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## COMPARATIVE WATER RELATIONS OF PHREATOPHYTES IN THE SONORAN DESERT OF CALIFORNIA<sup>1</sup>

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**Abstract.** The seasonal and diurnal water relations were compared among six desert phreatophytes, two evergreen shrubs, and one deciduous shrub. All species were located in one wash woodland in the Sonoran Desert of southern California. There are several mechanisms by which these phreatophytes have adapted to the desert environment. One group of winter-deciduous phreatophytes (*Olneya tesota*, *Prosopis glandulosa*, and *Acacia greggii*) experienced summer midday leaf water potentials below  $-4.0$  MPa. These phreatophytes had a series of physiological mechanisms for tolerating summer water stress, including seasonal and diurnal osmotic adjustment and the maintenance of high leaf conductance at low leaf water potential. Osmotic adjustment of these three phreatophytes was similar to or greater than that of two evergreen species (*Larrea tridentata* and *Simmondsia chinensis*). *Dalea spinosa*, a stem-photosynthetic phreatophyte, avoided water stress by maintaining a very small leaf area. The summer-deciduous phreatophytes (*Hyptis emoryi*, and *Chilopsis linearis*) demonstrated mechanisms of drought avoidance such as change in leaf biomass and low summer leaf conductance. Little osmotic adjustment occurred in the summer-deciduous phreatophytes.

The phreatophytic species studied in this investigation have evolved adaptations to water stress that are similar to those of deciduous and evergreen shrubs of the Sonoran Desert. Desert phreatophytes are a complex group of species with varied adaptive mechanisms to tolerate or avoid drought and should not be considered simply as a group of species that avoid desert water stress by utilizing deep ground water unavailable to other desert species of drought tolerance and avoidance.

**Key words:** *Acacia greggii*; *Chilopsis linearis*; *Dalea spinosa*; *Hyptis emoryi*; leaf conductance; *Olneya tesota*; osmotic adjustment; phreatophytes; *Prosopis glandulosa*; Sonoran Desert; water relations.

### INTRODUCTION

Comparative investigations of the water relations characteristics of various growth-forms within communities are available for many ecosystems. In Mediterranean ecosystems many comparisons of water relations in evergreen and drought deciduous species have been conducted (Mooney and Kummerow 1979, Poole and Miller 1981). Similar comparisons have been made in eastern deciduous forests between broadleaf evergreen and broadleaf deciduous taxa (Cline and Campbell 1976, Roberts et al. 1979). Some comparisons in desert ecosystems have been made between deciduous and evergreen shrubs (Bennert and Mooney 1979) and between a phreatophyte and an evergreen or deciduous shrub (Strain 1970, Szarek and Woodhouse 1977), but most detailed work has been limited to a few species.

While a large volume of literature is available on the water relations of desert shrubs (e.g., Walter and Sta-

delman 1974) and general studies of phreatophyte ecology (see Felker 1979), comparative studies of the water relations of desert phreatophytes and associated species have been limited (see Strain 1970, Szarek and Woodhouse 1976, Mooney et al. 1980, Nilsen et al. 1981, 1983). Generalizations have been commonly made that desert phreatophytes as a group have low water stress tolerance and high water stress avoidance as a result of their deep rooting system (Levitt 1980).

Observations of several phreatophytic trees in the Sonoran Desert made by our research group clearly indicated that there was great variability in adaptive strategies among species, particularly in relation to their phenology (E. T. Nilsen, *personal observation*). In this paper we compare the seasonal and diurnal water relations characteristics of a series of important desert phreatophytes and other perennial growth forms in the same habitat in the Sonoran Desert of southern California.

### SITE AND SPECIES DESCRIPTION

Our field measurements were carried out at Nude Wash in Anza Borrego State Park (San Diego County, California), a woodland community which is located

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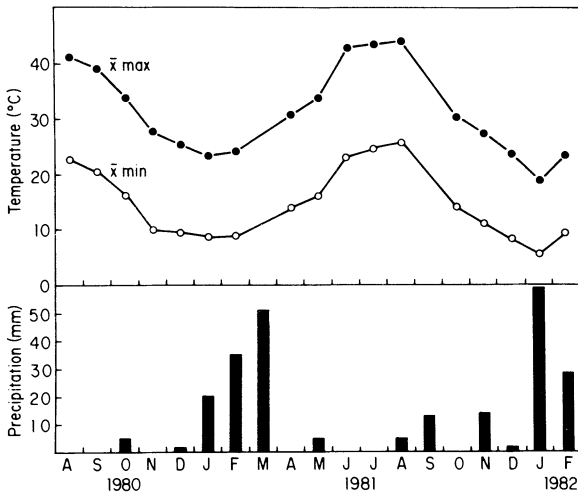


FIG. 1. Climatic conditions in Anza Borrego State Park headquarters (250 m elevation) near Nude Wash.

in an outwash canyon at 300 m elevation in the Vallecito Mountains. The wash vegetation is dominated by woody, phreatophytic, large shrubs and trees as well as scattered evergreen and drought deciduous shrubs. Most important upper Sonoran Desert wash woodland genera are represented in the flora of Nude Wash, with the exception of *Cercidium microphyllum*.

The climatic conditions of the region, as recorded at Anza Borrego State Park headquarters (elevation 250 m), from August 1980 to February 1982 are shown in Fig. 1. The highest mean-maximum temperatures are reached between July and September, when values are often  $>40^{\circ}\text{C}$ . At this time daily maximum values may reach  $48^{\circ}$ – $50^{\circ}$ . Lowest mean-minimum temperatures are reached between November and March with values as low as  $5^{\circ}$ – $7^{\circ}$ . Daily minimum temperatures may rarely reach  $0^{\circ}$  in January and February. Most precipitation occurs during the winter and early spring (December–March). Summers are dry with occasional fall thunderstorms. The mean annual precipitation at the Park Headquarters is 75 mm (20-yr record), less than the precipitation during 1980 (163 mm) and 1981 (147 mm).

Even though several species had individuals located on the walls of the wash canyon, only individuals on the floor of Nude Wash were used in this study so that all species would be in as uniform a habitat as possible.

The term phreatophyte is used in this article for those species capable of utilizing ground water outside the period of maximum rainfall. In this case water is accumulated from deep ground water resources. In this study *Hyptis emoryi* is an exception to the above definition, yet the water relations characteristics presented in this article indicated that *Hyptis emoryi* does have access to ground water unavailable to other nonphreatophytic shrubs in this wash. Six of the species chosen

were woody phreatophytes almost exclusively located in wash woodlands of the upper Sonoran Desert (Hastings et al. 1972). Three of these phreatophytes are winter-spring deciduous (*Prosopis glandulosa* var. *torreyana*, *Olneya tesota*, *Acacia greggii*). Two phreatophytes, *Chilopsis linearis* and *Hyptis emoryi*, are summer deciduous. One of the phreatophytes has very short-lived ephemeral leaves (*Dalea spinosa*) and is best classified as stem-photosynthetic. All are shrubs to small trees.

