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## Water relations of a perennial grass and seedling vs adult woody plants in a subtropical savanna, Texas

Joel R. Brown and Steve Archer

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Over  $52 \pm 16\%$  (Mean  $\pm$  SE) of the seeds of the arborescent legume *Prosopis glandulosa* var. *glandulosa* germinated within two weeks of dissemination in plots dominated by a perennial grass (*Chloris cucullata*) in July 1984 and  $63 \pm 7\%$  of those germinating survived through September 1985. Our observations spanned a period of normal temperatures and below-normal precipitation, suggesting the apparent increased abundance of *Prosopis* on this site in recent times has probably not been episodic with regard to moisture.

Over 60% of the herbaceous root biomass occurred in the upper 30 cm of soil. In contrast, tap roots of *Prosopis* seedlings had penetrated beyond 40 cm within 4 months of germination and their mean proportion of total biomass belowground increased from  $0.27 \pm 0.09$  in May to  $0.52 \pm 0.15$  in August. Net photosynthesis ( $P_n$ ) and conductance ( $g$ ) of *Chloris* were closely coupled to fluctuations in moisture in the upper soil horizons ( $<30$  cm), whereas  $P_n$  and  $g$  of one-year old *P. glandulosa* seedlings were correlated with soil moisture at depths between 30 and 90 cm. Among mature *Prosopis* plants,  $P_n$  and  $g$  varied as a function of soil moisture at depths  $>90$  cm.

We conclude that rapid development of roots of *Prosopis* seedlings during their first year of growth apparently enhanced survival by enabling them to access soil moisture beyond the zone effectively utilized by grasses. On sites with a history of grazing, competition for water from herbaceous vegetation may not play a significant role in limiting establishment of *P. glandulosa* seedlings or the growth of mature plants in most years. Partitioning of soil moisture between *P. glandulosa* and grasses, achieved early in the life cycle of *Prosopis*, helps explain how this woody plant can successfully establish in grasslands.

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### Introduction

Regulation of the proportion and local pattern of distribution of woody and graminoid lifeforms in savannas has been ascribed to edaphic, pyrogenic and climatic factors (Walter 1971, 1979, Monasterio and Sarmiento 1975). The observation that root systems of grasses intensively exploit a relatively small proportion of the soil profile, while woody plants utilize a much greater soil volume, prompted Schimper (1903: 173) to suggest “moisture in the subsoil has little influence on the covering of grass; only moisture in the superficial soil is

important to it” and that woody plants are favored by moist subsoil “regardless of whether rain falls frequently or rarely, or whether the rain falls during a period of activity or of rest.”

Variations in physical properties of soils may interact with rooting patterns to influence the distribution and abundance of plant lifeforms (Beard 1953, Cole 1982, San Jose and Farinas 1983). Coarse-textured soils permit greater infiltration and deeper percolation of water and should favor woody plants exploiting soil moisture at greater depths (Knoop and Walker 1985). Fine-textured soils that retain water in the upper soil layers

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should favor grasses with high root densities in upper horizons by limiting water penetration to lower horizons.

Disturbance regimes may also regulate the relative abundance of grasses and woody plants. In many instances, changes in community structure from grassland or savanna to woodland appear to be a consequence of shifts in herbaceous composition and standing crop resulting from grazing (e.g. Buffington and Herbel 1965, Madany and West 1983, van Vegten 1983). Defoliation of grasses reduces their biomass, both above- and belowground, adversely affecting their ability to pre-empt resources (Knoop and Walker 1985, Caldwell et al. 1987) and exclude invading woody plants. Reductions in herbaceous biomass and litter accumulations resulting from grazing would also decrease the frequency and intensity of fire, further favoring woody plant establishment and growth. As a result, decreased grass cover following grazing and drought has been followed by rapid invasion of the arborescent legume, mesquite (*Prosopis* spp.), in southwestern North America (Herbel et al. 1972, Archer et al. 1988). However, invasion of ungrazed grasslands by woody plants has also been reported in desert (Brown 1950, Humphrey and Mehrhoff 1958, Johnsen 1962, Hastings and Turner 1965) and tallgrass prairie systems (Bragg and Hulbert 1976, Towne and Owensby 1984). Thus, it is not clear how disturbance, resource partitioning, competition and edaphic heterogeneity interact to determine the balance between grasses and woody plants on a site.

