

## Summer Water Relations of the Desert Phreatophyte *Prosopis glandulosa* in the Sonoran Desert of Southern California \*

Erik T. Nilsen, Philip W. Rundel, and M. Rasoul Sharifi

Department of Ecology and Evolutionary Biology, University of California, Irvine, CA 92717 USA

**Summary.** *Prosopis* is a genus of phreatophytic trees inhabiting hot deserts and semiarid grasslands of the world. Although desert trees are exposed to unusual environmental temperature and water stress, few investigations have evaluated their water relations. This is particularly true for *Prosopis* species growing in areas where a large portion of their water use comes from ground water.

Water relations components for *Prosopis glandulosa* were studied at Harper's Well, near the Salton Sea, California during the summer months of 1980. Maximum temperatures (49° C), irradiance (2,000  $\mu\text{E}/\text{m}^2/\text{sec}$ ), and vapor pressure deficit (5.3 kPa) were reached in July. During this time *Prosopis glandulosa* pre-dawn xylem pressure potentials were below -3.0 MPa. *Prosopis glandulosa* at Harper's Well is able to maintain open stomata during high temperatures, high vapor pressure deficit and at low estimated turgor pressure. Leaf resistance measurements indicate that stomata are open primarily in the morning, but may reopen in the afternoon in trees with greater water resources. Osmotic potentials of juvenile shoots were higher (-1.0 to -2.5 MPa) than mature shoots (-3.5 MPa). Estimated turgor potential remained low (0.1-0.2 MPa) during the morning and early afternoon. Estimated turgor pressure increased from August to September as temperatures and vapor pressure deficit decreased. Leaf conductance was strongly associated with leaf vapor pressure deficit and estimated turgor potential but poorly associated with xylem pressure potential. *Prosopis* stomata seem to be uncoupled from tissue water potential until -4.8 MPa is reached.

in northern Chile by use of ground water alone (Mooney et al. 1980).

Although the ability to tap permanent or semi-permanent ground water supplies would be expected to minimize any potential physiological drought stress for desert phreatophytes, relatively low summer water potentials have been described for *Prosopis*. These water potentials may be as low at dawn as nearby xerophytes such as *Larrea tridentata* with far shallower roots (Strain 1970; Mooney et al. 1975). These few data in the literature are difficult to interpret and point out our poor understanding of the water relations of phreatophytic species.

In this paper we report on field investigations of the summer water relations of *Prosopis glandulosa* in the Sonoran desert of California. We describe patterns of diurnal cycles of leaf conductance and water potential over the peak yearly stress period from July through September at our study site near the Salton Sea. We also consider the relationship of leaf conductance to environmental stress of different types. Finally, we discuss the adaptive mechanisms of summer water relations in desert phreatophytes compared to those of other desert life forms.

### Methods and Materials

On July 15, August 26, and September 17, 1980, diurnal cycles of microclimatic conditions and water relations of *Prosopis glandulosa* were measured at Harper's Well, near the Salton Sea in the Sonoran Desert of California. This site has been previously described in some detail by Sharifi et al. (in press). Air temperature, soil temperature, leaf temperature, vapor pressure deficit, and wind speed were measured from before dawn to after sunset. Photosynthetically active radiation (PAR) was also measured over the diurnal cycle at each date using a LICOR quantum sensor. Separate measurements were recorded at maximum PAR (sensor perpendicular to sun's rays), at the angle of the leaves, and at the dawn leaf angle. Along with these microclimatic measurements, diurnal cycles of xylem pressure potential (XPP) were measured on two representative trees with the use of a pressure chamber (Ritchie and Hinckley 1975). Five replicate XPP measurements were taken for each tree from different compass directions each hour. Leaf conductance (k) was measured with a LICOR Model 1600 steady state porometer during diurnal cycles for two representative trees. Leaf relative saturation deficit (RSD) =  $[(\text{Turgid weight} - \text{fresh weight}) \div (\text{Turgid weight} - \text{dry weight}) \times 100]$  was also measured for two trees during the diurnal cycles in August and September. Leaves were collected each hour and placed in sealed containers on ice until fresh weights could be measured in the laboratory. The leaves were then saturated for 24 h, reweighed and dried at 70° C for 48 h to obtain dry weight. Three replicate RSD samples were measured for each tree at each time period. The RSD, leaf resistance, and XPP of the two intensively monitored trees were compared to those of three other trees periodically throughout this investigation. Also, the

