DIURNAL AND SEASONAL WATER RELATIONS OF THE DESERT PHREATOPHYTE *PROSOPIS GLANDULOSA* (HONEY MESQUITE) IN THE SONORAN DESERT OF CALIFORNIA[1]

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Abstract. Diurnal and seasonal water relations were monitored in a population of *Prosopis glandulosa* var. *torreyana* in the Sonoran Desert of southern California. *Prosopis glandulosa* at this research site acquired its water from a ground water source 4–6 m deep. Measurements of diurnal and seasonal cycles of aboveground environmental conditions, soil moisture, and soil water potential (to 6 m depth) were taken to ascertain environmental water availability and water stress. Leaf water potential, leaf conductance, leaf transpiration, relative saturation deficit of leaves, osmotic potential, and turgor potential were measured to evaluate plant adaptations to environmental water stress. Soil water potential was low (−4.0 to −5.0 MPa) in surface soil in relation to deep soil (−0.2 MPa). This difference was due to high surface soil salinity and low surface water content. The climatic conditions at the research site produced extreme water stress conditions in summer months when temperatures reached 50°C, vapor pressure deficit (VPD) reached 8 kPa, and surface soil water potential was below −4.5 MPa. Although considerable plant water stress developed in these trees (midday leaf water potential −4.8 MPa), osmotic adjustment occurred and turgor was maintained on a diurnal and seasonal cycle. *Prosopis glandulosa* has adapted to avoid water stress by utilizing deep ground water, but this phreatophyte has also evolved physiological adaptations, such as osmotic adjustment and seasonally changing stomatal sensitivity to VPD, which result in greater tolerance of water stress.

Key words: leaf conductance; osmotic adjustment; phreatophyte; Prosopis glandulosa; *Sonoran Desert; turgor potential; water relations.*

INTRODUCTION

Studies of water relations which concern plants of desert regions have emphasized the adaptations of shrub species which allow tolerance of water stress (see Osmond et al. 1980). These adaptations, for example, cover morphological adjustment to water stress (Cunningham and Strain 1969, Smith and Nobel 1977, Ehleringer and Mooney 1983), photosynthetic adaptation (Strain 1969, Hellmuth 1971, Odening et al. 1974), spatial distribution of individuals (Fonteyn and Mahall 1978), and osmotic adjustment (Walter and Stadelman 1974, Bennert and Mooney 1979, Monson and Smith 1982). Although considerable research has been done on the water relations of desert shrubs and ephemerals (e.g., Gulmon and Mooney 1977, Mulroy and Rundel

1977, Anderson and Szarek 1981), few studies have been concerned with the water relations of desert trees (e.g., Adams and Strain 1968, Haas and Dodd 1972, Szarek and Woodhouse 1976).

The phreatophytic species which has been most extensively studied in an ecological context is *Prosopis glandulosa* (mesquite). A large volume of available literature concerns the mechanisms to rid the landscape in Texas of this vigorous weed (see Parker and Martin 1952), while conversely, recent studies have evaluated the utility of mesquite as a crop for arid lands (Felker 1979, Nilsen et al. 1982). The water relation studies which concern mesquite have involved water use characteristics of communities in Texas and Arizona (e.g., McGinnes and Arnold 1939, Cable 1977, Webb et al. 1979). Few studies have evaluated the water relations of *Prosopis* (Haas and Dodd 1972, Nilsen et al. 1981) on an ecophysiological basis.

The available data suggest that phreatophytic species such as *Prosopis* avoid water stress in arid regions by tapping water at depth in soils. *Prosopis* roots have been found at a great depth (52 m) in soils (Phillips

1963), and stands of *Prosopis* survive in regions with little to no recorded rainfall by tapping underground water resources (Mooney et al. 1980). There is evidence for several phreatophytic species (*Olneya tesota, Cercidium floridum, Acacia greggii*) which indicated that only minor water stress (water potential not below −2.0 MPa) develops in desert phreatophytes (Adams and Strain 1968, Szarek and Woodhouse 1978, Monson and Smith 1982). Rainfall is relatively high for desert regions (350 mm/yr) in these study areas, and only suggestive evidence was presented indicating whether the *Olnea* and *Acacia* were growing phreatophytically. In the cases where phreatophytic growth was conclusive for *Prosopis*, considerable water stress (−4.0 MPa) has been measured in summer months (Mooney et al. 1980, Nilsen et al. 1981). Therefore, mechanisms of drought tolerance should exist. Because of the lack of intensive water relations information on desert phreatophytes, we believe that such a study on *Prosopis* could result in an understanding of the mechanisms of drought avoidance and drought tolerance in phreatophytic species.

STUDY SITE

This research was carried out in a mesquite woodland dominated by *Prosopis glandulosa* in the Sonoran Desert of southern California. Harper's Well, our study site, lies at an elevation of −30 m at the base of the Fish Creek Mountains, 15 km west of the southern tip of the Salton Sea (Fig. 1). *Prosopis glandulosa*, a tree or large shrub reaching 5 m in height, accounts for >90% of the vegetation cover. The few other shrubs which are present (*Larrea, Atriplex, Allenrolfia, Pluchea*), account for <4% coverage. Few ephemerals are present. The soils at Harper's Well are classified as a clay loam near the surface with lenses of sand and clay at depth (described in detail in Virginia and Jarrell 1983). There is a permanent, stable groundwater table which varies spatially between depths of 4 and 6 m (Meinzer 1927). Soil chemical characteristics are unusual with large quantities of nitrogen at the surface (Rundel et al. 1982, Virginia and Jarrell 1983). Harper's Well is a central research site for several ecosystem and ecophysiological studies including *Prosopis* water relations (Nilsen et al. 1981, 1982, 1983), nitrogen fixation (Shearer et al. 1983), nutrient cycling (Rundel et al. 1982, Virginia and Jarrell 1983), net primary production and biomass (Sharifi et al. 1982), and phenology (Sharifi et al. 1983) of a desert phreatophytic (*Prosopis glandulosa*) community.