The potential natural vegetation of southern Texas and northern Mexico has been classified as *Prosopis-Acacia* savanna (Kuchler 1964). However, many landscapes in this region are dominated by dense woodlands while others are savannas thought to be developing into closed-canopy woodlands. Mesquite (*Prosopis glandulosa* (Torr.) var. *glandulosa* Torr.) has been identified as the primary woody invader. Once established, it facilitates the ingress of additional woody species and may catalyze the conversion of grasslands to woodlands (Archer et al. 1988). To ascertain factors affecting the early establishment of *P. glandulosa*, we sought answers to the following questions: (1) Is there partitioning of soil moisture between grasses and *Prosopis* plants? (2) If so, how early in the life cycle of *Prosopis* is the partitioning achieved? and (3) To what extent might variation in seasonal, annual rainfall affect establishment and survival of *Prosopis* seedlings and adult plants?

### Site description

Research was conducted at the Texas Agricultural Experiment Station La Copita Research Area in Jim Wells County, 15 km from Alice, Texas (27°40'; 98°12'W; elevation 80 m) in the eastern Rio Grande Plains of the Tamaulipan Biotic Province. Contemporary vegetation of the region has been described by Davis and Spicer

(1965). The site was a savanna parkland consisting of discrete clusters of woody plants organized beneath *P. glandulosa*. Perennial grasses comprised about 90% of the biomass in herbaceous zones between clusters. The dominant grass, *Chloris cucullata*, accounted for >30% of the aboveground biomass (plant nomenclature follows Correll and Johnston 1979). Mean ( $\pm$  SE) peak herbaceous standing crop, estimated by clipping ten 0.5  $\times$  0.5 m plots, was 278  $\pm$  15 g m<sup>-2</sup> in July, 1984 and 289  $\pm$  14 g m<sup>-2</sup> in June, 1985. See Archer et al. (1988) for additional details on plant community structure and successional patterns.

Soils were fine sandy loams on 1–3% slopes (USDA 1979). Clay content and bulk density of soils above 40 cm were 18% and 1.3 g cm<sup>-3</sup>, respectively. Between 40 and 200 cm, clay content ranged from 31 to 37% and bulk density from 1.3 to 1.5 g cm<sup>-3</sup> (Weltz 1987). Climate is subtropical with warm winters and hot summers. Mean annual rainfall was 68 cm with maxima in May/June and September. Mean annual temperature was 22.4°C with a growing season of 289 d. The site had been grazed by cattle since the late 1800s. In May 1984, a 70 m  $\times$  40 m herbaceous zone was fenced to exclude cattle.

### Methods

Establishment of *P. glandulosa* in the herbaceous zone was evaluated by placing thirty scarified seeds on the soil surface in each of twelve 2  $\times$  1 m plots randomly located in the enclosure. The 360 seeds were disseminated in July 1984, coincident with seed production on mature trees. Germination exceeded 96% at 25°C in a growth chamber test of 1000 seeds. Emergence was noted two weeks after seed dissemination. Survival, expressed as a proportion of emerging seedlings, was assessed monthly through October 1984, and May through September, 1985.

Seasonal patterns of gas exchange and water relations of the dominant grass on the site and *Prosopis* plants at different stages of development were examined in 1985 with respect to precipitation, soil moisture, temperature and atmospheric vapor pressure deficits. Net photosynthesis (*P<sub>n</sub>*) and stomatal conductance (*g*) were measured on one-year-old *Prosopis* seedlings, leaves of mature *Prosopis* trees, and leaf blades of *Chloris cucullata* tillers. The same leaves were followed on each date. Diurnal measurements (0900, 1200 and 1600 hours) of gas exchange on clear days in May, June, July and August were made on both leaf surfaces with a closed-flow portable photosynthesis system (LI-6000, LI-COR, Inc., Lincoln, NE, USA) and a 0.25 l cuvette. Air and leaf temperature and vapor pressure deficit were also recorded. A minimum of three *Prosopis* seedlings and three *Chloris* tillers (3 to 4 blades per tiller) were followed through each day. Two leaves on each of three adult *Prosopis* trees were also monitored.

