

Ecophysiology of Two Solar-tracking Desert Winter Annuals. I. Photosynthetic Acclimation to Growth Temperature

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Abstract

The ability of two solar-tracking desert winter annuals, *Lupinus arizonicus* Watson and *Malvastrum rotundifolium* Gray, to acclimate their photosynthetic characteristics to different growth temperatures was examined. Plants were grown in growth chambers under 25/15°C and 40/30°C thermal regimes. The plants grown at 40/30°C were also subjected to a drying cycle in order to assess whether or not drought affected the photosynthetic acclimation to high temperatures. Both species exhibited shifts in their temperature optima and thermal death points for photosynthesis. The droughted plants showed no further acclimation than did the watered plants grown at 40/30°C. Using representative meteorological conditions measured in Death Valley, California, it was predicted that photosynthetic acclimation plays only a small role in enhancing daily carbon-gaining ability for late-season conditions. However, under conditions of drought stress and high temperatures, the acclimation may prevent thermal death and extend plant life.

Introduction

Desert winter annuals have historically been regarded as ephemerals with few adaptations beyond those restricting germination to favourable temperature and water regimes, accelerated growth responses and seed-dispersal mechanisms (Went 1948; Juhren *et al.* 1956; Beatley 1974; Evenari *et al.* 1975). Recently it has been observed that desert annuals possess several physiological and morphological adaptations beyond those suggested by early studies (Mooney *et al.* 1976; Mulroy and Rundel 1977; Monson and Szarek 1979; Forseth and Ehleringer 1980). One such morphological adaptation is that of leaf solar tracking, that is, diurnal leaf movements so that leaves remain perpendicular to the sun's direct rays. This property allows the leaves to operate potentially at maximum photosynthetic capacity throughout the day (Mooney and Ehleringer 1978) and is widespread in both winter and summer annuals in the deserts of the south-western United States (Ehleringer and Forseth 1980).

The thermal regime experienced by plants growing in North American deserts such as in Death Valley, California, is widely variable. Air temperatures can range from a mean daily maximum of 18°C in January to 37°C in May and up to 47°C in July (Mooney *et al.* 1978; Mooney 1980). Much of the work on potential for acclimation to temperature in desert plants has been conducted on species occurring

in Death Valley (for review see Berry and Björkman 1980). This work has largely concentrated on perennial species and has shown that many species have the ability to change their photosynthetic response to temperature throughout the season in concert with prevailing air-temperature regimes (Pearcy 1976, 1977; Mooney *et al.* 1978; Berry and Björkman 1980; Mooney 1980). These changes in photosynthetic acclimation to temperature are beneficial to the plant in terms of net carbon gain (Mooney 1980).

Recently, several studies have investigated the potential of desert annuals for photosynthetic acclimation to temperature. Monson and Szarek (1979) reported no photosynthetic acclimation in *Machaeranthera gracilis*, a winter annual of the southwestern United States. Other species have been found to adjust both their temperature optimum for photosynthesis as well as the point at which irreversible thermal damage to the leaf occurs (Seemann *et al.* 1979, 1980; Downton *et al.* 1980). Based on their studies, Seemann *et al.* (1979) and Downton *et al.* (1980) concluded that temperature itself is the primary environmental stimulus leading to photosynthetic acclimation. Additionally, they suggested that the effects of drought on acclimation occurred through the elevated leaf temperatures which were the result of reduced transpirational cooling.

As part of our studies on the ramifications of leaf solar-tracking movements in desert annuals, two Death Valley winter annuals were examined for their ability to adjust photosynthetic characteristics in response to changes in the temperature regimes. As a consequence of the enhanced solar-radiation levels experienced by solar-tracking species, it was hypothesized that the ability of these plants to acclimate photosynthetically to the higher ambient temperatures typical of mid- and late-season periods could play a significant role in the carbon balance of the plants. The two species used in this study, *Malvastrum rotundifolium* Gray and *Lupinus arizonicus* Watson, both exhibit solar tracking (diaheliotropism). However, under drought conditions leaf movements and energy balance differ markedly between the two species. While *M. rotundifolium* maintains leaf solar-tracking movements up to the wilting point of the plant, *L. arizonicus* exhibits increasing paraheliotropism (orientation of the leaf lamina parallel to the sun's direct beam) as leaf water potential declines (Forseth and Ehleringer 1980; Forseth and Ehleringer, unpublished data). This results in quite different incident solar-radiation levels, especially during drought, and can result in different leaf temperatures under similar microclimatic conditions (Ehleringer and Forseth 1980; Forseth and Ehleringer 1980). It was hypothesized that as a consequence of these morphological differences, the two species should exhibit different photosynthetic acclimation responses to growth temperature. Since the effects of drought on leaf temperature are pronounced, the plants grown at high temperature were also subjected to drought, and the photosynthetic responses to temperature were compared with those of non-droughted plants.

