Ecophysiology of two solar tracking desert winter annuals

III. Gas exchange responses to light, CO$_2$ and VPD in relation to long-term drought

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Summary. The gas exchange responses of potted, outdoor and greenhouse grown plants of the Sonoran Desert annuals *Lupinus arizonicus* (Wats.) and *Malvastrum rotundifolium* (Gray) were examined. Light saturation of leaf photosynthetic rates did not occur in either species at quantum flux densities exceeding 2.0 mmol m^{-2} s^{-1}. Decreasing water potentials due to long-term drought did not alter this pattern of light response, though it did lower both photosynthetic rates and leaf conductances. Absolute maximum net photosynthetic rates exceeded 60 µmol m^{-2} s^{-1} and 50 µmol m^{-2} s^{-1} for *M. rotundifolium* and *L. arizonicus*, respectively. Both species showed a two level control of leaf conductance, responding to bulk leaf water potential and vapor pressure deficit. There were non-stomatal effects of drought upon photosynthesis in each species. Leaves of *M. rotundifolium* exhibited a constant stomatal inhibition of approximately 19%, while in leaves of *L. arizonicus* stomatal inhibition ranged from 12–40% with decreasing leaf water potentials. These physiological data lend support to previous reports on the divergent water use patterns of these co-occurring species.

Introduction

Recent work on warm desert ephemerals has shown that this life form possesses a variety of potential adaptations to its physical environment. These include high degrees of developmental plasticity (Beatley 1974; Mulroy and Rundel 1977), high photosynthetic rates (Mooney et al. 1976; Seemann et al. 1980b), photosynthetic temperature acclimation (Seemann et al. 1980a; Forseth and Ehleringer 1982a), osmotic adjustment (Seemann et al. 1979; Forseth and Ehleringer 1982b) and heliotropic leaf movements (Wainwright 1977; Mooney and Ehleringer 1978; Ehleringer and Forseth 1980; Forseth and Ehleringer 1980, 1982b). Included in this list are properties that enhance the plant's ability to extend the period of carbon gain and plant life into the drought periods that occur at the end of the season.

The first paper in this series reported on the ability of the two study species, *Lupinus arizonicus* (Wats) and *Malvastrum rotundifolium* (Gray) to acclimate their photosynthetic response to growth temperature (Forseth and Ehleringer 1982a). The second paper of the series dealt with field studies on the plants' leaf movements (especially in relation to drought), seasonal patterns of diurnal microclimate and water relations, and the osmotic adjustment capabilities of the plants (Forseth and Ehleringer 1982b). This paper examines leaf gas exchange in response to the environmental parameters of light, humidity, CO$_2$ and long-term drought.

Leaf solar tracking (diaheliotropism) is a widespread phenomenon in the desert annuals of the southwestern United States (Ehleringer and Forseth 1980). But as pointed out by these authors there is little known about the physiological properties of these annuals. Without this data, little can be specified about the carbon gain and water loss ramifications of these leaf movements. Analysis and/or predictions of how leaf movements should or should not be varied by drought cannot be made. The experiments reported in this study were conducted in order to provide this basic information. Since both species have the ability to track the sun with their leaves, we hypothesized that they should have the physiological ability to utilize the high solar irradiances this property confers. Accordingly, the photosynthetic response to light was examined. Next, since transpiration peaks in the field were not concurrent with peaks in atmospheric evaporative demand (Forseth and Ehleringer 1982b), the response of leaf conductance and photosynthesis to vapor pressure deficit (VPD) was examined. Many desert species have a VPD response and this is hypothesized as conferring adaptive benefits to these plants (Lange et al. 1971; Schulze et al. 1972; Sheriff 1977; Lösch 1979; Schulze and Küppers 1979). Finally, bulk leaf water potential is a major factor in the leaf conductance and leaf movement patterns of these plants (Forseth and Ehleringer 1980, 1982b). We conducted all experiments with light and VPD at a variety of water potentials in order to determine its effects upon the photosynthetic characteristics of the plants. We also performed experiments at a variety of CO$_2$ levels in order to separate water potential effects on intrinsic photosynthetic capacity from effects caused by stomatal limitations to CO$_2$ diffusion.

Materials and methods

Growth conditions and experimental material have been described (Forseth and Ehleringer 1982a, b). Osmotic potentials, photosynthetic responses, and conductance re-

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sponses to drought of potted outdoor versus potted growth chamber grown *L. arizonicus* plants do not differ. The results reported here for *L. arizonicus* are from the same plants utilized in the temperature acclimation studies (Forseth and Ehleringer 1982a). These consisted of 10 droughted and 10 control plants grown in a growth chamber and droughted by lowering the watering regime by 1/2 for experimental plants. *M. rotundifolium* differed in the extent of osmotic adjustment between potted outdoor and potted greenhouse grown plants. The plants utilized for these experiments were grown outdoors and achieved osmotic potential values similar to those measured in field studies. There were eight control and 10 droughted plants. Drought was imposed over a 5 week period (Forseth and Ehleringer 1982b).