All measurements of gas exchange were made on

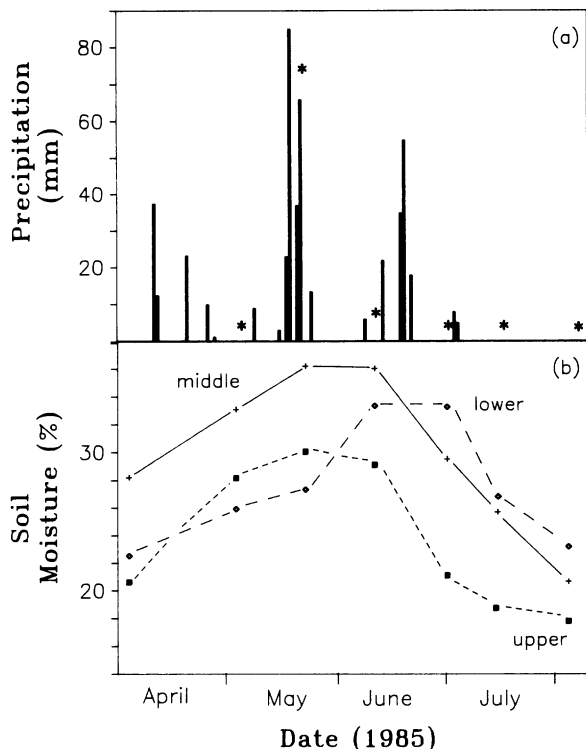


Fig. 1. Daily precipitation (mm) at the La Copita Research Area from April through July 1985 (a) and trends in percent soil moisture by volume measured with neutron probe (b). Asterisks in (a) denote dates of physiological measurement in Figs 2–4. Date, depth and the date by depth interaction were significant for soil moisture.

plants at light intensities  $\geq 90\%$  full sunlight. Because of the low height and density of herbaceous vegetation on the site, *Prosopis* seedlings did not experience shading. Levels of photosynthetically active radiation were determined with a quantum sensor (LI-190-S-1, LI-COR, Inc., Lincoln, NE, USA). Xylem water potential (*XWP*) was determined with a pressure chamber (Scholander et al. 1965). Seedling main stems, the newest fully expanded leaf of grass tillers, and petioles of mature *Prosopis* leaves were sampled predawn and following measurements of gas exchange on plants not monitored for gas exchange. Tissues were placed in plastic bags containing moistened filter paper just before excising, to minimize water loss during transport to the pressure chamber.

Soil water content in the enclosure was estimated at depths of 15 and 30 cm and at 30 cm increments to 1.5 m from 12 access tubes using the neutron scattering method (van Bavel 1958). Probe readings were calibrated from gravimetric estimates made on four dates. After preliminary analyses, soil moisture values were pooled into three depths: upper (<30 cm); middle (30–90 cm); and lower (>90 cm). Soil temperatures at 5 and 20 cm were determined with thermocouples placed in five plots. Daily precipitation and air temperatures

were recorded on a Campbell CR21 data logger at a weather station maintained 0.2 km from the enclosure.

Variations around means of physiological variables were similar for *Chloris* and *Prosopis* adult and seedling plants, thus, means of standard errors across species are displayed as indicators of variability in measurements. Repeated measures analysis of variance (AOV) was used to test for differences in *Pn* and *g* at  $P < 0.05$  (Keppel 1982). Standard AOV was used to test for differences in *XWP*. Multiple linear regression and Mallows's Cp statistic (SAS 1982) were used to relate maximum daily *Pn* and *g* to soil moisture, vapor pressure deficit and soil temperature.

Naturally occurring *Prosopis* seedlings in the area were located and excavated to quantify tap root development and the relationship of above- to belowground development. In May 1985, both newly germinated seedlings (cotyledons only) and recently established seedlings (at least one true leaf but cotyledons still intact) were excavated. Additional seedlings were tagged at this time and subsequently excavated in August 1985. Tap roots were excavated to 50 cm, severed and stored in a plant press. The number of lateral roots arising from the tap root were later counted beneath a binocular dissecting scope. Herbaceous root biomass was estimated by washing soils from 10 cm segments of ten 5.1 cm diameter cores to a depth of 1.2 m.