Several of these phreatophytic trees/shrubs are exclusively restricted to areas of ground water in the upper Sonoran Desert (*P. glandulosa*, *H. emoryi*, *C. linearis*, and *D. spinosa*). *Olneya tesota* and *A. greggii* are occasionally found on canyon walls and outwash bajadas, but their maximum distribution occurs in wash areas of the California Sonoran Desert (Hastings et al. 1972, Munz 1974). Deep rooting has been measured only with *P. glandulosa* (Phillips 1963, Sharifi et al. 1982), although personal observation of the roots in all phreatophytic species in this study indicate deep rooting ( $>1$  m).

Two evergreen shrubs were studied, *Larrea tridentata* and *Simmondsia chinensis*. Although these species are found in the wash, they are both more commonly found in rockier and higher areas of the Sonoran Desert (Munz 1974). Measurements were also taken on one drought-deciduous shrub, *Encelia farinosa*, which has been shown to lack access to deep ground water resources (Smith and Nobel 1977). Measurements were also made on the desert ephemeral vine *Cucurbita digitata*. Taxonomy used here follows that of Munz (1974).

#### METHODS AND MATERIALS

Seasonal and diurnal measurements of predawn and midday water potentials were collected with a pressure chamber (PMS Incorporated, Corvallis, Oregon; Model 1000) apparatus (Scholander et al. 1965, Ritchie and Hinckley 1975). Water potential measurements here refer to xylem-pressure-potential measurements of shoots in all cases except *P. glandulosa*, where leaves were used. Three individuals of each species were chosen and 2–3 measurements were taken per individual at predawn and midday. Values presented are means for each species. Diurnal cycles of leaf conductance were measured with a steady state porometer (LI-COR Incorporated, Lincoln, Nebraska; Model 1600). Five leaves were chosen on two plants of each species for the leaf conductance measurements.

Measurements of other water relations components (turgor, osmotic, and matric potential; water deficit at the turgor loss point) were determined by the pressure-volume (PV) technique (Scholander et al. 1965, Tyree and Hammel 1972). The particular method used for all species closely followed the "Hammel" method (Tyree et al. 1978) and has been explained in detail elsewhere (Tyree and Hammel 1972). Shoots were collected at dawn (except for the evaluation of diurnal

osmotic adjustment), recut under water and brought to full saturation (24 h) before the PV curve was determined. On each collection date 5–10 PV curves were determined for each species. For calculations and specifics about the PV technique see Tyree and Hammel 1972. Critical characteristics of PV curves, such as excess (noncollected) water loss, rate of pressure adjustment, length of resaturation period, attainment of the equilibrium pressure, etc., follow guidelines of Tyree and Hammel (1972).

Seasonal phenological patterns were determined by labeling branches ( $n = 10$  per species) and determining the number of leaves per branch. The percentage of the maximum number of mature leaves was calculated to indicate seasonal trends in leaf biomass. These values are presented as qualitative seasonal trends. Small changes in specific leaf mass occurred (data not reported) which did not influence the relationship of the number of leaves to the leaf biomass in shoots.

Diurnal cycles of microclimate were determined on 7 January, 22 May, and 4 August 1982. Photosynthetically active radiation (PAR) was measured at the leaf angle with a LI-COR quantum sensor. Temperature was recorded at 1 m elevation by a shaded copper-constantan thermocouple. Measurements of leaf temperature were determined by implanting 36-gauge copper-constantan thermocouples (0.13-mm diameter) into several leaves (abaxial surface) of each species. Wind velocity was measured at 1 m in the canopy every 15 s with a hot-wire anemometer (Weather Measure W241M) and the average for a 2-min span was recorded each hour. The vapor pressure gradient was calculated as per Campbell (1977) from measurements of wet and dry bulb temperatures (recorded by a sling psychrometer) and leaf temperature. Micrometeorological data were collected and stored with a Campbell Scientific Incorporated (Logan, Utah) data recording system; Model CR21 micrologger.

## RESULTS

Each phreatophyte species investigated had a distinct seasonal progression of leaf production and loss (Fig. 2). Every phreatophyte studied was deciduous, but the length of the deciduous period and the season when abscission occurred varied among species. Three legumes, *Prosopis glandulosa*, *Acacia greggii*, and *Olneya tesota*, were leafless for  $\approx 1$  mo during the late winter to spring, in February, March–April, and April–May, respectively. Although all the phreatophytes initiated productivity at the same time, *P. glandulosa* produced leaves before flowers, *A. greggii* produced flowers and leaves simultaneously, while *O. tesota* produced flowers before leaves.

*Chilopsis linearis* and *H. emoryi* were deciduous in the summer, losing most leaves during June and April–May, respectively. *Hyptis emoryi*, however, maintained a small population of small xeromorphic leaves

throughout the summer, as described by Smith and Nobel (1978). *Encelia farinosa* and *H. emoryi*, the drought-deciduous shrubs, had similar phenological patterns. Leaf production by *C. linearis* occurred later than that of *H. emoryi* but at a similar time to the winter-deciduous phreatophytes. *Chilopsis linearis* also had a small, second growth period following the main flowering period in August.

The two evergreen species (*L. tridentata* and *S. chinensis*) had phenological patterns distinctly different from each other. *Simmondsia chinensis* did not lose any leaves over the 18-mo observation period. In contrast, *L. tridentata* demonstrated a high rate of leaf turnover. Approximately 70% of the current leaves and all of the remaining last year's leaves abscised between July and October.

*Dalea spinosa* is considered an ephemeral-leaf species similar to *Cercidium microphyllum* (Adams et al. 1967) and *Fouquieria splendens*. The data presented here indicate that *D. spinosa* is winter deciduous (Fig. 2). However, the *D. spinosa* leaves are so small that they represent an insignificant portion of the total transpirational surface ( $>0.1\%$ ; E. T. Nilsen et al., *personal observation*), making *D. spinosa* virtually leafless during the summer as well. *Cucurbita digitata* was the most ephemeral species studied, with two equivalent periods of leaf development during January–March and August–September. These two growth periods corresponded to the periods of greatest rainfall (Fig. 1).

The species studied can be grouped on the basis of their phenology and their relative leaf water potentials ( $\psi$ ). The evergreen shrubs (*L. tridentata*, *S. chinensis*) had lower  $\psi$  than the phreatophytes during August 1981, while the drought-deciduous species *E. farinosa*, and *Beleporone californica* (used here for comparison), had equal or lower  $\psi$  than the phreatophytes (Fig. 3). Among the phreatophytes, the winter-deciduous species had considerably lower  $\psi$  than the summer-deciduous and stem-photosynthetic phreatophytic species. The root succulent (Hendrix 1982) *Cucurbita digitata* had the highest  $\psi$  values.