### Introduction

Desert phreatophytes, in particular the genus *Prosopis* (Mimosaceae), have long been known for their remarkable adaptations to desert environments. One of the most interesting of these adaptations is the presence of deep tap roots which are able to utilize underground water unavailable to other plants. Roots of one *Prosopis* species in Arizona have been reported as deep as 60 m below the soil surface (Phillips 1963). While there are some desert environments with sufficient summer rainfall to provide adequate surface soil moisture for *Prosopis* to survive without permanent ground water (Cable 1977), under more arid conditions *Prosopis* is restricted to areas with available ground water supplies. *Prosopis tamarugo* survives, for example, in the virtually rainless Pampa del Tamarugal of the Atacama desert

\* Dedicated to Dr. Konrad Springer and Professor Michael Evenari

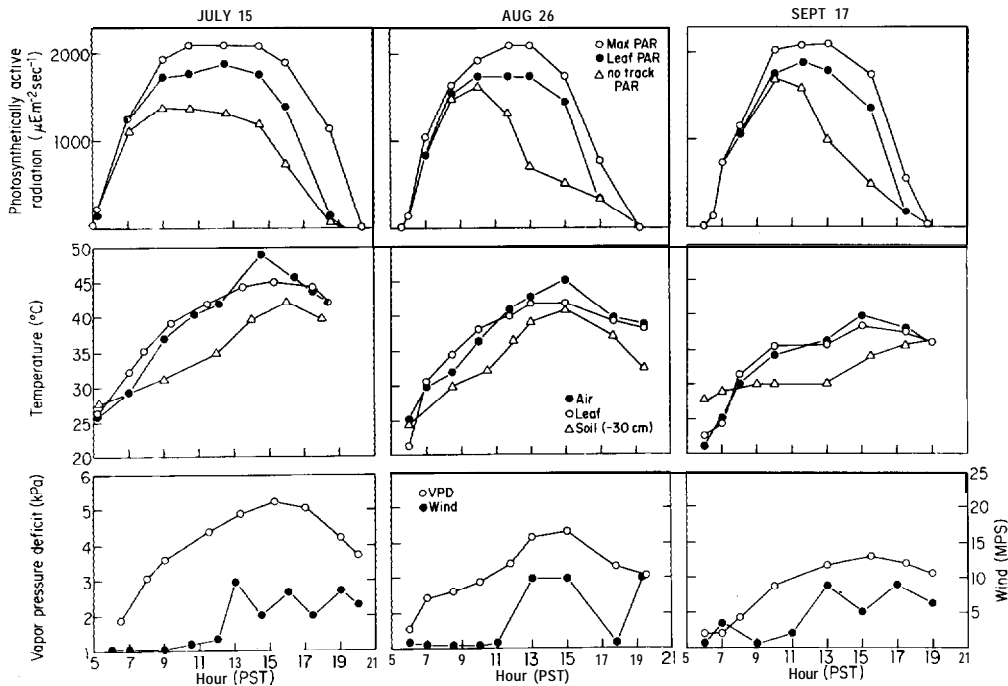


Fig. 1. Diurnal microclimatic conditions at Harper's Well during July, August and September 1980

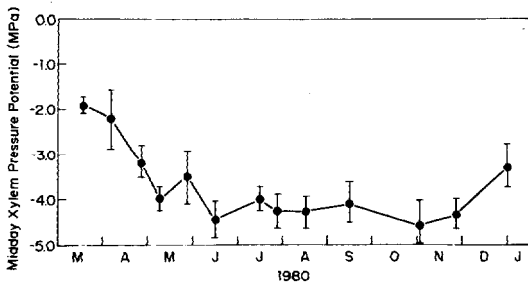


Fig. 2. Seasonal midday xylem pressure potentials for *Prosopis glandulosa* at Harper's Well during 1980. Values are means of 4-5 branches from each of five sample plants

leaf resistance, XPP, and RSD for leaves of different phenological status were compared.