Gas exchange measurements were performed following the techniques outlined in Forseth and Ehleringer (1982a). Only the youngest, fully expanded leaves were used. All photosynthetic and conductance values were derived from flow rates, humidities, and CO_2 concentrations corrected for temperature, altitude and water concentration differences. All measurements of gas exchange were performed at a leaf temperature of $30 \pm 0.5°$ C and 21% O_2. Photosynthetic responses to light were examined at CO_2 levels of 330 ± 15 µl l^{-1} and VPD levels below 10 mPa Pa^{-1}. Light levels started above 1.8 mmol m^{-2} s^{-1}, with stepwise decreases in light levels accomplished using neutral density filters. Data were recorded after a 20–30 minute equilibrium period at steady photosynthetic and leaf conductance levels. This was standard procedure for all the gas exchange response curves reported. Leaf conductance and photosynthetic responses to vapor pressure deficit were examined at light levels above 1.8 mmol m^{-2} s^{-1} and CO_2 levels of 330 ± 15 µl l^{-1}. VPD values were started below 10 mPa Pa^{-1} and increased stepwise through the use of a dry air shunt. Photosynthetic responses to carbon dioxide concentration were examined at light levels exceeding 1.8 mmol m^{-2} s^{-1} and VPD levels below 10 mPa Pa^{-1}. Measurements started at ambient CO_2 levels of 330 µl l^{-1} followed by stepwise decreases of 50–100 µl l^{-1}. After measurements at 80–100 µl l^{-1} ambient CO_2 levels, the leaf was brought back up to 330 µl l^{-1} ambient levels, allowed to equilibrate, and then exposed to higher concentrations of up to 1,000 µl l^{-1} CO_2. CO_2 concentrations in the intercellular spaces were calculated using an Ohm's Law analogy equation.

Water potentials of the leaf used in the photosynthetic measurements were taken immediately after removal from the chamber. Therefore, no leaf was used for more than one set of photosynthetic response curves. These sets usually consisted of an examination of photosynthetic response to CO_2 levels followed by either an examination of the photosynthetic response to light or VPD. Water potentials of neighboring leaves were measured periodically to see if gradients existed between them and the experimental leaf. These measurements were conducted with a Scholander type pressure bomb (PMS Instruments Inc.) (Scholander et al. 1965).

Results

Both species have very high net photosynthetic rates. Leaves of *M. rotundifolium* had rates exceeding 60 µmol m^{-2} s^{-1} and leaves of *L. arizonicus* approached levels of 50 µmol m^{-2} s^{-1}. The leaves of both species did not exhibit
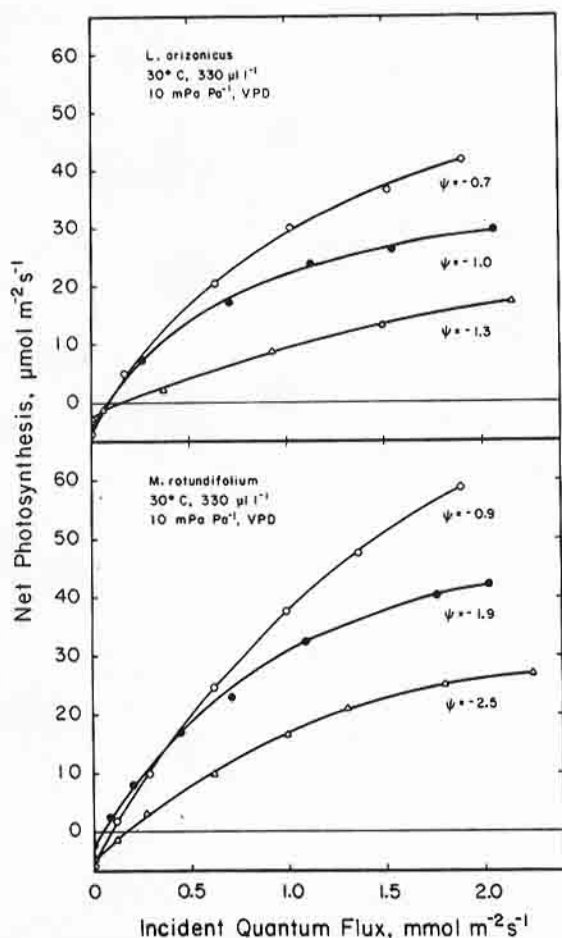

Fig. 1. Photosynthetic response to incident quantum flux density for three representative individuals of *L. arizonicus* and *M. rotundifolium*

light saturation of photosynthetic rates up to levels of incident quantum flux exceeding 2.0 mmol m^{-2} s^{-1} (Fig. 1). Although decreasing leaf water potentials reduced the maximum photosynthetic rate attained, they did not alter the light saturation characteristics of the plants (Fig. 1). It appeared that the positive portion of the photosynthetic light response curve was displaced to lower photosynthetic levels by increasing drought stress.