Drought-deciduous phreatophytes (*Chilopsis linearis*, *Hyptis emoryi*) experienced the highest seasonal  $\psi$ , while the winter-deciduous phreatophytes (*O. tesota*, *P. glandulosa*, *A. greggii*) experienced considerably lower  $\psi$  (differences significant at  $P < .01$ ;  $F$  test), particularly during the summer months (Fig. 4B). Although *O. tesota* is grouped with the winter-deciduous phreatophytes, its leaf phenology is intermediate, with the leafless period in late May–early June. This caused the summer decrease in midday  $\psi$  to be out of phase with the other winter-deciduous phreatophytes (Fig. 4A). As a result, the inclusion of *O. tesota* with the winter-deciduous phreatophytes decreased the difference between the water potentials of the summer- and winter-deciduous phreatophytes (Fig. 4B). The decrease in midday  $\psi$  during the summer is associated with increasing leaf biomass of the winter-deciduous

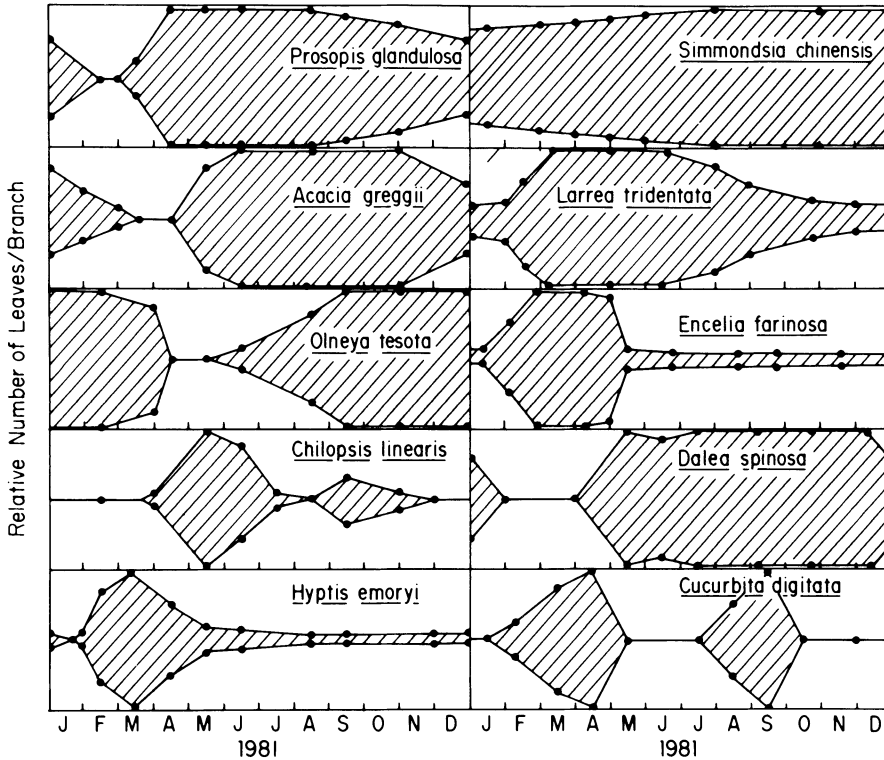


FIG. 2. Phenogram of relative number of leaves for 10 wash-woodland species in Nude Wash. Shaded area designates the number of leaves relative to the yearly maximum number of leaves for each species.

phreatophytes plus the increasing environmental water stress during this season.

The evergreen species in the wash (*S. chinensis* and *L. tridentata*) had the lowest midday  $\psi$  throughout the year (Fig. 4B). The summer decrease in  $\psi$  did not correspond to increasing leaf biomass in these species. The midday and predawn  $\psi$  values for the drought-decid-

uous shrub (*Encelia farinosa*) were intermediate between the evergreen shrubs and the winter-deciduous phreatophytes. The *Cucurbita digitata* midday  $\psi$  never decreased below  $-2.0$  MPa throughout the two growing seasons and was normally between  $-1.0$  and  $-1.25$  MPa. (Data for *E. farinosa* and *C. digitata* are not presented in Fig. 4B.)

The trends in predawn  $\psi$  (Fig. 5A), which indicate background water availability in the rooting zone (Slatyer 1967), were very similar to those of midday  $\psi$  (Fig. 4A). Thus, the summer-deciduous phreatophytes have the best water availability year-round. The winter-deciduous phreatophytes have intermediate water availability during July through December, during which time the evergreen shrubs have the least water available. During February and March, the predawn  $\psi$  indicates similar environmental water availability for all the species and growth forms (Fig. 5A, B). Decreases in predawn  $\psi$  reflect only general decreases in environmental water availability, since predawn  $\psi$  is also influenced by changes in the osmotic potential.

The microclimatic conditions for typical days during three seasons are shown in Fig. 6. PAR was similar on all three dates. The photoperiod increased from January to August as did the total daily photon flux. Temperature in January and May were similar, reaching a maximum of  $26^{\circ}\text{C}$  and  $29^{\circ}\text{C}$ , respectively, and a mini-

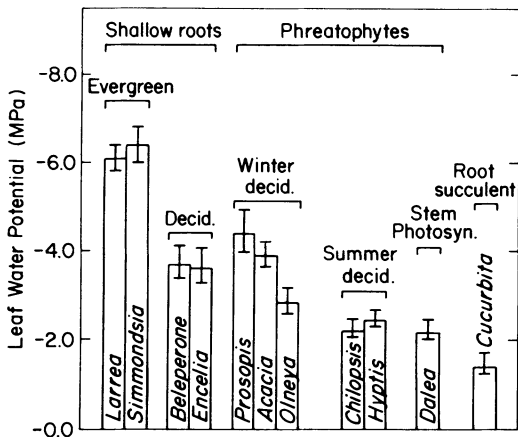


FIG. 3. Midday water potentials for species found in Nude Wash during August 1981. Error bars equal  $\pm 2$  standard errors of the means ( $n = 6$  measurements/species).