Estimated leaf osmotic potential was determined through the pressure-volume curve technique (Ritchie and Hinkley 1975) on shoots collected in the field. The shoots were cut from the trees at dawn and then recut under water, and immediately transported to the lab in sealed glass containers with the stems in water. After the shoots had been saturated for 24 h pressure-volume curves were determined by the Hammel method (Tyree and Hammel 1972, Tyree et al. 1977). Pressure-volume curves were done on five shoots for each tree. The osmotic and turgor potential relationships, along with the relative saturation deficit measurements, were used to estimate the diurnal cycle of turgor pressure in the field trees.

## Results

Maximum irradiance (PAR) of all three dates was similar (Figure 1 A), with cloud cover lacking. The PAR was over  $2,000 \mu\text{Em}^{-2} \text{s}^{-1}$  for six hours on July 15, and for 3.5 h on the other two days. The leaves on *Prosopis* at Harper's Well partially track the sun's movements, resulting in a higher incidence of light on leaf surfaces than would result without leaf movements (Fig. 1 A). The PAR at the angle of the leaves (leaf PAR) was

intermediate between the maximum possible PAR and the PAR at the dawn leaf angle on all three days (Fig. 1 A).

Maximum air temperature decreased from July 15 ( $49^\circ \text{C}$ ) to September 17 ( $40^\circ \text{C}$ ) (Fig. 1 B). Leaf temperatures were close to air temperature for the majority of the day, but leaf temperatures were higher in the morning and lower in the afternoon than the air temperatures. Maximum leaf temperature reached  $45^\circ \text{C}$  on July 15. Soil temperatures below the canopy at  $-30 \text{ cm}$  depth were below air temperature over the entire diurnal cycle with a maximum in July of  $42^\circ \text{C}$ . On all three days vapor pressure deficit (between the air and leaf) increased to a maximum between 1330 and 1530 h (Fig. 1 C). The highest vapor pressure deficits were on July 15, and decreased as the summer season progressed. Mean wind velocity was generally less than 10 mps with maximum wind velocities during the late afternoon (1330~1900 h) when vapor pressure deficits were the highest (Fig. 1 C).

Seasonal midday XPP, monitored as a relative indication of maximum physiological stress conditions for *Prosopis*, decreased to a minimum during the period from June through September ( $-4.4 \text{ MPa}$ ) (Fig. 2). These data indicate that the July through September period was the part of the growing season with the greatest relative water stress.

Xylem pressure potential (XPP) and leaf conductance have been shown to be closely associated with each other in some desert taxa (Szarek and Woodhouse 1977); therefore these two water relations components are shown together (Fig. 3). On all three days the XPP rapidly decreased, following sunrise, to a level below  $-4.0 \text{ MPa}$  by 900 h. The initial decrease in XPP was remarkably consistent even though climatic evaporative demand decreased from July through September. On all three days the XPP of Tree 1 remained near or below  $-4.0 \text{ MPa}$  until sunset. There was little increase in XPP due to gradually decreasing stomatal aperture for Tree 1. In contrast, the XPP of Tree 2 increased (became less negative) during the midday period of July 15 and August 26. Leaf conductance was maximum

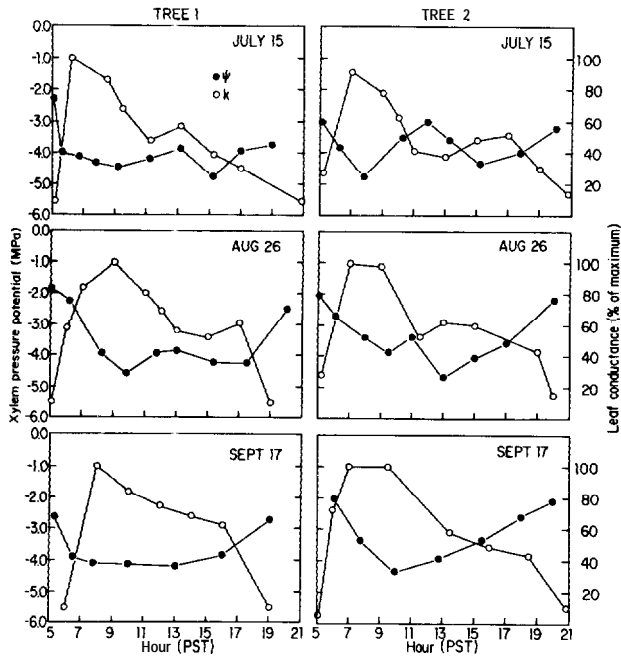


Fig. 3. Diurnal xylem pressure potential and leaf conductance for two *Prosopis glandulosa* trees at Harper's Well during July, August, and September 1980