The effect of decreasing leaf water potentials upon net photosynthesis at high irradiance resulted in a linear relationship between the two parameters (Fig. 2). *M. rotundifolium* had a very drought tolerant physiology, maintaining positive net photosynthesis at leaf water potentials more than twice as negative as observed in *L. arizonicus*. This photosynthetic-drought response is quite similar to the leaf conductance-drought relationship reported in Forseth and Ehleringer (1982b).

For leaves of *M. rotundifolium*, both the maximum attainable photosynthetic rate at high CO_2 concentrations and the initial slope of the CO_2-photosynthesis relationship at low CO_2 levels declined with decreasing leaf water potentials (Fig. 3). In leaves of *L. arizonicus* the maximum photosynthetic rate at high CO_2 concentrations was affected more by leaf water potentials than was the initial slope of the CO_2-photosynthesis relationship (Fig. 3).

The contribution of leaf conductance to the reduction in photosynthetic rate with decreasing leaf water potentials
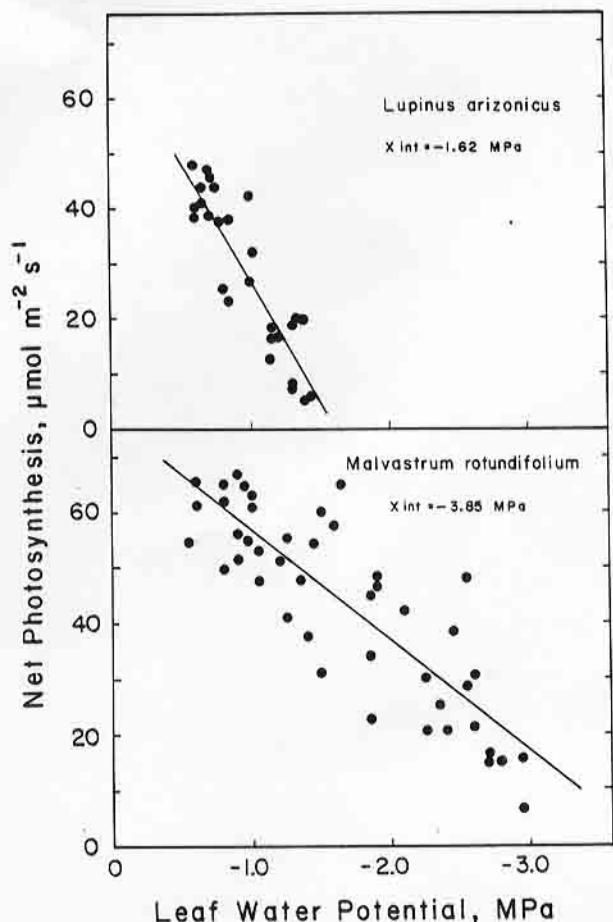
Fig. 2. Response of net photosynthesis to long-term drought in *L. arizonicus* and *M. rotundifolium*. Points were taken at light levels exceeding 1.8 mmol m^{-2} s^{-1}, 30° C leaf temperature, 330 ± 15 µl l^{-1} ambient CO_2 levels, 21% O_2 and VPDs below 10 mPa Pa^{-1}
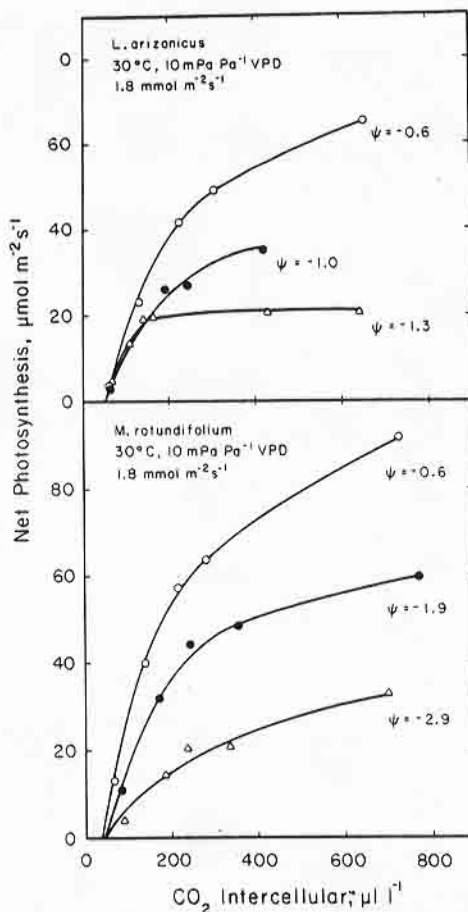
Fig. 3. Response of net photosynthesis to $CO_{2 int}$ concentrations for three representative individuals of *L. arizonicus* and *M. rotundifolium*