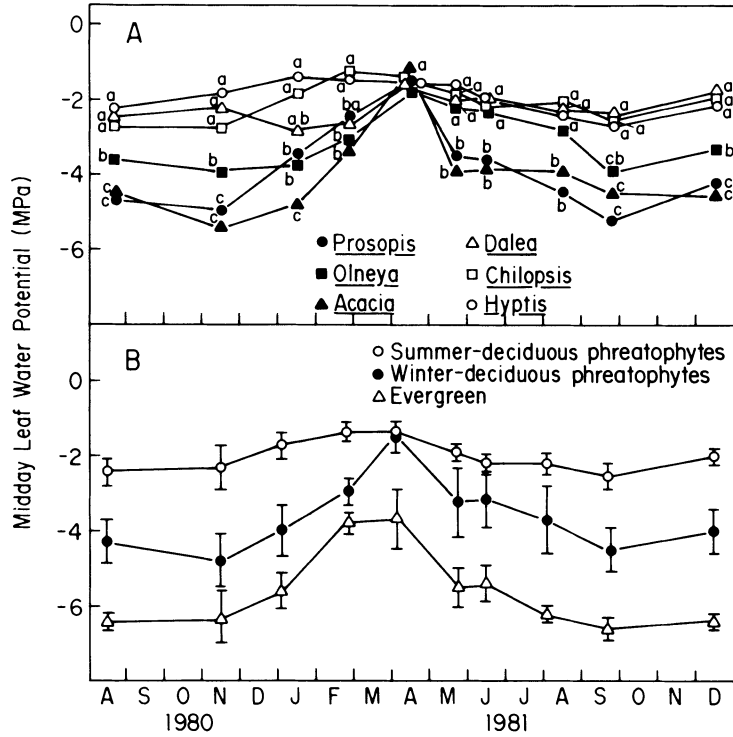


FIG. 4. A. Seasonal course of midday leaf water potential for six phreatophytic species in Nude Wash. Letters correspond to significant differences between species within a sampling date  $P < .05$  ( $F$  test). B. Seasonal course of mean, midday, leaf water potential for groups of species based on growth phenology. Errors bars equal 2 standard errors on each side of the mean.

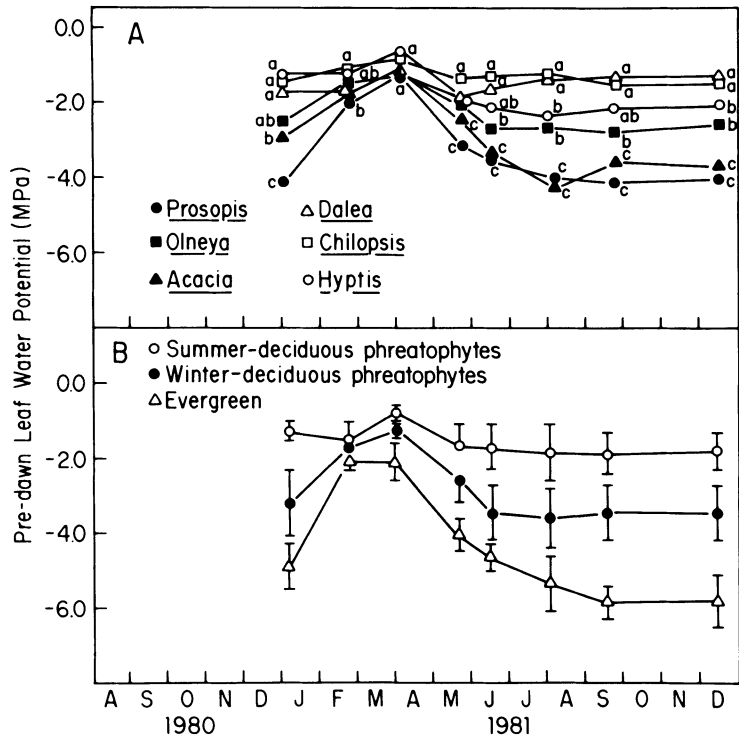


FIG. 5. A. Seasonal course of predawn leaf water potential for six phreatophytic species in Nude Wash. Letters correspond to significant differences between species within a sampling date at  $P < .05$  ( $F$  test). B. Seasonal course of mean predawn leaf water potential for several groups of species based on growth phenology. Error bars equal 2 standard errors on each side of the mean.

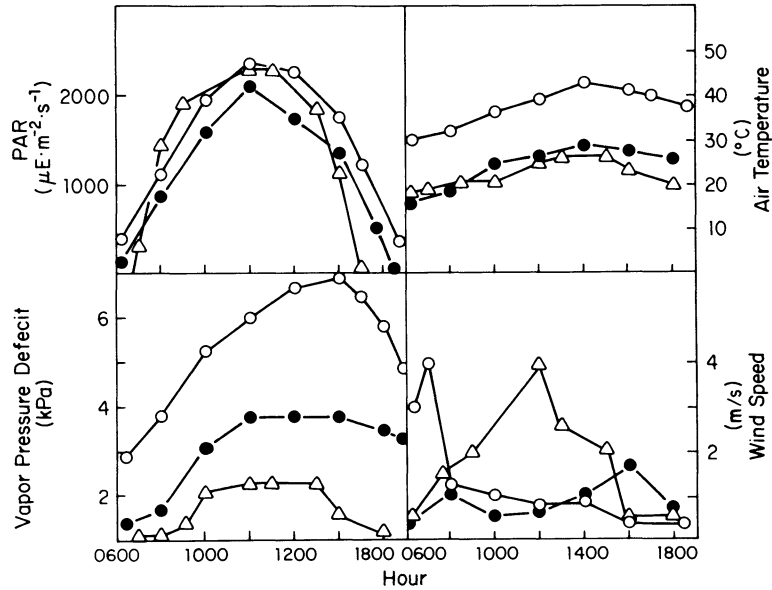


FIG. 6. Diurnal cycles (PST) of microclimatic conditions in Nude Wash on three dates;  $\Delta$  = 7 January 1981,  $\bullet$  = 22 May 1981,  $\circ$  = 4 August 1981. PST = Pacific Standard Time.

imum of 15.5° and 17.5°, respectively. August temperatures were much higher than January or May, reaching a maximum of 45°, with 8 h > 35°, and a minimum of 30°. January had the lowest vapor pressure deficit (VPD) values (maximum = 2.3 kPa), May was intermediate (maximum = 3.8 kPa) and August had the highest (maximum = 6.9 kPa). Wind characteristics were variable on the three chosen dates. In general, the microclimatic conditions of August were most desiccating because of the high temperatures, high VPD, and long photoperiod.

Diurnal cycles of leaf  $\psi$  for six species (Fig. 7) are consistent with species differences described for pre-dawn and midday  $\psi$ . The August  $\psi$  cycles showed the least diurnal variation in comparison to other dates, while the January cycles showed the greatest diurnal variation except for *H. emoryi* and *E. farinosa*. *Hyptis emoryi* only had a small diurnal variation in  $\psi$  in August and January because most leaves had abscised. There was an initial rapid drop in  $\psi$  during August for *E. farinosa* followed by a gradual increase.