Methods

Growth Conditions

Plants were grown from seed collected in Death Valley National Monument, California. They were potted in soil in plastic pots (15 or 25 cm diam.) and grown in growth chambers equipped with high-intensity discharge lamps. Average quantum flux density (400–700 nm) at leaf height was approximately $0.65 \text{ mmol m}^{-2} \text{ s}^{-1}$. Photoperiod was the same for both thermal regimes at 16/8 h

day/night. Temperature regimes were chosen to represent those temperatures present in the field during early to mid-season growth periods and late-season conditions: 25/15°C and 40/30°C day/night temperatures. At least 2 weeks were allowed for the plants to adjust to growth temperatures before gas exchange was measured, so the leaves measured for the gas exchange experiments were produced during this period.

Drying regimes differed between the two species. *L. arizonicus* plants, after adjustment to the 40/30°C growth temperatures, received half as much water as control plants. By the end of the experiment, the droughted plants were reaching the wilting point daily (-1.5 to -1.6 MPa) and leaf drop was starting to occur. *M. rotundifolium* plants, due to limited space, were in smaller pots (15 cm diam.). Since this species appears to be extremely drought tolerant (water potentials below -4.4 MPa have been measured in the field, I. Forseth, unpublished data), the plants grown at 40/30°C were subjected to 2 weeks of severe drought, during which plants wilted at least five or six times. The photosynthetic temperature response of both species was examined on unwatered plants and droughted plants that had been watered 24 h before measurement in order to alleviate some of the stomatal closure effects caused by the drought regime.

Gas-exchange Measurements

Gas exchange was measured on single leaves chosen from the youngest fully expanded leaves present on the plants. Measurements were conducted on an open gas-exchange system similar to that described by Ehleringer and Björkman (1977). Ambient CO₂ levels were maintained at $330 \pm 15 \mu\text{l l}^{-1}$ and vapour pressure deficit (VPD) levels were kept at less than 1.0 kPa, except at leaf temperatures above 40°C where the VPD averaged 3.0 kPa. No stomatal closure was observed at these elevated leaf temperatures. Thus, our results were probably not affected by the increasing VPD at high temperatures. This is supported by the fact that internal CO₂ concentrations increased at temperatures above the photosynthetic temperature optimum. All experiments were performed at ambient CO₂ levels because this was expected to yield results that were most ecologically significant. Curves of photosynthetic response to temperature were obtained by starting photosynthetic measurements at a leaf temperature of 30°C, then decreasing the leaf temperature stepwise to 15°C. The temperature was brought back to 30°C and when photosynthetic rates similar to those first recorded were achieved, the temperature was increased stepwise (3–5°C) until photosynthetically unstable points were reached. Photosynthetic rates at any one temperature were not recorded until they had been stable for 10–15 min.

Microclimatology

Field microclimatological conditions were measured in Death Valley, California following the procedure of Ehleringer *et al.* (1979). Data were taken hourly on several different days during the growing seasons of 1979 and 1980 of a sympatric population of *M. rotundifolium* and *L. arizonicus* located approximately 3.2 km east of the Saratoga Springs turnoff at an elevation of 100 m. Two representative days (23 March 1979 and 29 April 1979) were chosen to evaluate the effects of photosynthetic response to temperature on the daily carbon gain. This was achieved through the use of a microcomputer programmed with the measured leaf temperatures and regressions of the pooled photosynthetic data from each temperature treatment. The pooled data from each treatment were fed into a stepwise multiple regression of photosynthetic rate versus various powers of leaf temperature to generate the regression of best fit used in the simulation (Steel and Torrie 1960). For each hour the photosynthetic rate, as influenced by the leaf temperature measured in the field, was computed. Hourly photosynthetic rates between 0700 and 1500 h were integrated to estimate the total daily carbon gain. Light was assumed to be saturating and potential effects of humidity and water deficit were ignored. The results, therefore, represent the calculated effect of temperature alone on the daily carbon gain of the plant.