during the early morning for both trees on all dates. Leaf conductance rapidly decreased following the morning maxima in July and August, and slowly decreased in September. In the case of Tree 1, there was no increase in leaf conductance throughout the day cycle once leaf conductance began to decrease. Tree 2, on the other hand, reopened its stomata in the late afternoon following the recovery of XPP to a less negative value. These data indicate that both trees had limited transpiration due to limiting water resources, but Tree 2 had larger water resources (possibly larger rooting volume or lower stem resistance), allowing recovery of increased stomatal conductance during the afternoon.

Regressions were formulated between leaf conductance, micro-climatic conditions and water relations to ascertain the most influential factors associated with the diurnal changes in leaf conductance. Leaf conductance was found to be significantly correlated with vapor pressure deficit during the daylight hours (Tree 1,  $r=0.95$ ; Tree 2,  $r=0.83$ ). Leaf conductance was poorly associated with XPP and all other environmental characteristics. Stomatal closure, however, does seem to occur when XPP decreases below  $-4.8$  MPa (Fig. 3).

Osmotic potential and turgor pressure relationships investigated in August and September with pressure volume curves were similar. Juvenile shoots had distinctive pressure volume curves (Fig. 4) with higher osmotic potentials at full turgor ( $\psi_{II}^{1.00} = -1.59$  to  $-1.64$  MPa) than those of the mature shoots ( $\psi_{II}^{1.00} = -2.63$  to  $-2.90$  MPa). The relative saturation deficit at incipient plasmolysis was lower for juvenile shoots (10–25%) than for mature shoots (35%).

Osmotic potential, turgor pressure and total water potential of mature shoots are plotted against relative saturation deficit for two trees in Fig. 4. The osmotic potential at full turgor is lower for Tree 2 than for Tree 1. Also, Tree 1 has lower turgor pressure at any relative saturation deficit. These relationships indicate that as the relative saturation deficit increases during the day Tree 1 can have a greater increase in osmotic potential in relation to that of Tree 2. Therefore, Tree 1 should be able to maintain higher turgor potential at a given relative saturation deficit than Tree 2. In either tree turgor approaches zero at approximately 35%. These relationships were investigated for three other trees and the water potential components were found to fall within the range of values for these two trees.

The relative saturation deficit (RSD) for Tree 1 is generally higher than Tree 2 on both diurnal cycles in both August and September. Even though the RSD is higher in Tree 1, the estimated turgor (derived from the pressure volume curves) is also higher in Tree 1 compared to Tree 2 (Fig. 5). This again indicates that Tree 1 has a higher potential for diurnal osmotic change due to water loss or cell volume changes. The diurnal osmotic change for Tree 1 and 2 in August was 1.05 MPa and 0.40 MPa, respectively. Diurnal osmotic change was lower during Sep-

