon gain and water use efficiency. The study was not meant as a model of processes involved, but as a series of calculations based on empirical relationships, with the aim of providing insights into the plants' morpho-physiological patterns of response to their environment.

Materials and methods

The approach we used to combine empirical relationships between conductance and photosynthesis with environmental and internal plant factors was very similar to that utilized by Schulze et al. (1976) and Lösch and Tenhunen (1981). Most relationships were represented by linear equations for simplicity (Lösch and Tenhunen 1981). A flow-chart of the program used to calculate daily photosynthetic carbon gains is presented in Fig. 1. Climatic conditions were input using equations describing the path of the sun through the sky for a latitude of 36° N (Death Valley, California) and three different declinations (Table 1) (Campbell 1977). These equations also allowed us to compute incident radiation upon differently oriented leaf surfaces. Other parameters listed in Table 1 were derived from field measurements (Forseth and Ehleringer 1982b). The classification of the growing season into three major phenological periods, early, mid and late followed the procedure of Forseth and Ehleringer (1982b).

We calculated maximum photosynthetic rates (P_{max}) and conductances (g_{max}) according to the water potential of the plant. These relationships were derived from laboratory data (Forseth and Ehleringer 1983) (Table 2). Reductions of these maximum values were then calculated from multiple regressions derived from scaled (0 to 1) photosynthetic and leaf conductance response curves to light and

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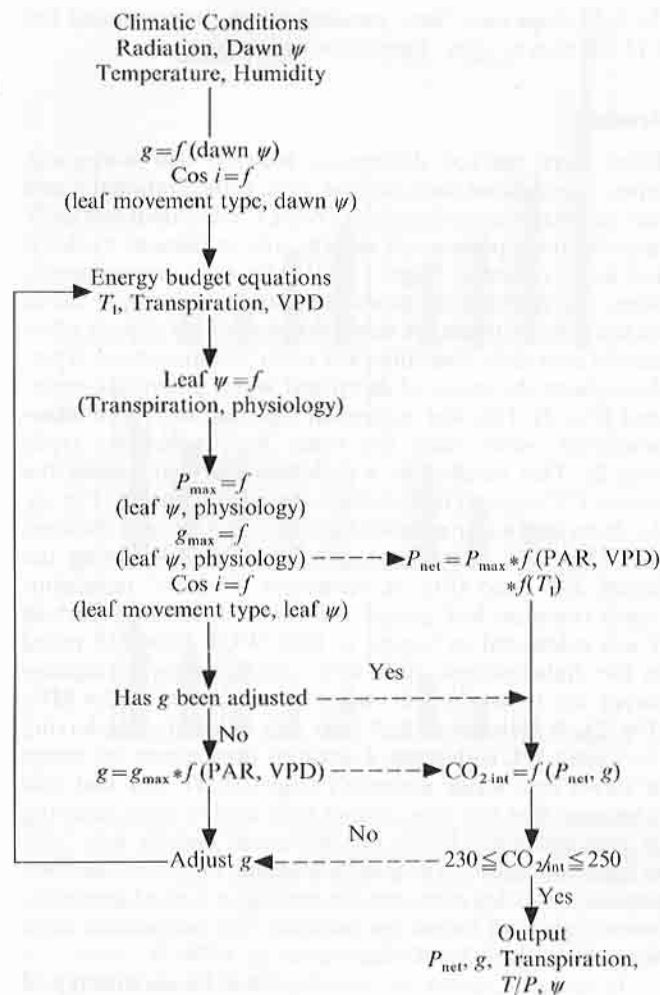


Fig. 1. Flowchart of the program used to calculate daily net carbon gain and transpirational water loss

VPD (Forseth and Ehleringer 1983). Water potential of the plant changed the shape of these response curves slightly, therefore several photosynthetic response curves (to light and VPD) and leaf conductance response curves (to light and VPD), at different leaf water potentials were regressed to give the final relationship (Table 2). Photosynthetic temperature responses were derived from the data of Forseth and Ehleringer (1982a) (Table 2). All effects were assumed to be multiplicative (Schulze et al. 1976).

Computing leaf conductance and photosynthetic rate separately with these regressions resulted in calculated intercellular carbon dioxide ($\text{CO}_{2\text{int}}$) concentrations generally above $250 \mu\text{l l}^{-1}$ (midday average value was $269 \mu\text{l l}^{-1}$). This was especially pronounced in early morning and late afternoon h when calculated leaf conductances were quite high in relation to photosynthetic rates. Our previous studies indicated that there was a very close balance of leaf conductances and photosynthetic rates. Most of the reductions in photosynthesis due to long-term drought were associated with direct effects of drought on the intrinsic photosynthetic capacity of the plants (Forseth and Ehleringer 1983). We felt that we could achieve more realistic results by computing photosynthesis with our regressions and then adjusting leaf conductance to this value in order to maintain $\text{CO}_{2\text{int}}$ values between 230 and $250 \mu\text{l l}^{-1}$. Leaf

Table 1. Climatic inputs used in the energy budget equations of the program used to calculate daily carbon gains, transpirational water losses and water use efficiencies for different leaf movement types. T_{air} and T_{soil} represent equations for calculating diurnal values of air temperature at leaf height and soil temperature, respectively

