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Ecophysiology of Two Solar Tracking Desert Winter Annuals

II. Leaf Movements, Water Relations and Microclimate

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Summary. The seasonal course of water relations in field populations of two leaf solar tracking desert winter annuals was examined. Measurements were made of leaf movements in relation to leaf conductance and water potential. *Malvastrum rotundifolium* maintained solar tracking movements up to the wilting point of the plant (−4 MPa). *Lupinus arizonicus* altered its morphology through paraheliotropic leaf movements as leaf water potentials declined to −1.8 MPa. Diurnal patterns of leaf conductance showed marked seasonal trends, with gas exchange activity being restricted to early morning hours as water availability declined. Studies of potted plants showed that *L. arizonicus* was not able to alter its osmotic potential in response to drought, while *M. rotundifolium* underwent a 1.86 MPa reduction in osmotic potential. The significance of the two contrasting patterns is discussed in terms of observed plant distribution and origin.

Introduction

Desert ephemerals have historically been regarded as possessing few adaptations beyond those controlling germination and rapid growth responses (Went 1948; Juhren et al. 1956; Beatley 1974; Turner 1979). Recent evidence suggests that these annuals not only possess several morphological and physiological adaptations necessary to the ephemeral habit, but may also possess features valuable during drought periods. These include extremely high photosynthetic rates (Mooney et al. 1976), photosynthetic temperature acclimation abilities (Seemann et al. 1980a; Forseth and Ehleringer 1982), seasonal photosynthetic pathway differentiation (Mulroy and Rundel 1977), morphological alteration of growth habit (Mulroy and Rundel 1977), and heliotropic leaf movements (Wainwright 1977; Mooney and Ehleringer 1978; Ehleringer and Forseth 1980).

Due to the highly variable length of the growing season experienced by winter ephemerals, very high growth rates under favorable conditions are quite advantageous (Mooney et al. 1976; Mulroy and Rundel 1977; Ehleringer et al. 1979). Diaheliotropic leaf movements (orientation of the leaf lamina perpendicular to the sun's direct rays) are recognized as being a morphological means to enhance radiation interception and potential photosynthetic carbon gain (Bonhomme et al. 1974; Shell and Lang 1976; Mooney and Ehleringer 1978; Ehleringer and Forseth 1980). The photosynthetic ability to utilize high solar radiation levels and heliotropic leaf movements are widespread properties in both winter and summer desert ephemerals of the southwestern United States (Ehleringer and Forseth 1980; Seemann et al. 1980b). A dichotomy exists within heliotropic species with some species displaying paraheliotropic leaf movements (orientation of the leaf lamina parallel to the sun's direct rays) under drought conditions (Ehleringer and Forseth 1980). This movement has been shown to lower leaf temperatures and transpiration rates and was an effective morphological means of drought avoidance in several arid land species (Begg and Torssell 1974; Shackel and Hall 1979; Forseth and Ehleringer 1980).

In this series of papers we have compared ecophysiological aspects of two winter annuals displaying these contrasting solar tracking traits. *Malvastrum rotundifolium* has simple, round leaves and accurate diurnal solar tracking leaf movements (Monney and Ehleringer 1978; Ehleringer and Forseth 1980). *Lupinus arizonicus* which grows sympatrically in many areas of the Sonoran and Colorado deserts of North America has palmately compound leaves and exhibits both solar tracking and paraheliotropic movements, depending upon the water status of the plant (Wainwright 1977; Forseth and Ehleringer 1980).

The studies reported in this paper were undertaken with several objectives in mind. The first was to examine the leaf movements of *M. rotundifolium* in response to plant water status, and to compare these with those reported for *L. arizonicus* (Forseth and Ehleringer 1980). Mooney and Ehleringer (1978) predicted that the carbon gain benefits of leaf solar tracking should be modulated by the water status of the plant so that when stress increased beyond a certain point, leaf movements ceased. Secondly, this study examines the seasonal ramifications of the two contrasting leaf movements to the interception of solar radiation. Third, we examine the seasonal course of microclimate and water relations of both species. Water relations characteristics of several desert annuals have been studied under high water availability, but the seasonal progression and late season responses to low water availability are poorly understood (Bennert and Mooney 1979; Ehleringer et al. 1979; Pavlik 1980; Wallace and Szarek 1981).

Materials and Methods

Field populations were located at several study sites. A sympatric population was located in Fossil Canyon, elevation 250 m, approximately 5 km NW of Ocotillo, Imperial

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Co., California. Microclimatic and water relations studies were conducted at this site in March, 1979 and February and March, 1980. The other field populations were located in Death Valley National Monument, California. Microclimatic and water relations studies were conducted on a sympatric population located in Jubilee Pass approximately 3.2 km east of the Saratoga Springs turnoff at an elevation of 100 m in March and April, 1979. In 1980, this same site was virtually devoid of *M. rotundifolium* and measurements were made only on *L. arizonicus*. An additional study site with *M. rotundifolium* but without *L. arizonicus* was located at an elevation of −50 m, approximately 3 km NNW of Ashford Mills. It was studied in April 1979 and March and April, 1980. A sympatric population located in Salsberry Pass at an elevation of 300 m was sampled in March, April and May, 1980.

The time of season (early or late) will be defined throughout the paper by the water potentials and leaf to air vapor pressure deficits (VPD) experienced by the plants. Early season air temperatures are close to 20 C and leaf-air VPD is less than 2.0 kPa. Mid-season air temperatures are 25–30 C and leaf-air VPD is approaching 3.0 kPa or more. Finally, in late season conditions air temperatures are at or above 30 C and leaf-air VPD can exceed 4.0 kPa. Mid and late season conditions can occur within several days of each other at any locality or be separated by several weeks depending upon the timing of precipitation and general weather events (Mulroy and Rundel, 1977; personal observations).