Leaf conductance values for *P. glandulosa* and *A. greggii* were significantly higher than for all other species ( $P < .01$ ;  $F$  test, Fig. 8), and both had midday stomatal closure in May but not in August, as did *E. farinosa* and to some degree *O. tesota*. Similar results were found for *P. glandulosa* at another wash community (Nilsen et al. 1983). Even though  $\psi$  values were considerably lower in August than in May for *P. glandulosa*, *A. greggii*, and *O. tesota* (Fig. 7), leaf conductance values were the same or higher in August than in May (Fig. 8). This indicates a change in the relationship between leaf conductance and water potential (Nilsen et al. 1981).

Pressure-volume (PV) relationships of leaf water po-

tential ( $\psi$ ), osmotic potential ( $\pi$ ), and turgor potential ( $\tau$ ), and matric potential ( $m$ ) for eight species in September 1982 are shown in Fig. 9. Considerable vari-

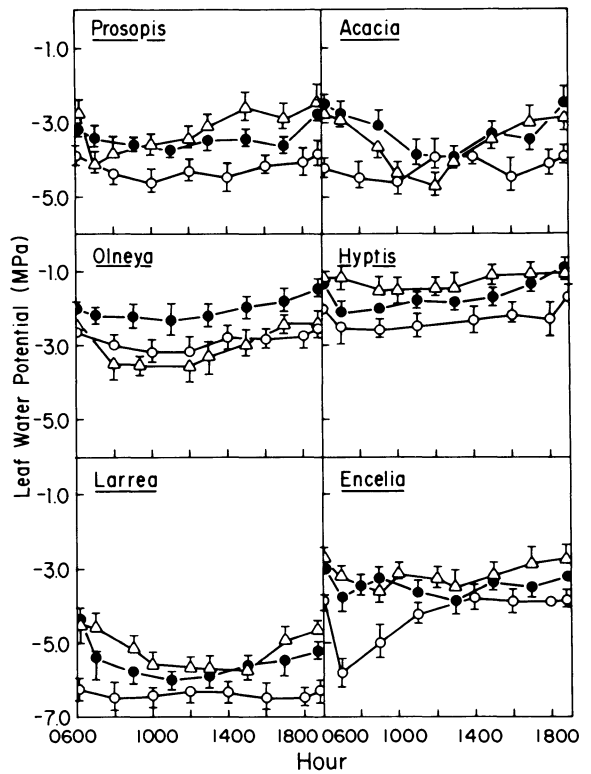


FIG. 7. Diurnal cycles (PST) of leaf water potential for six species in Nude Wash, on three dates;  $\Delta$  = 7 January 1981,  $\bullet$  = 22 May 1981,  $\circ$  = 4 August 1981.

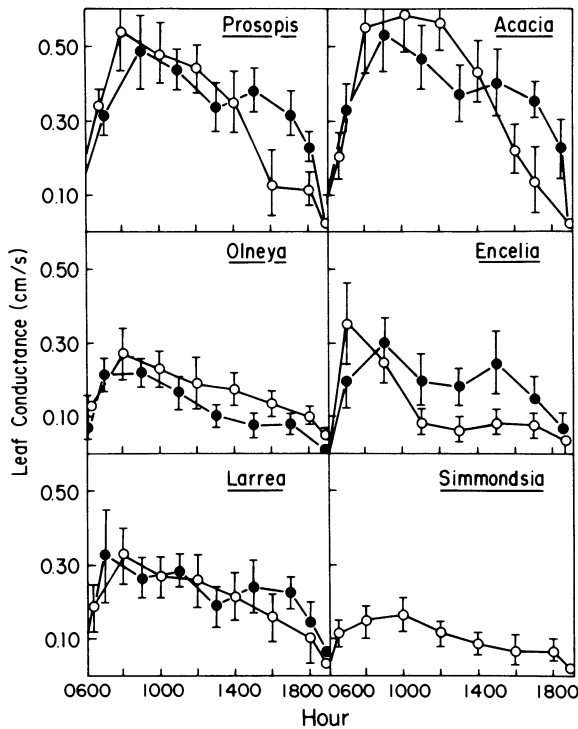


FIG. 8. Diurnal cycles (PST) of leaf conductance for six species in Nude Wash on two dates, ● = 22 May 1981, ○ = 4 August 1981.

ability in osmotic potential was found among the five phreatophytes represented. *Prosopis glandulosa* and *A. greggii* had the lowest osmotic potential at the turgor loss point ( $\psi_s^0$ ), *O. tesota* and *C. linearis* were intermediate, and *H. emoryi* had the highest. There was a similar relationship for the osmotic potential at full turgor ( $\psi_s^{100}$ ). There were only small differences in the water deficit at the turgor loss point ( $WD^0$ ) between the phreatophytes (0.22–0.30). *Prosopis glandulosa* and *O. tesota* maintained turgor to the lowest water deficits. The osmotic potential characteristics of *L. tridentata* and *S. chinensis* were most similar to *A. greggii* and *P. glandulosa* values (Fig. 9).

These data indicate that *P. glandulosa*, *A. greggii*, *L. tridentata*, and *S. chinensis* are the most drought tolerant in September because of their ability to maintain turgor at lower leaf water potentials. *Olneya tesota*, *C. linearis*, and *E. farinosa* seem to be intermediate and *H. emoryi* is the least drought resistant because of the high water potential and low water deficit at the turgor loss point. The pressure-volume diagrams were from only one point in time and there is a diversity of phenologies among these species. Therefore, seasonal PV data will be a better representation of relative drought tolerance.

The annual minimum osmotic potential values were lowest in *P. glandulosa*, *A. greggii*, *L. tridentata*, and *S. chinensis* (Table 1). These low osmotic potentials oc-