Season	Climatic inputs
Variable parameters	
Early	Dawn $\psi = -0.20 \text{ MPa}$ to -2.00 MPa
	Declination = -8.0 (March 1)
	Vapor pressure = 10 mPa Pa^{-1}
	$T_{\text{air}} = -0.025 (\text{h})^3 + 0.59 (\text{h})^2 - 1.77 (\text{h}) + 3.05$
	$T_{\text{soil}} = -0.03 (\text{h})^3 + 0.65 (\text{h})^2 + 0.93 (\text{h}) - 16.00$
Middle	Dawn $\psi = -0.20 \text{ MPa}$ to -2.00 MPa
	Declination = 4.1 (April 1)
	Vapor pressure = 8 mPa Pa^{-1}
	$T_{\text{air}} = -0.017 (\text{h})^3 + 0.16 (\text{h})^2 + 5.03 (\text{h}) - 23.60$
	$T_{\text{soil}} = -0.029 (\text{h})^3 + 0.23 (\text{h})^2 + 9.0 (\text{h}) - 50.00$
Late	Dawn $\psi = -0.20 \text{ MPa}$ to -2.55 MPa
	Declination = 14.8 (May 1)
	Vapor pressure = 7 mPa Pa^{-1}
	$T_{\text{air}} = -0.008 (\text{h})^3 - 0.14 (\text{h})^2 + 8.5 (\text{h}) - 30.80$
	$T_{\text{soil}} = -0.030 (\text{h})^3 + 0.30 (\text{h})^2 + 8.7 (\text{h}) - 46.00$
Constant parameters	
Wind	$= 1 \text{ m s}^{-1}$
Latitude	$= 36^\circ \text{ N}$
Leaf diameter	$= 0.03 \text{ m}$ (<i>M. rotundifolium</i>)
	$= 0.02 \text{ m}$ (<i>L. arizonicus</i>)
Leaf absorptance	$= 0.5$ total solar
	0.85 PAR

conductance values were adjusted (usually decreased) through the use of an Ohm's Law analogy equation so that appropriate $\text{CO}_{2\text{int}}$ values were achieved (Fig. 1). This constraint did not alter the qualitative results of leaf orientation effects. It did result in overall decreases of 21% and 24% in calculated transpiration rates and T/P ratios, respectively. The cosine of the angle of incidence ($\cos i$) for *Lupinus* – type leaves (paraheliotropic) was set by the water potential of the plant, according to the relationship reported in Forseth and Ehleringer (1980) (Table 2). Finally, the water potential – transpiration relationship was derived from data reported in Forseth and Ehleringer (1982b) (Table 2). The early season relationship was linear. However, as the season advanced and dawn water potentials became more negative, transpiration rates declined and rates at equivalent water potentials were lower in the afternoon than in morning hours. This may have been due to drying of the soil surrounding the roots or changes in plant resistance (Jones 1978). It was compensated for by including a seasonal and an hourly term in the relationship for mid and late season calculations (Table 2) (Jones 1978). The seasonal term in the regression was given values of 10, 20 and 30 for early, mid and late, respectively.

Calculations were carried out for several combinations of season (early, mid and late), leaf movement type (diaheliotropic, two types of paraheliotropic, and horizontal) and physiological type of drought response (osmotic adjustment or no osmotic adjustment). The drought response type was classified as Type 1, or drought tolerant, for *M. rotundifolium* type responses of leaf conductance and photosynthesis to long-term drought (Forseth and Ehleringer 1982b, 1983).

Table 2. Equations for the empirical relationships used in the program to calculate daily carbon gains, transpirational water losses, and water use efficiencies of different leaf movement types. The relationships were derived from data presented in Forseth and Ehleringer (1980, 1982a, b, 1983). Symbols are the same as in Fig. 1

Program relationships

P_{\max} (type 1) = $20.29 * \psi + 78.8$ ($\mu\text{mol m}^{-2} \text{s}^{-1}$)
P_{\max} (type 2) = $34.75 * \psi + 65.3$ ($\mu\text{mol m}^{-2} \text{s}^{-1}$)
g_{\max} (type 2) = $0.0118 * \psi + 0.0498$ (m s^{-1})
g_{\max} (type 2) = $0.0198 * \psi + 0.0352$ (m s^{-1})
Prop. reduction of P_{\max} due to PAR, VPD (type 1)
= $0.45 * \text{PAR} - 0.014 * \text{VPD} - 0.03 * \psi + 0.24$ $r^2 = 0.94$
Prop. reduction of P_{\max} due to PAR, VPD (type 2)
= $0.45 * \text{PAR} - 0.018 * \text{VPD} + 0.21 * \psi + 0.45$ $r^2 = 0.86$
Prop. reduction of P_{\max} due to T_1 (type 1)
= $(0.22 * T_1^2 - 0.005 * T_1^3 + 37.7)/100$ $r^2 = 0.94$
(early and mid season)
= $(13.9 * T_1 - 0.21 * T_1^2 - 128.2)/100$ $r^2 = 0.89$
(late season)
Prop. reduction of P_{\max} due to T_1 (type 2)
= $(0.25 * T_1^2 - 0.006 * T_1^3 + 29.8)/100$ $r^2 = 0.90$
(early and mid season)
= $(0.35 * T_1^2 - 0.007 * T_1^3 - 29.9)/100$ $r^2 = 0.87$
(late season)
Prop. reduction of g_{\max} due to PAR, VPD (type 1)
= $0.30 * \text{PAR} - 0.017 * \text{VPD} + 0.08 * \psi + 0.59$ $r^2 = 0.70$
Prop. reduction of g_{\max} due to PAR, VPD (type 2)
= $0.35 * \text{PAR} - 0.018 * \text{VPD} + 0.14 * \psi + 0.56$ $r^2 = 0.78$
Leaf ψ (type 1) = $-0.08 * \text{Transpiration} + \text{dawn } \psi$ $r^2 = 0.65$
(early season)
= $-0.05 * \text{Transpiration} + \text{dawn } \psi - 0.06 * h$
= $-0.04 * \text{season} + 0.97$ $r^2 = 0.85$
(mid and late season)
Leaf ψ (type 2) = $-0.10 * \text{Transpiration} + \text{dawn } \psi$ $r^2 = 0.79$
(early season)
= $-0.05 * \text{Transpiration} + \text{dawn } \psi - 0.03 * h$
= $-0.01 * \text{season} + 0.30$ $r^2 = 0.77$
(mid and late season)
$\cos i = 0.29 * \psi$ (fast response)
$\cos i = 0.15 * \psi$ (slow response)

