

EFFECTS OF PLANT SIZE ON PHOTOSYNTHESIS AND WATER RELATIONS IN THE DESERT SHRUB *PROSOPIS GLANDULOSA* (FABACEAE)¹

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The Jornada del Muerto basin of the Chihuahuan Desert of southern New Mexico, USA, has undergone a marked transition of plant communities. Shrubs such as mesquite (*Prosopis glandulosa*) have greatly increased or now dominate in areas that were previously dominated by perennial grasses. The replacement of grasses by shrubs requires an establishment phase where small shrubs must compete directly with similar-sized grass plants. This is followed by a phase in which large, established shrubs sequester nutrients and water within their biomass and alter soil resources directly under their canopy, creating "islands" of fertility. We hypothesized that these two phases were associated with shrubs having different physiological response capacities related to their age or size and the resource structure of the environment. As a corollary, we hypothesized that responses of small shrubs would be more tightly coupled to variation in soil moisture availability compared to large shrubs. To test these hypotheses, we studied gas exchange and water relations of small (establishing) and large (established) shrubs growing in the Jornada del Muerto as a function of varying soil moisture during the season. The small shrubs had greater net assimilation, stomatal conductance, transpiration, and xylem water potential than large shrubs following high summer rainfall in July, and highest seasonal soil moisture at 0.3 m. High rates of carbon assimilation and water use would be an advantage for small shrubs competing with grasses when shallow soil moisture was plentiful. Large shrubs had greater net assimilation and water-use efficiency, and lower xylem water potential than small shrubs following a dry period in September, when soil moisture at 0.3 m was lowest. Low xylem water potentials and high water-use efficiency would allow large shrubs to continue acquiring and conserving water as soil moisture is depleted. Although the study provides evidence of differences in physiological responses of different-sized shrubs, there was not support for the hypothesis that small shrubs are more closely coupled to variation in soil moisture availability than large shrubs. Small shrubs may actually be less coupled to soil moisture than large shrubs, and thus avoid conditions when continued transpiration could not be matched by equivalent water uptake.

Key words: Chihuahuan Desert; Fabaceae; photosynthesis; plant size; *Prosopis glandulosa*; shrub; water relations.

Mesquite (*Prosopis glandulosa* (Torr.) var. *glandulosa* Torr.) is a winter-deciduous, leguminous shrub that has greatly increased in abundance during the last century in valleys and basins throughout the southwestern U.S. where grasses previously dominated. The replacement of grass by mesquite and other shrubs may be due to a number of interacting factors, including grazing, drought, climate shifts, and perhaps fire (Buffington and Herbel, 1965; Schlesinger et al., 1990). To be able to predict which life form (shrub vs. grass) will predominate, particularly with respect to climatic change or environmental perturbation, depends on understanding how the two interact. In this context there may be two rather different

levels of interaction. Small, establishing shrubs may be functionally similar to the perennial bunch grasses that they displace (Reynolds et al., in press), and must compete more directly with them for water and nutrient resources. As the shrubs increase in size and become established, their roots exploit a larger volume of soil, accessing deeper soil moisture than is available to grasses (Nilsen et al., 1983). They simultaneously sequester increasing water and nutrients within an increasing biomass, and effectively "focus" resources into soil regions under their canopy through accumulations of litter, airborne particulates, and interception and stemflow of rainfall—and thus by changes in size and morphology alone become more effective competitors for limited soil moisture and nutrient resources (Gadzia and Ludwig, 1983; Schlesinger et al., 1990).

However, there is a question as to whether these morphological, size-related changes in the shrubs are accompanied by physiological changes that would allow them to make more effective use of the changing resource structure of the environment, and thus be more effective competitors during these different phases. Factors such as stomatal sensitivity to soil and atmospheric water and photosynthetic sensitivity to reduced plant water and ni-

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trogen could change either as an inherent aspect of plant age, as found in *Hedera helix* (Bauer and Bauer, 1980), or, perhaps more simply, as an aspect of size-dependent capacity related to the shrub's water, nutrient, and osmotic reserves. Size (age) dependent differences in photosynthesis and stomatal conductance have been reported in mesquite (Brown and Archer, 1990), and size (age) dependent differences in water-use efficiency have been found in the desert shrub *Chrysothamnus nauseosus* (Donovan and Ehleringer, 1992).