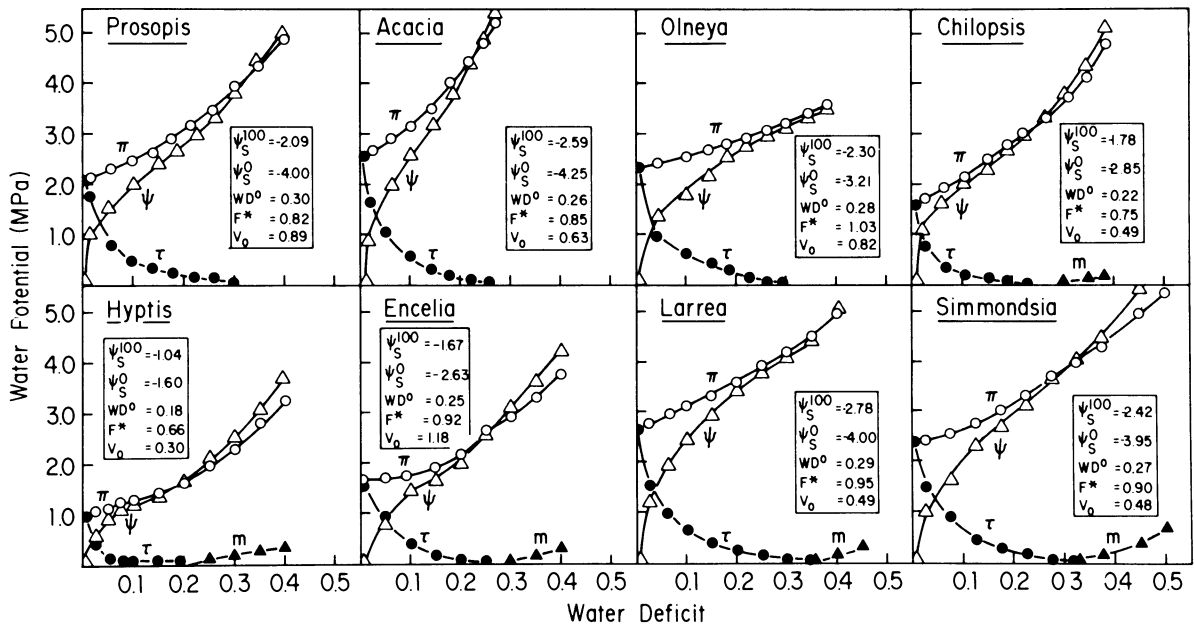


FIG. 9. Diagrams of water relations components against water deficit for eight species from Nude Wash, California. Symbols are:  $\psi$  = leaf water potential,  $\pi$  = osmotic potential,  $\tau$  = turgor potential,  $m$  = matric potential,  $\psi_s^{100}$  = osmotic potential at full turgor,  $\psi_s^0$  = osmotic potential at zero turgor,  $WD^0$  = water deficit at zero turgor,  $F^*$  = relative volume of nonbound symplastic water,  $V_o$  = volume of osmotically active water. All water potentials are negative except turgor ( $\tau$ ), which is positive.



TABLE 1. Mean values for osmotic potentials at full turgor ( $\psi_s^{100}$ ) and zero turgor ( $\psi_s^0$ ), and water deficits at the turgor loss point ( $WD^0$ ) derived from pressure-volume curves for several desert species. Values with the same letter superscripts are not significantly different ( $n = 5$ ;  $P < .05$ ,  $F$  test).

Species	Seasonal minimum			Maximum		
	$\psi_s^{100}$ (MPa)	$\psi_s^0$ (MPa)	Date	$\Delta\psi_s^0$ (MPa)	$WD^0$	$\Delta WD^0$
<i>Prosopis glandulosa</i>	-2.98 <sup>b</sup>	-4.00 <sup>ab</sup>	Sep 81	1.56 <sup>b</sup>	0.34 <sup>a</sup>	0.10 <sup>ab</sup>
<i>Olneya tesota</i>	-2.98 <sup>b</sup>	-3.74 <sup>b</sup>	Jan 82	2.14 <sup>a</sup>	0.28 <sup>ab</sup>	0.04 <sup>b</sup>
<i>Acacia greggii</i>	-2.20 <sup>bc</sup>	-4.25 <sup>a</sup>	Sep 81	1.00 <sup>c</sup>	0.30 <sup>ab</sup>	0.04 <sup>b</sup>
<i>Chilopsis linearis</i>	-1.70 <sup>c</sup>	-2.51 <sup>c</sup>	Aug 81	1.50 <sup>b</sup>	0.24 <sup>b</sup>	0.06 <sup>ab</sup>
<i>Hyptis emoryi</i>	-1.18 <sup>d</sup>	-1.72 <sup>d</sup>	May 81	0.52 <sup>d</sup>	0.20 <sup>b</sup>	0.15 <sup>a</sup>
<i>Encelia farinosa</i>	-1.67 <sup>c</sup>	-2.63 <sup>c</sup>	Aug 81	1.05 <sup>c</sup>	0.25 <sup>b</sup>	0.15 <sup>a</sup>
<i>Larrea tridentata</i>	-2.78 <sup>b</sup>	-5.26 <sup>a</sup>	Feb 82	1.65 <sup>b</sup>	0.39 <sup>a</sup>	0.08 <sup>ab</sup>
<i>Simmondsia chinensis</i>	-3.70 <sup>a</sup>	-5.00 <sup>a</sup>	Sep 82	1.24 <sup>bc</sup>	0.32 <sup>ab</sup>	0.12 <sup>ab</sup>

occurred in September for *S. chinensis*, *A. greggii*, and *P. glandulosa*, but *L. tridentata* did not reach its lowest value until February 1982 (January for *O. tesota*). *Chilopsis linearis* and *E. farinosa* had intermediate minimum osmotic potentials, which occurred in August. The minimum osmotic potential of the season for *H. emoryi*, occurring in May, was significantly higher than for the other species.

The magnitude of seasonal osmotic adjustment is a good index of a species' ability to adapt to changing water stress (Walter and Stadelman 1974, Hellebust 1976). Although *O. tesota* did not have the lowest osmotic potential, this species had the largest seasonal osmotic adjustment (Table 1). *Prosopis glandulosa*, *C. linearis*, and *L. tridentata* had seasonal osmotic adjustments of  $\geq 1.5$  MPa. *Simmondsia chinensis*, *A. greggii*, and *E. farinosa* also had seasonal osmotic adjustments between 1.0 and 1.25 MPa, while *H. emoryi* had the lowest seasonal osmotic adjustment.

Maximum water deficits ( $WD^0$ ) at the turgor loss point ( $\psi_s^0$ ) were quite similar among species except for *H. emoryi*, which had a low value (0.20), and *L. tridentata*, which had a high value (0.39), relative to the other studied species. Only *E. farinosa*, *S. chinensis* and *H. emoryi* had a  $\Delta WD^0 > 0.10$ .

Variability in the volume-averaged elastic modulus (Tyree and Hammel 1972, Richter et al. 1980), or  $E_{vat}$ , has been considered as a mechanism of adaptation to water stress (Roberts et al. 1981). The  $E_{vat}$  is the slope of turgor potential vs. water deficit. The larger the value of  $E_{vat}$  the more rapidly turgor decreased with increasing water deficit. There is very little variation among species values of  $E_{vat}$ . Therefore, because of the considerable error potential in measuring  $E_{vat}$  (Richter et al. 1980) and the small variation in  $E_{vat}$  between species, there seems to be no significant difference in elastic modulus characteristics between species.

*Larrea tridentata*, *S. chinensis*, *A. greggii*, and *P. glandulosa* had lower field, midday, leaf water potential than the leaf water potentials at the turgor loss point derived from predawn PV curves. This suggested either that diurnal osmotic adjustment may have been occurring because the reported PV relationships were col-

lected on branches cut at dawn, or that negative turgor may have existed (Tyree 1976). For this reason, samples for PV analyses were collected at dawn and midday during September 1982.

