

Effects of Summer Drought on the Water Relations, Physiology, and Growth of Large and Small Plants of *Prosopis glandulosa* and *Larrea tridentata*

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Abstract—Large and small plants of creosotebush and mesquite were subjected to drought during summer 1993. Large and small plants responded to drought with lowered xylem water potential and lowered photosynthetic gas exchange. Large plants appear to maintain a reduced but constant photosynthetic rate during drought, and responded to precipitation with increased photosynthesis. However, small plants attempted to maintain a high photosynthetic rate throughout the season, responding less strongly to precipitation events, but probably depleting reserves more and causing photosynthesis to decline more when droughted. Our results suggest that large, established plants are better able to withstand drought than are small, establishing shrubs.

Mesquite (*Prosopis glandulosa* (Torr.) var. *glandulosa* Torr.) and Creosotebush (*Larrea tridentata* D.C. (Cov.)) are two shrub species that have greatly increased in abundance during the last century, in valleys and basins throughout the southwestern U.S. where perennial grasses previously dominated. The replacement of perennial bunch grasses by shrubs may be due to many interacting factors including drought, grazing, climate shifts, and fire (Buffington and Herbel 1965; Schlesinger and others 1990). In light of continued climate change and environmental perturbation, the ability to predict fluxes in life-form (shrub versus grass) composition will depend on understanding how they respond to the

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various factors. Here, we consider the responses of the two shrub species to artificially induced drought, particularly in the context of the degree of establishment of a shrub. Small, establishing shrubs with underdeveloped, shallow root systems may be functionally similar to the perennial bunch grasses they displace. The root systems of larger established shrubs probably exploit a larger volume of soil and access moisture from deeper soil, which is not normally available to grasses (for example, Nilsen and others 1983). Larger, established plants simultaneously sequester increasing water and nutrient resources and effectively "focus" these resources into soil regions under their crowns. Establishment and the relative abundance of water and nutrient resources may also translate into morphological differences such as differences in stem angle (Whitford and others 1996).

Here we ask 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. In some species, for example, *Hedera helix*, some physiological characters such as stomatal aperture and photosynthesis exhibit age-dependent sensitivity to environmental factors (Bauer and Bauer 1980). Perhaps more simply, this sensitivity may occur as a result of size-dependent responses to shrub water, nutrient and osmotic reserves. Size-dependent differences in photosynthesis and stomatal conductance have been reported in mesquite (Brown and Archer 1990), and size-dependent differences in water-use efficiency have been found in the desert shrub *Crysothamnus nauseosus* (Donovan and Ehleringer 1992). Franco and others (1994) found some indication that large plants of creosotebush may access deeper soil water reserves even when not artificially droughted.

We hypothesize that mesquite and creosotebush shrubs of different sizes would have different physiological responses to artificially induced drought. Under drought, large established shrubs with greater access to, or greater "stored", nutrients and water should exhibit only a slow decline in photosynthesis until resource reserves are depleted. Drought should induce a greater decline of photosynthesis in small shrubs, which probably do not have a substantial store of nutrients or water. This leads to the corollary hypothesis that the physiological responses of small shrubs are more closely coupled to variation in soil moisture than are the physiological responses of large shrubs.

To investigate these hypotheses we examined the relationships among plant and soil water contents and photosynthesis of small and large plants of mesquite and creosotebush growing in two mutually exclusive habitats in the Jornada Basin of the Chihuahuan Desert. Plants growing in this stressful, hot desert environment should show the clearest evidence of size-dependent coupling of physiological response with the availability of soil moisture.

Materials and Methods

Study Sites

Both study sites were in the Jornada del Muerto Basin in southern New Mexico, USA. The area has an elevation of 1,200 to 2,000 m, and is close to the northern limit of the Chihuahuan Desert. The climate is semiarid, with a mean annual precipitation of 233 mm (Conley and others 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 and others 1992). Freezing temperatures may occur from late October to mid April (data from the Jornada LTER Weather Station).