We hypothesized that mesquite shrubs of different sizes would have different physiological responses to soil water availability. Small shrubs that must compete with grasses to become established would be expected to have high rates of carbon gain, high stomatal conductance, and to use soil moisture rapidly when it was available (thus having low water-use efficiency; Donovan and Ehleringer, 1994), whereas larger shrubs with greater biomass, and greater stored nutrients and water, would be expected to have greater stomatal control of water loss, lower carbon gain, and higher water-use efficiency than small shrubs. Small shrubs should be impacted more quickly by soil drying, but this might be offset by a quicker response to rainfall due to a more rapid rehydration of the smaller plant body and greater rooting in shallow layers. This suite of expected differences, in terms of sensitivity to moisture availability and rapidity of response, is summarized as a second, corollary hypothesis: small shrub response is more closely coupled to variation in soil moisture than large shrub response (i.e., large shrubs have greater inertia).

To investigate these hypotheses we examined the relationships among plant and soil water content, and the gas-exchange characteristics of small and large plants of mesquite growing in a sand dune habitat developed from former grassland communities. This site is severely degraded, having low concentrations of organic C, N, and P, and lower soil moisture than any other mesquite habitat in the Jornada Basin (Virginia et al., 1992). We expected that plants growing in this stressful environment would show the clearest evidence of size-dependent coupling of physiological response with moisture availability.

MATERIALS AND METHODS

Study site—The study site was on the United States Department of Agriculture (USDA) Jornada Experimental Range in the Jornada del Muerto Basin, 40 km NNE of Las Cruces, Doña Ana County, New Mexico, USA. The area has an elevation of 1200–2000 m, and is close to the northern limits of the Chihuahuan Desert. The climate is semiarid, with a mean annual precipitation of 233 mm (Conley, Conley, and Karl, 1992), of which 64% occurs as summer (July–October) rainfall from brief convective storms. Summer mean maximum and minimum temperatures are 31 C and 10 C (Conley, Conley, and Karl, 1992), while freezing temperatures may occur from late October to mid-April (data from the Jornada LTER Weather Station). The experimental site, near Waggoner Well, in the northwest flank of the USDA Experimental Range, is a sand dune area, which began forming ≈ 80 yr ago following intensive grazing and drought (Buffington and Herbel, 1965; Hennessy et al., 1983).

Sample plots and shrub size classes—At the study site, *Prosopis glandulosa* grows as a multistemmed shrub. We considered clumps having a discrete canopy to represent a single shrub, and from this popu-

lation we selected eight large (established) shrubs and eight small (establishing) shrubs on the basis of height, diameter, and litter accumulation under the shrubs. Root excavations have shown that adjacent clumps are not connected, although root systems may overlap to some degree (Ludwig, 1977). The root systems of the selected shrubs were isolated from the surrounding soil by digging a trench 0.6 m from the edge of the shrub's crown to a depth of ≈ 1.5 m, lining the trench with black plastic sheeting, and returning the soil to the trench. Trenching was done between January and February 1991. The trench also minimizes the effects of neighboring plants on the water relations of these selected shrubs. Crown volume (calculated as a cone) and height of small shrubs averaged 0.079 ± 0.026 m³ and 0.49 ± 0.06 m, respectively, and of large shrubs averaged 2.598 ± 0.55 m³ and 1.062 ± 0.13 m, respectively.