METHODS AND MATERIALS

Climatic measurements were taken diurnally on 12 occasions (approximately monthly) during 1980–1981. Temperatures of leaves (n = 5), air, and soil (1 m, −1 cm, −30 cm) were measured hourly from 500 to 1900 Pacific Standard Time (PST) with copper constantan thermocouples. Similar cycles of measurements were
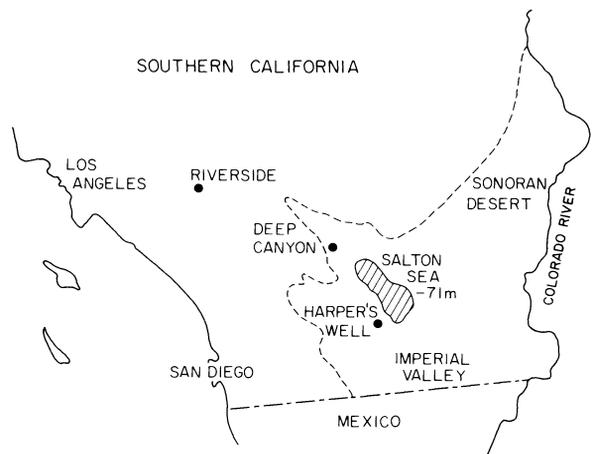

FIG. 1. Location of the primary research site, Harper's Well, in the Sonoran desert of southern California.

made for relative humidity (sling psychrometer), PAR (quantum sensor), and wind (hot-wire anemometer). The vapor pressure gradient was calculated from leaf temperature, air temperature, and relative humidity. Precipitation and seasonal air temperature were recorded at the official United States Department of Agriculture weather station (National Oceanic and Atmospheric Administration 1980, 1981) in Brawley (20 km south of the study site). Our field measurements indicate that maximum temperatures at Harper's Well are ≈3°C higher than those at Brawley. Soil water content was measured throughout the rooting profile at 25 cm increments to a maximum of 550 cm with the use of the neutron activation technique (Gardner 1965). Neutron probe access tubes were inserted under the canopies of five representative trees and midway between the selected trees. Measurements of volumetric moisture content were taken by the neutron activation technique approximately monthly from July 1980–September 1981.

Soil matric potential was determined for nine representative surface soil samples (both 0–30, and 30–60 cm depth) by use of a pressure plate apparatus (Gardner 1965). Curves relating soil volumetric water content to potentials as low as −1.5 MPa were constructed. Deep soil samples (0–60 cm above groundwater level) were at or near saturation throughout the year. Soil osmotic potential was estimated from data on field soil water content (neutron probe) and the osmotic potential of soil saturation extracts measured using a vapor pressure osmometer. Surface soil osmotic potential was based on saturation extract data reported by Virginia and Jarrell (1983) and the osmotic potential of deep soil was based on saturation extracts of samples recovered from drilling 10 neutron access tubes. We assumed a linear inverse relationship between soil water content and the osmotic potential of the soil solution. This assumption ignores possible changes in
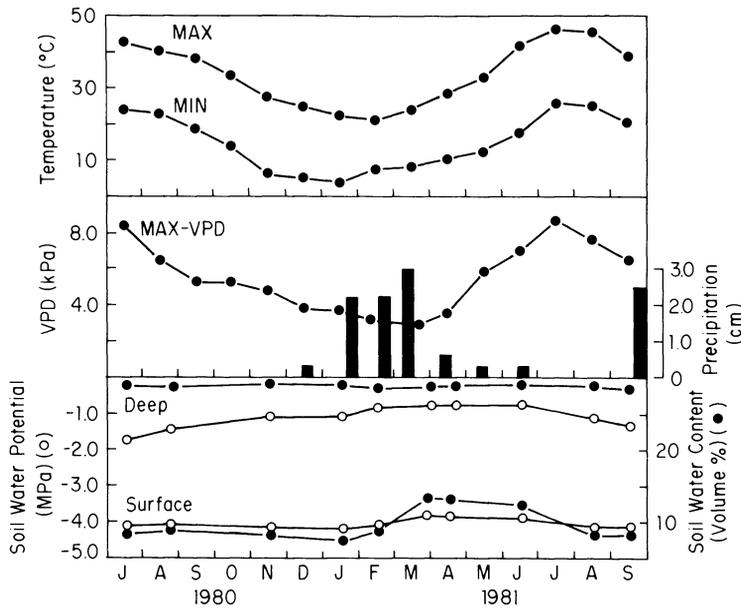
FIG. 2.   Seasonal climatic conditions and soil water parameters.

the osmotic potential of the soil solution at low water content caused by precipitation of some salts.

All plant water relations were followed on five selected trees. The results are reported as means for the five individuals. Mean values are used because we are trying to characterize the diurnal and seasonal water relations of a population, not an individual. Some results will be presented on an individual plant basis to clarify a particular interaction of climate and water relations which is masked by average values. During the 12 diurnal cycles mentioned above, leaf water potential (ψ_l) was determined with the use of a pressure chamber (Scholander et al. 1965). Water potential measurements were made in triplicate on each of five individuals every 2 h from 500 to 1900 (PST). Over a similar time course, leaf conductance (g) and leaf transpiration were determined (J). Leaf conductance was measured on five leaves of each sample individual ($n = 25$), with a steady state porometer (LICOR-1600). Simultaneous measurements of transpiration were determined from the equation $J = g \cdot \text{VPD}$, where transpiration (J) is calculated from measurements of conductance and the vapor pressure deficit (VPD).

The predawn and midday leaf water potential was determined from July 1980 to September 1981 with a pressure chamber (four samples per individual; $n = 20$). Twig and leaf samples were also collected on each sample date for pressure-volume (PV) determinations of water relations components (Tyree and Hammel 1972, Cheung et al. 1976, Nilsen et al. 1983). Samples were cut in the field, recut underwater, and rapidly transported to the lab for analysis. Techniques for PV analysis on phreatophytes have been previously described (Nilsen et al. 1983) and are based on those of

Tyree and Hammel 1972. On each sample date, five PV curves were formulated on each of four individuals. All PV curve samples were cut before dawn for uniformity. Diurnal osmotic adjustment was assessed by cutting similar, even-aged twig samples at midday as well as predawn for PV curve analyses.

RESULTS

Climatic conditions

Seasonal meteorological conditions at Harper's Well during 1980–1981 were characteristic of extreme warm deserts. Air temperature at Brawley increased from December to July reaching a mean maximum of 44°C (Fig. 2), with maximum diurnal temperatures >50° during July and August. Mean minimum temperatures never reached below 0° and there were no individual air temperatures below 0° during the measured diurnal cycles. Leaf temperature was within 1° of air temperature on all diurnal cycles. Soil temperature of surface soil (−1 cm) reached >80° and minimum soil surface temperature was often below air temperature. Soil temperature below −30 cm showed only slight seasonal variability around a mean of 25°.

The vapor pressure deficit followed a similar pattern to that of temperature (Fig. 2) reaching a maximum in July (8.5 kPa). Annual precipitation at Brawley during 1980 (65 mm) and 1981 (45 mm) was slightly lower than the yearly average of 70 mm (Sharifi et al. 1983). Most precipitation occurred during the winter with only a few small summer storms in 1981, although normally August and September are the months when most precipitation occurs. Maximum daily photon flux was 53.3 $\text{E} \cdot \text{m}^{-2} \cdot \text{d}^{-1}$. Seasonal soil moisture content is plotted as an average of all measurements (between and under

trees) because active roots extend well beyond tree
canopies. The soil moisture at depth remained fairly
constant at ≈25% except during July 1980 and August
1981, when a significant decrease occurred (Fig. 2). In
1980 and 1981, surface soil water content was highest
during the winter months (February–April) but the
yearly average volumetric content was much lower (8–
10%) than that of the deep soil.