Leaf angle and conductance measurements were made following the procedure of Forseth and Ehleringer (1980). Leaf conductance measurements were made on 3–8 leaves hourly. Water potentials were measured with a Scholander pressure chamber (Scholander et al. 1965). Water potential measurements were collected at dawn and then every two hours until sunset on 3–5 leaves of each species.

The relationships between leaf conductance, cosine of incidence and water potential for *M. rotundifolium* were determined from measurements on Death Valley populations in April, 1979. The measurements were made between 1,000 and 1,400 hours to minimize any light effects upon stomatal conductance. Plants were randomly selected and angle and azimuth measurements were made on 2–5 leaves of the plant. Leaf conductance and water potential were measured on the same leaf and these values were associated with the mean cosine of incidence generated from the angle and azimuth measurements on that plant. Microclimatic measurements were made following the procedure of Ehleringer et al. (1979).

Transpiration rates were calculated using the wet bulb temperature, leaf temperature and air temperature at leaf height to calculate leaf to air vapor density gradients for any hour. This value was then multiplied by the average stomatal conductance for that hour. Boundary layer conductances were not used in the calculation, so these calculated transpiration rates are slightly higher than might actually have occurred. However, at leaf sizes of 1–3 cm and the generally high wind speeds measured in the field (1–3 m s^{-1}) boundary layer conductances are much higher than stomatal conductances.

A combination of pressure-volume curve analysis and thermocouple psychrometry was used to determine osmotic potentials of field and potted plants. Thermocouple psychrometer samples were taken by harvesting leaflets of *L. arizonicus* and leaf discs of *M. rotundifolium*, placing the samples in small sealed plastic vials and dropping them immediately into liquid N_2. Samples were then kept frozen until analysis with thermocouple psychrometers (J. Merril Co., Logan, Utah). Pressure volume curves were performed following the procedure of Jones and Turner (1980). Field samples of 8–10 leaves were collected in March, April, and May 1980. Due to experimental difficulties with petiole breakage these sample sizes were reduced to 2–6 complete curves per sample day.

Laboratory studies of osmotic adjustment were conducted on plants grown from field collected seed. Plants were grown in 25 cm diameter pots. These experiments were repeated several times in order to achieve osmotic potential values similar to those measured in the field. The first experiment was performed on outdoor, potted plants in July–August, 1980 and lasted 21 days for *L. arizonicus* and 15 days for *M. rotundifolium*. This experiment yielded osmotic potentials similar to field values for *L. arizonicus*, but not for *M. rotundifolium*. Osmotic adjustment values for *M. rotundifolium* similar to field values were measured in outdoor grown plants in July, 1981. Drought was imposed by withholding water for 2–3 day spans followed by slight re-watering. This was continued for a period of five weeks.

Results

Both plants exhibited very accurate diaheliotropic leaf movements. Measured cosine of incidence (cosine of the angle between the sun's direct rays and a normal to the leaf surface) for early season plants (little or no water stress) was approximately 1.0 for *M. rotundifolium* and 0.6 for *L. arizonicus* (Fig. 1). A cosine of incidence value of 1.0 indicates that the full direct beam of the sun is incident upon the leaf lamina. Even when plants are very small and the soil profile is well charged with water *L. arizonicus* exhibited some paraheliotropic movement. This was accomplished primarily through the orientation of the leaflets which are bent around their midvein.

The seasonal radiation regime resulting from these contrasting leaf movements is quite different (Fig. 2). The values were generated from equations describing the path of the sun through the sky at a latitude corresponding to Death Valley, California (36° N) (Campbell 1977). Reflected and diffuse radiation are assumed to be equal for each leaf type (i.e., nondirectional sources). The parahelio-

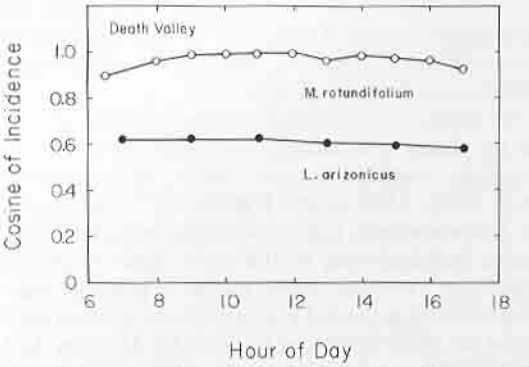

Fig. 1. The diurnal course of cosine of incidence exhibited by *M. rotundifolium* and *L. arizonicus*