can be derived from the curves in Fig. 3, using the method of Farquhar and Sharkey (1982). In leaves of *L. arizonicus*, the value of intercellular CO_2 concentration ($CO_{2 int}$) varies with bulk leaf water potential (Fig. 4). We included this in the calculation of stomatal limitation. Leaves of *M. rotundifolium* maintained constant $CO_{2 int}$ concentrations (Fig. 4), and a virtually constant value of stomatal limitation to photosynthesis of approximately 19%. In leaves of *L. arizonicus*, the proportion of stomatal limitation to photosynthesis showed a tendency to increase as water deficits increased (Fig. 5). These data were not significant at the 5% level of confidence.

Both species had very strong photosynthetic and leaf conductance responses to VPD (Figs. 6, 7). These responses were influenced by leaf water potential. Maximum photosynthetic and leaf conductance values were determined by leaf water potential, with VPD exerting its influence in addition to this factor. The response of leaf conductance to VPD resulted in reduced transpirational water losses relative to that which would have occurred without a leaf conductance response (Fig. 8). In six out of eleven VPD response curves conducted on *L. arizonicus*, transpiration temporarily decreased with a step increase in VPD. Six out of twenty-one VPD curves with leaves of *M. rotundifolium* showed this same response. The decrease was not permanent and usually transpiration increased with the next increment in VPD.

The response of photosynthesis to VPD could not be completely explained by the leaf conductance response. Intercellular CO_2 concentrations do not change sufficiently to account for all of the response, and often the change is in the opposite direction to one that would reduce photosynthesis (Fig. 9). We examined this response further with an additional five *M. rotundifolium* plants grown in a greenhouse with supplemental H.I.D. lamp lighting. The plants were grown from seed in large (25 cm dia.) volume pots and achieved photosynthetic rates comparable to outdoor grown plants. The response was analyzed by examining the response of photosynthesis to CO_2 concentration at various VPD levels. The results indicated that there was a nonstomatal effect of VPD upon photosynthesis (Fig. 10). All five plants used showed the same response (Fig. 10). When VPD levels were returned to 10 mPa Pa^{-1} from higher values, photosynthetic rates recovered to only 85% of original values after a two hour period, although stomatal values had recovered 100% by this time.

Discussion

The bulk of the data on photosynthetic characteristics of desert ephemerals has not dealt with the effects of drought upon photosynthesis (Mooney et al. 1976; Mooney and Ehleringer 1978; Ehleringer et al. 1979; Monson and Szarek 1979; Pavlik 1980; Seemann et al. 1980b). Studies that have
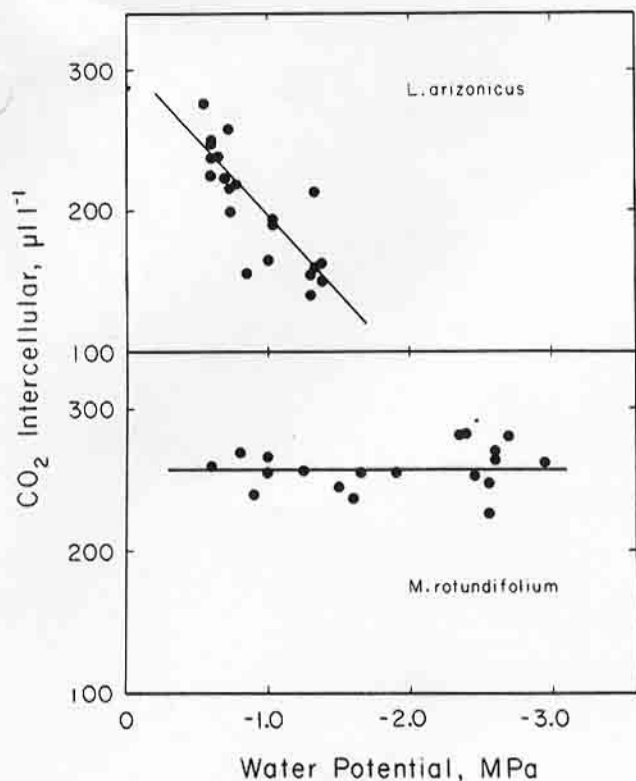
Fig. 4. $CO_{2\,int}$ concentrations calculated for a range of water potentials. Conditions under which measurements were made were; incident quantum flux exceeding 1.8 mmol m^{-2} s^{-1}, 30° C leaf temperature, 330±15 µl l^{-1} ambient CO_2 concentrations, 21% O_2 and VPDs below 10 mPa Pa^{-1}. Equation for *L. arizonicus* is $y = 110.7\,x + 304.8\ r^2 = 0.67$