The surface soil had higher salinities than deep soil
(Virginia and Jarrell 1983) due to limited infiltration
and high evaporation rates. Therefore, the osmotic po-
tential in surface soil was lower than that of deep soil
throughout the year. Matric potentials for surface soils
exceeded −1.5 MPa, the limit of quantification using
the pressure plate technique. The summation of os-
motic and a minimum matric potential of −1.5 MPa
indicates that surface soil water potential decreased
below −4.5 MPa in July (Fig. 2), far lower than the
water potential in deep soils (−0.2 MPa). Results from
the soil cores indicated that there was a root mat at
the surface (above −30 cm depth) and deep roots ex-
tending to −4 to −6 m, where they proliferate. There-
fore, each portion of the dual rooting system of *Pro-
sopis* experiences a widely different water potential
regime. The seasonal surface soil water potentials plus
seasonal meterological data all clearly indicate that June
through August constitutes a period of extreme envi-
ronmental water stress, particularly for the roots in
surface soil.

Phenology

Diurnal cycles and seasonal water relations char-
acteristics were influenced by both environmental
conditions (as described above) and by leaf phenolog-
ical characteristics. These seasonal trends of leaf pro-
duction, leaf number, and leaf maturation are shown
in Fig. 3. A majority of leaf production occurred dur-
ing March and April and a secondary period of leaf
production occurred in August on a much smaller scale.
Leaves matured rapidly to full leaf area after produc-
tion and initiated senescence, as defined by chlorosis
or leaflet abscission, in September. Senescent leaves
then remained on the branches until February and
complete abscission did not occur until early March
when the new set of leaves was being produced. The
majority of leaves on the plants were of one cohort
produced during late March to early April. This even-
aged cohort of leaves was used exclusively for the
water relations studies, and therefore influences of age
on water relations were easily controlled. The second
cohort of leaves produced in August was clearly iden-
tifiable through the morphological characteristics of
the leaves.

Diurnal cycles

Diurnal cycles of environmental conditions support
similar conclusions concerning the period of maximum
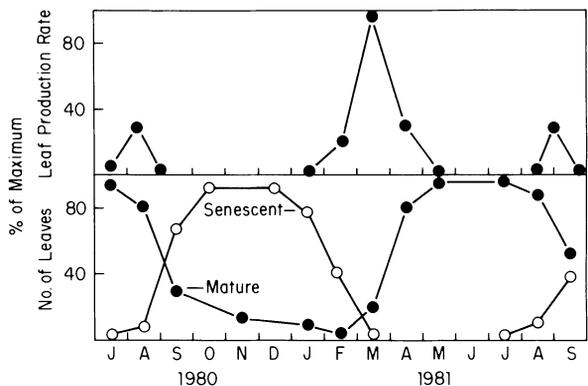environmental water stress. Of the 12 diurnal cycles

FIG. 3. Seasonal progression of leaf production rate and
the number of senescent or mature leaves, as a percent of
the yearly maximum, for *Prosopis glandulosa*.

measured, 4 are chosen to represent major character-
istics of diurnal aboveground conditions. On all 4 dates
presented, maximum air (Fig. 4) and leaf temperature
was reached between 1300–1700. Leaf temperature was
close to air temperature on all dates except in July,
when midday leaf temperature rose 1° above air tem-
perature. Maximum surface soil temperature reached
80° in July but only 30° in February. Below 30 cm soil
temperature varied little diurnally and from 15°–25°
seasonally. Wind increased to a maximum in the after-
noons, which is consistent with thermally driven wind
currents.

The VPD also increased to a maximum between
1300–1500 on all dates measured, with the difference
between dawn and midday VPD largest during July
and September. Only small variability in VPD oc-
curred during the February diurnal cycle.

The photosynthetically active radiation (PAR) arriv-
ing at the leaf surface is little influenced by cloud cover
since such cover is infrequent. Maximum PAR, oc-
curring between 1100–1500, is close to the potential
maximum arriving at the earth's surfaces (Nobel 1977).
Prosopis leaves track the motion of the sun during the
morning and early afternoon hours, resulting in higher
irradiance impinging on leaf surfaces than would be
expected without solar tracking ability (Nilsen et al.
1981).

In general, leaf water potential decreases with in-
creasing environmental water stress brought on by in-
creasing irradiance, temperature, and vapor pressure
deficit. Water potential at midday decreased to ≈−4.0
to −4.5 MPa after which it either increased or re-
mained constant, except for the curve of diurnal water
relations in February (Fig. 5). Minimum leaf water po-
tential was only −2.8 MPa in February. Leaf conduc-
tance reaches a maximum early in the day (0800–0900),
following which there is a general decline through the
rest of the day (Fig. 5). There is an indication of sto-
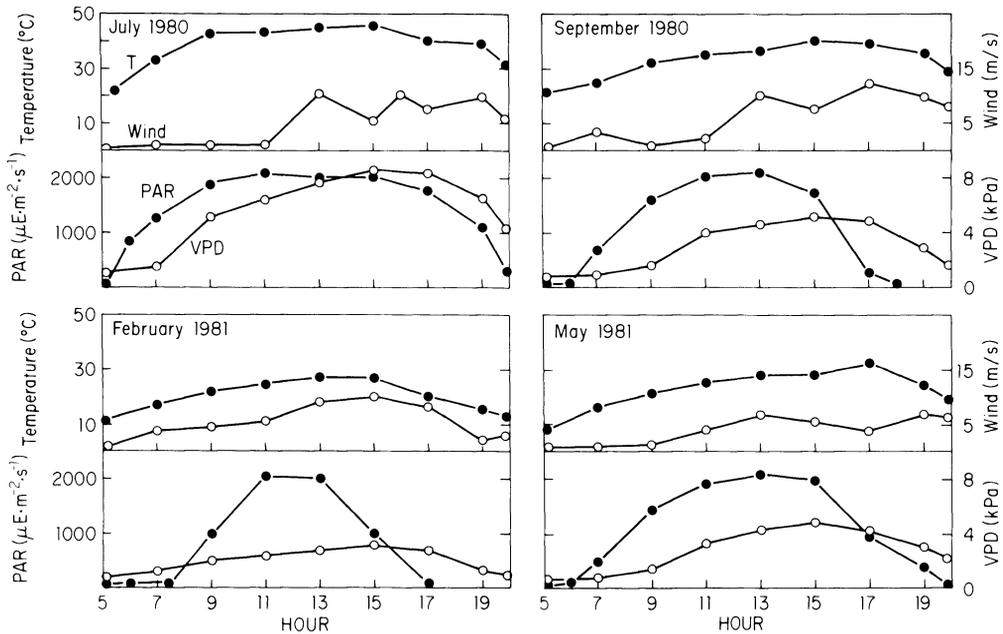matal closure at midday in the July and the May diur-

FIG. 4.   Diurnal cycles of environmental conditions on four dates during 1980–1981.

nal cycles. The magnitude of the midday stomatal clo-
sure was variable among individuals; therefore, these
cycles of mean leaf conductance mask some of the
midday stomatal closure. While this midday stomatal
closure is evident in the leaf conductance data, the
pattern is not mimicked in the mean leaf water poten-
tial data. In fact, previously reported data (Nilsen et
al. 1981) indicate that the leaf conductance is clearly
better associated with the VPD than with water po-
tential until a leaf water potential below −4.0 MPa is
reached, at which time stomata close rapidly. The
magnitude of secondary diurnal increases in stomatal
conductance decreased in accordance with leaf age
rather than with changes in diurnal meteorological
conditions.