L. arizonicus type responses, drought intolerant, were classified as Type 2 (Forseth and Ehleringer 1982b, 1983). Two types of paraheliotropic leaf movements were examined. The slope of the $\cos i$ vs leaf water potential relationship was examined at values of 0.29 (actually observed in *L. arizonicus*) and 0.15 (Table 2). The value of 0.15 was chosen because analysis of the leaf conductance vs leaf water potential and the photosynthesis vs leaf water potential relationships of *L. arizonicus* and *M. rotundifolium* indicated that *M. rotundifolium* had approximately one half of the slope in these relationships when compared to the responses observed in leaves of *L. arizonicus* (Forseth and Ehleringer 1982b, 1983). We felt that calculations of paraheliotropic leaf types with drought tolerant (Type 1) physiologies was unrealistic because the degree of paraheliotropism severely limited incident radiation loads, compared to leaf water potential effects on photosynthesis. The decreased slope of 0.15 for the $\cos i$ vs leaf water potential relationship may represent a more realistic morpho-physiological combination of paraheliotropic leaf movements with Type 1 physiologies.

The reverse analysis, a drought intolerant physiology (Type 2) with a 0.15 slope for the $\cos i$ vs leaf water potential relationship was also examined for comparative purposes. For simplicity, the rest of the paper will refer to

the 0.29 slope as a 'fast' paraheliotropic response and the 0.15 slope as a 'slow' paraheliotropic response.

Results

There were marked differences between leaf movement types in calculated daily carbon gain, transpirational water loss and water use efficiencies (WUE). The calculated daily rates for these parameters were greatly influenced by dawn leaf water potential (Figs. 2–4). Under early season conditions, our calculations predicted that diaheliotropic leaves with a Type 1 (drought tolerant) physiology gained more carbon on a daily basis than any other leaf movement types, throughout the range of dawn leaf water potentials examined (Fig. 2). This leaf movement type also lost more transpirational water than the other leaf movement types (Fig. 2). This resulted in a diaheliotropic leaf having the lowest T/P ratios at high dawn leaf water potentials (Fig. 2). As dawn leaf water potential declined this pattern changed with the 'slow' paraheliotropic response leaf having the lowest T/P ratio (Fig. 2). Although the 'fast' paraheliotropic response leaf gained the lowest total daily carbon it was calculated as having as high WUE (low T/P ratio) as the diaheliotropic and 'slow' paraheliotropic response leaves up to dawn leaf water potentials of -0.6 MPa (Fig. 2). A horizontal leaf type was calculated as having the lowest WUE (highest T/P ratio) throughout the range of dawn leaf water potentials (Fig. 2). We feel that this is because that leaf type cannot fully exploit early morning or late afternoon hours for maximum carbon gain, due to light limitations. These early morning and late afternoon periods of the day represent the periods of highest humidity, lowest light and lowest temperature, i.e., the periods most favorable to high WUE (Rawson et al. 1978).

In the same season, we calculated that leaves with type 2 physiologies (drought intolerant) showed very different WUE patterns (Fig. 2). These leaves were also calculated to have enhanced daily carbon gains, because of diaheliotropism. However, the calculated WUE of diaheliotropic leaves was the lowest for all leaf movement types until dawn leaf water potentials had reached levels of -1.4 MPa. At that point a horizontal leaf was calculated as having the lowest WUE (Fig. 2). With these Type 2 physiologies and early season climatological conditions a 'fast' response paraheliotropic leaf type was calculated as having the highest WUE of any leaf type examined (Fig. 2).

Different patterns for calculated daily carbon gain, transpirational water loss and WUE in leaves with Type 1 physiologies were evident under the higher temperatures, radiation levels and VPDs of mid season (Fig. 3). In fact, our calculations indicated that the carbon gain and WUE enhancements exhibited by diaheliotropic leaves were even more pronounced under these mid season conditions (Fig. 3). In contrast to early season results, lower dawn leaf water potentials in mid season did not result in a 'slow' response paraheliotropic leaf type becoming more water use efficient than the diaheliotropic leaf (Fig. 3).

The calculated WUE pattern for leaves with Type 2 physiologies also changed from early season to mid season conditions (Fig. 3). Three different leaf movement types were calculated as having the lowest T/P ratios depending upon dawn leaf water potential. At high (-0.2 MPa) and at low (-1.4 MPa) dawn leaf water potentials, a diaheliotropic leaf had the lowest T/P ratios (Fig. 3). At intermediate