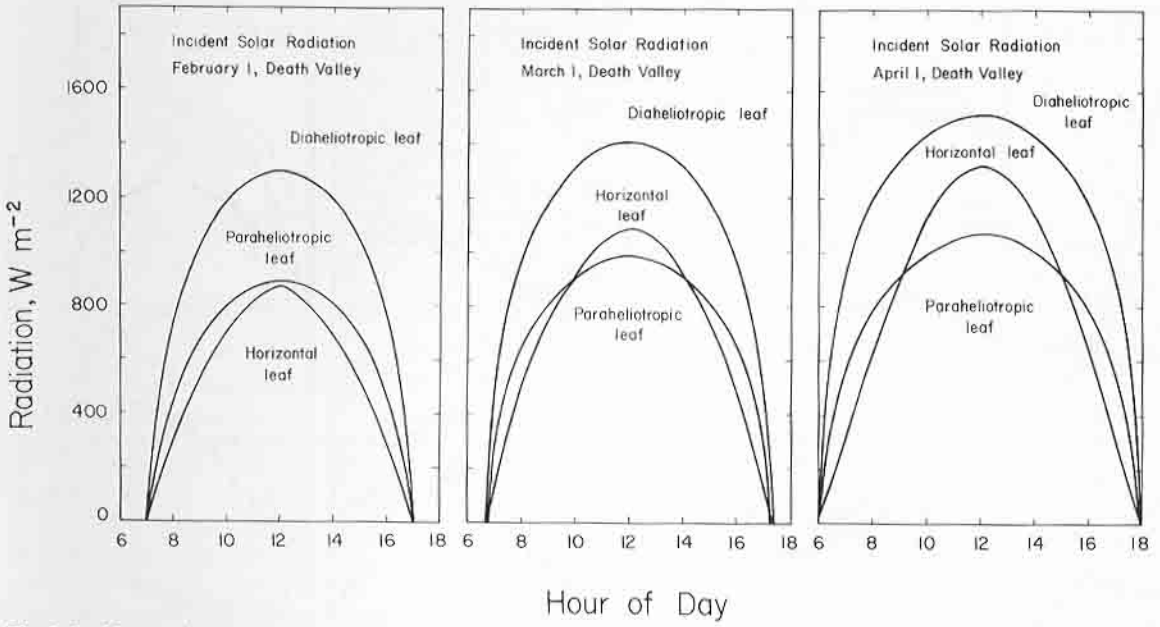

Fig. 2. Incident solar radiation throughout the day computed for three different times of the season for three different desert winter annual leaf types. The latitude used was that of Death Valley, California. Diffuse and reflected solar radiation are included in the calculations. Ratios of total daily solar radiation incident upon diaheliotropic, paraheliotropic and horizontal leaves are; 1:0.68:0.56; 1:0.69:0.63; 1:0.69:0.71 for February, March and April, respectively

tropic leaf was given a cupping angle of approximately 75 degrees (a flat leaf would have a cupping angle of 180 degrees). This angle is representative of the paraheliotropism exhibited by *L. arizonicus* under well-watered conditions in the field (Fig. 1, Forseth and Ehleringer 1980). Quantum flux (400–700 nm) is a constant percentage of the total solar radiation, hence the same patterns would hold for photosynthetically active radiation (PAR).

Early in the season both the dia- and the paraheliotropic leaf are receiving more total daily radiation than a fixed, horizontal leaf. As the season progresses, and temperatures and drought levels increase, the paraheliotropic leaf has lower midday solar irradiances than a horizontal leaf. On a daily total basis, the paraheliotropic leaf is receiving exactly the same total radiation as the horizontal leaf on April 1. In contrast, the diaheliotropic leaf experiences high solar radiation loads throughout the day.

Leaf solar tracking movements changed as the season progressed (and as drought caused changes in plant water status) in *L. arizonicus* (Forseth and Ehleringer 1980). *M. rotundifolium* maintained tracking movements over a much wider range of leaf water potentials (Fig. 3). The *L. arizonicus* data have been published previously and are presented here to contrast with those of *M. rotundifolium*. The dichotomy in leaf movements in response to plant water status increases the differences in incident solar radiation (Fig. 2) between the dia- and paraheliotropic leaves.

This morphological difference is mirrored in the physiological responses of the plants to decreasing leaf water potentials. The water potential at complete stomatal closure is much lower in *M. rotundifolium* than in *L. arizonicus* (Fig. 4). The relationship between conductance and water potential is the result of long term soil drought effects. Daily patterns due to short term effects could vary from

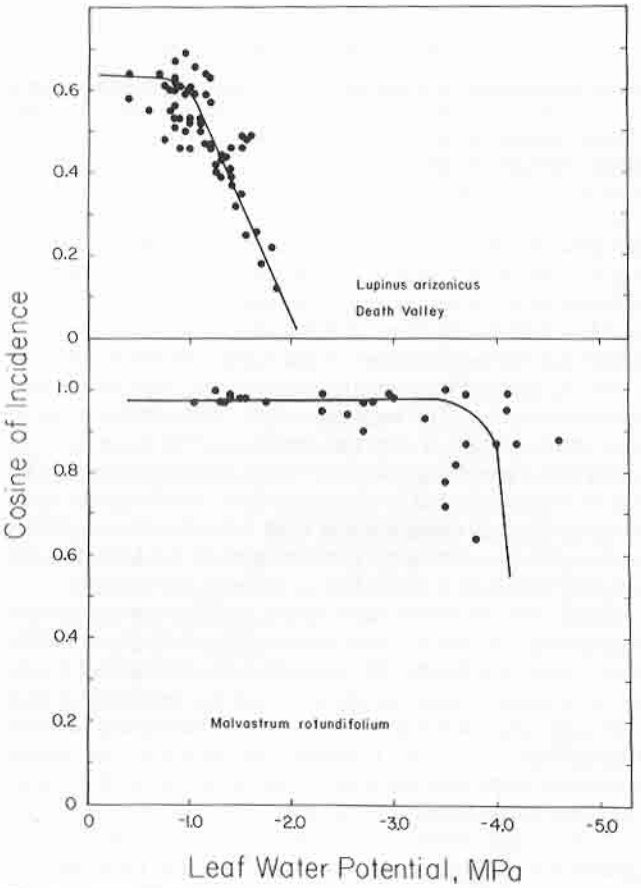

Fig. 3. Relationship between cosine of incidence and leaf water potential for randomly selected plants in Death Valley, California in April of 1979