The mesquite study site was near Waggoner Well, in the northwest flank of the United States Department of Agriculture (USDA) Jornada Experimental Range. This is a sand dune area, which began forming about 80 years ago, following intensive grazing and drought (Buffington and Herbel 1965; Hennessy and others 1983).

The creosotebush study site was on the coarse-loamy soils of the northeast-facing piedmont slope of Mt. Summerford, the northernmost peak of the Doña Ana Mountain range.

Experimental Plots and Shrub Size Classes

While small creosotebush may have a single primary stem, both creosotebush and mesquite commonly occur in multi-stemmed clumps, and clumps having a discrete canopy were considered to represent a single shrub. From these we selected sixteen large (established) and sixteen small (establishing) shrubs of each species on the basis of height, diameter, and litter accumulation under the shrubs. The root systems of 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 approximately 1.5 m, lining the trench with black plastic sheeting, and returning the soil to the trench. All trenching was done between January and February 1991.

Open-sided rain-exclusion shelters, constructed of metal two-by-fours, with a greenhouse quality transparent plastic (CT Film, Harrington, DE) pitched roof, having a minimum vertical clearance of 1.5 m from the top of the plant and extending approximately 0.6 m beyond the edge of the trench, were placed over half the plants of each size class of mesquite and creosotebush. The architecture of these shelters allowed free movement of air through the shelter, and minimized light exclusion, while effectively excluding meteoric water.

Water Relations and Gas Exchange

Net photosynthetic rate was measured on leaf clusters on marked terminal stem segments (creosotebush) or leaves (mesquite) with an LI 6200 Portable Photosynthesis System (LI-Cor Inc., Lincoln, NE) on seven days for each species during the summer of 1993. Volumetric water content of soil (VWC) and plant water potential (Ψ_L) were also measured on these days. Photosynthesis measurements were repeated at approximately 1.5 hour intervals, from approximately 0700 to 1700 Mountain Daylight Savings Time. These measurements were used to obtain an integrated daily value for photosynthesis (A_i) over a standard time period for all measurement days. Soil water content was measured at 0.3, 0.6, and 0.9 m through an aluminum tube permanently installed in each plot, with a 503 DR hydroprobe (CPN Corp., Santa Barbara, CA). Plant water potential was measured on stem segments (creosotebush) or leaves (mesquite) with a model 3005-1422 Plant Water Status Console (Soil Moisture Corp., Santa Barbara, CA).

Results

Volumetric Water Content of Soil

At the beginning of summer 1993 VWC of creosotebush plots at 0.3 m was similar in large control ($0.11 \pm 0.01 \text{ m}^3 \text{H}_2\text{O m}^{-3} \text{ soil}$) and large droughted ($0.14 \pm 0.05 \text{ m}^3 \text{H}_2\text{O m}^{-3} \text{ soil}$) plant plots, and in small control ($0.18 \pm 0.02 \text{ m}^3 \text{H}_2\text{O m}^{-3} \text{ soil}$) and small droughted ($0.17 \pm 0.01 \text{ m}^3 \text{H}_2\text{O m}^{-3} \text{ soil}$) plant plots. One-way Analysis of Variance (ANOVA) was used to investigate differences in soil VWC between treatment and control plots with large or small plants.

Control plots developed significantly greater mean VWC by July 20. Small plant control plots remained significantly wetter than did treatment plots throughout the summer. Plots with large plants had similar VWC except on August 5 and September 6, when the VWC of large plant control plots increased dramatically following major precipitation events.

There were no significant differences between control and drought treated plants of either size at the 0.6 m and 0.9 m depths. We found no consistent differences in VWC in mesquite treatment and control plots. However, on July 19 and again on August 19, soil in small mesquite control plots held significantly more moisture than did the treatment plots. These dates coincided with or were immediately after the two major precipitation complexes of summer 1993 at this site.