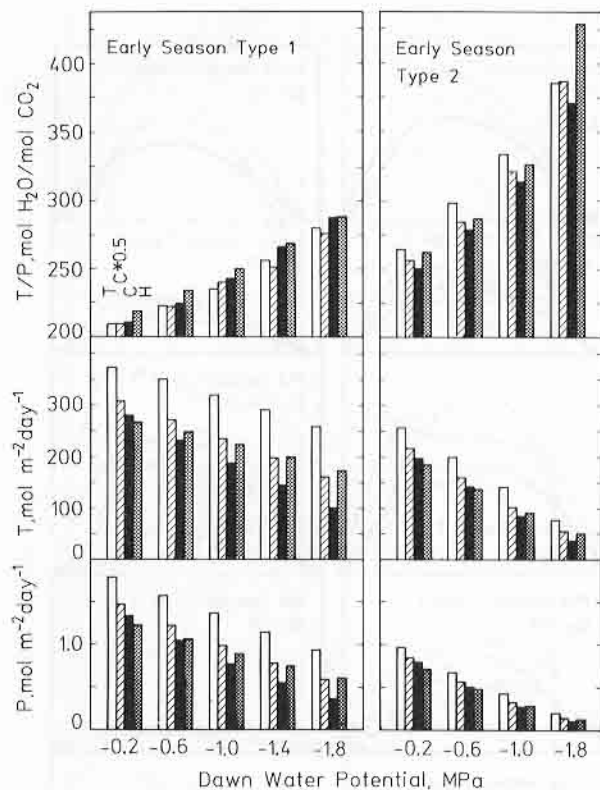


Fig. 2. Calculated rates of daily net carbon gain, transpirational water loss and the ratio of transpirational water to carbon gain (T/P) for four different leaf movement types under early season microclimatic conditions as a function of dawn water potential. \square = solar tracking leaf; diagonal lines = slow paraheliotropic response leaf (0.15 slope); \blacksquare = fast paraheliotropic response leaf (0.29 slope); cross-hatched = horizontally fixed leaf

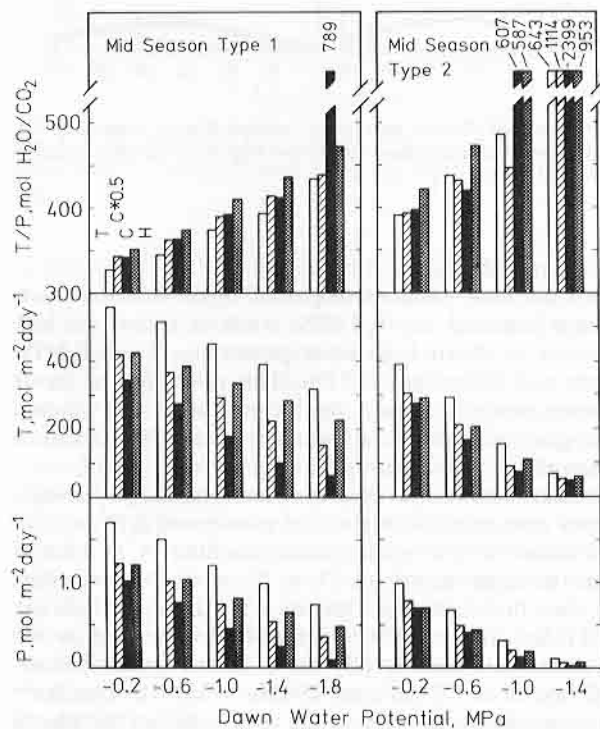


Fig. 3. Same calculations as in Fig. 2 for mid season conditions

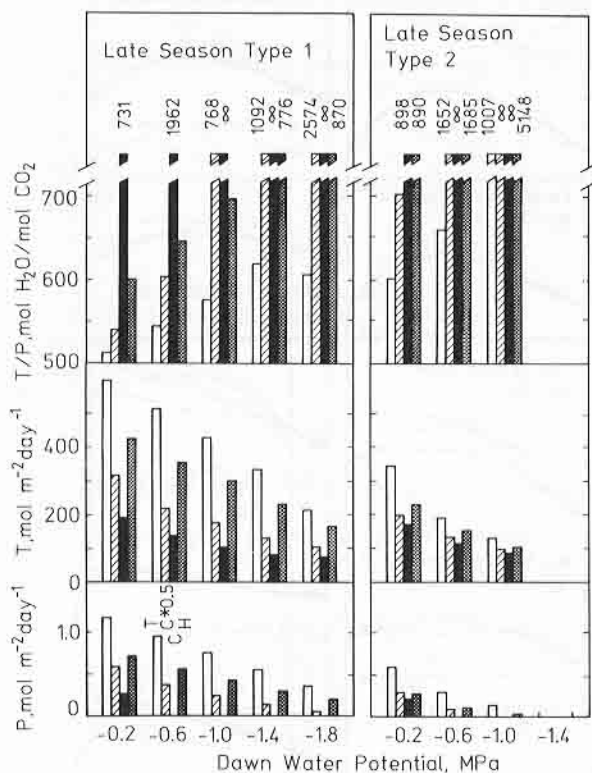


Fig. 4. Same calculations as in Fig. 2 for late season conditions

dawn leaf water potential values, a 'fast' response paraheliotropic leaf had the lowest T/P ratios. This occurred at dawn leaf water potentials of approximately -0.6 MPa. A 'slow' response paraheliotropic leaf had the lowest T/P ratio at dawn leaf water potentials of -1.0 MPa.

With the increased ambient temperatures, solar radiation loads and VPDs characteristic of late season conditions, even larger changes in calculated patterns of carbon gain and WUE resulted (Fig. 4). 'Fast' response paraheliotropic leaves were predicted to reach negative daily carbon gains at dawn leaf water potentials below -0.6 MPa (Fig. 4). With both Type 1 and Type 2 physiologies, diaheliotropic leaves were calculated to have the highest WUE and also to gain the most daily carbon. This is primarily a result of the non-saturating photosynthetic response to light these plants possess (Forseth and Ehleringer 1983). Under late season conditions, paraheliotropic leaves (both 'slow' and 'fast' response) were severely limited, in terms of carbon gain, by the effects of VPD on net photosynthesis, and leaf water potential on the cosine of incidence (i.e. light interception), combined with the effect of low leaf water potentials on net photosynthesis. Diaheliotropic leaves, in contrast, were never limited by light effects and therefore only responded to water potential and VPD.