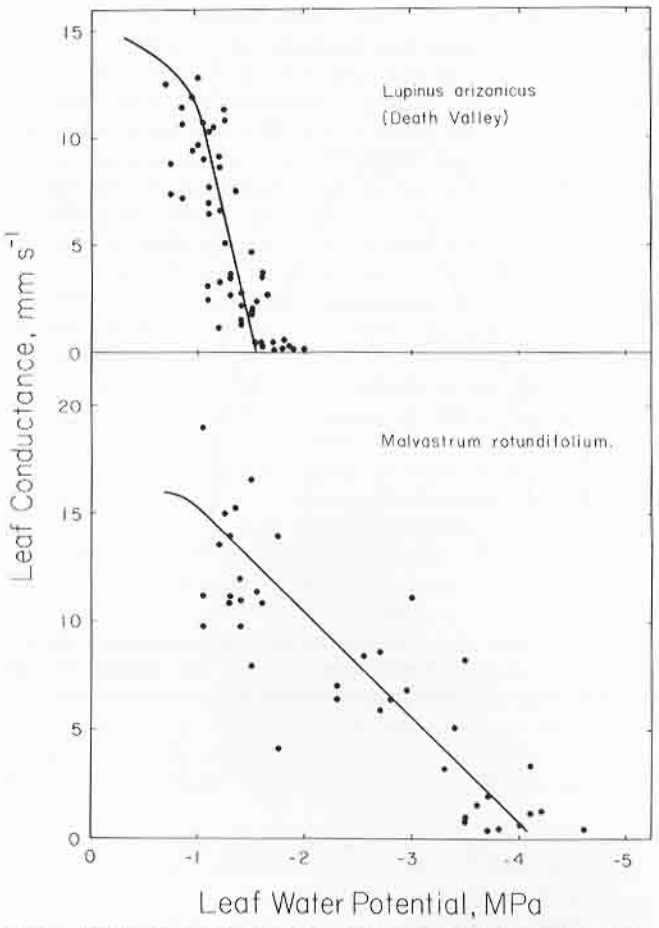

Fig. 4. Relationship between leaf conductance and leaf water potential for Death Valley populations of *L. arizonicus* and *M. rotundifolium*. Measurements were taken between 1,000 and 1,400 hours to alleviate light factors

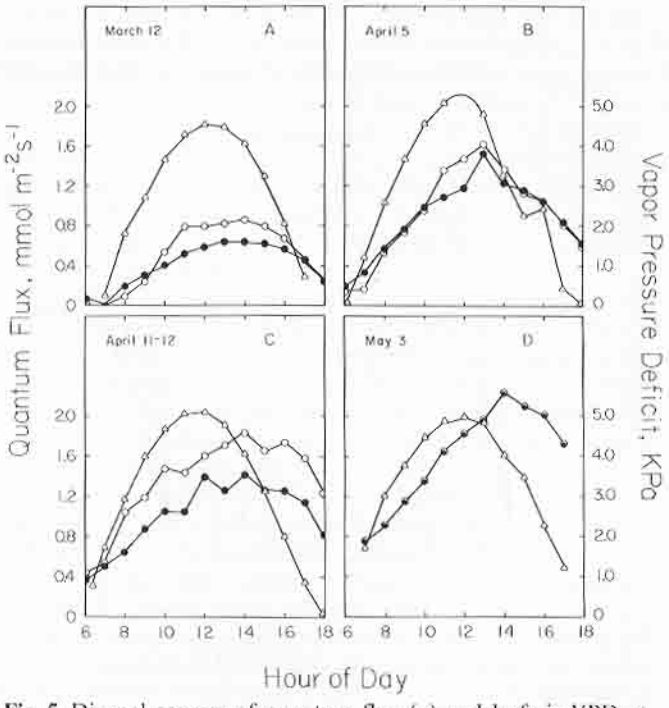

Fig. 5. Diurnal courses of quantum flux (△) and leaf-air VPD at four phenological periods. *M. rotundifolium* leaf-air VPD (○), *L. arizonicus* leaf-air VPD (●), May 3 data is air-air VPD and is assumed to be equal for both plants (◉)

this pattern. In the *M. rotundifolium* data there is considerable scatter, which may be indicative of changes in the relationship either seasonally or from plant to plant.

March 12 microclimatological and water relations measurements were conducted on the sympatric population at Fossil Canyon. Plants in this population were small and pre-reproductive. The majority of *M. rotundifolium* leaves were within 2 cm of the soil surface, while *L. arizonicus* leaves were generally within 5 cm of the soil surface. The day was characterized by cloudless skies, resulting in a sinusoidal pattern of quantum flux (Fig. 5A). Leaf to air VPDs were moderate, reaching peak values of 2.1 kPA for *M. rotundifolium* and 1.6 kPa for *L. arizonicus* (Fig. 5A).

Leaf conductances were quite similar and constant throughout the day for both species (Fig. 6A). Even in this early stage of growth, *M. rotundifolium* leaves had lower (more negative) water potentials than *L. arizonicus*. Daily variation in leaf water potential was 0.56 MPa for *L. arizonicus* and 0.9 MPa for *M. rotundifolium*. Minimum leaf water potentials were 0.69 MPa lower in *M. rotundifolium* than in *L. arizonicus* (1.67 vs. 0.98) (Fig. 6A).

Leaf height distribution as well as the radiation regime differences resulted in *M. rotundifolium* leaf temperatures that were 2–3° C higher than *L. arizonicus* leaf temperatures throughout the day. Leaves of both species were 4–5° C cooler than ambient temperatures during the middle of the day (Fig. 7A). Transpiration rates exhibited sinusoidal patterns, reflecting the diurnal course of VPD (Fig. 7A).