Water relations and gas exchange—Soil water content, shrub water relations, and diurnal courses of gas exchange were measured at four times during the summer season: 29 July, 21 August, 5 September, and 30 September, 1991. These measurement times corresponded, respectively, to (a) following relatively high rainfall and soil water recharge of the upper profile, (b) following relatively high rainfall, but soil water depletion of upper layers, (c) following relatively little rainfall and further soil water depletion, and (d) following moderate rainfall and partial soil water recharge of the upper profile (see Results for details). Soil volumetric water contents (VWC) were measured in each plot (eight each, large and small shrubs), at three depths (0.3 m, 0.6 m, and 0.9 m) using the neutron attenuation (scatter) method (e.g., Rundel and Jarrell, 1989) with a 503DR hydroprobe (CPN Corp., CA). Aluminum access tubes for the hydroprobe were installed in the southern side of each plot, midway between the edge of the canopy and the edge of the plot at the plastic liner. Neutron probe access tubes were installed several weeks before any measurements were taken. A calibration equation relating neutron counts to volumetric water content of soil samples was derived from numerous samples of coarse-textured soils taken from surrounding areas, though not specifically within the experimental plots. The soils were generally uniform among the experimental plots and with depth; thus, neutron counts provided a good relative measure of VWC between shrub size classes.

Shrub water potentials and gas exchange were measured on a subsample of three or four shrubs of each size class at each sample time. Predawn xylem water potentials (ψ_L) were determined with a model 3005-1422 Plant Water Status Console (Soil Moisture Corp., Santa Barbara, CA) from one stem of each small shrub and two stems of each large shrub. Only one small stem segment was sampled from each of the small shrubs in order to avoid excessive defoliation. Thus, mean values of ψ_L for each size class were based on 3–4 individual values for small or 6–8 values for large shrubs.

Diurnal courses of net assimilation (A), transpiration (E), and stomatal conductance (g_s) were measured using a LI6200 portable photosynthesis system (LI-COR, Inc., Lincoln, NE). At the start of each measurement day we selected two compound leaves at the outer edge of the canopy of each shrub, for ease of access and for best light interception. These leaves were marked for repeat gas exchange measurements during that day with yarn tied lightly onto the stem at the base of the petiole. Each measurement took 10 sec, and a leaf was inside the LI6200 leaf chamber for < 20 sec. Any data points indicating large changes in chamber conditions (e.g., chamber temperature, relative humidity) were excluded from the final data set. The LI6200 measures leaf and air temperatures, photosynthetically active photon flux density (PPFD; 400–700 nm wavelength), CO₂ concentration, and the vapor pressure of the air, and from this information calculates values of A , E , and g_s . From the diurnal measurements, we calculated daily values of A and E (A_d and E_d) by integrating (trapezoidal) from the first measurement to the last ($\approx 8:30$ a.m. to 4:30 p.m. Mountain Daylight Time [MDT]). Integrations were adjusted slightly so that all integrated values

were based on 8 hr. Thus, actual daily values of A and E were greater than those reported since we did not extrapolate to sunrise or sunset.

Statistical analysis—Differences between large and small shrubs were investigated by one-way analysis of variance (ANOVA). Where skewed or kurtotic data was encountered the nonparametric Kruskal-Wallis test was used, and in every case confirmed the ANOVA results that were reported. Repeated-measures ANOVA (rANOVA) was used to test for significant changes in VWC, PPFD, and ψ_L through time. However, rANOVA was not used to investigate gas exchange factors because successive measurements were taken on different individuals, different branches, and with different light and microclimate conditions, and thus were largely independent of each other. In order to quantify the degree of coupling of shrub physiological response to environmental moisture, as well as relate responses to internal plant controls, we used least-squares regression models to test for significant relations of A , E , and A_i/E_i with soil VWC, atmospheric VPD, shrub ψ_L , and g_s .

RESULTS

Water relations—Air temperature and precipitation recorded at the study site during the summer 1991 growing season are shown in Fig. 1A. The preceding spring (data not shown) was characteristically warm and dry (April–June rainfall was 13 mm, compared to the long-term average of 28 mm; Conley, Conley, and Karl, 1992). The total July–September precipitation was 154 mm, $\approx 25\%$ greater than the long-term mean (Conley, Conley, and Karl, 1992). However, the precipitation was distributed such that there were distinctly moist and dry periods. Late July (prior to the first sample date, 29 July) was moist with ≈ 60 mm of rainfall; 29 July to 21 August (the second sample date) received moderate (48 mm) rain. This was followed by a dry period from 21 August to 5 September (the third sample date) with only 10 mm of rain. A large rainfall of 24 mm on 18 September resulted in partial soil water recharge by the final sample date of 30 September.