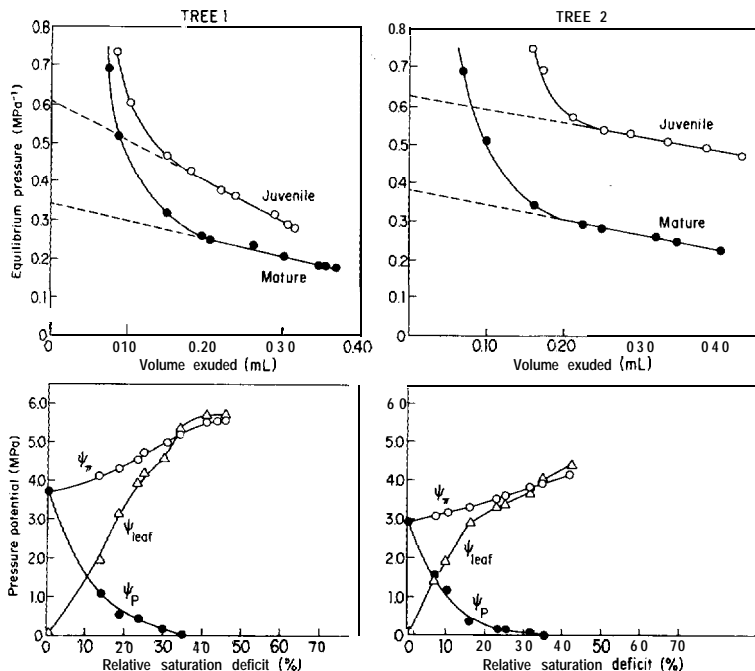


Fig. 4. Pressure volume curves for juvenile and mature shoots of *Prosopis glandulosa* from two trees at Harper's Well during August 1980. Lower figures represent water potential components for mature leaves of tree 1 and tree 2

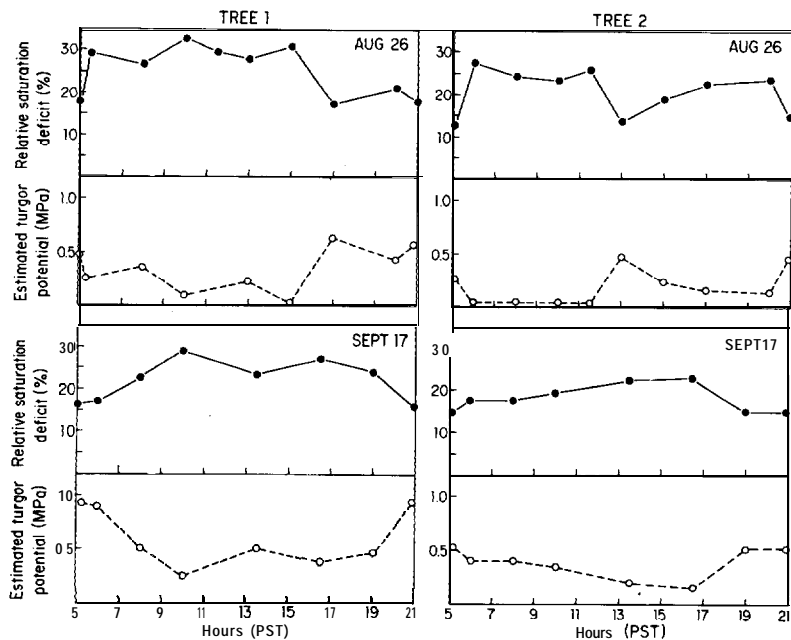


Fig. 5. Diurnal cycles of relative saturation deficit and estimated turgor potential for two *Prosopis glandulosa* trees at Harper's Well, during August and September 1980

tember (Tree 1 = 0.6 MPa, Tree 2 = 0.2 MPa). Also, during September both trees maintained lower RSD and higher estimated turgor potential. Investigations are continuing to evaluate diurnal osmotic adjustment by active changes in solute content.

The diurnal water relations characteristics of these two trees indicate a variable species response to the desert climatic conditions. Tree 1 maintained turgor by changing the osmotic potential during water loss. In contrast, Tree 2 lost turgor potential rapidly during desiccation, but was able to recover rapidly from loss of turgor by water replenishment from the environment. Tree 1 seems to have smaller water resources and did not reduce water deficit even when stomata were closed considerably.

The relative saturation deficit of juvenile leaves on both trees was characteristically 10–20% greater than the mature leaves. In relation to their pressure volume characteristics, the juvenile leaves rapidly lost turgor during the diurnal cycle throughout the summer period, with a RSD less than 20% resulting in zero turgor.

## Discussion

Desert regions of the world, particularly warm deserts, are characterized by high environmental evaporative demand, high heat load, low water availability, and high irradiance. The diurnal microclimatic factors measured during this investigation indicate that Harper's Well is particularly stressful in this regard (Fig. 1). This high environmental evaporative demand imposes considerable water stress to which desert species must adapt to survive. Phreatophytes, by the traditional definition, avoid this water stress by utilizing large water resources reached by a deep proliferation of their tap root systems. *Prosopis*, a classically cited phreatophyte, certainly has been shown to have a deep root system (Phillips 1963, Cable 1977). At Harper's Well *Prosopis* taps permanent ground water supplies at 5 m depth.