The dawn leaf water potential effect upon daily carbon gains, transpirational water losses and WUE greatly influences the analysis of Figs. 2, 3 and 4. Due to the higher water use of a diaheliotropic leaf, soils would either dry out faster around the roots, or the plant would be forced to invest more carbon in root biomass in order to maintain dawn leaf water potentials similar to that of a paraheliotropic or horizontal leaved species. The pattern observed

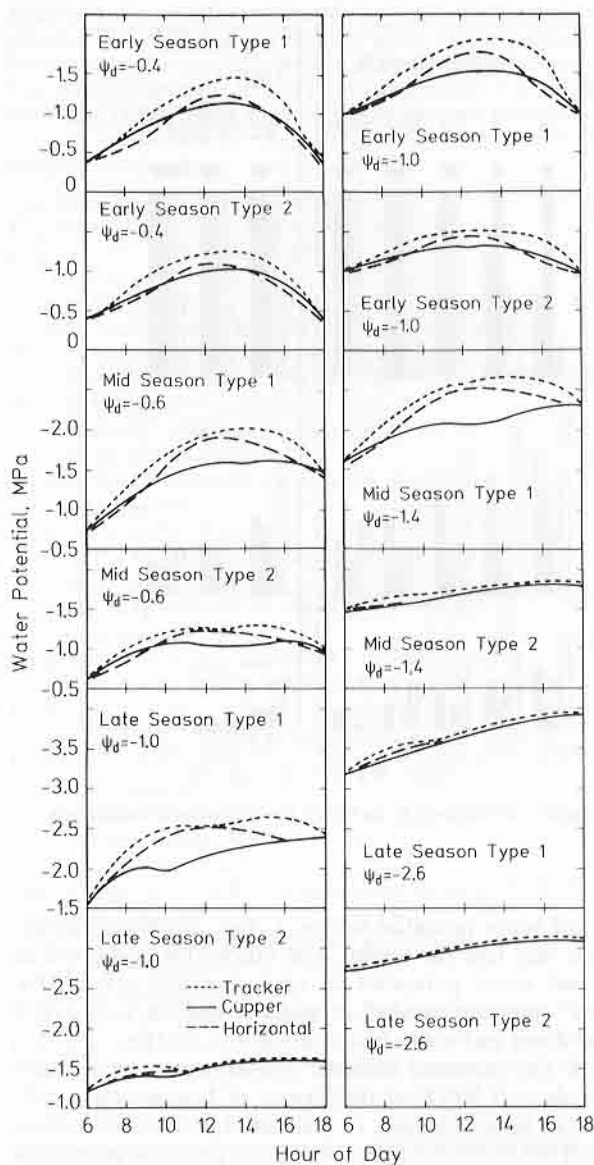


Fig. 5. Calculated diurnal pattern of bulk leaf water potential for three different leaf movement types, three different growing season periods, two different dawn water potentials, and two different physiological responses to drought. Dawn water potentials were chosen for each season to represent typical values experienced by *M. rotundifolium* (Type 1) and *L. arizonicus* (Type 2) (Forseth and Ehleringer 1982b). Physiological types are derived from drought responses of *M. rotundifolium* (Type 1) and *L. arizonicus* (Type 2) (Forseth and Ehleringer 1982b, c).

in field water relations parameters suggests that even at very early phenological periods, diaheliotropic leaf types have lower dawn leaf water potentials than paraheliotropic leaved species. This pattern became more pronounced as the season advanced (Forseth and Ehleringer 1982b). Our calculations showed that the daily course of leaf water potentials reflected the transpirational differences between leaf movement types (Figs. 5, 6). A more realistic comparison of leaf types may be represented by comparing values in Figs. 2, 3 and 4 for the different leaf movement types at different dawn leaf water potentials. For example, our field studies indicated that in sympatric populations, under early

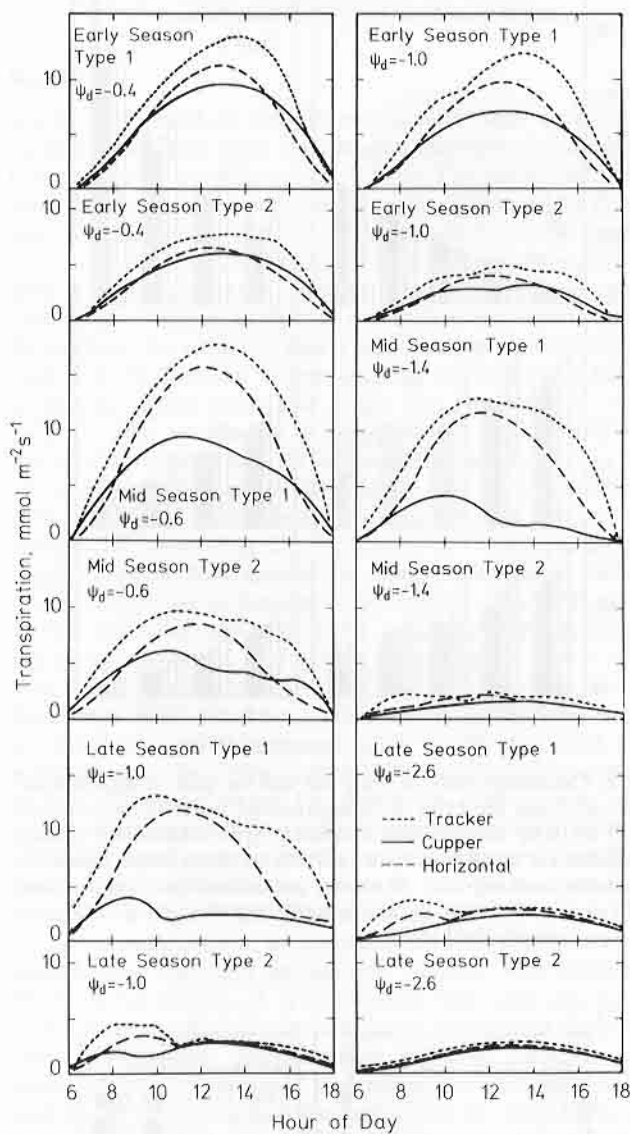


Fig. 6. Calculated diurnal pattern of transpirational water loss for three different leaf movement types. See Fig. 5 for further description.

season conditions, paraheliotropic leaf types were at a dawn leaf water potential of -0.4 MPa, while diaheliotropic leaf types were at dawn leaf water potentials of -1.0 MPa (Forseth and Ehleringer 1982b). This difference in dawn leaf water potential would significantly alter the relative carbon gain, transpirational water loss and WUE values of different leaf movement types (Fig. 2).