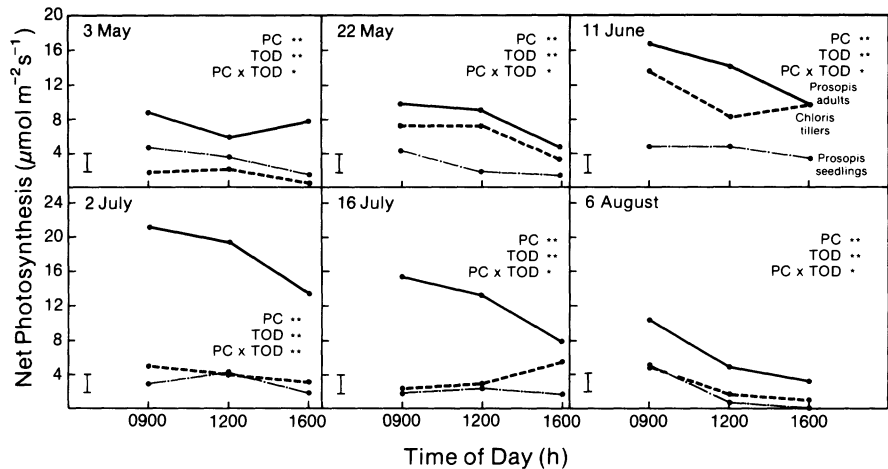
## Results

Over 52% of the *P. glandulosa* seeds disseminated in July 1984 emerged within two weeks (SE = 16%; range = 30 to 77% across the 12 plots). Mean ( $\pm$  SE) survival of emerging seedlings at the end of the growing season was  $74 \pm 4\%$  even though precipitation during the three months after germination was substantially below normal. Soil moisture (*SM*) was 16% in the upper 30 cm of soil at the time of emergence, 19% on August 21 and 17% on September 20. Overwinter mortality of seedlings was 7% and by the end of the second growing season  $63 \pm 7\%$  (range = 55 to 71% across the 12 plots) remained alive. Monthly precipitation in January through May of the second growing season was 25 to 80% higher than normal, whereas precipitation in August and September was 20 and 53% of normal. Mean monthly temperatures for the 1984 and 1985 growing season were within 1 to 2°C of long-term (30 yr) monthly means.

Relative to the upper depths, *SM* in lower depths displayed a lag in both recharge and depletion (Fig. 1b). *SM* in the upper 90 cm was rapidly depleted in June in spite of a series of showers yielding a total of 13 cm of rain (Fig. 1a). The substantial lag in recharge of deep soils after rainfall events in both April and May presumably reflected the higher clay content and bulk density in horizons below 30 cm.

Adult *Prosopis* plants had the highest rates of net photosynthesis (*Pn*) and *Prosopis* seedlings the lowest

Fig. 2. Net photosynthesis ( $P_n$ ) of *Prosopis* trees, *Prosopis* seedlings and tillers of *Chloris cucullata* on six dates in 1985 at the La Copita Research Area. Each point is the mean of 3–5 samples. Vertical bar is the mean SE of all observations. Significance levels (\* =  $p < 0.05$ ; \*\* =  $p < 0.01$ ; ns =  $p > 0.05$ ) determined by repeated measures AOV are given for main effects (PC = plant category; TOD = time of day) and PC by TOD interactions.



(Fig. 2).  $P_n$  was generally greatest in the morning and lowest in the afternoon for each plant category (PC) throughout the season. However, PC and time of day (TOD) interactions were significant on each date. Mature *Prosopis*  $P_n$  was greatest during June and July when soil moisture in the lower horizons was highest (Fig. 1b).  $P_n$  of mature *Prosopis* plants significantly exceeded that of *Chloris* tillers on each date except 3 and 22 May.  $P_n$  of *Chloris* tillers was highest in late May and early June when soil moisture in the upper 90 cm was highest.  $P_n$  was generally  $< 6 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$  the remainder of the season, even during periods when soil moisture at depths below 30 cm was relatively high.  $P_n$  of *Prosopis* seedlings never exceeded  $6.5 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ . With the exception of the 11 June date,  $P_n$  did not differ significantly between *Prosopis* seedlings and *Chloris* tillers.

Stomatal conductance ( $g$ ) of *Prosopis* seedlings was comparable with or greater than that of mature plants and *Chloris* tillers on each date (Fig. 3). The PC by

TOD interaction was significant on each date. Xylem water potential ( $XWP$ ) of *Prosopis* at predawn was similar or slightly lower than that of *Chloris* throughout the season, with the exception of 2 July, when *Chloris* tillers were substantially more negative (Fig. 4). Through the day,  $XWP$  of *Chloris* tillers, which generally had lower  $g$  than *Prosopis* plants (Fig. 3), was usually less negative than those of *Prosopis*. Patterns of  $XWP$  varied significantly between plant categories on each date.

Multiple regression analysis indicated maximum daily  $g$  and  $P_n$  of *Chloris* tillers were most closely correlated with  $SM$  in the upper ( $< 30$  cm) zone (Tab. 1). In contrast,  $SM$  at depths  $> 90$  cm and  $VPD$  explained most variation in  $g$  and  $P_n$  among *Prosopis* trees. Performance of one-year-old *Prosopis* seedlings was primarily a function of  $SM$  at middle and lower depths.