There are several cases in which phreatophytes are reported to maintain higher diurnal water potentials than other desert species (Szarek and Woodhouse 1977, Strain 1970). Even though phreatophytes traditionally have relatively high water potentials, *Prosopis* at Harper's Well maintained water potentials considera-

bly lower than other reported values for phreatophytic species (Szarek and Woodhouse 1976; 1977; 1978; Strain 1970; Hass and Dodd 1972; Mooney et al. 1980; Easter and Sosebee 1975). From July to August predawn xylem pressure potential averaged -2.3 MPa (Fig. 3) and minimum xylem pressure potential averaged -4.65 MPa. Stomata closure caused a rapid increase in xylem pressure potential (Fig. 3), indicating large available water resources, particularly for Tree 2. Thus, *Prosopis* at Harper's Well encountered low diurnal water potentials during the summer but generally exhibited rapid increases in water potential upon stomata closure due to pools of available water resources.

Osmotic potential has not been measured often in desert phreatophytes. Mooney et al. (1980) estimated an osmotic potential of -2.13 MPa for *Prosopis tamarugo*. The summer osmotic potentials for *Prosopis* at Harper's Well ranged from -2.75 MPa to -5.25 MPa during the July diurnal cycle. Diurnal osmotic change is present but this is likely due to changing RSD alone. We are now carrying out sequential determinations of osmotic potential over diurnal cycles using pressure-volume curves to evaluate if true diurnal osmotic adjustment is occurring.

Varying degrees of osmotic adjustment in response to moisture stress have been found to occur in plant tissue with age (Hsiao et al. 1976) and with season (Jefferies et al. 1977; Roberts et al. 1980). Our data indicate that true osmotic adjustment (Hinkley et al. 1980) occurs with age in *Prosopis* where the mature shoots have lower osmotic potential relationships than juvenile shoots (Fig. 4). Therefore, mature shoots maintain positive turgor at lower leaf water potentials than juvenile shoots. In fact, incipient plasmolysis occurs at a leaf water potential of about -2 MPa and a relative saturation deficit of 20% in juvenile shoots as compared to -5 MPa and 35% respectively for mature shoots. Tissue variability in water relation characteristics and photosynthetic characteristics have been found in other desert taxa (DePuit and Caldwell 1973). Considerable variability of osmotic potentials from -2.60 to -4.40 MPa was observed in five *Prosopis* studied at Harper's Well. This variability of osmotic potential between trees may be due to the size of the water resources utilized by each individual tree, since individuals with the lowest osmotic potentials had the most rapid recovery

from the minimum diurnal water potential. This general level of osmotic potential is within the range reported for desert plants by Walter and Stadelmann (1974).

Stomatal conductance of desert taxa are commonly high in the early morning and low during the afternoon (Szarek and Woodhouse 1976, Strain 1970, Strain 1968, Schulze et al. 1974). This pattern often occurs even though leaf water potentials (or the bulk leaf water status) are lower in the morning than the afternoon (Schulze et al. 1974). Similar relationships were found with *Prosopis* in the present study (Fig. 3). Stomatal conductance has been shown to be associated with vapor pressure deficit in several species (Lange et al. 1971; Schulze et al. 1974, 1975; Hall and Hoffman 1976; Federer and Gee 1976; Osonubi and Davis 1980). Schulze et al. (1975) found that stomatal resistance in desert grown *Prunus armeniaca* had a greater association with vapor pressure deficit than with internal CO<sub>2</sub> concentration or bulk leaf water potential. The epidermis and guard cells are hypothetically decoupled from the mesophyll water relations and respond most closely to environmental evaporative demand.

The present data for *Prosopis* indicate a strong exponential correlation between leaf conductance and leaf-air vapor pressure deficit ( $r=0.95$ ) and a poor association between leaf conductance and leaf bulk water potential ( $r=0.33$ ), suggesting that the stomata are responding to vapor pressure deficit, not leaf bulk water potential. The response of stomata to vapor pressure deficit was previously suggested for *Prosopis* (Mooney et al. 1977). Estimated turgor potential also has a strong significant linear association with leaf conductance ( $r=0.90$ ). The linear relationship between leaf conductance and estimated turgor potential suggests that vapor pressure deficit influences turgor potential, which then controls stomatal conductance. Further experiments are planned to clarify the relationships between water potential components and stomatal conductance and to investigate seasonal variability in the leaf conductance – VPD response curves in leguminous desert trees.