Plant Xylem Water Potential

Xylem water potential (Ψ_L) of small droughted creosotebush ranged from -2.5 to -5.4 MPa and was significantly (ANOVA, $p < 0.05$) lower than Ψ_L of small control plants (-1.7 to -4.8 MPa) through most of the summer. Large droughted creosotebush had Ψ_L ranging from -2.2 to -5.4 MPa and did not vary significantly from Ψ_L of large control plants, which ranged from -2.1 to -5.0 MPa. Xylem water potential of small droughted mesquite ranged from -1.2 to -2.5 MPa and was significantly lower than the Ψ_L of small control plants,

which ranged from -0.75 to -1.7 MPa. Statistically significant differences in Ψ_L were detected between large mesquite control plants (range -1.1 to -1.95 MP) and large droughted plants (range -1.3 to -2.4 MPa) on August 4, August 17, and September 4 only.

Photosynthesis

Overall, large and small creosotebush had similar seasonal patterns of daily net photosynthetic carbon assimilation rates (A_i), reaching maximal values around mid July and decreasing thereafter. Large control plants of creosotebush occasionally (on two out of seven measurement days) had A_i greater than that of large droughted plants (fig. 1A). On the same measurement days, control plants of small creosotebush showed clearly greater A_i than did droughted plants (fig. 1B).

Large droughted mesquite A_i reached a relatively stable maximum around mid-July and decreased substantially only at the end of the growing season, while at the same time A_i of large control plants fluctuated from treatment plant levels to significantly greater rates and back (fig. 2A). Small droughted mesquite A_i began to decrease and diverge from the A_i of control plants around early August, and this condition persisted throughout the summer (fig. 2B).

A simple regression model was used to investigate the relationship between VWC and Ψ_L , and between Ψ_L and A_i . For measurements taken during summer 1993, mesquite

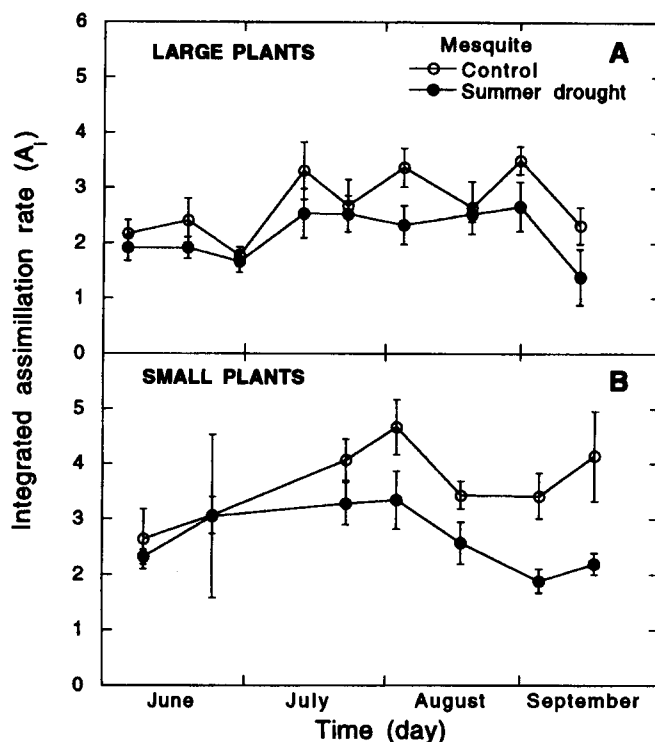


Figure 2—Net photosynthetic assimilation rate (A_i) of (A) large, and (B) small mesquite control plants and plants droughted during summer 1993, integrated between 7:00 and 17:00 Mountain Daylight Savings Time.