All species exhibited diurnal osmotic adjustment except for *L. tridentata* (Fig. 10). The magnitude of diurnal osmotic adjustment varied among species, as shown in Table 2. Here we present the predawn and midday leaf water potential ( $\psi$ ), osmotic potentials ( $\psi_s^0$ ,  $\psi_s^{100}$ ), and water deficit at the turgor loss point ( $WD^0$ ) for each species studied. Maximum diurnal osmotic adjustment occurred in *S. chinensis*, *A. greggii*, and *P. glandulosa*. *Olneya tesota* had little diurnal osmotic adjustment. There was no diurnal adjustment of the  $WD^0$  for any species. At predawn *P. glandulosa* and *L. tridentata* seemed to have slightly negative turgor, but these negative values are so small that it is most likely that small errors in leaf water potential and PV curve measurements are responsible. All other species had positive turgor at predawn, ranging from 1.21 MPa for *A. greggii* to 0.63 MPa for *S. chinensis*. At midday, *P. glandulosa* still had close to zero turgor even though there was an osmotic adjustment of 0.91 MPa. *Acacia greggii* and *S. chinensis* maintained turgor potential at midday only because of their large osmotic potential adjustment. *Olneya tesota* would have maintained turgor even if the small osmotic adjustment of 0.37 MPa had not occurred. *Larrea tridentata* had a large estimated negative turgor at midday because no diurnal osmotic adjustment was measurable.

## DISCUSSION

In past reports (Levitt 1980) phreatophytes have been described as deep-rooted trees with poor water use efficiency which survive in deserts by utilizing ground water to avoid the complications of water stress. However, the data collected in this study indicate that the phreatophytes are a diverse group which exhibit several mechanisms of avoiding and tolerating water stress, as previously suggested for *P. juliflora* and *P. glandulosa* (Mooney et al. 1977, Nilsen et al. 1983). The phreatophytes studied in this investigation can be placed in three categories based on their phenology and water

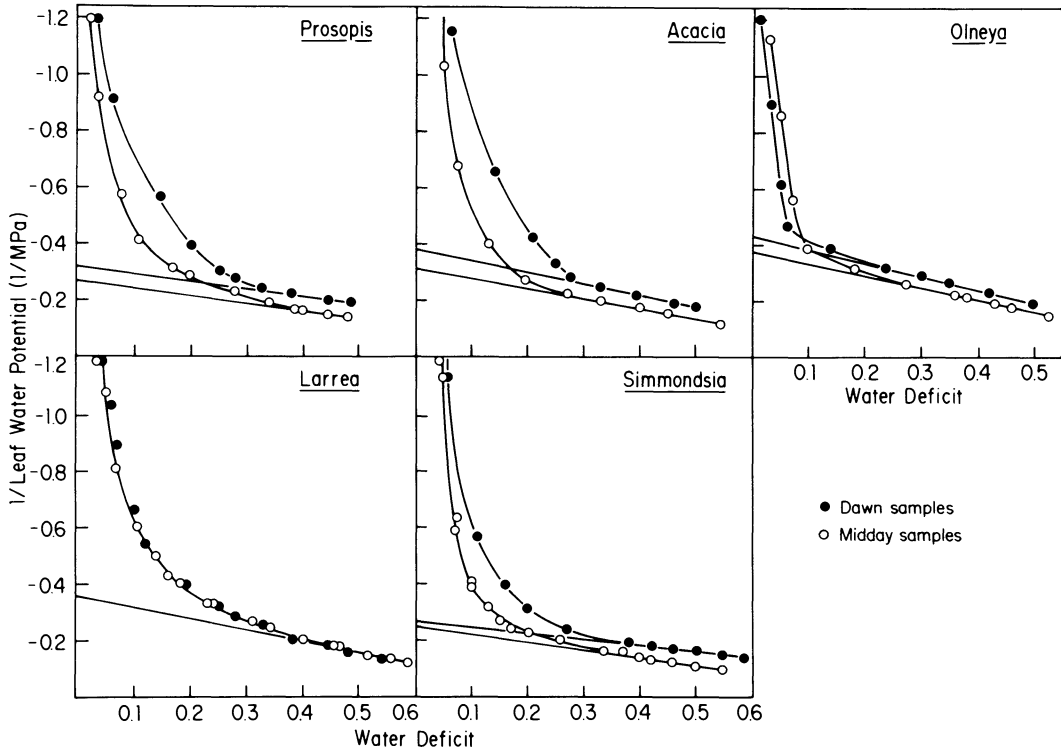


FIG. 10. Plots of pressure-volume (PV) curves derived from midday and dawn PV curve samples of five species from Nude Wash during September 1982. (● = dawn samples, ○ = midday samples).

relations parameters. Each category has a different suite of adaptations to the water deficiency imposed by the desert environment. These categories are winter-deciduous, summer-deciduous, and stem photosynthetic phreatophytes.

*Mechanisms of drought avoidance*

One classic mechanism of drought avoidance in desert plants is deciduousness during the driest and hottest period of the year, resulting in a reduction of transpi-

TABLE 2. Predawn and midday water relations parameters for five desert species derived from representative pressure-volume analyses for individuals during September 1982, in Nude Wash of the Sonoran Desert, California.  $\psi$  = leaf water potential;  $\psi_s^{100}$  = leaf osmotic potential at full turgor;  $\psi_s^0$  = leaf osmotic potential at the turgor loss point;  $WD^0$  = leaf water deficit at the turgor loss point;  $\tau$  = leaf turgor potential.

	<i>Prosopis glandulosa</i>	<i>Acacia greggii</i>	<i>Olneya tesota</i>	<i>Larrea tridentata</i>	<i>Simmondsia chinensis</i>
<b>Predawn</b>					
$\psi$ (MPa)	-3.96	-2.96	-2.23	-5.37	-4.33
$\psi_s^{100}$ (MPa)	-3.03	-3.23	-2.70	-2.77	-3.70
$\psi_s^0$ (MPa)	-3.85	-4.17	-3.33	-5.26	-5.00
$WD^0$	0.34	0.30	0.23	0.39	0.32
$\tau$ (MPa)	-0.11	1.21	1.10	-0.11	0.63
<b>Midday</b>					
$\psi$ (MPa)	-4.75	-4.58	-3.10	-6.40	-5.90
$\psi_s^{100}$ (MPa)	-2.70	-2.67	-2.33	-2.77	-4.00
$\psi_s^0$ (MPa)	-4.76	-5.13	-3.70	-5.26	-6.25
$WD^0$	0.34	0.30	0.23	0.39	0.32
$\tau$ (MPa)	0.01	0.53	0.60	-1.14	0.85
<b>(Midday)-(predawn)</b>					
$\Delta\psi_s^{100}$ (MPa)	-0.33	-0.56	-0.36	0.0	-0.30
$\Delta\psi_s^0$ (MPa)	-0.91	-0.96	-0.37	0.0	-1.25
$\Delta WD^0$	0.0	0.0	0.0	0.0	0.0

rational surface area (Orshan 1954). There are many drought-deciduous species in the Sonoran Desert of California, including the widespread *Encelia farinosa*. The small leaf area during the summer also reduces water use and prevents the development of extremely low water potentials in these plants. Both *H. emoryi* and *C. linearis* utilize the drought-deciduous avoidance mechanism. *Dalea spinosa* is virtually leafless all year and similarly avoids water loss during the summer. Because the phreatophytes also utilize deep water, the water potentials of the summer-deciduous phreatophytes are not so low as summer-deciduous shrubs (*E. farinosa*, *B. californica*) during June through November. The phenology of the other phreatophytes is out of phase with temporal evaporative demand, since they are deciduous in the winter and maximum leaf area occurs during the summer. These species utilize ground water at depth to maintain high dawn water potentials in relation to the shallow-rooted species.