Diurnal cycles of transpiration were the product of
VPD and conductance. Maximum transpiration oc-
curred later in the day than maximum conductance
because the VPD was low in the early morning. The
midday depression in stomatal conductance was not
reflected by decreasing transpiration (Fig. 5) because
the VPD remained high (Fig. 4).

The interactions between leaf water potential, con-
ductance, VPD, and transpiration are not clear in the
mean values because the trees were not precisely in
temporal agreement and the magnitude of the various
water relations parameters varied between individu-
als. For this reason a diurnal cycle for one tree in
August 1981 is presented in Fig. 6. As in July 1980,
the PAR reaches a maximum by 1100 and remains full
until 1500, after which time the light intensity de-
creases. The VPD increases slowly through the morn-

ing hours, reaching a maximum of 8 MPa by 1300. The
VPD then remains high, only decreasing slowly fol-
lowing 1700.

Leaf water potential (ψ_l) oscillated over the course
of the day. When ψ_l decreased below −4.0 to −4.5
MPa, it then began to increase again. Two such oscil-
lations occurred during the diurnal cycle. The leaf con-
ductance pattern followed that of leaf water potential.
When leaf water potential decreased below −4.0 MPa,
stomata began to close, causing an increase in leaf
water potential. Although the 1300 leaf water potential
approached that of the morning, the resulting conduc-
tance at 1500 was much lower than that at 0700. This
was the result of higher VPD at midday than at 0700.
Also, even though the conductance decreased from
0900–1300, transpiration increased until 1100, and at
1300 a slight decrease occurred. This is likewise the
result of increasing VPD. The secondary increase in
conductance at 1500 caused a renewed increase in
transpiration since the VPD was still high.

Leaf turgor potential was calculated from the mea-
surements of leaf water potential and the pressure-
volume relationship for August 1981 (data presented
later in the article). Zero turgor is reached at 0800 at
the time when stomata begin to close. Turgor potential
then increases towards the afternoon (1000 to 1300)
when leaf water potential increases as a result of re-
duced conductance. Thus, turgor potential increases
as a result of reduced conductance. Turgor potential
comes close to zero again at 1600, following increased
conductance. At dusk (1800) turgor is once again re-
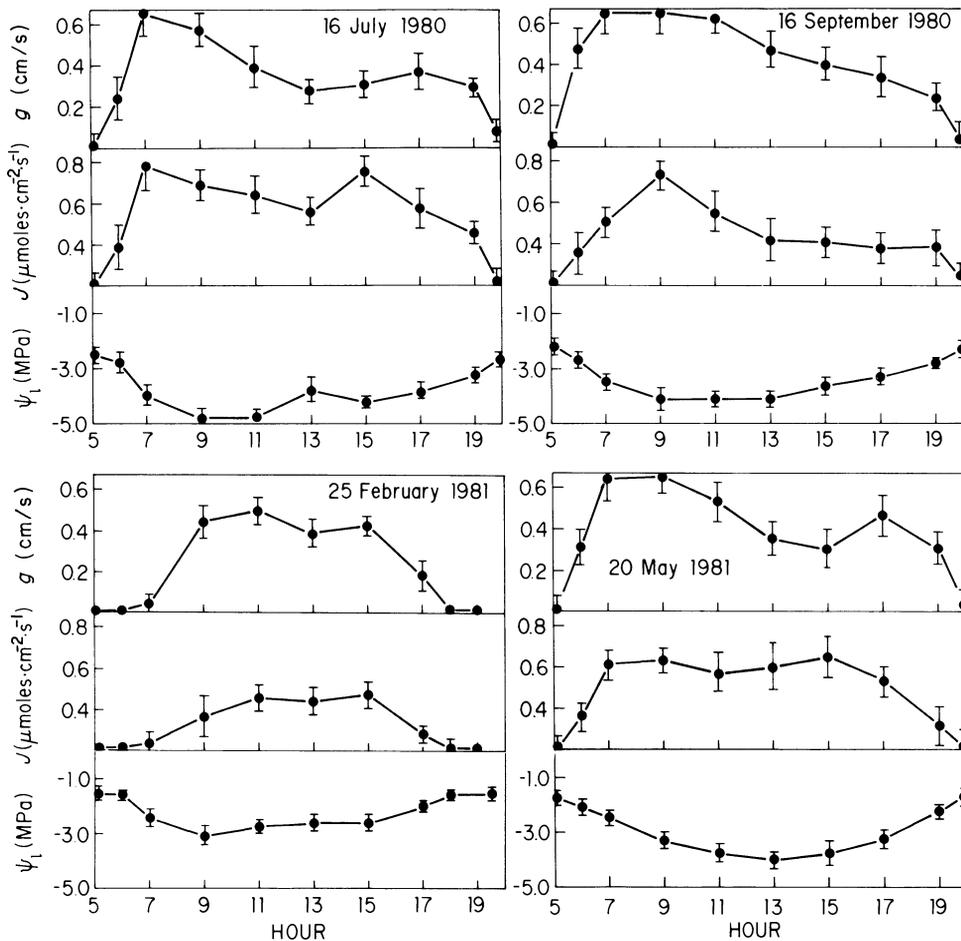newed in response to the decreasing conductance.

FIG. 5. Diurnal cycles of leaf conductance (g), transpiration (J), and leaf water potential (ψ_l) for *Prosopis glandulosa*. Each point is a mean of five individuals with five samples per individual per time period.

Seasonal parameters

The seasonal water relations parameters reflect the important characteristics of the 12 diurnal cycles of water relations measured on this desert phreatophyte. Seasonal leaf water potential characteristics are shown in Fig. 7. Predawn leaf water potential remains fairly constant at −2.5 MPa throughout 1980–1981, except during February through March, when an increase of 1 MPa occurs. Midday water potential is lowest during July–September, reaching as low as −4.5 MPa. There is a gradual increase from September through February to a maximum value of −1.7 MPa. The gradual increase is due partly to a reduction of environmental water stress and a reduction in plant leaf area (Fig. 3; and Sharifi et al. 1983). Because −4.0 MPa leaf water potential initiated stomatal closure (Fig. 6; and Nilsen et al. 1981) the number of hours below −4.0 MPa during a diurnal cycle is thought to be a good index of relative water stress for *Prosopis glandulosa*. During June–August there are nine or more hours (64% of daylight hours) with a water potential below −4.0 MPa.