In order to assess the combined effects of drought and high temperature late in the season on the plants, an energy-budget program [constructed from equations in Campbell (1977)] was used to predict leaf temperatures of leaves with closed stomates (conductance to water loss, 0.5 mm s^{-1}) under the microclimatic conditions measured on 29 April 1979. This energy-budget model has been tested previously using actual parameters measured in the field and has been found to predict leaf temperatures within 1–2°C of those actually measured.

Results

Photosynthetic Responses

The pattern of photosynthetic response to temperature shows a very broad temperature optimum for all treatments in both species (Fig. 1). In both species, the optima are in the 28–33°C range. The main difference between treatments is at the extreme lower and upper temperature ranges.

The curves of photosynthetic response to temperature for both species were analysed in greater detail using multiple regression analysis for each individual temperature curve (Steel and Torrie 1960) (Table 1). All the individual multiple regressions had correlation coefficients greater than 0.92. Temperature optima were then found by differentiating photosynthetic rate with respect to temperature and solving for zero ($dPS/dT = 0$) (Lange *et al.* 1974). The temperatures at which photosynthesis reached half of its maximum value were then found using an iterative procedure with the regressions.

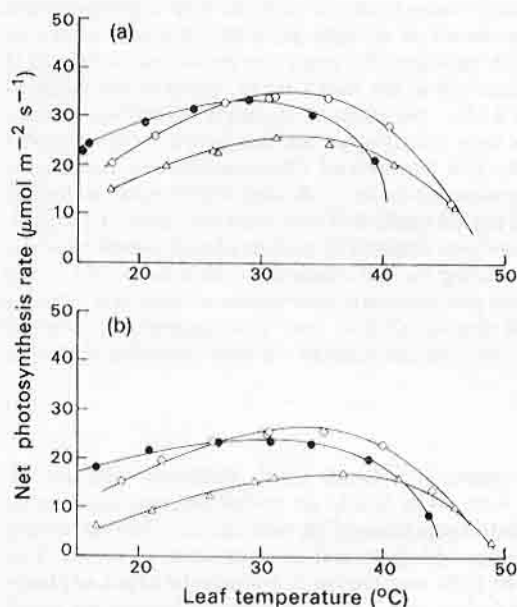


Fig. 1. Photosynthetic response to temperature by representative individuals of *Lupinus arizonicus* (a) and *Malvastrum rotundifolium* (b). ● 25/15°C thermoperiod. ○ 40/30°C thermoperiod. △ 40/30°C droughted thermoperiod. Ranges of response are given in Table 1 and other growth conditions are given in text.

Temperature optima shifted upwards approximately 4°C in *L. arizonicus* and 3.5°C in *M. rotundifolium*. The temperature at which photosynthesis reached half that of its maximum also shifted upwards with higher growth temperatures. This temperature was examined because it is considered to coincide with the temperature at which irreversible damage to the photosynthetic apparatus occurs, i.e. the thermal death point (Seemann *et al.* 1979; Berry and Björkman 1980). Photosynthetic rates were not significantly different between treatments except for the droughted plants, whose rates were significantly lower (droughted plants of *M. rotundifolium* had significantly lower photosynthetic rates at the 0.10 level). The differences between treatments in the lower and upper temperature ranges are reflected by the fact that the mean photosynthetic rate at 15°C of *L. arizonicus* grown at 25/15°C was 3.9 times that of the value for the plants grown at 40/30°C. However, the mean photosynthetic rate at 45°C was only 0.4 that of the plants grown at 40/30°C. This same

Table 1. Photosynthetic response to temperature by *Lupinus arizonicus* and *Malvastrum rotundifolium* when grown under different thermal regimes in growth chambers