The April 5 data were collected on a sympatric population located in Salsberry Pass, Death Valley. At this time both species were actively flowering. Leaves were arrayed 10 cm or more above the warm soil surface. Both species were producing new leaves as well as flowers. A small percentage of flowering apices (*L. arizonicus*) or axillary meristems (*M. rotundifolium*) bore mature seeds at this phenological period. Quantum flux again showed a characteristic sinusoidal pattern (Fig. 5B). Leaf-air VPDs were markedly higher than earlier. *L. arizonicus* experienced slightly lower VPDs than *M. rotundifolium*, reaching a maximum value of 3.8 kPa compared with 4.0 kPa for *M. rotundifolium*.

Leaf conductance and water potential diurnal courses were markedly different in both species from earlier season values. Although peak conductances were similar to those on March 12 (Fig. 6B), they occurred quite early in the morning. *L. arizonicus* exhibited generally higher leaf conductances than *M. rotundifolium*. The range in daily water potential values increased to 0.81 MPa and 1.15 MPa for *L. arizonicus* and *M. rotundifolium*, respectively. *L. arizonicus* reached a minimum value of −1.43 MPa at 1,130 hours, while *M. rotundifolium* reached a minimum of −2.58 MPa at 1,530 hours. *L. arizonicus* water potentials became more positive after 1,200 hours, indicating a recovery of water status, whereas *M. rotundifolium* values continued to decline until sunset.

Leaf temperatures were very close to ambient, with *M. rotundifolium* having slightly higher temperatures than *L. arizonicus* (Fig. 7B). Transpiration rates showed a sinusoidal pattern for *L. arizonicus* with a peak value at 1,100 hours. The pattern for *M. rotundifolium* changed from the earlier season pattern with a flat transpiration response

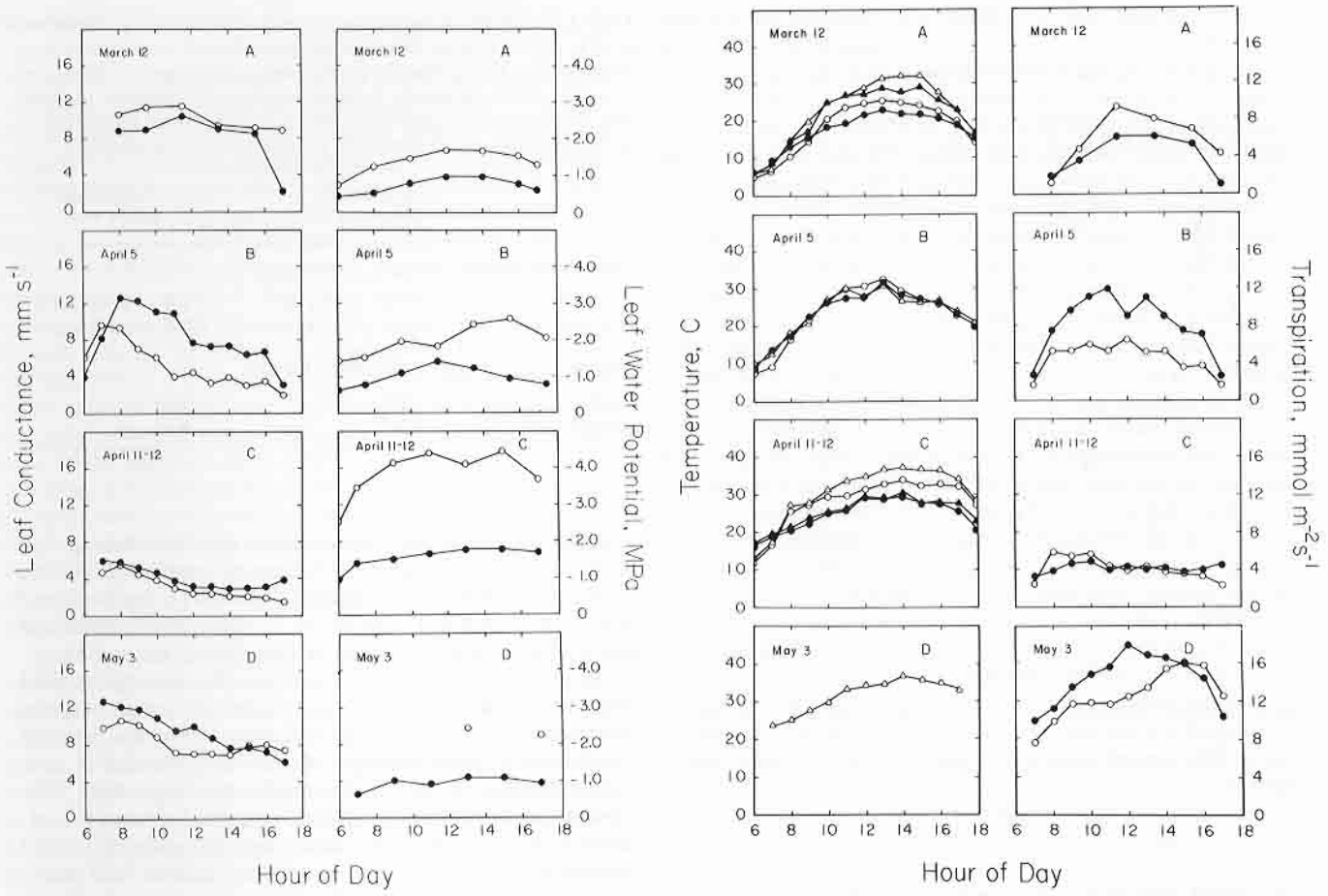

Fig. 6. Diurnal courses of leaf conductance and leaf water potential for *M. rotundifolium* (○) and *L. arizonicus* (●) at four phenological stages in 1980

Fig. 7. Diurnal courses of air temperatures, leaf temperatures, and transpiration rates at four different phenological periods in 1980. *M. rotundifolium* leaf temperatures and transpiration rates (○), *L. arizonicus* leaf temperatures and transpiration rates (●). Air temperature at *M. rotundifolium* leaf height (△). Air temperature at *L. arizonicus* leaf height (▲). For April 5 and May 3 data (△) denotes air temperature experienced by both species

between 0800 and 1,400 hours (Fig. 7B). Both of these patterns indicated that the stomata were exerting a dominant influence over transpiration rates, since in neither species did the peak in leaf-air VPDs occur at the same time as the peak in transpiration rate.