During the period from 29 July and 21 August, VWC at 0.3 m in soil of both shrub size classes declined slightly, though not significantly (Fig. 1). From 21 August to 5 September, VWC at 0.3 m declined significantly ($P < 0.05$) in soils of both shrub size classes (Fig. 1). During the period from 5 September to 30 September, VWC at 0.3 m increased slightly, though not significantly in soils of both shrub size classes (Fig. 1). The VWC at 0.6 m and 0.9 m did not change significantly during the course of the study (Fig. 1). However, at 0.6 m, there was significantly less water throughout the study in soils of large shrubs (rANOVA, $P < 0.05$, $df = 15$). Shrub ψ_L varied significantly during the course of the study (rANOVA, $P < 0.05$, $df = 15$), but not in a manner entirely consistent with the variation in soil water content. The ψ_L of both shrub size classes decreased slightly from the first to second measurement periods (Fig. 1D), though not significantly, and ψ_L was not significantly different between shrub size classes during the first two measurement dates. At the third measurement date (5 September), the ψ_L of small shrubs had increased, and was significantly greater than the large shrubs (Fig. 1D; rANOVA, $P < 0.05$, $df = 15$). This result is rather puzzling, in view of the lack of rain, or recharge of soil moisture. The ψ_L of small shrubs had decreased at the final sample date and was not significantly different from ψ_L of large shrubs, which