Data presented are the mean values ± 1 s.e. Upper stable temperature limit is assumed to be the temperature at which the photosynthetic rate is one half of the value measured at the temperature optimum. Sample size was 4-6. Values in each column are significantly different at the 0.05 level if they are followed by different letters [*t*-test for the difference between means (Daniel 1977)]. The use of *x*, *y* and *z* in the *M. rotundifolium* data signifies that these values were not compared with the respective *L. arizonicus* values. The acclimation ratio of photosynthetic rate was obtained by dividing the photosynthetic rate at 25°C of the plants grown at 25/15°C by the photosynthetic rate at 40°C of the plants grown at 40/30°C

Treatment	Temperature optimum (°C)	Photosynthetic rate at optimum ($\mu\text{mol m}^{-2} \text{ s}^{-1}$)	Upper stable temperature limit (°C)	Photosynthetic rate at 15°C ($\mu\text{mol m}^{-2} \text{ s}^{-1}$)	Photosynthetic rate at 45°C ($\mu\text{mol m}^{-2} \text{ s}^{-1}$)	Photosynthetic rate acclimation ratio
<i>L. arizonicus</i>						
25/15°C	28.8±1.4 <i>a</i>	33.5±4.3 <i>a</i>	41.9±0.9 <i>a</i>	21.7±4.4 <i>a</i>	6.4±5.5 <i>a</i>	1.18
40/30°C	32.9±1.1 <i>b</i>	33.1±3.6 <i>a</i>	44.5±0.3 <i>b</i>	5.6±7.6 <i>b</i>	15.1±1.9 <i>b</i>	
40/30°C, drought	32.4±1.2 <i>b</i>	22.5±9.3 <i>b</i>	44.7±1.6 <i>b</i>	5.6±6.4 <i>b</i>	10.3±6.7 <i>ab</i>	
<i>M. rotundifolium</i>						
25/15°C	29.5±0.6 <i>a</i>	25.0±8.8 <i>x</i>	42.8±0.8 <i>a</i>	16.9±6.2 <i>x</i>	7.4±4.5 <i>x</i>	1.01
40/30°C	33.0±1.5 <i>bc</i>	27.2±8.4 <i>x</i>	46.7±2.1 <i>c</i>	9.2±3.2 <i>y</i>	16.7±7.4 <i>y</i>	
40/30°C drought	34.6±0.6 <i>c</i>	19.1±7.2 <i>x</i>	48.8±1.8 <i>c</i>	8.2±5.0 <i>y</i>	14.1±5.9 <i>xy</i>	

pattern is evident in *M. rotundifolium* where the plants grown at 25/15°C had a mean photosynthetic rate at 15°C that was 1.8 times that of the plants grown at 40/30°C and at 45°C 0.4 times. In all treatments, though, the absolute photosynthetic rates