The magnitude of stomatal conductance can also be viewed as a mechanism of drought avoidance. As suggested by Monson and Smith (1982), very low conductance values act to inhibit water loss and conserve water to avoid water stress. *Olneya tesota* and *H. emoryi* both have low conductance values compared to the other phreatophytes. The low conductance reduces water loss, resulting in the maintenance of higher water potentials than for those species with high conductance rates. The evergreen species in our study also had low conductance values for water conservation similar to those found by Strain (1975). It may be advantageous for evergreens to conserve water because they have relatively large leaf areas during the summer, and minimal competition for water exists between species of evergreens (Fonteyn and Mahall 1978). *Dalea spinosa* effectively maintains high dawn and midday water potentials by having a small leaf area, as does *C. microphyllum* (Adams et al. 1967).

*Cucurbita* was the most efficient avoider of low water potential. Its water potential values were always high (midday not below  $-1.5$  MPa) due to the short leaf longevity and the succulent root.

#### Mechanisms of drought tolerance

Several of the phreatophytic species maintained low seasonal and diurnal water potential in contrast to previous reports for phreatophytes (Szarek and Woodhouse 1977, Monson and Smith 1982). The low water potential values for *P. glandulosa*, *A. greggii*, and *O. tesota* suggest that mechanisms of drought avoidance must exist. The winter-deciduous phreatophytes did not experience water potentials so low as the evergreen, shallow-rooted species which are considered to have mechanisms of drought tolerance (Strain 1975, Bennett and Mooney 1979).

The maintenance of low plant osmotic potential is considered a mechanism of drought tolerance because turgor can be maintained at low plant water potentials (Hellebust 1976, Hsiao et al. 1976). The winter-decid-

uous phreatophytes had low seasonal osmotic potentials which were almost as low as the shallow-rooted, evergreen species. The summer-deciduous and stem photosynthetic phreatophytes had high osmotic potentials. The ability to adjust osmotic potential over the season as water stress becomes more severe is also a mechanism for tolerating water stress. *Prosopis glandulosa*, *O. tesota*, *A. greggii*, and *C. linearis* had considerable seasonal osmotic adjustment in comparison to the other phreatophytes. Even though *C. linearis* is summer deciduous, there was a second growth period in the late spring/early summer. The leaves of the second growth period had lower osmotic potential than the leaves produced in the winter, resulting in large seasonal osmotic adjustments. The evergreen species had lower osmotic adjustments than the winter deciduous phreatophytes because their osmotic potentials were low throughout the year.

The ability to maintain turgor at low leaf water content (measured by  $WD^0$ ) was fairly consistent between species (0.22–0.39). Only *L. tridentata* maintained turgor to water deficits close to 0.40. *Hyptis emoryi*, on the other hand, lost turgor at low water deficits. The ability to maintain turgor at low leaf water content varied minimally between the studied phreatophytes in relation to the seasonal variation in osmotic adjustment.

Two of the winter-deciduous phreatophytes were able to maintain high conductance values at low water potentials. This enabled *P. glandulosa* and possibly *A. greggii* to have high productivity in the desert environment (Felker 1979, Nilsen et al. 1982, Sharifi et al. 1982). The other phreatophytes, including the winter deciduous *O. tesota*, had lower conductance values similar to the evergreen and summer-deciduous shrubs.

The presence of diurnal osmotic adjustment was indicated by the midday water potentials, which were lower than those at the turgor loss point derived from the PV analyses. Diurnal osmotic adjustment occurred in *S. chinensis*, *P. glandulosa*, *A. greggii* and *O. tesota*, but not in *L. tridentata*, in September 1982. This diurnal osmotic adjustment was required to maintain turgor at midday for *S. chinensis*, *A. greggii*, and *P. glandulosa*. The diurnal adjustment for *P. glandulosa* just maintained zero turgor at midday. For *O. tesota* the small diurnal osmotic adjustment which occurred was not necessary for the maintenance of positive turgor. *Larrea tridentata* did not exhibit diurnal osmotic adjustment; as a result a large negative turgor ( $-1.14$  MPa) seemed to develop. Other authors have found the same discrepancy for *L. tridentata* (Monson and Smith 1982). Since negative turgor is theorized not to exist (Tyree 1976) the lack of diurnal osmotic adjustment in *L. tridentata* remains unexplainable.

#### CONCLUSIONS

Phreatophytes of the Sonoran Desert have a complex suite of water stress avoidance and tolerance mechanisms. Each species has a different complex of water

stress adaptations. *Prosopis glandulosa* and *A. greggii* tolerate summer water stress by adjusting osmotic potential and maintaining high conductance in the morning through the summer months. Therefore, they attain maximum leaf area for photosynthesis during the summer. On the other hand, *O. tesota* adjusts osmotic potential to maintain turgor during the late summer, but this species also avoids early-summer water stress by maintaining low conductance rates. *Chilopsis linearis* and *H. emoryi* minimize water stress by their summer deciduous habit, and *C. linearis* adjusts the osmotic potential in a second set of leaves produced in early summer to maintain turgor at the early-summer, low, leaf water potential. *Dalea spinosa* has extremely small leaves, and therefore has a reduced leaf area all year, thus minimizing water stress in the summer. On the basis of the general adaptations to water stress, these phreatophytes can be placed into three categories which correspond with phenological categories: (1) winter-spring deciduous (*P. glandulosa*, *A. greggii*, *O. tesota*); (2) summer deciduous (*H. emoryi*, *C. linearis*); (3) stem photosynthetic-leafless (*D. spinosa*).

The variation in phreatophyte adaptations to water stress includes all mechanisms exhibited by the evergreen and deciduous desert shrubs in this study. In the study site the evergreen shrubs had lower osmotic potential and lower midday water potentials, but the winter deciduous phreatophytes had equivalent seasonal osmotic adjustment. This study clearly indicates that the desert phreatophytes are a diverse group with a complex set of adaptations to the desert environment.

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