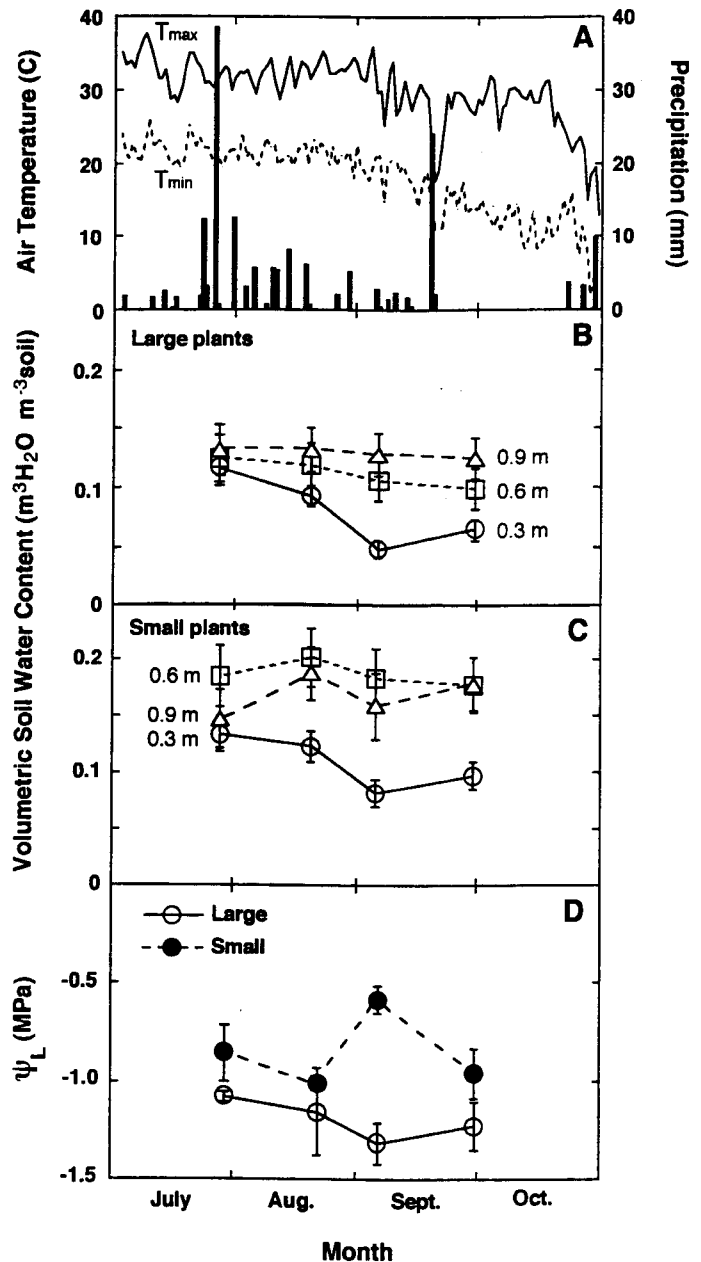


Fig. 1. (A) Changes in maximum (T_{max}) and minimum (T_{min}) air temperatures, and precipitation from July through October 1991. (B), (C) Changes in volumetric soil water content (mean ± 1 SE; $N = 8$) at three different depths for large (B) and small (C) shrubs. Readings were taken near the edge of the canopy of each shrub. (D) Mean pre-dawn xylem water potentials (ψ_L) in large and small shrubs ($N = 3$ or 4 plants ± 1 SE).

had changed little from the previous sample date. The ψ_L of small shrubs through time was not significantly correlated with soil VWC at any depth, whereas the ψ_L of the large shrubs was highly correlated with soil VWC of 0.3 m ($r^2 = 0.84$; $P < 0.01$).

Leaf gas exchange—Results from the diurnal measurements of gas exchange are shown in Fig. 2. Air temperature (T_{air}) and leaf-to-air Vapor Pressure Deficit (VPD) were generally very similar between small and