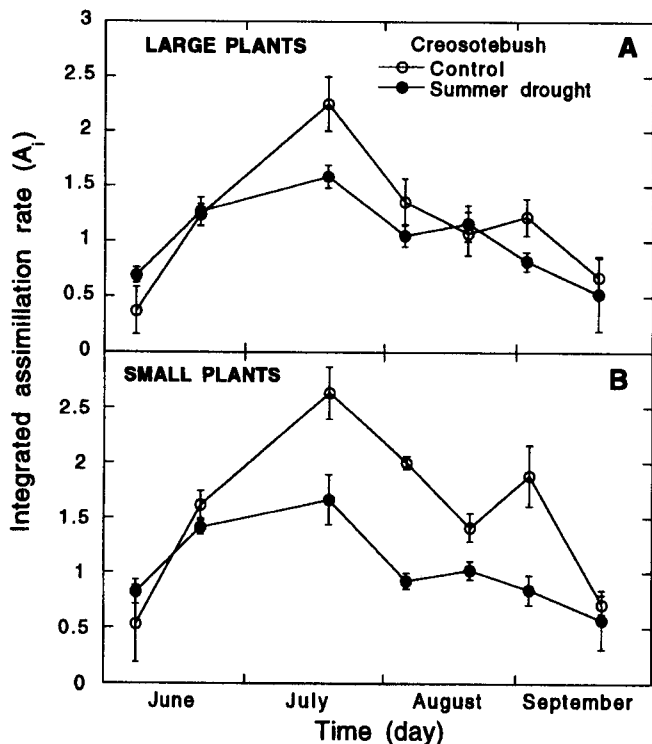


Figure 1—Net photosynthetic assimilation rate (A_i) of (A) large, and (B) small creosotebush control plants and plants droughted during summer 1993, integrated between 7:00 and 17:00 Mountain Daylight Savings Time.

VWC at 0.3 m was significantly and positively related to Ψ_L of large plants ($n=28$; $p < 0.05$), but Ψ_L was not significantly related to A_i in droughted or control plants ($n=28$; $p > 0.05$). In creosotebush VWP at 0.3 m was significantly and positively related Ψ_L of control plants of both size classes ($n=23$ to 27, $p < 0.05$), and Ψ_L was significantly and positively related to A_i of control and treatment plants of both size classes ($n=23$ to 27, $p < 0.05$). In both species there was no significant relationship between Ψ_L and VWC at 0.6 or 0.9 m.

Discussion and Conclusions

Although there were differences in physiological responses of the two species to induced drought, our data support the hypothesis that large and small plants may respond differently to environmental perturbation.

The rain-out shelters were effective in excluding meteoric water from experimental plots, as seen from the differences in soil VWC between control and treatment plots, particularly at the most shallow soil depth. In control plots soil VWC at the 0.3 m depth also appears to relate directly to plant xylem water potential in both species. The absence of a relationship between Ψ_L of droughted plants and VWC at any of the three soil depths suggests that under drought conditions plants of both species and size classes obtain some moisture from deep soil reserves.

Overall, if control plant A_i is representative of potential A_i , drought depressed the A_i of small plants more than the A_i of large plants. Interestingly, this was due to small control plants having an overall greater photosynthetic rate than large control plants— A_i of large and small droughted plants was very similar. Photosynthetic assimilation rate of large control creosotebush was only rarely different from that of large droughted plants. Days when control plant A_i was greater than treatment plant A_i coincided with recent precipitation events. This suggests that (1) large creosotebush A_i is not severely limited by depletion of soil water reserves, and (2) large creosotebush can respond to short-term environmental perturbation—for example, precipitation events—but the magnitude of the response is relatively small and short-lived. Drought caused small creosotebush to have significantly lower photosynthetic rates than did small control plants through most of the summer. However, while small control plants also responded to precipitation events, their A_i did not decline to droughted plant levels until the final measurement of the summer.

In mesquite also, if control plant A_i is representative of potential A_i under prevailing environmental conditions, the drought treatment caused significant declines in large and small plant A_i . While overall A_i levels were greater in small plants than in large plants, large droughted plant A_i remained approximately unchanged for much of the summer and small droughted plant A_i declined substantially from midsummer. In small plots, continued rapid loss of water with no replenishment may deplete water resources to levels that are limiting to photosynthetic gas exchange. The absence of a similar decline in large droughted plants suggests that these plants have access to other sources of moisture, probably from deeper soil layers.

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