Herbaceous root biomass was  $466 \pm 24 \text{ g m}^{-2}$  and  $628 \pm 17 \text{ g m}^{-2}$  in the upper 30 and 60 cm of soil, respectively. This represented  $60 \pm 11$  and  $80 \pm 13\%$  of the

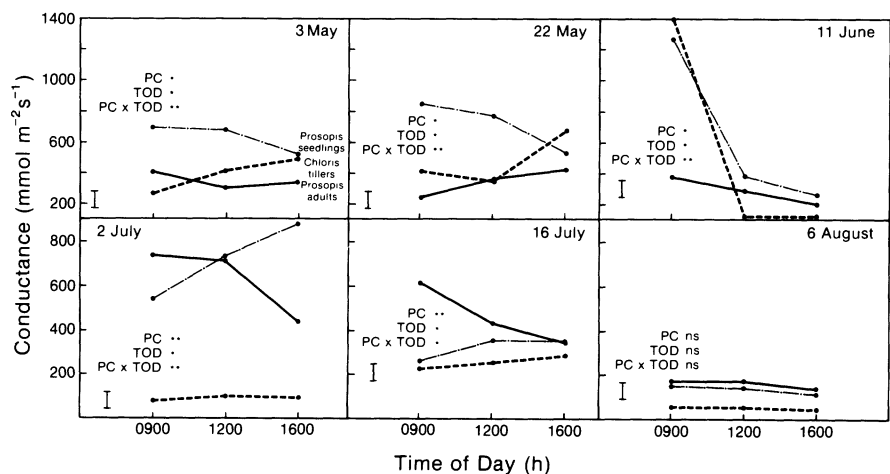


Fig. 3. Conductance ( $g$ ) of *Prosopis* trees, *Prosopis* seedlings and tillers of *Chloris cucullata* on six dates in 1985 at the La Copita Research Area. Insert statistical summaries are described in Fig. 2.

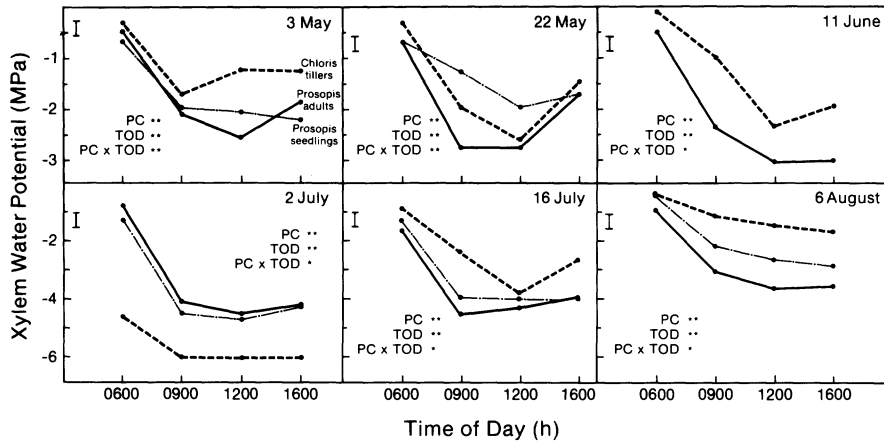


Fig. 4. Xylem water potential (*XWP*) of *Prosopis* trees (—), *Prosopis* seedlings (---) and tillers of *Chloris cucullata* (· · ·) on six dates in 1985 at the La Copita Research Area. Insert statistical summaries are described in Fig. 2.

total herbaceous root biomass in the 1.2 m profile. Only  $6 \pm 2\%$  ( $49 \pm 10 \text{ g m}^{-2}$ ) of the roots in the 1.2 m profiles occurred between 1.0 and 1.2 m. *Prosopis* seedlings with one true leaf and cotyledons still attached had tap roots extending beyond 20 cm and an average of six lateral roots, most of which were in the upper 10 cm (Tab. 2). Tap roots of four-month-old seedlings extended beyond 40 cm and had increased the mean number of lateral roots to ten, half of which were concentrated in the upper 10 cm of the profile. The proportion of total seedling biomass belowground increased from 0.27 in May to 0.52 in August. This ratio was underestimated, since excavations were terminated at 50 cm and lateral roots were not collected for biomass determinations.