Another factor to be considered is the actual physiological types associated with the leaf movement types in the field. Paraheliotropic species, as represented by *L. arizonicus*, are drought intolerant (Type 2), while *M. rotundifolium*, the diaheliotropic species, is drought tolerant (Type 1). But, the drought tolerant physiology used in our calculations represents a fully osmotically adjusted phenotype (Forseth and Ehleringer 1982b, 1983). It is unlikely that this would occur early in the season before the plants have experienced low soil water potentials. In fact, the early

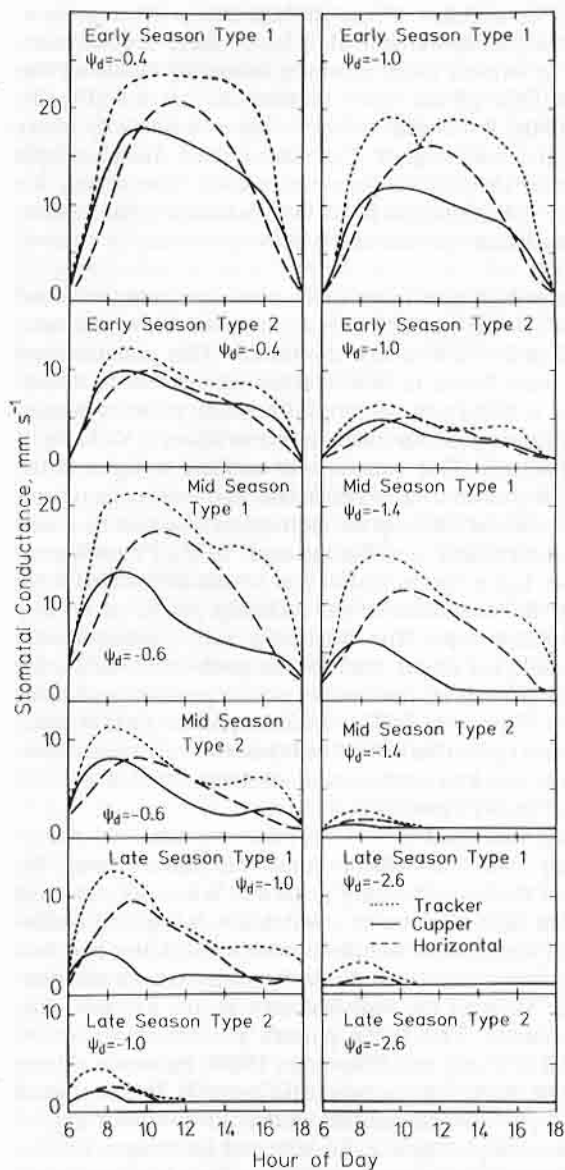


Fig. 7. Calculated diurnal pattern of stomatal conductance for three different leaf movement types. See Fig. 5 for further description

season values of osmotic potential at incipient plasmolysis for *M. rotundifolium* were not very different from those of *L. arizonicus* (Forseth and Ehleringer 1982b). Depending on the previous water stress history of the leaf, it may not be osmotically adjusted at all or may have an intermediate osmotic potential. This would then alter the appropriate comparisons in Figs. 2, 3 and 4. Further field studies are needed to fully elucidate the consequences of these differences in water usage and osmotic adjustment between leaf movement types. However, we would expect that the speed of soil drying and osmotic adjustment of a diaheliotropic species would be critical to carbon gain patterns in the field.

The diurnal patterns of leaf conductance, photosynthesis, water potential and transpiration we calculated for the three different seasons were very similar to those actually measured in field studies (Figs. 5–8) (Forseth and Ehleringer 1982b). The dawn leaf water potentials chosen for these figures are those reported for *M. rotundifolium* (the

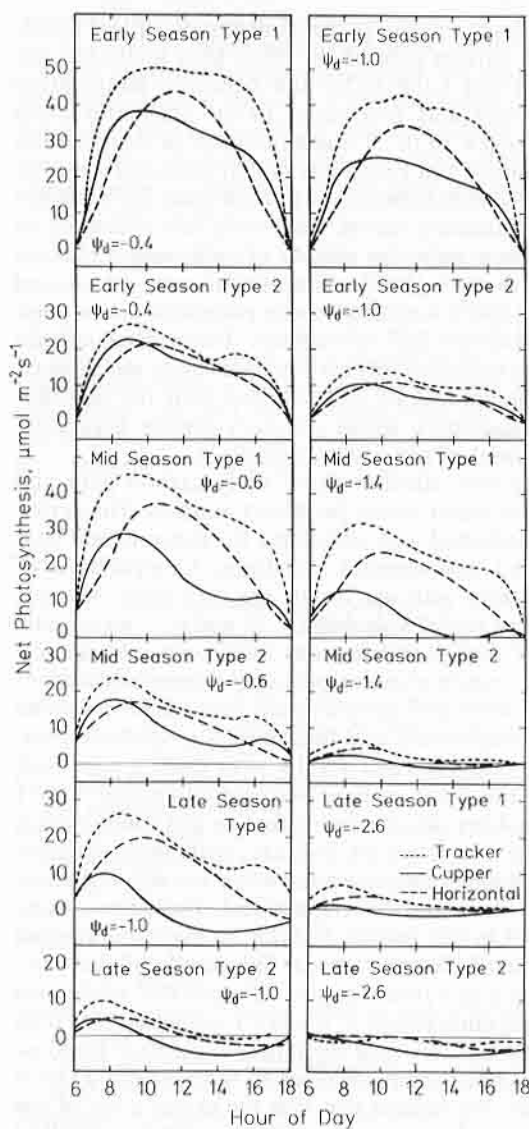


Fig. 8. Calculated diurnal pattern of net photosynthesis for three different leaf movement types. See Fig. 2 for further description