Fig. 2

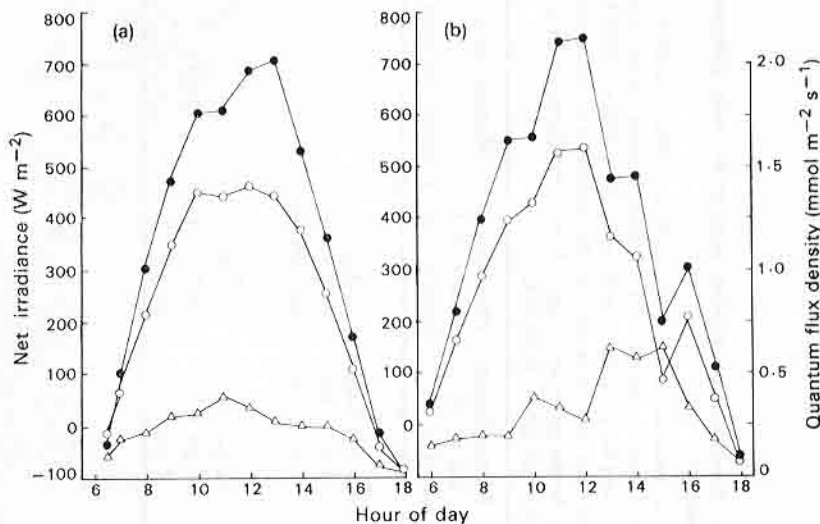


Fig. 3

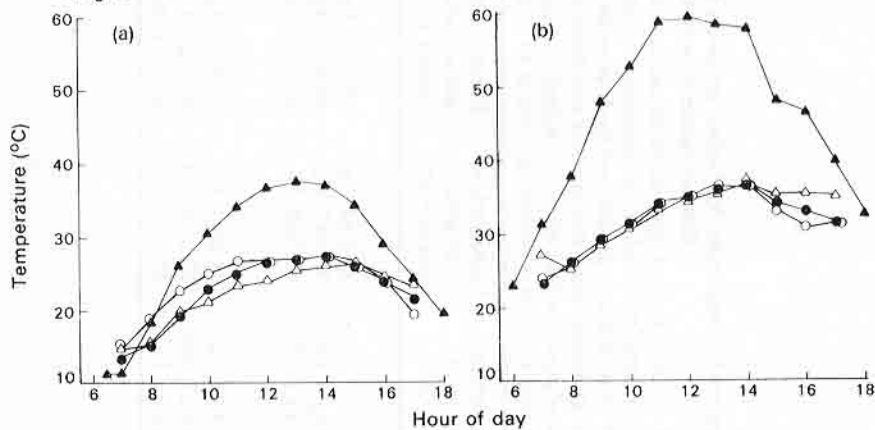


Fig. 2. Measured radiation regimes on a horizontal surface on 23 March 1979 (a) and 29 April 1979 (b) near Jubilee Pass, Death Valley. ● Quantum flux density. ○ Net irradiance. △ Diffuse quantum flux density.

Fig. 3. Measured temperatures on 23 March 1979 (a) and 29 April 1979 (b) near Jubilee Pass, Death Valley. ● *L. arizonicus* leaf temperature. ○ *M. rotundifolium* leaf temperature. △ Ambient temperature at leaf height. ▲ Soil-surface temperature.

were lower than have been measured under different growth regimes. Photosynthetic rates of well watered and fertilized *M. rotundifolium* and *L. arizonicus*, grown outdoors, can exceed $60 \mu\text{mol m}^{-2} \text{s}^{-1}$ and $50 \mu\text{mol m}^{-2} \text{s}^{-1}$, respectively. We attribute these reduced rates to the lower light levels in the growth chambers.

Droughted plants of *M. rotundifolium* undergo a greater upward shift in temperature optima than found in the well watered plants grown at 40/30°C. However,

since at all temperatures their photosynthetic rates were lower than the watered plants grown at 40/30°C, this shift would not be considered as true acclimation (Mooney 1980). Moreover, under comparable growth conditions, *M. rotundifolium* has a slightly higher thermal death point than *L. arizonicus*. This is especially evident under the 40/30°C growth treatment, where its mean extrapolated thermal death point is 2.2°C higher than that of *L. arizonicus*.

Microclimatology

Two days of microclimatic data, representative of mid- and late-season conditions, were used for productivity analysis. Mid-day leaf temperatures for these 2 days are quite similar to the ambient temperature regimes used in the growth-temperature experiments (Fig. 3). The microclimatological conditions at these times of the season were used to assess the potential daily carbon-gaining capacity of the photosynthetic characteristics measured in the different treatments. The solar radiation regime measured on each day is shown in Fig. 2. As is common in these desert regions, solar radiation levels are high, and most of the incident radiation is direct, not diffuse. The soil, leaf and air temperatures at plant height are presented in Fig. 3.