## Discussion

### Lifeform utilization of soil moisture

Seasonal variations in *Pn* and *g* among lifeforms in response to changes in *SM* with depth were consistent with Walter's (1971, 1979) two-layer soil moisture hypothesis and other comparative studies of grasses and mature woody plants from geographically diverse savannas (Sariano and Sala 1983, Hesla et al. 1985, Knoop and Walker 1985). Our data further indicate that *Prosopis* plants began partitioning soil moisture with grasses early in their life cycle (Tab. 1) when competition from grasses, both above- and belowground, would probably be most acute. In controlled environment pot studies where rooting volumes were restricted, competition between grasses and *Prosopis* seedlings can be intense (van Auken and Bush 1988, 1989). However, in field experiments on a more productive central Texas site, survival, shoot development, and gas exchange of *Prosopis* seedlings were comparable on rangelands differing in grazing history, graminoid species composition, and above- and belowground biomass (Brown and Archer 1989). These experimental data and the high

levels of survival observed on our site suggest root stratification achieved early in the life cycle of *Prosopis* may promote sharing of soil resources, thus, minimizing competitive exclusion by grasses.

Sixty percent of the herbaceous root biomass was concentrated in the upper 30 cm of soil on our site and

Tab. 1. Partial and multiple  $R^2$  values and significance levels (\* =  $P < 0.05$ ; \*\* =  $P < 0.01$ ; ns = not significant) for variables potentially regulating  $g_{\text{max}}$  and  $Pn_{\text{max}}$  in *Prosopis* seedlings, mature *Prosopis* trees, and *Chloris* tillers. Factors evaluated were % soil moisture (*SM*) in the upper (<30 cm depth), middle (30–90 cm depth) and lower (>90 cm depth) horizons, vapor pressure deficit (*VPD*) and soil temperature. All multiple  $R^2$  values were significant at  $P < 0.01$ . *VPD* was negatively correlated with *Pn* and *g*; all other variables reported were positively correlated.

Plant category	Variables	Partial $R^2$	P	Multiple $R^2$
Conductance <i>Chloris</i>	SM-Upper	0.64	**	0.88
	SM-Middle	0.21	**	
	SM-Lower	0.03	ns	
<i>Prosopis</i> Seedlings	SM-Upper	0.11	*	0.82
	SM-Middle	0.47	*	
	SM-Lower	0.24	*	
Mature	SM-Upper	0.02	*	0.89
	SM-Middle	0.07	*	
	SM-Lower	0.65	**	
	VPD	0.15	*	
Photosynthesis <i>Chloris</i>	SM-Upper	0.43	**	0.47
	SM-Middle	0.04	*	
	SM-Lower	0.00	ns	
<i>Prosopis</i> Seedlings	SM-Upper	0.06	*	0.49
	SM-Middle	0.00	ns	
	SM-Lower	0.28	*	
	Temp	0.15	*	
Mature	SM-Upper	0.01	*	0.92
	SM-Middle	0.09	*	
	SM-Lower	0.47	**	
	VPD	0.25	**	

Tab. 2. Aboveground height and biomass, taproot length, diameter and biomass, partial root to total plant biomass ratio, root diameter and lateral root development of *Prosopis* seedlings excavated on 3 May and 22 August, 1985. Seedlings were newly emerged (cotyledons only = NE; n = 10) and recently established with at least one true leaf (EST; n = 10) on 3 May and approximately 4 months old (4 mo; n = 7) on 22 August. Each value is mean  $\pm$  SE. Excavations were terminated at 50 cm.

Age	Aboveground		Belowground		Partial root to total plant ratio (g g <sup>-1</sup> )	
	Height (cm)	Biomass (g)	Length (cm)	Biomass (g)		
NE	2.8 $\pm$ 0.2	0.11 $\pm$ 0.01	5.5 $\pm$ 0.0	0.04 $\pm$ 0.00	0.27 $\pm$ 0.09	
EST	7.4 $\pm$ 0.8	0.63 $\pm$ 0.11	20.7 $\pm$ 3.7	0.45 $\pm$ 0.12	0.41 $\pm$ 0.13	
4 mo	8.1 $\pm$ 1.1	0.68 $\pm$ 0.15	41.3 $\pm$ 5.1	0.73 $\pm$ 0.14	0.52 $\pm$ 0.15	
Tap root diameter (mm) with depth						
	0 cm	10 cm	20 cm	30 cm	40 cm	50 cm
NE	0.1 $\pm$ 0.05	–	–	–	–	–
EST	2.7 $\pm$ 0.03	0.9 $\pm$ 0.2	0.7 $\pm$ 0.1	0.5 $\pm$ 0.1	0.5 $\pm$ 0.0	–
4 mo	5.3 $\pm$ 0.80	2.4 $\pm$ 0.4	1.4 $\pm$ 0.4	0.9 $\pm$ 0.3	0.4 $\pm$ 0.1	0.3 $\pm$ 0.0
Number of lateral roots with depth (cm)						
		10 cm	20 cm	30 cm	40 cm	50 cm
NE		–	–	–	–	–
EST		5.8 $\pm$ 1.2	1.6 $\pm$ 0.4	–	–	–
4 mo		4.5 $\pm$ 1.4	1.3 $\pm$ 0.2	0.1 $\pm$ 0.2	1.0 $\pm$ 0.2	1.6 $\pm$ 0.3