By mid-April both species were in an active seed setting stage, although a few new flowers and leaves continued to be produced as long as the plants were viable. Leaves were at least 10–15 cm above the soil surface. The *L. arizonicus* population located in Jubilee Pass was measured on April 11, and the *M. rotundifolium* population near Ashford Mills was measured on April 12, 1980. The quantum flux on both days was nearly identical (Fig. 5C). Leaf-air VPDs were quite high, exceeding 3.0 KPa (Fig. 5C).

Leaf conductances were markedly lower than earlier values. They declined throughout the day from a peak at 0700–0800 hours (Fig. 6C). *L. arizonicus* had a range of 0.81 MPa between the maximum water potential value and the minimum value. *M. rotundifolium* showed a much larger diurnal range of 1.91 MPa (Fig. 6C). Its daily minimum water potential was over two and one half times more negative than that reached by *L. arizonicus* (−4.46 vs. −1.77 MPa).

April 12 was a warmer day than April 11, and this is reflected in the ambient temperatures experienced by the plants (Fig. 7C). Both plants maintained leaf temperatures close to ambient. Transpiration rates peaked in the morning, decreased at 1,100 hours and then stayed relatively constant, despite peak leaf-air VPDs occurring at 1,400 hours (Fig. 7C).

Data collected on May 3 illustrated the plasticity of these annuals to precipitation. The data were collected on the sympatric population at Salsberry Pass (same population as the April 5 data). Only four viable *M. rotundifolium* plants could be found, and the *L. arizonicus* population was also significantly reduced. On April 30 to May 1 a rare storm had passed through the area, recharging the topmost portions of the soil profile with 14.5 mm of precipitation. Leaf temperatures were not measured and thus only air-air VPDs are calculated (Fig. 5D). However, these data show that at this late stage in the season the VPD can be quite pronounced.

Although there had been severe mortality in the population, those plants that survived were able to recover to peak leaf conductances similar to those measured earlier (Fig. 6D). The diurnal pattern of leaf conductance was sim-

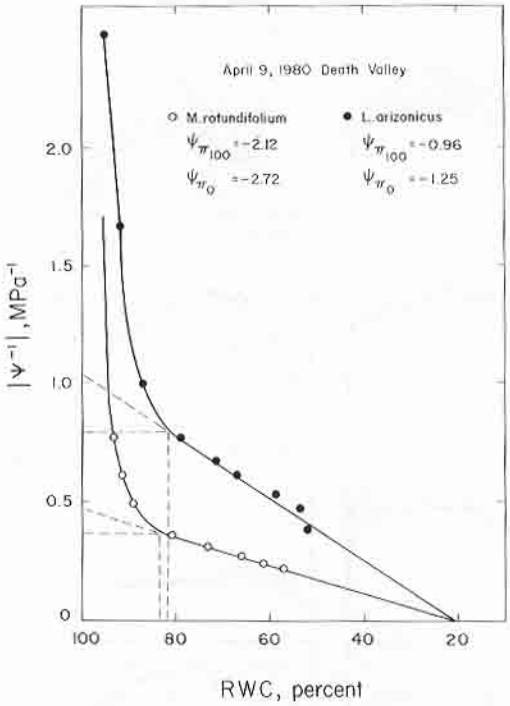

Fig. 8. Pressure-volume curves for *M. rotundifolium* and *L. arizonicus* on April 9, 1980. $\Psi\pi 100$ denotes osmotic potential at 100% relative water content while $\Psi\pi_0$ denotes osmotic potential at zero turgor

ilar to mid and late season patterns in that there was a steady decrease after 0800 hours. Leaf water potentials for *L. arizonicus* reached a midday minimum of −1.1 MPa. Due to the paucity of *M. rotundifolium* plants only midday and 1,700 hours values of leaf water potential were measured. The average midday value for three leaves on three different plants was −2.43 MPa, quite comparable to the minimum value of −2.58 MPa measured on April 5.

Transpiration rates on May 3 were the highest measured all season, reflecting the combination of large VPDs and high leaf conductances (Fig. 7D). They showed a sinusoidal pattern typical of early and mid-season patterns. These data must be interpreted cautiously since the combination of high ambient air temperatures and leaf conductances are likely to result in leaf under temperatures. Therefore, the VPDs and transpiration rates may have been overestimated. However, the diurnal pattern would not be altered significantly by these factors.

In 1979 osmotic potential samples were collected from the sympatric population at Fossil Canyon on March 30. The population at Fossil Canyon was in an advanced flowering, mid-seed setting stage. Daily minimum leaf water potentials were −1.9 MPa and −3.3 MPa for *L. arizonicus* and *M. rotundifolium*, respectively. Psychrometric analyses revealed that *M. rotundifolium* had an osmotic potential at zero turgor of −3.43 MPa. The *L. arizonicus* samples had an osmotic potential value of −1.9 MPa. The difference in these values suggested a difference between the osmotic adjustment capabilities of the two species.