Fig. 6. Response of leaf conductance to VPD for three representative individuals of *L. arizonicus* and *M. rotundifolium* at three different water potentials
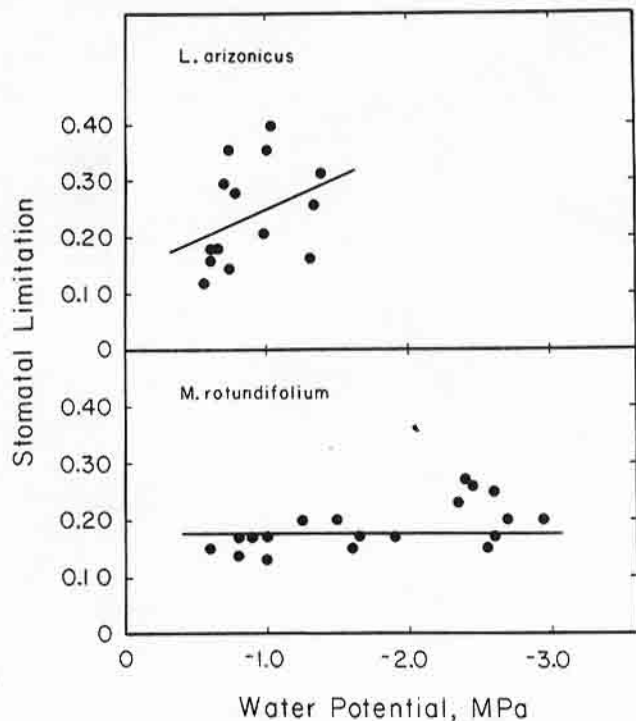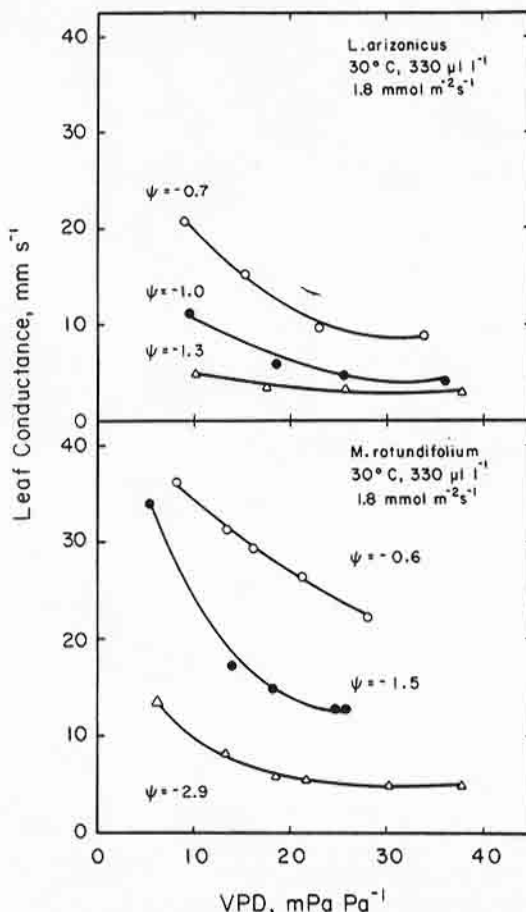

Fig. 5. Proportion of stomatal limitation to net photosynthesis as determined from the CO_2 response curves of *L. arizonicus* and *M. rotundifolium*. Regression for *L. arizonicus* is $y = -0.11\,x + 0.14$ $r^2 = 0.13$

looked at lowered leaf water potentials include a field study by Wallace and Szarek (1981), temperature acclimation studies (Seemann et al. 1980a; Forseth and Ehleringer 1982a) and an examination of photosynthetic response to CO_2 concentration (Mooney 1980). Our data represent the most extensive studies documenting responses to factors such as CO_2, VPD and long-term drought. Work conducted so far has shown that the desert ephemeral life form has the highest reported photosynthetic rates for the C_3 photosynthetic pathway (Mooney et al. 1976; Seemann et al. 1980b). Our data support this finding for plants grown under unlimited nutrient, light and water regimes.

The lack of a saturation point in photosynthetic light response curves has been reported in other desert annuals, desert perennials, and early successional ephemerals of sunny habitats (Wieland and Bazzaz 1975; Mooney et al. 1976; Ehleringer and Bjorkman 1978). This is an important point, especially for diaheliotropic species. It allows them to exploit the higher irradiances consequent from their leaf movements for carbon gain. Long-term drought did not result in photosaturation (Fig. 1). As pointed out in Forseth and Ehleringer (1982b) this is significant in view of the continued diaheliotropic leaf movements *M. rotundifolium* exhibits with reduced leaf water potentials.