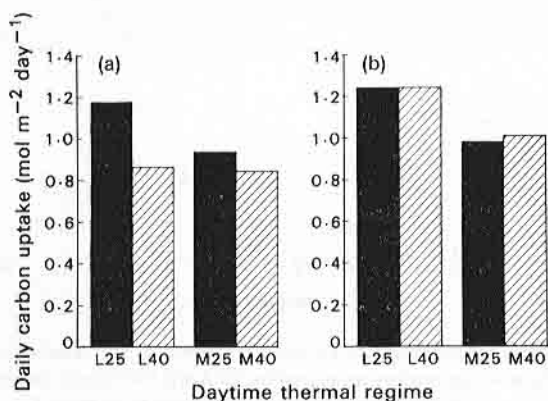


Fig. 4. Predicted daily carbon uptake due to temperature alone on 23 March 1979 (a) and 29 April 1979 (b), representative of mid- and late-season conditions experienced by winter annuals in Death Valley. L25, *L. arizonicus*, 25/15°C thermoperiod; L40, *L. arizonicus*, 40/30°C thermoperiod; M25, *M. rotundifolium*, 25/15°C thermoperiod; M40, *M. rotundifolium*, 40/30°C thermoperiod.

On 23 March, air temperature was within 2°C of 25°C (the daytime temperature of the 25/15°C growth regime) between 1100 and 1700 h; leaf temperatures of both *L. arizonicus* and *M. rotundifolium* were generally within 3°C of ambient temperatures throughout the day. Leaf temperatures of the two species were again very similar to each other and to air temperature on 29 April.

Using the measured leaf temperatures and the pooled data regressions of photosynthesis versus temperature, the hourly and daily rates of carbon uptake for both species on the 2 days were calculated (Fig. 4). The calculated differences in total daily carbon gain were large on 23 March, when the predicted daily carbon uptake of *L. arizonicus* and *M. rotundifolium* grown at 25/15°C was 36 and 11% higher

respectively than that of plants grown at 40/30°C. However, as a consequence of the wide temperature optima exhibited by both species, little differences in total daily carbon gain were calculated between treatments on 29 April: the plants grown at 40/30°C were predicted to have daily carbon uptake totals 0.2 and 2.9% greater than the plants grown at 25/15°C for *L. arizonicus* and *M. rotundifolium*, respectively. These results must be interpreted carefully because of the compounding effects that VPD, plant water potential and leaf conductance could exert upon the calculations. If water-stress effects could be ignored, the photosynthetic acclimation to growth temperature observed in experimental plants would play only a small role in enhancing carbon gain under the late-season conditions. But for conditions in March, it appears that the plants grown at 25/15°C would perform significantly better than plants acclimated to warmer growth conditions.

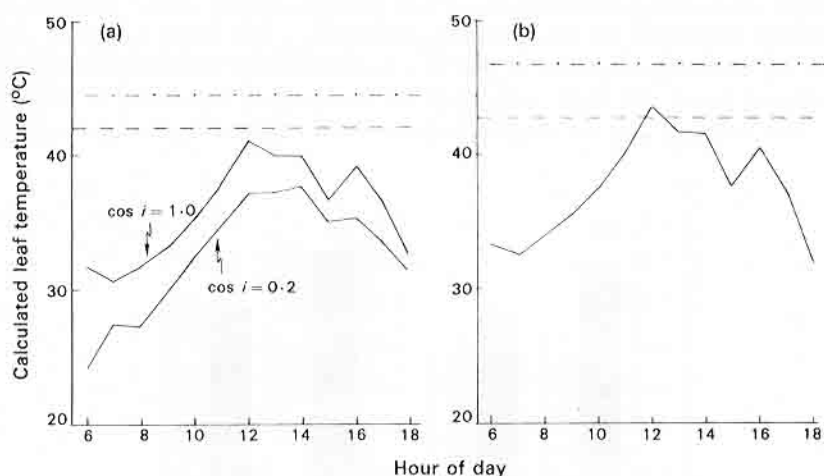


Fig. 5. Predicted leaf temperatures of *Lupinus arizonicus* (a) and *Malvastrum rotundifolium* (b) using microclimatic parameters measured on 29 April 1979 and a stomatal conductance of 0.5 mm s^{-1} . — — — Thermal death point of plants grown at 40/30°C. — · — Thermal death point of plants grown at 25/15°C.