Representative pressure-volume curves during mid-flowering stages in Death Valley show a definite dichotomy in internal water relations (Fig. 8). *M. rotundifolium* is able

Table 1. Summary of osmotic water potentials of field and outdoor grown, potted plants. The osmotic potentials at zero turgor were measured by thermocouple psychrometry techniques. The lowest recorded water potentials indicate single measurements of plants with the Scholander pressure bomb. Experiments on potted plants were performed on 20 plants. 10 control and 10 droughted

	L. arizonicus (July 1980)	*M. rotundifolium* (July 1981)
Osmotic potentials at zero turgor (MPa)		
Control	−1.28 ± 0.14 (s.d.)	−1.85 ± 0.39 (s.d.)
Droughted	−1.44 ± 0.31 (s.d.)	−3.71 ± 0.40 (s.d.)
Lowest recorded water potentials (MPa)		
Field	−2.00	−4.60
Potted	−1.60	−4.15

to shift this relationship from a curve closely matching that of *L. arizonicus* in the early stages of vegetative growth to one even further left and under the curve depicted here (data not presented). Leaves of *L. arizonicus* maintained essentially the same relationship throughout the season.

Results with potted *L. arizonicus* plants support field observations. There were no significant differences between droughted and control *L. arizonicus* in any of the pressure volume curve parameters or in osmotic potential at zero turgor (measured by thermocouple psychrometry). The most negative osmotic potentials measured during the experiment were −1.80 MPa, which were comparable to field measured values (Table 1). The observation that field plants have never been measured at water potentials below −2.0 MPa (Table 1), suggests that the osmotic adjustment capabilities of *L. arizonicus* were extremely limited. Similar results have been obtained with other legumes (Wilson et al. 1980). On potted outdoor grown *M. rotundifolium* the lowest recorded osmotic potential at zero turgor was −4.17 MPa. This is comparable to values for field plants (Table 1). Midday water potentials were as low as −4.15 MPa during this experiment. None of the reduction in osmotic potential can be explained by changes in the percent of bound water or turgid weight/dry weight (TW/DW) ratios. In fact, the bound water fraction changed in the opposite direction from one that would lower osmotic potentials. Results on field plants showed no consistent trend in bound water fraction with increasing drought. However, the TW/DW ratio did tend to decline with declining water potentials. Assuming a starting point for osmotic potential at zero turgor of −1.65 MPa and using the largest range found in the TW/DW ratio for Death Valley plants (7.6 to 4.7), only a 0.63 MPa reduction in osmotic potential at zero turgor would be realized.

The value of osmotic adjustment to the plant is illustrated in the *M. rotundifolium* experiment. At the end of the experiment, control plants reached midday water potentials of −1.78 ± 0.19 (s.d.) MPa. Droughted plants reached water potentials of −3.37 ± 0.35 (s.d.) MPa. Osmotic potentials measured at the same time as the total water potentials gave values of −1.85 ± 0.18 MPa and −3.71 ± 0.4 MPa for control and droughted plants, respectively. Thus it appears that the droughted plants had greater turgor potentials at midday than did controls (0.34 vs 0.07 MPa).

Discussion

The length of the growing season for winter ephemerals can range from six weeks to six months, but the time available for rapid growth is much shorter (Beatley 1974; Mulroy and Rundel 1977). In the Death Valley region biomass is accrued primarily in March and April. This pattern suggests that there has been selection for plants with high growth rates that can flower and set seed within this short period of mild climatic conditions, before the limited soil water supply is depleted. Both *M. rotundifolium* and *L. arizonicus* possess high photosynthetic rates and their leaves do not saturate at full noon irradiances (Ehleringer and Forseth 1980). These characteristics are shared by other desert ephemerals and are considered to be adaptations to the short growing season (Mooney et al. 1976; Ehleringer et al. 1979; Seemann et al. 1980b). The solar tracking leaf movements of these plants allow them to fully exploit these photosynthetic characteristics by enhancing light interception, especially in early morning and late afternoon hours when VPD levels are most favorable in terms of water use efficiency (Fig. 2) (Mooney and Ehleringer 1978; Ehleringer and Forseth 1980).

But there are drawbacks to solar tracking as well. The increased radiation loads increase leaf temperatures and transpiration rates over those of stationery leaves of the same size and with equal leaf conductances and absorptances. While this may result in higher carbon gains during earlier, cooler growth periods it may lead to water deficits in later phenological periods. These two species exhibited marked differences in their late season morphological responses. *L. arizonicus* modulated its intercepted radiation according to its water potential (Fig. 3) (Forseth and Ehleringer 1980). There was a tight coupling between leaf movements, water potential and stomatal conductance. This allowed *L. arizonicus* to maintain high water potentials despite increasing levels of environmental drought (this ability is defined as drought avoidance by Hall (1981)). While this morphological response (paraheliotropism) reduced leaf temperatures and transpirational water loss it also reduced the interception of PAR and photosynthetic rates. The response was plastic and with recovered water potentials paraheliotropism was reduced and light interception increased (Forseth and Ehleringer 1980).

Leaves of *M. rotundifolium* showed a different response to drought. They did not change morphology or leaf movements but rather exhibited drought tolerance characteristics (Hall 1981). As soil water potentials declined, leaves of *M. rotundifolium* changed osmotic potential, enabling them to maintain positive turgor to much lower leaf water potentials than would have been possible without this osmotic potential change. If leaf solar tracking and the enhanced radiation interception that accompanies these movements are to be maintained throughout the season, then this drought tolerance ability may be essential. Ludlow (1980) points out the advantages and disadvantages of this type of stomatal adjustment. The additional carbon gained through this mechanism can be used to produce more roots, assist in maintenance of existing structures, further osmotic adjustment, further shoot growth, and perhaps the most important in our context, to produce seeds in annuals. The disadvantages include the probability that severe water deficits may occur at critical stages of development such as floral initiation and anthesis. This is especially crucial for annuals which must produce some seeds every year in order to contribute to future generations.