Many plants have been found to have reduced photosynthetic rates associated with decreasing leaf water potentials (Hsiao 1973; Odening et al. 1974; Wieland and Bazzaz 1975; Szarek and Woodhouse 1976, 1978; Bunce et al.
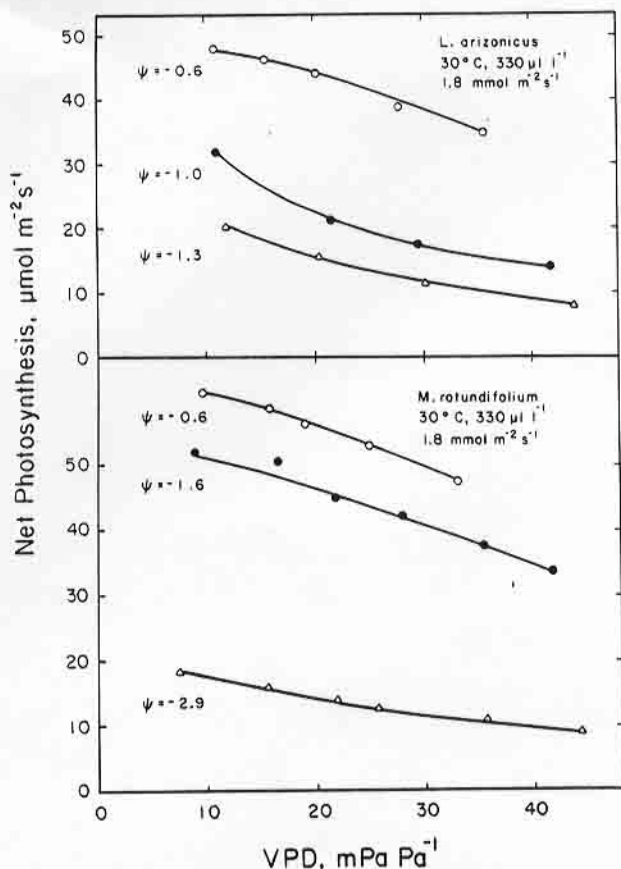
Fig. 7. Response of net photosynthesis to VPD for three representative individuals of *L. arizonicus* and *M. rotundifolium* at three different water potentials

Fig. 8. Response of transpiration to VPD for three representative individuals of *L. arizonicus* and *M. rotundifolium* at three different water potentials

Fig. 9. Calculated $CO_{2\,int}$ concentrations plotted vs VPD for the same individuals as in Fig. 7

1979; Osmond et al. 1980). Differences in this response have been used to explain differences in distribution (Bunce et al. 1979) and life history characteristics (Odening et al. 1974; Szarek and Woodhouse 1976, 1978). The results here were interesting in that such a large difference existed between the species in their drought tolerance (Fig. 2). Differences in drought tolerance of this magnitude are usually not found in species of the same life history (Wieland and Bazzaz 1975). But they are present in different life histories such as desert drought deciduous vs desert evergreen perennial species (Odening et al. 1974; Szarek and Woodhouse 1976, 1978). It would appear that the life history of desert ephemerals has representatives spanning a range of photosynthetic sensitivity to drought from the most drought intolerant, mesophytic ephemerals to drought tolerant perennials such as *Encelia farinosa* (Odening et al. 1974; Wieland and Bazzaz 1975; Szarek and Woodhouse 1976, 1978; Bunce et al. 1979).