During the summer period in the lower Sonoran Desert *Prosopis* is placed under severe climatic conditions of high heat load, high irradiance, and high water stress. Under these conditions *Prosopis* is able to maintain open stomata in the morning and early afternoon through a hypothetical decoupling of the guard cells from the bulk leaf water potential. Maintenance of positive turgor, as a result of osmotic adjustment due to water loss, allows carbon fixation during a period of lower vapor pressure deficit in the morning hours. In this way *Prosopis* has adapted to the severe summer climatic conditions by the ability to maintain growth during extreme conditions (Sharifi, et al. in press) when most desert perennials are dormant. While these phreatophytic trees may experience constraints on productivity induced by high water stress during the summer, recovery is rapid on a diurnal cycle due to their large water resources and low osmotic potentials.

The phreatophytic life form, as exemplified by *Prosopis*, has distinctive adaptations to severe desert environments from those of other desert growth-forms. During the summer desert growth-forms which survive on surface water sources commonly are subject to extremely low leaf water potentials at dawn (Szarek and Woodhouse 1976 ; Odening et al. 1974 ; Bennett and Mooney 1979) and diurnal fluctuations of water potentials is less than – 1.5 MPa. Desert phreatophytes, in contrast, may have relatively high dawn water potentials (Szarek and Woodhouse 1977, 1978; Strain 1970; Hass and Dodd 1972), and diurnal fluctuation in water potential can be more than -3.0 MPa, as seen in the present study. Non-phreatophytic desert taxa tolerate the severely arid summer conditions by conserving water use and limiting

the extent of diurnal decreases in water potential. Desert phreatophytes, on the other hand, can have high summer productivity rates because water loss is not curtailed, and diurnal leaf water potential decreases rapidly while stomata stay partially open. Under these conditions there must be a considerable diurnal osmotic adjustment so turgor pressure is not lost rapidly during the day. Thus, maximum diurnal osmotic change may be lower in nonphreatophytic taxa 0.7 MPa (Bennett and Mooney 1979) in comparison to *Prosopis* (1.1 MPa). Phreatophytic taxa can maintain this lavish water use system in deserts because plant water content can be recharged from deep ground water during the evening.

We are currently studying the water relations characteristics of *Prosopis glandulosa* over a seasonal cycle to investigate the possibility of seasonal osmotic adjustment in response to present and previous climatic conditions. Seasonal water use and water use efficiencies will be evaluated in relation to the seasonal water relation components. In this way we hope to fully describe the dynamics of the soil-plant-atmosphere continuum and the water use characteristics of *Prosopis*.

*Acknowledgements.* Drs. Wes Jarrell and Ross Virginia (Riverside) aided our field work greatly. We thank Dr. O.L. Lange (Würzburg) and Dr. A. Hall (Riverside) for suggestions with the steady state porometer. This research was supported by National Science Foundation grant number DEB 79-21971.

## References

- Bennett WH, Mooney HA (1979) The water relations of some desert plants in Death Valley, California. *Flora* 168 :405-427
- Cable DR (1977) Seasonal use of soil water by mature velvet mesquite. *J Range Manag* 30:4-11
- DePuit EJ, Caldwell MM (1973) Seasonal pattern of net photosynthesis of *Artemisia tridentata*. *Amer J Bot* 60:426-435
- Easter SJ, Sosbee RE (1975) Influence of soil water potential on the water relationships of honey mesquite. *J Range Manag* 28 : 230-232
- Federer CA, Gee GW (1976) Diffusion resistance and xylem potential in stressed and unstressed northern hardwood trees. *Ecology* 57:975-984
- Haas R, Dodd J (1972) Water stress patterns in honey mesquite. *Ecology* 53 : 674-680
- Hall AE, Hoffman CJ (1976) Leaf conductance responses to humidity and water transport in plants. *Agron J* 68 :876-881
- Hinckley TM, Dume F, Hinckley AR, Richter H (1980) Water relations of drought hardy shrubs: osmotic potential and stomatal reactivity. *Plant, Cell and Environment* 3: 131-140
- Hsiao TC, Acevedo E, Fereras E, Henderson DW (1976) Stress metabolism. Water stress, growth, and osmotic adjustment. *Phil Trans Roy Soc Lond B* 273 :479 500
- Jefferies RL, Davy AJ, Rudnick T (1979) The growth strategies of coastal halophytes. In: Jefferies RL, Davy AJ (eds), *Ecological processes in coastal environments*. Blackwell Scientific Publications, Oxford, pp 243-268
- Lange OL, Lösch R, Schulze E-D, Kappen L (1971) Responses of stomata to changes in humidity. *Planta* 100:76-86
- Mooney HA, Simpson BB, Solbrig OT (1977) Phenology, morphology, physiology. In: BB Simpson (ed), *Mesquite. its biology in two desert ecosystems*. Dowden, Hutchinson and Ross Inc: Stroudsburg, Penn. pp 26 43
- Mooney HA, Gulmon SL, Rundel PW, Ehleringer J (1980) Further observations on the water relations of *Prosopis tamarugo* of the northern Atacama desert. *Oecologia (Berl)* 44: 177-180
- Odening WR, Strain BR, Oechel WC (1974) The effect of decreasing water potential on net CO<sub>2</sub> exchange of intact desert shrubs. *Ecology* 55:1086-1095
- Osonubi O, Davies WI (1980) The influence of plant water stress