The unpredictability of the end of the growing season may actually favor stomatal adjustment capabilities. Unlike the annuals discussed by Ludlow (1980), where the end of the growing season is predictable and flowering and seed set are concentrated near the end of the growth period, desert ephemerals in Death Valley start flowering very early and at a small size. They continue to flower, set seed and produce new leaves for the rest of the growing period. In essence this pattern is a way of hedging their bets against an early end to the growing season. Under this type of selective regime stomatal adjustment may be quite advantageous in terms of extending carbon gain periods, extracting more soil water and extending seed setting periods. In drier areas, where initial rains which trigger germination are not followed by more precipitation, stomatal adjustment may be the only mechanism which allows annuals to achieve substantial seed sets. As the amount of rainfall rises and the unpredictability of the season decreases the more conservative pattern of *L. arizonicus* would be viable. The increase in the probability of late precipitation events would maintain soil water potentials at a level that would allow the drought avoiding *L. arizonicus* to extract water from the soil. The distribution of *M. rotundifolium* and *L. arizonicus* within Death Valley support this hypothesis. *M. rotundifolium* is found on sandy soils from elevations below sea level on the valley floor to elevations above 1,000 m in the surrounding passes. *L. arizonicus* does not occur below 100 m and cannot be found in Death Valley proper. It seems to be restricted to the higher elevations in Jubilee and Salsberry Pass. These areas receive more precipitation as well as precipitation later in the spring than the valley itself.

This distribution appears to have a historical facet as well. The *Lupinus* species in the California flora are derived from a northern, Arcto-Tertiary origin. *Lupinus* occurs from moist forest habitats out into adjoining desert regions with many of the annual species having evolved within the Californian floral regime. *Malvastrum*, in contrast is derived from a southern, Madro-Tertiary origin and invaded the California flora from desert ancestors (Raven and Axelrod 1978). *Lupinus* has invaded the desert areas from mesophytic mountainous areas while *Malvastrum* has been associated with arid areas for a much longer evolutionary time period.

The diurnal patterns of stomatal conductance and water potential in both species exhibit marked seasonal trends. In response to declining soil water availability and increasing VPD, the plants exhibited increased stomatal control over transpirational water loss. More of the gas exchange activity of these plants took place in early morning hours as water potentials declined. Patterns similar to our March 12 data have been measured on other winter annuals (Bennert and Mooney 1979; Ehleringer et al. 1979; Wallace and Szarek 1981). However, the only other work showing the seasonal course of leaf conductance was that of Wallace and Szarek (1981). Their findings for three species of winter annuals growing in sunny environments in Arizona were quite similar to ours, although the maximum conductances were not as high. Water potentials were not reported in their study. Work on desert perennials is more readily available. This work generally shows gas exchange being restricted to early morning and late afternoon hours as plant water potentials decline. This is true for cool and warm

desert species in North American deserts (Oechel et al. 1972; Pearcy et al. 1974; Odening et al. 1974; Depuit and Caldwell 1975; Bjorkman et al. 1981), and for perennial species in other desert areas of the world (Schulze et al. 1980). It appears that flat or single peaked gas exchange patterns under conditions of high water availability followed by double peaked and finally early morning peaks as water availability declines is a general feature of all life forms, including agricultural systems (Rawson et al. 1978; Muchow et al. 1980).

The dichotomy in sympatric drought avoidance and drought tolerance patterns is also found elsewhere. Two legumes in semi-arid regions of northeastern Australia *Macroptilium atropurpureum* and *Desmodium uncinatum* showed contrasting gas exchange responses to declining water potentials. Leaves of *M. atropurpureum* display drought avoidance characteristics including paraheliotropism and tight stomatal control over transpirational water loss, while *D. uncinatum* experiences much lower water potentials under the same conditions (Ludlow and Ibaraki 1979). *M. atropurpureum* can also be found in mixed pastures with several osmotically adjusting grass species, with quite contrasting water potential values (Wilson et al. 1980).

The question of why *M. rotundifolium* maintains leaf solar tracking movements throughout the season is still hard to resolve. Although the stomatal adjustment capabilities of the plant allow it to utilize the high radiation loads to much lower water potentials than would be possible without this ability, stomatal conductances are still quite low at late stages of the season. The plant would still achieve higher rates of carbon gain but the enhancement becomes very small at these lower conductances. We can only speculate that since these leaf movements are turgor mediated processes (Schwartz and Koller 1978; Wainwright 1977), either the plant does not have the ability to stop these movements until turgor is at such a low level that gradients cannot be maintained or the energy from the light harvesting reactions is utilized in some unknown processes other than photosynthesis. An advantage to these solar tracking movements even under low water availability is that light would not be limiting in the early morning hours when the leaf conductances are highest.

In summary, these two species both show leaf movements which enhance radiation loads and potential photosynthetic carbon gain during periods of high water availability. As water availability declines the physiological and morphological responses of the two species become increasingly divergent. *M. rotundifolium*, derived from warm region and desert ancestors displays pronounced drought tolerance properties and maintains leaf solar tracking movements and stomatal opening to very low water potentials. *L. arizonicus* derived from north temperate, mesophytic ancestors displays a well developed drought avoidance pattern with tightly coupled leaf movements and stomatal opening in order to maintain high water potentials. The fact that we have found two such contrasting drought response patterns within the same life history category is consistent with the wide diversity of life forms found in the warm deserts of North America. The harsh, highly variable abiotic characteristics of this region lead to a variety of successful coexisting physiological suites of characters even within the same life form.

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