This relative index of plant water stress decreases rapidly from September, to 0 h in January.

Several characteristics of diurnal leaf conductance and transpiration over the seasonal cycle are shown in Fig. 8. Maximum leaf conductance remains approximately constant (>0.65 cm/s) from March through August. Following August, maximum leaf conductance decreases to a minimum during November through February, a period when most leaves are senescent and vapor pressure deficit is the lowest. Midday leaf conductance increased from July through January and remained low from late February through June. The difference between the maximum leaf conductance and the midday leaf conductance should be a significant indicator of plant water stress, since this index represents the magnitude of the midday stomatal closure in leaf conductance, previously considered a good indicator of plant water stress (Klepper 1968, Tenhunen et al. 1980). The maximum difference between midday and maximum leaf conductance occurred during May (Fig. 8). This index gradually in-
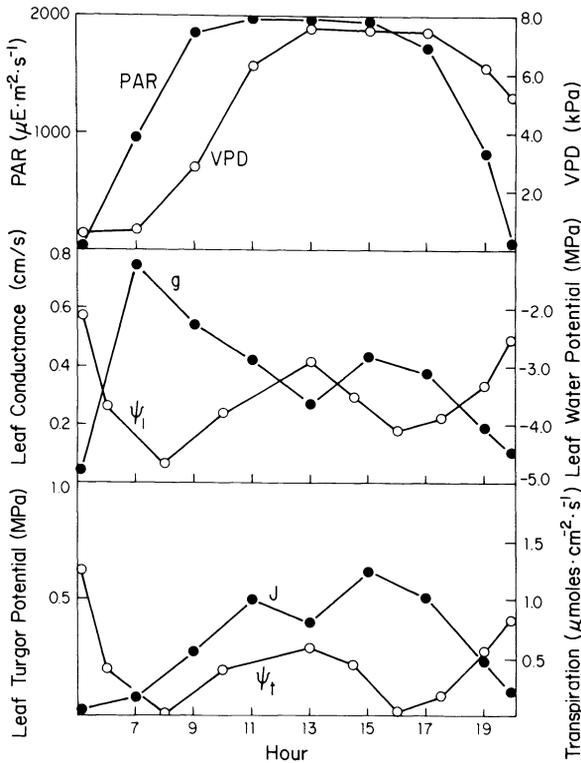
FIG. 6.   Diurnal cycle of photosynthetically active radiation, vapor pressure deficit, leaf conductance (g), leaf water potential (ψ_l), transpiration (J), and leaf turgor potential (ψ_t) for a *Prosopis glandulosa* individual during August 1981.

creased from January through May and decreased thereafter. The midday decrease in leaf conductance has been found to be related to both plant water potential (e.g., Biscoe et al. 1976, Nilsen and Muller 1981) and vapor pressure deficit (Schulze et al. 1974). In this case, the maximum midday stomatal closure occurs 2 mo before the period of minimum leaf water potential (Fig. 7) and maximum vapor pressure gradient (Fig. 2). Leaf age influenced the magnitude of the midday stomatal closure; therefore, young leaves (April–May) respond more rapidly to smaller changes in VPD and leaf water potential, resulting in a greater midday decrease in leaf conductance. The seasonal variability in the midday stomatal closure may be strongly influenced by a variable sensitivity of stomata to changing VPD.

Regressions between VPD and leaf conductance were formulated for each diurnal cycle. These linear regressions were significant $(P = .05)$ and r^2 values ranged from 0.95 to 0.47. Lower r^2 values were found during diurnal cycles which contained water potentials below -4.5 MPa. Such low leaf water potentials were associated with rapid stomatal closure (Nilsen et al. 1981). The sensitivity of stomata to changes in VPD is best represented by the slope of the regression equations relating leaf conductance to VPD (Fig. 8). The

greatest sensitivity of leaf stomata to VPD occurred during April and May when leaves were young (Fig. 3). As the leaves aged gradually and became senescent from May to February, stomatal sensitivity to VPD decreased as the slope of the regression increased. The slope became positive following September, after which the r^2 of VPD : conductance decreased to below 0.50 (Fig. 8). The significance of the variable sensitivity of stomata to VPD will be discussed later.

Seasonal transpiration characteristics are represented as a diurnal sum of water loss per unit leaf area (Fig. 8). Maximum water loss occurred during July through September when temperature and VPD were maximum. On a per plant basis, this maximum water loss during the summer is magnified because this is also the period of maximum leaf area (Sharifi et al. 1982, 1983, Nilsen et al. 1983).

Other water relations components such as osmotic potential, modulus of elasticity, and turgor potential (see Tyree and Hammel 1972, Tyree and Richter 1981) were derived from pressure-volume analyses. Such analyses done over a diurnal cycle (predawn vs. midday) indicated that a maximum diurnal osmotic adjustment of 0.5–0.7 MPa occurred during June–October (Nilsen et al. 1983). There was considerable variability in water relations components among individuals (Nilsen et al. 1981, 1983) but here we present the mean water relations characteristics for the five studied individuals.

The seasonal osmotic potential at full turgor $(\psi_s{}^{100})$ and at the turgor loss point $(\psi_s{}^0)$ (Fig. 9) decreased from late February through August in accordance with increasing environmental water stress. The total sea-
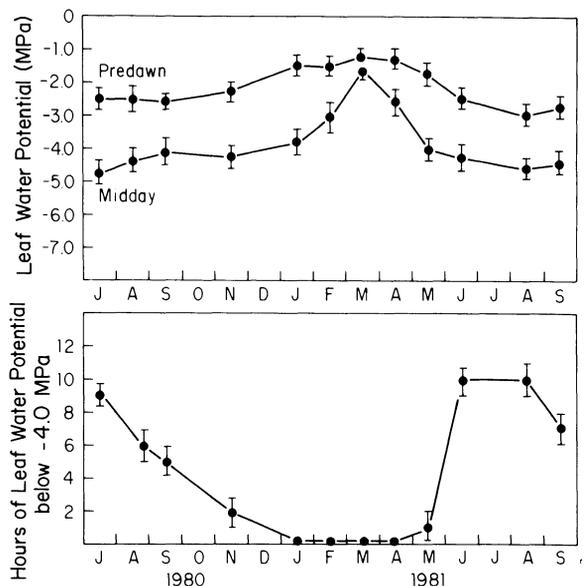