The results indicated a direct effect of long-term drought upon intrinsic photosynthetic capacity (Fig. 3). Investigations on agricultural as well as native species have shown that both stomatal and non-stomatal effects of long-term drought on photosynthesis are common (Boyer 1971; Hsiao 1973; Plaut and Bravdo 1973; Lawlor 1976; Collatz 1977; Mooney et al. 1977; O'Toole et al. 1977; Mooney 1979; Bjorkman et al. 1980; Osmond et al. 1980). In *Larrea divaricata*, an evergreen perennial of the southwestern deserts of the United States, the stomatal vs non-stomatal limitations to photosynthesis caused by drought are similar to those observed in *M. rotundifolium* (Mooney et al. 1977).
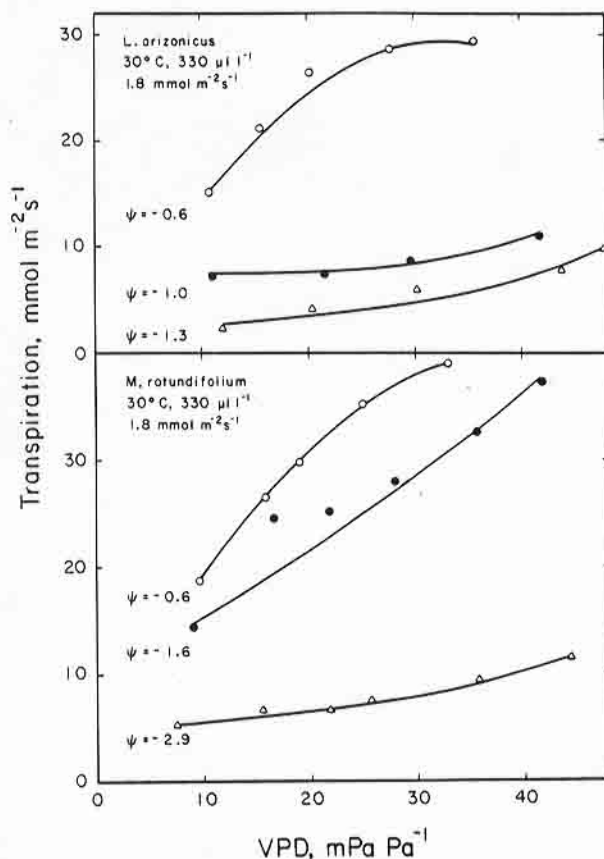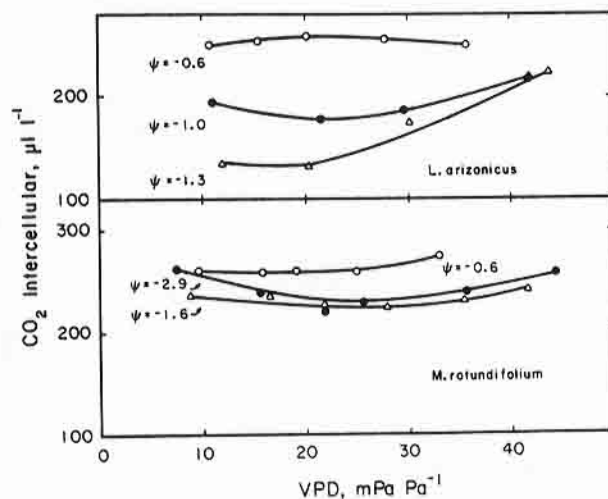
The photosynthetic response to CO_2 concentration at different leaf water potentials in *Camissonia brevipes* was very similar to that of *L. arizonicus* (Mooney 1980). An interesting corollary to this is the pattern observed in $CO_{2\,int}$ concentrations under ambient CO_2 conditions of 330 µl l^{-1} (Fig. 4). Wong et al. (1979) reported that in a number of species under a variety of treatments a constant $CO_{2\,int}$ concentration was maintained. This implied a tight coupling
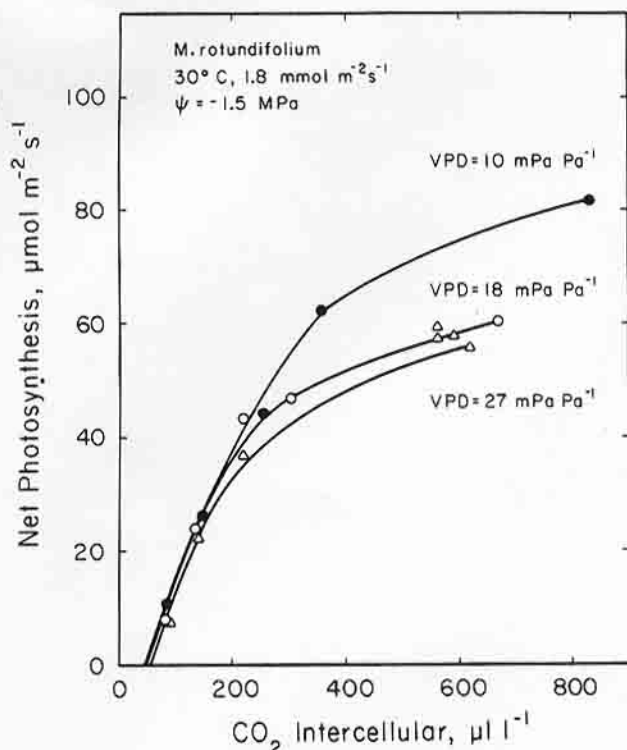
Fig. 10. Response of an individual *M. rotundifolium* leaf net photosynthesis to $CO_{2\,int}$ concentration at three different VPD levels

of stomatal functions and photosynthetic capacity. *L. arizonicus* did not hold $CO_{2\,int}$ concentrations constant. But there appeared to be a correlation between $CO_{2\,int}$ concentrations under ambient conditions of 330 μl l⁻¹ CO_2, and the break point of the photosynthetic response curve to CO_2 (Figs. 3, 4).