- on stomatal control of gas exchange at different levels of atmospheric humidity. *Oecologia (Berl)* 46: 1-6
- Phillips WS (1963) Depths of roots in soil. *Ecology* 44:424
- Ritchie GA, Hinkley TM (1975) The pressure chamber as an instrument for ecological research. *Adv Ecol Res* 6: 165-254
- Roberts SW, Strain BR, Knoerr KR (1980) Seasonal patterns of leaf water relations in four co-occurring forest tree species: Parameters from pressure volume curves. *Oecologia (Berl)* 46:330-337
- Schulze E-D, Lange OL, Evenari M, Kappen L, Buschbom U (1974) The role of air humidity and leaf temperature in controlling stomatal resistance of *Prunus armeniaca* L. under desert conditions. I. A simulation of the daily course of stomatal resistance. *Oecologia (Berl)* 17: 159-170
- Schulze E-D, Lange OL, Kappen L, Evenari M, Bushbom U (1975) The role of air humidity and leaf temperature in controlling stomatal resistance of *Prunus armeniaca* L. under desert conditions. II. The significance of leaf water status and internal carbon dioxide concentration. *Oecologia (Berl)* 18 : 219-233
- Sharifi MR, Nilsen ET, Rundel PW (in press) Biomass and net primary production of *Prosopis glandulosa* (Fabaceae) in the Sonoran Desert of California. *Amer J Botany*
- Strain BR (1968) Seasonal adaptations in photosynthesis and respiration in four desert shrubs growing in situ. *Ecology* 50: 511-513
- Strain BR (1970) Field measurements of tissue water potential and carbon dioxide exchange in the desert shrubs *Prosopis juliflora* and *Larrea divaricata*. *Photosynthetica* 4: 118-122
- Szarek SR, Woodhouse RM (1976) Ecophysiological studies of Sonoran desert plants. I. Diurnal photosynthetic patterns of *Ambrosia deltoidea* and *Olnea tesota*. *Oecologia (Berl)* 26: 226-234
- Szarek SR, Woodhouse RM (1977) Ecophysiological studies of Sonoran desert plants. II. Seasonal photosynthesis patterns and primary production of *Ambrosia deltoidea* and *Olnea tesota*. *Oecologia (Berl)* 28:365-375
- Szarek SR, Woodhouse RM (1978) Ecophysiological studies of Sonoran desert plants. III Daily course of photosynthesis for *Acacia greggii* and *Cercidium microphyllum*. *Oecologia (Berl)* 35:285-294
- Tyree MT, Hammel HT (1972) The measurement of the turgor pressure and the water relations of plants by the pressure bomb technique. *J Exp Bot* 23:267-282
- Tyree MT, MacGregor ME, Petrov A, Upenieks MI (1978) A comparison of systematic errors between the Richards and Hammel methods of measuring tissue-water relations parameters. *Can J Bot* 56:2153-2161
- Walter H, Stadelmann E (1974) A new approach to the water relations of desert plants. In: GW Brown (ed), *Desert Biology*, Vol 2. Academic Press, New York, pp 213-309

Received June 6, 1981