most negative values) and *L. arizonicus* (the most positive values) in Forseth and Ehleringer 1982b. The predicted diurnal courses highlight differences between leaf movement types, dawn leaf water potentials and physiological response to drought. Paraheliotropic leaf movements had their greatest gas exchange activity during early morning hours (Figs. 7, 8). Diaheliotropic leaves also displayed this pattern, with the addition of afternoon peaks in their gas exchange patterns (Figs. 7, 8). Horizontal leaves had their peak gas exchange activities during the middle of the day, or in morning hours, depending upon the dawn leaf water potential (Figs. 7, 8). The overall effect of later seasons and lower dawn leaf water potentials on all leaf movement types was to curtail gas exchange activity and restrict it to earlier periods of the day (Figs. 7, 8). Leaves with Type 2 physiologies had reduced and earlier diurnal peaks in gas exchange compared to leaves with Type 1 physiologies (Figs. 7, 8).

Discussion

Earlier attempts to evaluate the contribution of leaf movements to the carbon gain of the plant have included light effects (Shell and Lang 1976) and light and temperature effects (Mooney and Ehleringer 1978). Shell and Lang (1976) predicted a 10 to 23% enhancement of daily carbon gain and Mooney and Ehleringer (1978) predicted approximately a 15% enhancement of carbon gain for diaheliotropic over stationary leaves. Our study has attempted to incorporate not only the effects of enhanced radiation loads, but also the higher transpirational water losses, leaf temperatures and lowered leaf water potentials that accompany diaheliotropic leaf movements. Our results encompassed a wide range of daily carbon gain values and showed that the enhancement of daily carbon gain for diaheliotropic over stationary leaves can vary greatly depending upon the amount of soil water available.

There are few calculations of daily carbon gain and transpirational water losses for desert annuals. Those that have been conducted were calculated for constant leaf conductances and non-stressful situations. Comparisons of these calculations with our results are very close. Mooney and Ehleringer (1978) calculated $1.33 \text{ mol m}^{-2} \text{ day}^{-1}$ and $1.25 \text{ mol m}^{-2} \text{ day}^{-1}$ carbon gains for *Camissonia claviformis* and *M. rotundifolium*, respectively. These calculations assumed constant leaf conductances, but allowed for the differential temperature and light effects of diaheliotropic vs horizontal leaves. Their results were quite comparable to values in Fig. 2 for early season conditions and Type 1 physiologies. They also predicted that as leaf conductances declined, T/P ratios would increase, with their diaheliotropic leaf actually becoming more water use efficient under these conditions than the horizontal leaf. These trends were also predicted in our results, but not for the same reasons as Mooney and Ehleringer stated. They used different temperature response curves for the different leaf movement types, and this contributed to the WUE advantage for their diaheliotropic leaf. We used the same temperature response curves for all leaf movement types so this was not a factor in our results. We believe that it is the exploitation of the early morning and later afternoon hours (with lower VPDs) for carbon gain that allows diaheliotropic leaves to have higher WUE than horizontal leaf types.

Using an energy budget approach combined with microclimatic measurements, Ehleringer et al. (1979) calculated a daily carbon gain of $1.42 \text{ mol m}^{-2} \text{ day}^{-1}$ and a daily transpirational water loss of $308 \text{ mol m}^{-2} \text{ day}^{-1}$ for *C. claviformis* on March 21. These are slightly higher than the values we calculated in Fig. 2 for a Type 1 physiology. This difference can be explained by the higher water potentials and leaf conductances used in their calculations. T/P ratios in their study ranged from $216 \text{ mol H}_2\text{O/mol CO}_2$ to $493 \text{ mol H}_2\text{O/mol CO}_2$, depending on midday leaf conductances. Over the same range of midday leaf conductances our results are quite comparable (Fig. 2).

The pattern of increasing drought stress restricting gas exchange activity to early morning peaks in desert and agricultural systems is well documented (Oechel et al. 1972; Odening et al. 1974; Pearcy et al. 1974; Depuit and Caldwell 1975; Rawson et al. 1978; Bjorkman et al. 1980; Muchow et al. 1980; Schulze et al. 1980; Wallace and Szarek 1981; Forseth and Ehleringer 1982b). This general response of gas exchange activity to stress points out an

important component in the diaheliotropic phenomenon. Due to the leaf movement abilities of these species, they are able to exploit early morning hours by reducing the limitation light places upon photosynthetic rate (Fig. 8). We calculated horizontal leaves to have consistently lower carbon gains and higher T/P ratios than diaheliotropic leaves under the conditions we examined. The reason for the higher T/P ratios for horizontal leaves was the restriction of maximum gas exchange activity to midday periods (Figs. 7, 8).