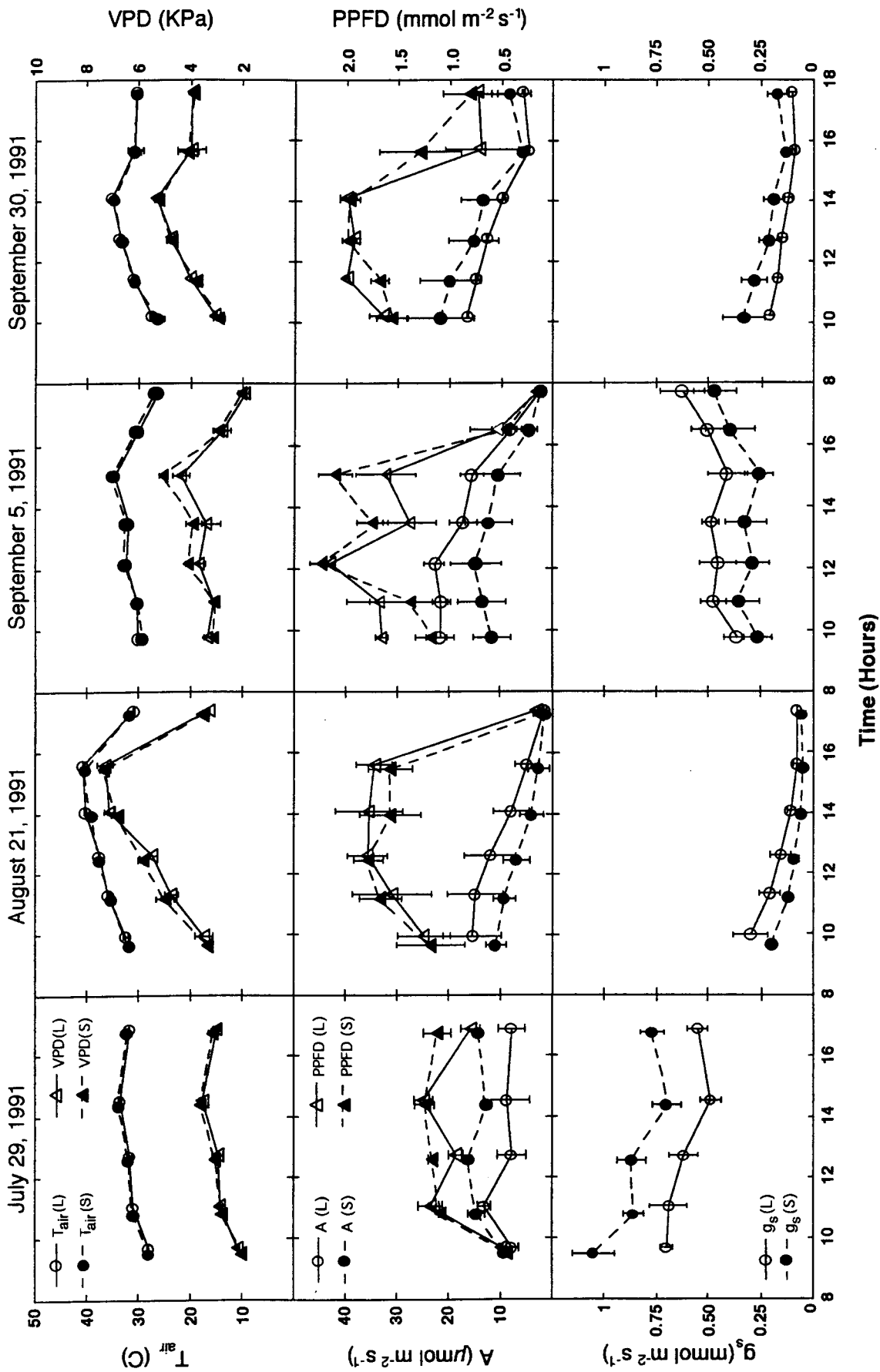


Fig. 2. Diurnal courses for air temperature (T_{air}), leaf-to-air vapor pressure deficit (VPD), photosynthetic photon flux density (PPFD), net assimilation (A), and stomatal conductance (g_s) for large and small shrubs on 4 d, 29 July (sunrise 6:10 MDT), 21 August (6:30 sunrise MDT), 5 September (sunrise 6:45), and 30 September (sunrise 7:06 MDT). Values are means \pm 1 SE for 3-4 plants.

large shrubs at all times. Photosynthetic Photon Flux Density (PPFD) varied between shrub size classes at infrequent times during the day (due to changing cloud cover between measurements), but integrated values of PPFD during the day were not significantly different between shrub size classes (ANOVA, $P < 0.05$, $df = 14$ to 20). Values of PPFD (both integrated and daily maximums) were similar on all dates except 29 July, when the maximum value was about half as great as the other days; however, the integrated values were not significantly different among days (rANOVA, $P > 0.05$, $df = 59$).

Net CO_2 assimilation rates (A) of both shrub size classes had a similar diurnal pattern, in that rates were greatest early in the day and declined throughout the day, except on 29 July when they were about constant through the day. Values of A of small shrubs were greater than those of large shrubs on 29 July (ANOVA, $P < 0.05$, $df = 28$), similar between the size classes on 21 August, greater in large shrubs on 5 September, and similar again on 30 September. These differences are summarized in the integrated daily A (A_d) shown in Fig. 3A. Stomatal conductances were also greatest early in the day and decreased thereafter, except on 30 September, when they increased somewhat during the day. Small shrubs had significantly greater rates of stomatal conductance on 29 July, shrubs were similar on 21 August and 30 September, and large shrubs had greater stomatal conductances on 5 September.

In addition to the integrated values of A , we also show the integrated values of E (E_d) and ratio of A_d/E_d (Fig. 3). The pattern of E_d during the season was similar for both shrub size classes, relatively high on 29 July, low on 21 August, moderate-high on 5 September, and moderate-low on 30 September. The ratio (A_d/E_d), daily plant water-use efficiency, also had a similar pattern for both shrub size classes, increasing through the season, with large shrubs having significantly higher A_d/E_d on 5 September.

We further investigated the internal and environmental control of shrub physiological responses (A , E , and A_d/E_d) using regression models. The A_d of small shrubs was not correlated with environmental moisture (soil VWC or atmospheric VPD), shrub moisture status (ψ_L), or stomatal conductance. The A_d of large shrubs was significantly negatively correlated with both soil VWC ($r^2 = 0.75$; $P < 0.05$) and shrub ψ_L ($r^2 = 0.81$; $P < 0.01$), but not with mean daily g_s or VPD. The E_d of both small and large shrubs was not correlated with soil or plant water status, but was strongly related to atmospheric VPD ($r^2 = 0.66$ and 0.75 , respectively). This relationship was due to the strong control of g_s by VPD. Linear regression models revealed that the g_s of large shrubs were strongly related to VPD on 29 July, 21 August, and 30 September, while the g_s of small shrubs were strongly related to VPD on 29 July and 21 August (Fig. 4). The g_s to VPD relationship in both size classes deteriorated during the drought period and recovered by 30 September in large shrubs only. During the drought period large changes in VPD elicited only very small changes in g_s . The ratio A_d/E_d was not correlated with soil and plant water status, nor with VPD in either shrub class.