*Pn* and *g* of *Chloris* tillers was correlated with *SM* in this zone. The limited ability of *Chloris* to utilize subsoil moisture was particularly evident during July and August, when upper horizons had a much lower water content than lower horizons (Fig. 1). During these times, *Pn* and *g* were generally highest in adult and seedling *Prosopis* and lowest among *Chloris* tillers. In addition, *Pn* (Fig. 2) and *g* (Fig. 3) of *Chloris* was substantially enhanced on 11 June, apparently in response to a small precipitation event (Fig. 1a) which did not register on the neutron probe measurement of *SM*. The importance of these small rainfall events in contributing to primary production of semi-arid grasslands has been summarized by Sala and Lauenroth (1982). Herbaceous zones were not shaded by adult *Prosopis* and herbaceous plants were not shading *Prosopis* seedlings. Thus, the plants monitored on this site all experienced comparable light regimes. Mature *P. glandulosa* plants were consistently superior to either *Chloris* tillers or one-year-old *Prosopis* seedlings with respect to *Pn*, even when water content was high at shallow depths. This suggests adult *Prosopis* plants have (1) the ability to access shallow as well as deeper sources of soil moisture and/or (2) a higher photosynthetic capacity than *Chloris* or seedling *Prosopis*. *Pn* was low in *Prosopis* seedlings relative to mature trees even though conductance was comparable to substantially higher. This suggests developmental shifts in water-use efficiency and may reflect ontogenetic constraints on photosynthetic capacity in seedlings relative to adult plants (Kozlowski 1971) as well as differential access to moisture at deeper depths.

Coarse-textured soils, which occurred to 40 cm on our site, permitted a substantial recharge of moisture deep into the soil profile during May and June (Fig. 1b). The recharge of soils to depths >90 cm observed in 1985 followed a series of rainfall events over 10 d in May which totaled 23 cm (Fig. 1a). We examined daily precipitation records from 1930 to 1986 for Alice, Texas, 15 km from the study site, and found at least one occurrence of >23 cm of rainfall over a 10 d period in 23 of the 52 yr for which there were data. For years in which this pattern of rainfall occurred, there was an average ( $\pm$  SE) of 1.5  $\pm$  0.2 such events. All but one of the events noted over the 52 yr of records examined occurred during the growing season, between April and October. During the dormant season, smaller rainfall events might contribute to subsoil recharge (Cable 1977). In addition, *SM* was measured from access tubes located in grass-dominated zones. Thus, with respect to adult *Prosopis* plants, these frequencies of subsoil recharge are probably underestimated, since trees and shrubs may enhance the water content of subsoil by intercepting rain and funnelling it down the stem and into soils with higher infiltration rates (Pressland 1973, Brock et al. 1982).

Average time elapsed between years receiving at least one event capable of generating subsoil recharge under the conditions prevailing during our study was 1.9  $\pm$  0.5 yr (maximum = 5). This appears to be well within the limits of *Prosopis* survival. For example, during a severe 7 yr drought in the 1950s, Carter (1964) observed mortality (ca. 40%) occurred primarily during the last 2 yr of the drought period. He also noted *Prosopis* mortality

was greatest on sites with fine-textured soils and least on sites with coarse-textured soils.

#### Establishment of *Prosopis* in grass stands

High rates of emergence (52%) and survival (74%) were observed for *P. glandulosa* seedlings in 1984. Survival among naturally occurring populations of *Prosopis* seedlings in the area ranged from 78 to 95% over this same period (Brown and Archer 1987). Soil moisture in the upper 30 cm averaged only 16% at the time seeds were disseminated in July and precipitation during the 3 months following germination was substantially below normal. Mean monthly temperatures for the 1984–85 growing seasons were comparable to the long-term means, suggesting effectiveness of precipitation would not have been increased over the period of observation. The high rates of survival observed under these conditions and the population size structure on the site (Archer 1989) leads us to believe establishment of *Prosopis* on this site has not been episodic with regard to moisture. Monthly precipitation from January through May of 1985 was above normal. Thus, the survival observed during the second growing season may have been unusually high.