FIG. 7.   Seasonal progressions of leaf water potential for five *Prosopis glandulosa*.
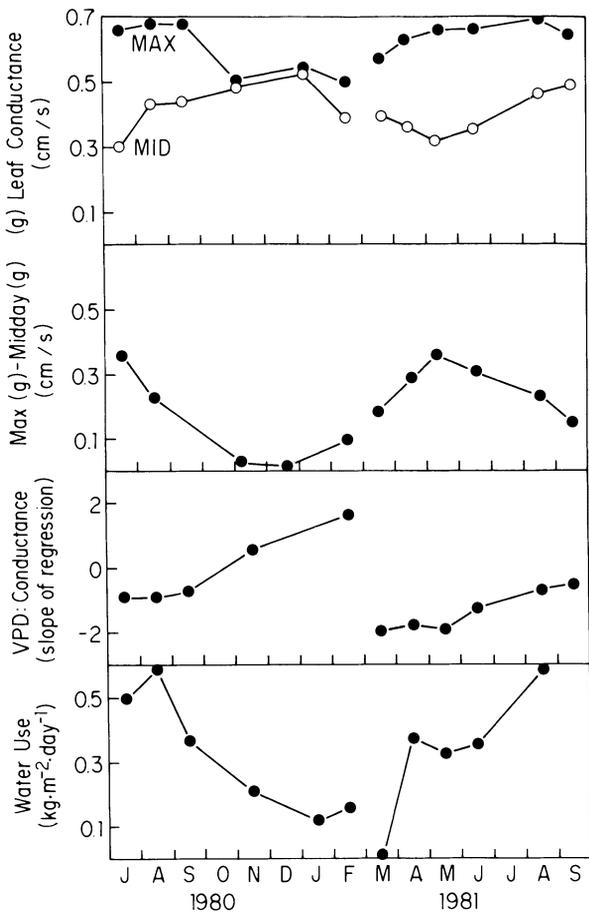
FIG. 8. Seasonal progression of leaf conductance and transpiration characteristics for *Prosopis glandulosa*.

mum turgor potential of 0.10 MPa was reached during the early growing season (May) and remained low until November when environmental water stress became less severe. Seasonal dawn turgor potential remained quite stable at 0.80 MPa throughout the measured period. During diurnal cycles of turgor potential of individual plants, zero turgor was occasionally reached from June through August. For example, during August of 1981 turgor potential was lost at 0800 and almost lost at 1600 for the individual used as an example in Fig. 6. From May through November these plants, taken as a group, had minimal mean turgor potential (<0.1 MPa) from 0900 to 1600, yet stomata remained open.

The modulus of cell elasticity (E, calculated as per Cheung et al. 1976) is plotted seasonally as $\bar{E}$ (maximum modulus of elasticity) and E_k, which represents the slope of E plotted against turgor potential. The modulus of elasticity is an indication of the ability of cells to change volume with decreasing water potential. The larger the E, the smaller the cell elasticity. Maximum E ($\bar{E}$) and E_k rapidly decreased from March through April (Fig. 9) during the leaf maturation period (Fig. 3). Following leaf maturation, $\bar{E}$ and E_k remained

sonal osmotic adjustment at full turgor was from -1.51 to -3.30 MPa, or a difference of 1.80 MPa. Some individuals had an osmotic adjustment up to 2.5 MPa. Osmotic potential at full turgor then increased from August through February as environmental conditions became less stressful. This seasonal osmotic adjustment also coincides with leaf maturation (decreasing osmotic potential) and leaf senescence (increasing osmotic potential) as indicated in Fig. 3. Osmotic potential at zero turgor varied similarly to that at full turgor. In this case the variation was from -1.75 to -4.20 MPa or 2.45 MPa.

The water deficit at the turgor loss point (WD⁰) followed a seasonal pattern similar to that of the osmotic potential. Young leaves in March lost turgor at a WD of 0.17 while mature leaves in July did not lose turgor until they reached a WD of 0.28. The WD⁰ decreased from September to February, to a value similar to that of the next year's leaves in March.

Turgor potential was determined from the diurnal cycles of leaf water potential (ψ_l) and the PV-curve relating turgor potential to ψ_l. The mean, daily mini-
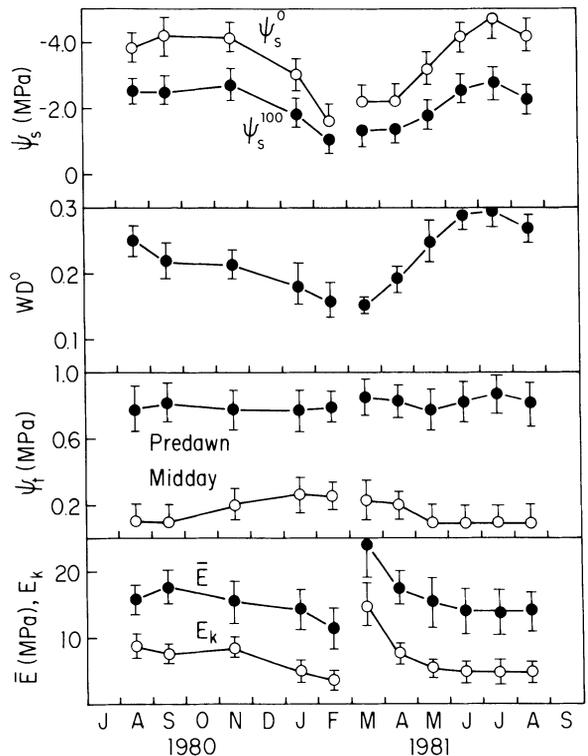

FIG. 9. Seasonal progression of water relations components in *Prosopis glandulosa*. $\psi_s{}^{100}$ = osmotic potential at full turgor; $\psi_s{}^0$ = osmotic potential at incipient plasmolysis; WD⁰ = relative water deficit at incipient plasmolysis; ψ_t = turgor potential; $\bar{E}$ = maximum elastic modulus; E_k = slope of line comparing E to RSD.

constant until November, after which a slight decrease occurred. There is some indication that $\bar{E}$ and E_k were slightly lower in 1980 in comparison to 1981. The seasonal progression of cell elasticity, as measured by $\bar{E}$ and E_k, was most consistent with leaf maturation and senescence.

Discussion
Environmental water characteristics

The climatic data collected at this site in the Sonoran Desert clearly represent extreme conditions of water limitation as indicated by the VPD and the low plant osmotic potentials. This water stress is most severe from May to August when temperatures reach 50°C, VPD approaches 8 kPa, photoperiod is 14 hr, wind velocities are high, and irradiance is maximum. These environmental data are similar to those of the most water-limited climates in the California deserts (Hunt 1966, Major 1977) and some of the most stressful deserts of the world (Fuchs 1973). Even though this is a site of extreme aridity (precipitation = 45–65 mm), Prosopis production at this site is the highest measured in desert communities to date (Nilsen et al. 1983, Sharifi et al. 1983); therefore, the Prosopis individuals must be well adapted to conditions of water stress.

Soil moisture characteristics at Harper's Well are unusual for desert environments. Surface soil has very low volumetric moisture content (8–10%), while deep soils are at or near saturation most of the year. For this reason, and due to high salinity in the surface soil, the surface soil water potential is low in comparison to deep soil. On the basis of the soil-plant-atmosphere-continuum models of water uptake (Nobel 1977: 401–408) it seems clear that the large majority of water transpired by these Prosopis trees is derived from ground water. Resistance in the 4-m column of water in tap roots would not compensate for the soil water potential gradient from deep to surface soils. Another indication of the minimal root resistance is the rapidity with which the plant water potential returns to the predawn value after sunset (Fig. 5).