The absolute maximum daily photosynthetic rates we calculated for the plants never approached the maximums measured under laboratory conditions. This phenomenon has also been found in field studies (Seeman et al. 1980). There are a variety of factors influencing photosynthesis, including nutrient status, drought stress history, VPD, light and temperature. Our results were realistic in light of the large number of internal plant factors and external environmental factors influencing the expression of a plant's maximum photosynthetic rate (Lange et al. 1975). Physiological type, dawn leaf water potential and season all exerted large effects on the magnitude of gas exchange predicted for any leaf movement type. The extremely high photosynthetic rates possible for desert annuals are probably reached for only short periods of time under actual growth conditions in the field (Figs. 2-4, 8). This would represent further selective pressure upon this life history type to evolve leaf movements that allowed exploitation of these limited periods of optimal growth conditions.

Shackel and Hall (1979) hypothesized that leaf movements may evolve in order to allow the plant to meet the demand of the most limiting resource. When demands for carbon are high and water availability is high, diaheliotropic leaf movements will predominate. As water becomes more limiting paraheliotropic leaf movements should predominate. Most of the time leaf movements will probably be intermediate. This is the pattern *L. arizonicus* displays in the field (Forseth and Ehleringer 1980). However, *M. rotundifolium* displayed the opposite pattern. It maintained diaheliotropic leaf movements under all conditions, until turgor was completely lost (Forseth and Ehleringer 1982b). Another approach to conceptualizing these leaf movement types is to look at them as two extremes in water use patterns. Leaves with *L. arizonicus* type movements had the highest WUE for Type 2 physiologies under early and mid season conditions and high dawn leaf water potentials, when the highest growth rates and carbon gains would be realized in the field (Figs. 2, 3). But this WUE was achieved by sacrificing carbon gain in comparison to both a diaheliotropic and a horizontal leaf (Figs. 2, 3). *L. arizonicus* leaf movements appear to be conserving water at all stages of the season, even under conditions of high water availability (Figs. 2-4). These leaf movements were oriented towards allowing maximal rates of carbon gain only during those periods of the day which contribute to high WUE (i.e. early morning and late afternoon) (Figs. 7, 8). *L. arizonicus* was able to divorce its peak transpiration periods from peak ambient evaporative demand periods through a combination of its leaf movements and stomatal responses to VPD and leaf water potential (Fig. 6, note the shift to the early morning hours of the paraheliotropic leaf transpiration curve in comparison to other leaf movement types) (Forseth and Ehleringer 1983). The tradeoff to this pattern of transpirational water loss is that photosynthesis is also restricted (Fig. 8).

M. rotundifolium represents the opposite end of the spectrum in water use. Its leaf movement responses appeared to maximize carbon gain under all conditions examined (Figs. 2–4). With a Type 1 (drought tolerant) physiology, *M. rotundifolium* achieved this high carbon gain without sacrificing WUE. The carbon costs of osmotic adjustment are unknown and may have a considerable impact upon the net carbon gain of this morpho-physiological pattern. A major component of this water use pattern would be the speed of development of drought tolerance. *M. rotundifolium* experienced drier soils in its root environment than *L. arizonicus* (Forseth and Ehleringer 1982b). Periods of high ambient temperatures before sufficient root development and osmotic adjustment have occurred may be quite critical to the survival of this water use pattern. Diaheliotropic leaves' relative carbon gain and WUE values compared to other leaf movement types would be directly proportional to the speed and the extent of osmotic adjustment and soil drying in the root zone. This would determine the relevant bars of Figs. 2, 3 and 4 which would be compared to each other.

The sensitivity of carbon gain to dawn leaf water potential predicted in our results for a paraheliotropic leaf supports the distribution differences pointed out in Forseth and Ehleringer (1982b) between *M. rotundifolium* and *L. arizonicus*. The predictability and amount of rainfall in deserts varies dramatically with elevation (Hunt 1975). *L. arizonicus* at our study sites is restricted to higher, more mesic elevations (Forseth and Ehleringer 1982b). This distribution occurs in other parts of the Sonoran desert also (Wainwright 1978). This is consistent with the pattern shown in Figs. 2, 3 and 4 for Type 2 physiologies and paraheliotropic leaf movements. High WUE and carbon gain were realized for this morpho-physiological type only under mild climatic conditions and high dawn leaf water potentials (Figs. 2–4). *M. rotundifolium*, in contrast, is found below sea level on the floor of Death Valley. Here, ambient temperatures are highest and rainfall is the lowest and most unpredictable (Hunt 1975). Our calculations predict that a Type 1 (drought tolerant) physiology and a diaheliotropic leaf movement type would have higher carbon gains and WUE under higher temperatures and lower dawn leaf water potentials than paraheliotropic leaf types (Figs. 3, 4). We do not know if these distributional differences are present in other representatives of these morpho-physiological types. But our simulations predict that as long as diaheliotropic leaves can osmotically adjust in concert with soil drying, they would gain more carbon and have higher WUE than paraheliotropic leaves in drier, more unpredictable environments. The tradeoffs between carbon gain and water loss involved in the conservative water use pattern of *L. arizonicus* may limit it to environments with higher and more predictable precipitation regimes.

Ehleringer and Forseth (1980) outlined the possible advantages and disadvantages of diaheliotropic leaf movements in plants. The authors pointed out that the physiological data needed to examine leaf movement patterns in terms of the consequences to the plants were lacking. This study has synthesized laboratory physiological and field microclimatic data collected on two contrasting heliotropic leaf movement types in order to give us insights into the ramifications of these leaf movements. The importance of the unique combinations of physiological and morphological properties that these plants possess is clear. Paraheliotropic

is not beneficial to a drought tolerant (Type 1) physiological type, either in terms of carbon gain or WUE. Diaheliotropic, due to its greater water use ramifications, has low WUE when associated with drought intolerant (Type 2) physiologies and mild climatic conditions. Our calculations indicated that with a drought tolerant physiology, a diaheliotropic leaf need not stop diaheliotropic leaf movements under drought conditions, since other leaf types under identical conditions would gain less carbon as well as being less water use efficient.

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