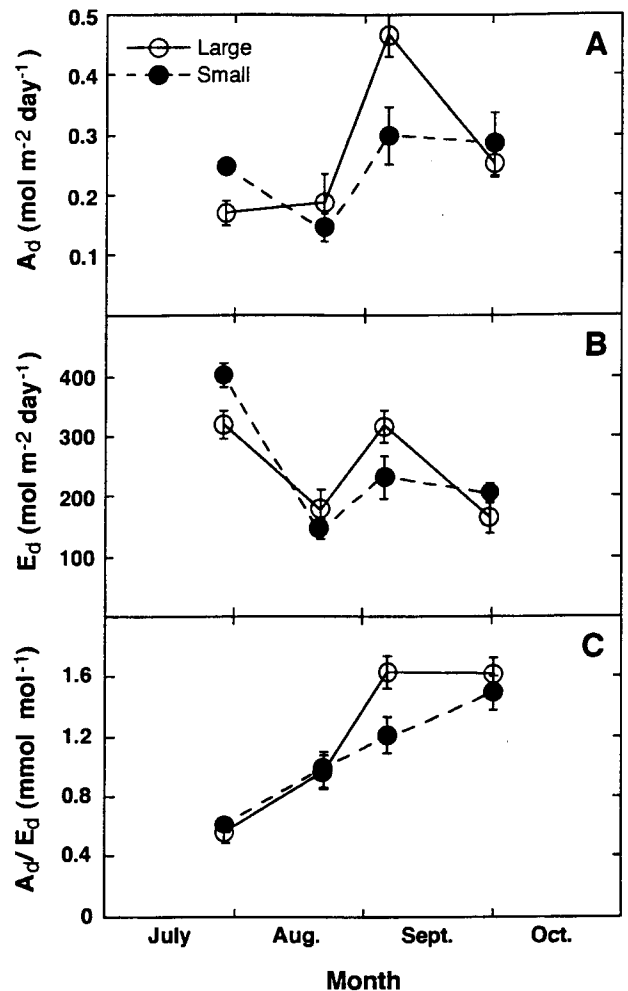


Fig. 3. (A) Daily assimilation rates (A_d), (B) daily transpiration rates (E_d), and (C) water-use efficiency (A_d/E_d) for large and small shrubs on the four measurement days 11 July, 21 August, 5 September, and 30 September. Net assimilation and transpiration rates of individual shrubs were derived by integrating diurnal values between 8:30 a.m. and 4:30 p.m. Values are means \pm 1 SE for 3–4 plants.

DISCUSSION

There were three principal differences between the large and small shrubs found in this study: (a) soil water at 0.6 m was greater under small shrubs during the entire study; (b) small shrubs had greater A_d , E_d , g_s , and ψ_L than large shrubs on the first measurement date (29 July) when soils had greatest VWC at 0.3 m; and (c) large shrubs had greater A_d , A_d/E_d , and g_s , but lower ψ_L than small shrubs on 5 September, when soil VWC at 0.3 m was lowest. The first of these differences, VWC at 0.6 m, is most easily explained by the differences in size and rooting mass of the two shrub classes. Small shrubs have less total transpirational surface, less demand for water, and probably less root mass in the deeper soils (e.g., Freckman and Virginia, 1989), and should therefore deplete soil water less than large shrubs, particularly in deeper soils. However, during the course of the study, water was depleted largely from the region around 0.3 m similarly by both shrub size classes. Thus, the difference in VWC at 0.6 m was essentially established before the study was