Drought avoidance

The seasonal and diurnal water relations characteristics for Prosopis at Harper's Well indicate mechanisms of both avoidance and tolerance of water stress. Clearly, Prosopis is able to avoid some aspects of water stress by utilizing the deep groundwater. The ability of Prosopis to utilize groundwater was demonstrated in this investigation by the relatively constant seasonal predawn leaf water potential (Fig. 7). Root mats of Prosopis at Harper's Well were found to occur at 10–100 cm and again at 400–600 cm. Also, the rapid recovery of leaf water potential after sunset to predawn values, indicates large available water resources. Even though these Prosopis predominantly utilized the water

in deep soil, their predawn leaf water potential (−1.5 to −2.8 MPa) did not match the water potential of the deep soil (−0.2 MPa). As previously explained, there seems to be minimal stem and root resistance to water flow so that the plants at predawn may become equilibrated with the combined influences of surface and deep soil moisture relationships. In fact, the predawn leaf water potential (−1.5 to −2.8 MPa) appeared to equilibrate with the average value of surface (−3.0 to −4.5+ MPa) and deep (−0.2 MPa) soil water potential. Another investigation of Prosopis water relations in the Atacama Desert (Mooney et al. 1980) indicated that since the plant water potential at night is higher than that of the surface soil, water may flow from deep soil layers and from the plant into surface soils. Although there were similar water potential gradients in this study, the surface soil moisture was so low that increases in soil moisture at night could not be measured. The activity of surface roots, limited to a short period (February–April) by low water potentials the rest of the year, may function predominantly for nutrient accumulation, particularly for nitrogen (Rundel et al. 1982), to complement the amount of nitrogen accumulated by N-fixation (Shearer et al. 1983).

Other phreatophytic species have been demonstrated to have mechanisms which allow avoidance of water stress. For example, Olneya tesota in Arizona does not experience low leaf water potentials (minimum = −2.5 MPa), presumably due to accumulation of water from deep soils (Szarek and Woodhouse 1976, 1977, Monson and Smith 1982). But in this case, annual precipitation was as high as 250–350 mm, in comparison to 70 mm at Harper's Well. Cercidium seems to maintain high plant water potentials by maintaining leaves for only a short period in winter (Strain 1970, Szarek and Woodhouse 1978).

Drought tolerance

Although phreatophytes are generally considered to be drought avoiders and water spenders (Levitt 1980), these data for Prosopis indicate several mechanisms of drought tolerance. First of all, the phenological development of Prosopis leaves does not suggest any phenological drought avoidance mechanism (Fig. 3). Maximum leaf area occurs during the hottest and driest part of the year, and leaves which become morphologically senescent remain on the trees until January–February. Both of these temporal leaf characteristics result in maximal water loss of up to 116 Mg·tree⁻¹·yr⁻¹ (Nilsen et al. 1983).

One of the mechanisms of drought tolerance in Prosopis is the observed seasonal variation of stomatal control of water loss. Maximal conductance remained >0.65 cm/s from April through September (Fig. 8), even though water potential dropped to −4.5 MPa in July. The ability to maintain such a high maximum conductance value during summer months was related to the diurnal cycles of conductance. Maximum con-

ductance occurred in the morning (800–1000, Fig. 5) when leaf water potential was high and the VPD was low. As VPD increased and leaf water potential decreased, conductance decreased until a leaf water potential reached ≈−4.0 to −4.5 MPa, at which time an equilibrium was reached. Since the water potential and conductance varied among individuals, this maintenance of a specific water potential by stomatal control is best shown on the basis of an example individual (Fig. 6).

Regressions between mean leaf conductance and other average water relations characteristics resulted in best correlations with VPD. There has been recent evidence that stomatal conductance is well correlated with the VPD in desert and nondesert species (Lange et al. 1969, 1971, Schulze et al. 1974, Hall and Hoffmann 1976). The midday depression in conductance may be best related to the VPD in some species (Tenhunen et al. 1980). Although this is basically true for the mean values of conductance for *Prosopis*, on an individual basis, a leaf water potential below −4.0 MPa causes stomatal closure irrespective of the VPD (Fig. 6).

There has been considerable information in the literature concerned with osmotic adjustment as an adaptation to water stress (Hellebust 1976, Hsiao et al. 1976, Osonubi and Davies 1978, Turner and Jones 1980, Meyer and Boyer 1981). Osmotic adjustment in such drought-hardy shrubs may range up to 2.5 MPa (Walter and Stadelman 1974) of adjustment during severe water stress. *Prosopis* at Harper's Well had a similar value of osmotic adjustment: 2.45 MPa. Diurnal osmotic adjustment, also considered an important adaptation to water stress, was present up to 0.7 MPa in these *Prosopis* (Nilsen et al. 1983). The seasonal and diurnal osmotic adjustment resulted in the maintenance of turgor potential, found to be critical for drought avoidance (Hsiao 1973), throughout the season.

Plants can adapt to seasonal water stress through osmotic adjustment or by alterations in the bulk elastic modulus, which is an indication of cell wall elasticity (Tyree and Hammell 1972, Cheung et al. 1976, Roberts et al. 1981). Maximum measured elastic modulus ($\bar{E}$) decreased from March through April, as did (E_k), the relationship between E and turgor potential. Therefore, cellular elasticity increased as leaves matured from March through April, but after leaf maturation there was little change in cellular elasticity. There is no evidence for turgor maintenance by adjusting cellular elasticity during periods of extreme water stress, as was reported for several Sonoran desert plants (Monson and Smith 1982).

The relationship between turgor potential, water deficit, and cell elastic modulus (Fig. 10A, B) is critical to understanding the way in which *Prosopis* adjusts its water relations in response to severe water stress. During June (high water stress) the leaves of *Prosopis*
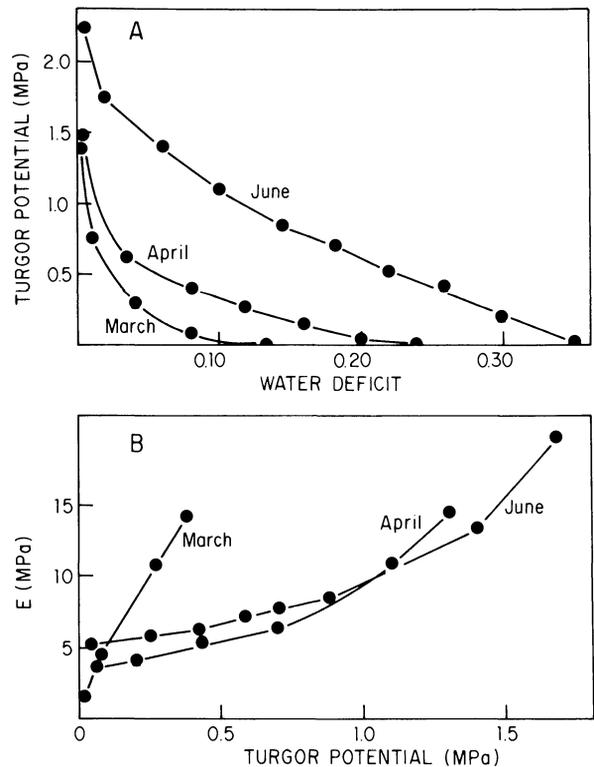