The pattern of drought-response shown by *L. arizonicus* is indicative of a conservative water use pattern. Along with its paraheliotropic leaf movements (Forseth and Ehleringer 1980), lowered $CO_{2\,int}$ concentrations would reduce water loss under drought and high evaporative demand conditions in relation to a constant $CO_{2\,int}$ level. In contrast, the pattern in *M. rotundifolium* of continued diaheliotropic leaf movements, osmotic adjustment (Forseth and Ehleringer 1982b), constant $CO_{2\,int}$ concentrations and constant stomatal limitations represent a pattern of much higher water use under equal conditions.

As many as 70 species including C_3, C_4 and CAM representatives are now reported to have stomatal responses to VPD (Lange et al. 1971; Schulze et al. 1972; Aston 1973; Hall and Hoffman 1976; Hall et al. 1976; Sheriff 1977; Lange and Medina 1979; Pallardy and Kozlowski 1979; Schulze and Küppers 1979; Tibbitts 1979; Hall and Schulze 1980; Lösch and Tenhunen 1981). This property is hypothesized to be a major adaptive pattern for plants exposed to arid conditions, both in terms of water use efficiency and survival (Hall et al. 1976; Ludlow 1980). In addition, it is thought that a two-stage control involving bulk leaf water potential (as determined by long-term drought effects) and VPD determines leaf conductance responses to ambient conditions (Fig. 6) (Lösch 1979; Ludlow and Ibaroki 1979; Schulze and Küppers 1979; Hall and Schulze 1980; Osonubi and Davies 1980). VPD determines the value of leaf conductance within a range set by leaf water poten-

tial. Both species in this study showed this two stage control over leaf conductance (Fig. 6).

The response of photosynthesis to VPD was quite pronounced (Fig. 7). There is a great range of responses in the literature ranging from small decreases (Schulze et al. 1972; Osmond et al. 1980; Osonubi and Davies 1980) to a reduction of over 50% over a 30 mPa Pa⁻¹ VPD range (Schulze et al. 1972; Aston 1973; Schulze and Küppers 1979). The reductions were explained through stomatal closure and reduction of $CO_{2\,int}$ concentrations, although $CO_{2\,int}$ values were usually not reported. It is generally accepted that VPD levels do not have a direct effect upon photosynthesis (Schulze et al. 1975; Rawson et al. 1977; Tibbitts 1979). Our data indicated that there were combined stomatal and non-stomatal effects of VPD upon photosynthesis (Figs. 9, 10). We do not know a mechanism for the non-stomatal effect. It may be explained by localized water potential depressions in the leaf being examined, which could not be discerned using bulk leaf water potential measurements. Differences in leaf water potential of 0.1 to 0.3 MPa were measured between experimental leaves and neighboring leaves on the same stem two to three times during the course of the experiments. Since these plants have such high photosynthetic rates, large changes in leaf conductance and CO_2 concentration would be needed to explain the reductions in photosynthesis with VPD. Plants in the literature with such high photosynthetic rates have not been examined for VPD responses. Further investigation with larger sample sizes and more species are needed before definitive statements can be made about this phenomenon.

Although many species have been reported as possessing stomatal responses to VPD, the consequence for transpiration varies. Leaves of species such as *Corylus avellana* L. were able to reduce transpiration levels at higher VPDs (Schulze and Küppers 1979), while sunflower displayed a linear relation of transpiration to VPD (Aston 1973). Our test plants showed a response intermediate between sunflower and *Betula pendula* Roth (Osonubi and Davies 1980). Some curves were linear or steadily increasing, while others showed depressions in transpiration in mid-ranges of VPD followed by an increase at more extreme VPD levels (Fig. 9). However, transpiration rates were reduced below those rates that would have occurred without a stomatal response.

In summary, these species possessed very high photosynthetic capacities. The magnitude of the photosynthetic light response was reduced but not qualitatively changed by exposure to long-term drought. This is very important in leaves of diaheliotropic species, especially *M. rotundifolium*, which maintains leaf movements to the wilting point of the leaf. Despite low leaf water potentials, *M. rotundifolium* is able to exploit enhanced radiation levels for carbon gain purposes. This, combined with the morphological and physiological properties outlined in earlier papers of this series show a complex and varied combination of potential adaptations in the desert ephemeral life form. The two species investigated represent two opposite ends of a spectrum of water use. *L. arizonicus* is very conservative, reducing water loss through stomatal and morphological mechanisms. It is a drought evader, maintaining high leaf water potentials as drought increases. *M. rotundifolium* represents a pattern of greater water use. While it does have stomatal responses reducing water loss, it also displays leaf move-

ments and osmotic adjustment patterns that result in high water losses. It is a drought tolerant morpho-physiological type.

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