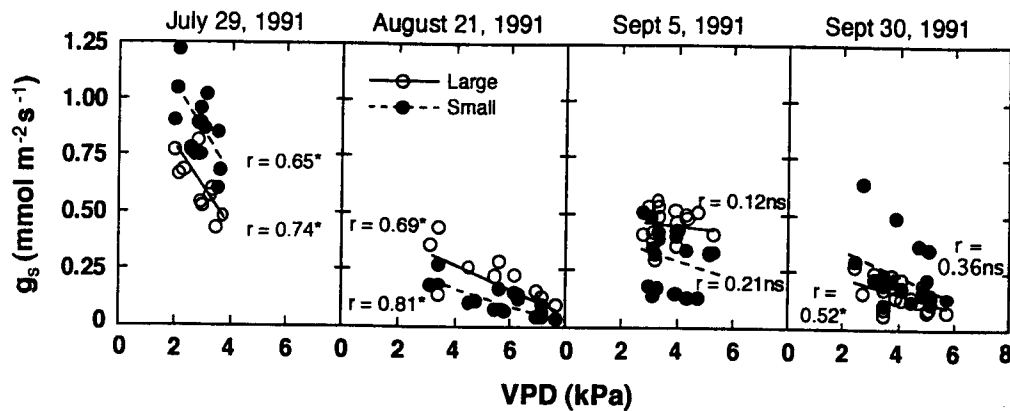


Fig. 4. Relationship between stomatal conductance (g_s) and leaf-to-air vapor pressure deficit (VPD) on 29 July, 21 August, 5 September, and 30 September, for large and small shrubs. Significant least squares regressions are indicated with *, and not significant with ns.

initiated, perhaps as a source of water for growth of large shrubs during the dry spring period.

The differences observed in gas exchange patterns in the different shrub size classes provide rudimentary support for the primary hypothesis that large and small shrubs differ in physiological responses to moisture availability. Small shrubs apparently have higher photosynthesis and stomatal conductance than large shrubs when upper soil (0.3 m) moisture is high after initial, large summer rains. High rates of photosynthesis and water use would be an advantage during establishment when small shrubs must compete with warm-season perennial grasses that also utilize the moisture in the upper soil. On the other hand, large shrubs appear to have higher photosynthesis, stomatal conductance, and particularly, higher water-use efficiency after upper soil moisture has been depleted during a dry period, indicating either greater physiological activity at reduced soil water, or access to and (limited) utilization of deeper soil water. At this time, high water-use efficiency would be advantageous in preventing desiccation while moisture is brought into the plant at slower rates from deeper soils or at lower availability. The larger shrubs maintained lower ψ_L than small shrubs during this dry period, which would be an advantage in extracting soil moisture at low soil water availability.

In contrast to the above differences, however, there were many general similarities in the response patterns between the two shrub size classes. Both shrub classes appeared to use water preferentially from the upper soil. Both shrub classes had similar stomatal responses to drying soil and to atmospheric vapor deficit. Both shrub classes exhibited increased water use efficiency during the course of the season and neither shrub class responded strongly to the rainfall following the dry period. Furthermore, there was little evidence from this study to support the second hypothesis, that small shrubs would be more strongly coupled to environmental moisture than large shrubs. In fact, large shrubs appeared more strongly coupled to soil water than small shrubs. Xylem water potentials of large shrubs were highly correlated with soil VWC at 0.3 m, whereas ψ_L of small shrubs were not. The ψ_L of the small shrubs was completely independent of soil drying between 21 August and 5 September. The ψ_L of small shrubs increased during this period, perhaps as

a result of greater reduction of g_s (compared to large shrubs), allowing for greater plant rehydration during a period of low water loss. In this case, uncoupling from soil water would be accomplished through a greater sensitivity of stomata of small shrubs to soil water availability (Turner, Schulze, and Gollan, 1985), and could protect small shrubs from desiccation.

The evidence found in this study for differences in responses of shrub size classes to variation in environmental moisture is significant in that it encompasses only moderate variation in soil moisture. Further study is needed of how the functional responses of different-sized mesquite plants are affected by greater variation in soil moisture during the entire year and, especially, during long-term drought. Such studies should help reveal how the establishment phase, involving direct competition with grasses, differs from the established phase where shrubs may access substantially different pools of resources than are available to grasses.

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