FIG. 10. Relationships of turgor potential, water deficit, and modulus of elasticity for leaves during March, April, and June (1981) on *Prosopis glandulosa*.

are able to maintain turgor to lower leaf water contents (higher water deficits) than the same leaves in March and April (Fig. 10A). Since turgor potential is vital for growth and photosynthesis of plants (Hsiao et al. 1976), the ability to maintain turgor at high water deficit is an important adaptation to the severe water stress conditions of the Sonoran desert. Turgor potential can be maintained at low leaf water content either by an adjustment of cell volume through cellular elasticity or an adjustment of osmotic potential. Often the maximum elastic modulus ($\bar{E}$) is used as an indication of possible adjustment of cell elasticity (Monson and Smith 1982), but there are many reasons why this value may contain considerable variability (Cheung et al. 1976, Roberts et al. 1981) and error (Tyree and Richter 1982). The best measure of the variation in cell elasticity is a comparison of the way in which E changes with turgor potential (E_k). There was no difference in the relationship between E and turgor potential for *Prosopis* when comparing April to June values (Fig. 10B). However, there is a considerable influence of leaf maturation on this relationship because March values (immature leaves) are quite different from those of April and June (mature leaves). These data indicate that changes in cell elasticity are due to leaf development, rather than a response to water stress. *Pro-*
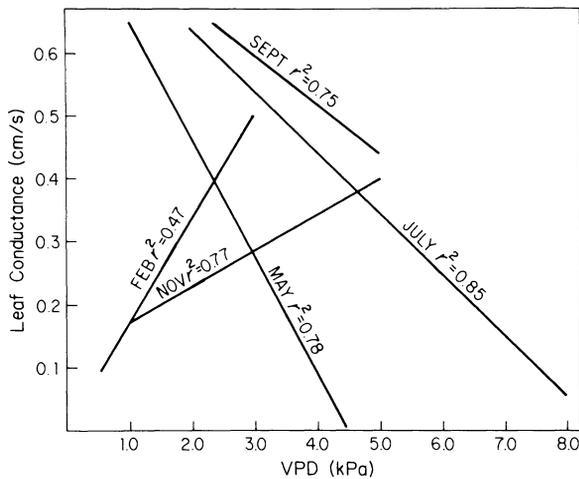
FIG. 11. Regressions between VPD and conductance for different aged leaves in a field population of *Prosopis glandulosa*. May = 2 mo old, July = 4 mo old, September = 6 mo old, November = 8 mo old, February = 11 mo old.

sopis responds to water stress by adjusting osmotic potential (Fig. 9) after leaf maturation, thereby maintaining turgor potential at low leaf water contents.

Some researchers have argued that rapid loss of turgor at relatively low WD may be an adaptation allowing water conservation in times of severe water stress (Monson and Smith 1982). Rapid loss of turgor would cause stomatal closure and this would result in water conservation. This may be reasonable for shallow-rooted evergreen species which have small water resources and large evaporative demand in summer months when major leaf area is maintained. But these species, such as *Larrea tridentata*, generally have sclerophyllous leaves which maintain turgor to low leaf water contents. Also, maintaining a large leaf area with closed stomata creates considerable problems for the leaf energy budget in environments with high irradiance (Nobel 1977), and photo-oxidation of photosystems can result. Therefore, water conservation by rapid loss of turgor at high leaf water content would seem to be a disadvantage to water stress in desert plants, especially since growth and photosynthesis are severely curtailed by loss of turgor potential. On the other hand, the ability to maintain turgor at low leaf water content has clear advantages for plants in arid regions, since conductance can be maintained and growth can continue.

Influences of leaf age

Leaf age (and/or development) clearly influences leaf water relations characteristics. The phenology of leaf production in *Prosopis* (Fig. 3) results in an even-aged cohort of leaves produced in March. After production the leaves mature rapidly, as indicated by leaf specific mass which becomes constant in early April (Rundel et al. 1982). The main cohort of leaves then remains

mature until early September when the first signs of senescence appear. Juvenile leaves have lower osmotic potentials at full turgor and reach incipient plasmolysis at a lower WD (Nilsen et al. 1981). This suggests that the seasonal osmotic adjustment (Fig. 9) might be a result of leaf maturation, not a response to increasing water stress, from February to July. But leaves mature (based on specific leaf mass and leaf area) by late April (see Fig. 3 and Sharifi et al. 1983) while most osmotic adjustment occurs between April and June. Therefore, the major portion of observed seasonal osmotic adjustment is most associated with increasing water stress, not with leaf morphological maturation.

There also seems to be a relationship between leaf conductance and leaf age. First of all, the largest midday depression in leaf conductance occurred during April and May, while the greatest environmental water stress did not occur until June through August. This suggests that stomata are more sensitive to the VPD and leaf water potential during the late spring (April–May) and when they are young mature leaves. During April and May turgor potential is lost at a higher water potential and lower WD^0, which is one reason why conductance is more sensitive to changes in leaf water potential in April + May as compared to June to September. Furthermore, the regression between VPD and leaf conductance varies with leaf age (Fig. 8), as plotted in Fig. 11. As the leaves age (1 mo to 6 mo) the slope of the regressions becomes less steep but remains negative. Therefore, at a VPD of 4.0 KPa in May and July, leaf conductance will be 0.10 cm/s and 0.60 cm/s, respectively. As drought stress becomes more severe, higher conductances are maintained at lower VPD due to the change in slope of the VPD : conductance regression. Higher leaf conductances (and higher photosynthetic rates) can be maintained in July due to the changing association of VPD with leaf conductance. Following the initiation of senescence (September) the VPD : conductance regressions became positive and had a poorer fit ($r^2 = 0.47 - 0.77$). This suggests a fundamental change in stomatal control following early signs of senescence.

The data collected during this investigation indicate that *Prosopis* by its phreatophytic habit can avoid severe physiological water stress as defined by loss of turgor, severely reduced leaf conductance, or reduced growth. However, this study also indicated that this phreatophytic species has several mechanisms of tolerating drought stress such as seasonally changing stomatal sensitivity to VPD, and seasonal and diurnal osmotic adjustment to maintain turgor potential during severe environmental drought. These mechanisms of avoiding and tolerating water stress are highly adaptive in desert wash envirionments, because they allow relatively high productivity (Salinas and Sanchez 1971, Sharifi et al. 1983) in environments with extreme aridity.

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