Another important aspect of photosynthetic acclimation to temperature is that of the point at which irreversible damage occurs. In order to assess the importance of shifts in this parameter between treatments, an energy-budget model was used to calculate the leaf temperatures that would be experienced by plants undergoing drought stress. Droughted plants were assumed to have stomatal conductances to water loss of 0.5 mm s^{-1} . The leaf and climatic parameters used in the energy-budget model were those measured on 29 April 1979 and included leaf widths of 1 cm for *L. arizonicus* and 3 cm for *M. rotundifolium*, leaf absorptance (400–3000 nm) of 0.5 for both species, a water-vapour pressure of 0.8 kPa for 29 April, and wind speeds of $0.5\text{--}1.7 \text{ m s}^{-1}$.

Plants were experiencing high ambient temperatures and drought simultaneously under late-season conditions (29 April). At this time, the highest leaf temperature predicted for *M. rotundifolium* was 43.6°C (Fig. 5). This leaf temperature exceeds the thermal death point of the plants grown at 25/15°C but is 3°C below the temperature at which thermal damage occurs in plants grown at 40/30°C. Under these

late-season conditions, *L. arizonicus* grown at 25/15°C are also predicted to be very close to the thermal death point. The predicted maximum leaf temperature was 41.2°C and the thermal death point of plants grown at 25/15°C is 41.9°C. Again, the plants grown at 40/30°C would still be 2.6°C below the temperature at which thermal damage would occur. However, since *L. arizonicus* exhibits paraheliotropism under drought conditions, leaf temperatures should be less than 41.9°C. At a leaf conductance of 0.5 mm s⁻¹, leaves of *L. arizonicus* will have cupped so that the leaves will receive only 20% of the direct solar beam (Forseth and Ehleringer 1980). Using this value, the predicted leaf temperatures with stomatal closure on 29 April would be 37.6°C, well below the thermal death point of plants grown at 25/15°C or 40/30°C.

The mean standard deviation of the mean-maximum air temperature at three surrounding weather stations (Indio, Calif.; Barstow, Calif.; and Boulder City, Nevada) for April, May and June is 2.08°C (calculations based on United States Weather Bureau data). This variability would be extremely critical for unacclimated plants under late-season conditions. A shift of 2°C in the curves of Fig. 5 would result in plants grown at 25/15°C exceeding their thermal death point for several hours and would also raise predicted leaf temperatures to values very close to the thermal death point for plants grown at 40/30°C. The temperatures measured on 29 April 1979 were fairly mild for this time of season. The mean maximum air temperature for May at Furnace Creek, Death Valley is approximately 38°C (Furnace Creek Ranger Station records). At plant height, temperatures exceeding 40°C can be experienced anytime from mid-April on. This indicates that in wet years with flowering and seed set continuing into May and June, plants without the ability to acclimate would be quite likely to suffer thermal damage to their photosynthetic apparatus.

Discussion

Recent studies of photosynthetic acclimation in desert plants have indicated that many species are able to shift their photosynthetic temperature optimum and thermal death point in response to changes in growth temperatures (Lange *et al.* 1974; Pearcy 1977; Björkman *et al.* 1978; Mooney *et al.* 1978; Berry and Björkman 1980). The acclimation to high temperatures seems to involve changes in the composition of the thylakoid membrane resulting in increased heat stability of photosystem II activity, transfer of excitation energy from chlorophyll *b* to chlorophyll *a*, whole-chain electron transport, and non-cyclic photophosphorylation (Armond *et al.* 1978; Björkman *et al.* 1978; Berry and Björkman 1980; Björkman *et al.* 1980). Acclimation to high temperatures was found to occur with a concomitant decrease in photosynthetic performance at low temperatures. This result is supported by the results of this investigation in which the plants grown at 40/30°C had significantly lower photosynthetic rates at leaf temperatures below 20°C than those grown at 25/15°C. We have little information on the physiological basis for the acclimation responses, but we can conclude that CO₂ diffusion factors did not influence the results since stomatal conductance generally increased with temperature and internal CO₂ concentrations reached minimum values at the temperature optima for photosynthesis (data not presented).

In a survey of several annual species in Death Valley, conducted by Seeman *et al.* (1979, 1980), shifts of about 6–9°C were found in both photosynthetic temperature

optima and thermal stability. These shifts were found over seasonal, altitudinal and microsite gradients as well as in plants grown in a growth chamber (Downton *et al.* 1980). The extent of the temperature shift that these authors reported was not found in this study (3–6°C), but this could be because of the wider range of temperature used in their studies. This study supports the conclusion that temperature and not drought is the primary environmental stimulus for the changes in photosynthetic characteristics, since there were no significant differences in the photosynthetic responses to temperature between the droughted and the watered plants of both species grown at 40/30°C (Table 1).