Developmental of lateral roots in shallow soil layers (Tab. 2) may have enabled *Prosopis* seedlings to successfully compete for resources with grasses while other roots were developing and growing into deeper zones. In addition, natural establishment and early root development of *Prosopis* seedlings may occur during periods when competition for soil moisture is minimal. Brown and Archer (1987) documented recruitment of naturally occurring seedlings over two growing seasons on this site and observed most emergence occurred in autumn and spring, coincident with bimodal peaks in annual precipitation.

Seedling *Pn*, although low, was positive throughout 1985 and generally comparable to that of *Chloris* tillers (Fig. 2). The proportion of total biomass belowground increased markedly in seedlings, indicating preferential allocation of resources to roots (Tab. 2). Rapid root development has also been quantified in *Prosopis* seedlings by Paulsen (1950). In semi-desert grassland of Arizona, *Prosopis* tap roots averaged 33 cm in length three weeks after emergence. At the end of their second growing season tap roots averaged 68 cm. An ability to quickly develop a deep, extensive root system would enhance survival by enabling seedlings to access deeper supplies of soil moisture relative to competing grasses (Tab. 1) and vegetatively regenerate following defoliation (Scifres and Hahn 1971) and fire (Wright et al. 1976).

#### Implications for the conversion of grasslands to woodlands

The geographic range of mesquite has apparently not changed in the past 500 yr (Johnston 1963) but abun-

dance within its historic range appears to have increased substantially since the late 1800s (Bogusch 1952, Humphrey 1958, Herbel et al. 1972, Archer 1989). Given the ready establishment of *Prosopis* observed in this study, one must wonder why its encroachment into grasslands had not occurred earlier. Most hypotheses attempting to explain woody plant invasion into North American grasslands during the past century have centered around decreased fire frequencies, climatic change and grazing by livestock (Hastings and Turner 1965, Neilson 1986).

In their model of savanna stability, Walker et al. (1981) concluded there were but two stable loci: grass-dominated and woody plant-dominated. They identified graminoid biomass as the factor limiting woody plant encroachment. Once grass production was reduced below a threshold, succession toward woodland would occur. Other models of savanna stability make similar predictions (McMurtrie and Wolf 1983, Eagleson and Segarra 1985). Field studies have shown savannas protected from grazing can be maintained despite low fire frequencies, whereas nearby sites experiencing livestock grazing developed into woodlands (e.g. Madany and West 1983). In these studies, the close geographic proximity of the sites suggest climatic change was not a factor. Repeated defoliation of grasses removes transpiring leaves and results in decreased root initiation, extension, biomass and resource uptake (Carmen and Briske 1982, Archer and Tiezen 1983, Caldwell et al. 1987). Such alterations would reduce shading and the ability of grasses to limit percolation of water to deeper soil layers (Knoop and Walker 1985) and, thus, their ability to competitively exclude woody plants. Trampling by ungulates may also create gaps in the grass sward and increase soil surface strength such that recruitment of woody plants is favored relative to grasses (Braunack and Walker 1985).

Gaps in the grass sward created by dung deposition (Brown and Archer 1987) and experimental reductions of herbaceous plant density and biomass (Brown 1987) did not enhance *Prosopis* seedling emergence or establishment on this site. Long-term grazing by livestock may therefore have altered graminoid species composition and reduced above- and belowground biomass such that the present assemblage could not pre-empt resources sufficiently to limit the establishment of *Prosopis* seedlings (e.g. Eissenstat and Caldwell 1988). However, in other systems, rates of *Prosopis* establishment can be high, despite high levels of herbaceous standing crop and/or protection from grazing (Brown 1950, Humphrey and Mehrhoff 1958, Smith and Schmutz 1975, Meyer and Bovey 1982, Brown and Archer 1989). This, coupled with the fact that mesquite is highly tolerant of fire within 2 to 3 yr of emergence (Wright et al. 1976) and that sheep, cattle and horses disseminate large numbers of viable *Prosopis* seeds (Mooney et al. 1977), suggests poor dispersal may have limited its encroachment into North American grasslands before the



introduction of livestock (see Brown and Archer 1987, 1989 and Archer et al. 1988 for elaboration).

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