One of the ways to examine the extent of acclimation to different growth temperatures is to look at the acclimation of the photosynthetic rate. This is the ratio between the photosynthetic rate at one growth temperature to the rate achieved at a different growth temperature (Mooney 1980). A ratio of 1.0 represents perfect acclimation of the rate. The results of rate acclimation in this study are presented in Table 1. The ratios for both species are very close to 1.0, indicating good acclimation of the photosynthetic rate. The value of 1.18 for *L. arizonicus* indicates that the plants performed slightly better under the 25/15°C treatment. Another means of examining acclimation is to look at the slope of the line obtained by plotting temperature optimum versus daytime growth temperature (Mooney 1980). Perfect adjustment would be represented by a slope of 1.0. Most studies have shown a slope between 0.3 and 0.4 (Billings *et al.* 1971; Percy 1977; Slatyer 1977). However, *Heliotropium curassavicum*, an herbaceous perennial from Death Valley, exhibited a slope of 0.65 (Mooney 1980). *L. arizonicus* and *M. rotundifolium* exhibited slopes of 0.27 and 0.23, respectively. These values are comparable to the lower range cited above.

Few studies have attempted to examine the impact of photosynthetic acclimation upon carbon uptake at various times during the season. A notable exception is the work of Lange *et al.* (1978), whose results indicated that plants which can change their photosynthetic responses to temperature do not always enhance their daily or seasonal carbon uptake. The results of this study also showed a very marginal increase in daily photosynthetic carbon gain due to temperature acclimation to higher temperature regimes (Fig. 4), although it appears that significant gains would be realized under mid-season conditions by the plants grown at 25/15°C.

An important component of the similarity in the predicted photosynthetic performances of the two desert annuals under the conditions on 29 April was the broad nature of the photosynthetic response to temperature. This seems to be a common feature of all desert winter annuals examined thus far. In fact, photosynthetic rates exceeding 90% of maximum occur over temperature ranges of 12–16°C (Ehleringer *et al.* 1979; Monson and Szarek 1979; Seemann *et al.* 1979). This could be an important aspect of the performance of desert annuals in their native habitat. Since a wide range of temperatures results in high photosynthetic rates, the importance of a high degree of plasticity in acclimation abilities would be diminished.

The lengths of the growing seasons of desert winter annuals are very variable, ranging from 8 weeks to as long as 6 months (Beatley 1974; Mulroy and Rundel 1977). The physiological ability to shift thermal death point with rising ambient temperatures is probably most important during those years when high availability of soil water extends growth into the very warm months of May and June. This property of life extension could be an important determinant of the life span under

these conditions and may influence an individuals' reproductive output by lengthening the period available for seed filling. Another important facet of this property is the benefit to plants in poorer microsites. The desert habitat is quite variable, and spatial heterogeneities can result in quite different water regimes. This, in turn, can result in substantially different leaf temperatures between plants of the same population. The ability to withstand higher leaf temperatures may extend the life of these plants growing in poorer microsites.

In summary, the results of this study indicate that both *L. arizonicus* and *M. rotundifolium* possess the ability to adjust their photosynthetic responses to temperature in concert with changes in growth temperature. This ability is predicted to result in increased carbon gain for plants acclimated to a 25/15°C thermoperiod under mid-season conditions when compared to plants grown under higher temperatures. However, due to the ability of these plants to maintain high photosynthetic rates over a very broad temperature range, the acclimation to higher temperatures does not result in significant increases in carbon gain over plants acclimated to lower temperature for the late-season conditions examined in this study. Perhaps most important is the prediction that plants acclimated to warm conditions are better able to avoid thermal damage under late-season conditions of low water availability and high ambient temperatures. We feel that this broad photosynthetic response to temperature along with the shift upwards in thermal death point are important components of the photosynthetic adaptation of desert winter annuals to their environment.

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