Tree-shrub interactions in a subtropical savanna parkland: competition or facilitation?

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Abstract. *Prosopis glandulosa* var. *glandulosa* has played a central role in the encroachment of woody plants in southern Texas, grasslands and savannas by acting as a nurse plant for various shrubs that establish in its understory. To test for continued facilitation of established understory shrubs by *Prosopis* and to determine if established shrubs compete with the *Prosopis* nucleus, selective removal experiments were conducted and monitored over a 2 - 5 yr period. Short-term (1 - 3 days) and long-term (2 yr) growth and physiological activities (midday net photosynthesis and leaf/shoot water potential) of two common understory shrubs, *Zanthoxylum fagara* and *Berberis trifoliolata*, growing with *Prosopis*, were generally comparable to those of individuals occurring in clusters where *Prosopis* was removed. Shrubs growing with an intact *Prosopis* occasionally showed significantly higher leaf-[N] and pre-dawn water potentials than those in clusters lacking a live *Prosopis*, especially under drought conditions; however, these differences did not translate into greater midday leaf gas exchange or shoot growth. By comparison, removal of understory shrubs elicited large increases in *Prosopis* net photosynthesis, annual trunk growth in each of the 5 yr monitored, and seed pod production in three of the four years monitored. Seven of 26 *Prosopis* plants in experimental clusters with an intact understory died over a 5-yr period, compared to only two of the 26 plants in clusters with the cleared understory.

Results indicate that (1) the founding overstory *Prosopis* plant may continue to facilitate understory shrubs following their establishment, but these beneficial effects appear to be small and transitory, and (2) the understory shrubs have a pronounced negative effect on *Prosopis*, such that competition between overstory and understory woody plants is strongly asymmetrical. These findings suggest that understory shrubs will likely persist despite changes in microclimate and soils (potentially) that occur after the *Prosopis* plant, which facilitated their ingress or establishment, has died. Soil resource depletion by shallow-rooted understory shrubs appears to be a primary factor contributing to the demise of the deeply rooted, overstory *Prosopis* plants, especially on upland sites with duplex soils where below-ground competition is accentuated.

Keywords: Asymmetric competition; *Berberis trifoliolata;* Nitrogen; Nurse plant; Overstory-understory interaction; Photosynthesis; *Prosopis glandulosa;* Removal experiment; Water relation; Woody patch dynamics; *Zanthoxylum fagara.*

Nomenclature: Correll & Johnston (1979).

Introduction

Studies of plant-plant interactions in savannas have traditionally emphasized effects of individual trees on grasses, soils and microclimate; far fewer studies have examined interactions between woody species (Vetaas 1992; Belsky & Canham 1994; Scholes & Archer 1997). Although woody plant 'clumping' phenomena and the occurrence of 'tree islands' have been widely reported in savannas, 'parklands' (e.g. Whittaker et al. 1979; Archer et al. 1988; McPherson et al. 1988; Mordelet et al. 1993), and other arid and semi-arid ecosystems (e.g. Fuentes et al. 1984; Callaway 1992; Kellman & Kading 1992), little is known of the nature of interactions among the constituent woody plants. These woody clumps or patches are often initiated when a pioneering woody plant facilitates the dispersal or establishment of other species and thereby serves as a 'nurse plant' and 'nucleation' site for subsequent vegetation development (Yarranton & Morrison 1974). In time, and depending on soils, these woody clumps may eventually expand and coalesce to form closed-canopy woodlands (Archer 1995). Thus, woody patch development is often a key element of the more general phenomenon of woody plant invasion of grasslands and savannas that has been documented worldwide over the past century (Archer 1994).

Facilitation has long been viewed as an important process in succession (Clements 1916) and there is a growing recognition that beneficial interactions between plants may be more widespread and important than previously thought (Callaway & Walker 1997; Holmgren et al. 1997). Many examples exist of the nurse plant aspect of facilitation in arid and semi-arid ecosystems (Callaway 1995), and also in entirely different alpine systems (Kikvidze & Nakhutsrishvili 1998). However, the mechanisms enabling facilitation, the circumstances under which it occurs, and the extent to which facilitation persists beyond the seedling establishment phase are not well documented. In the Clementsian model of succession, [i.e. the facilitation model of Connell & Slatyer (1977)], facilitation is thought to operate for a relatively short time and to be of greatest importance

early in succession. For many nurse plant associations, facilitation eventually gives way to competition as seedlings develop into adults and resource limitations increase (Franco & Nobel 1990; Aguiar et al. 1992). In some cases, the original nurse plant is thought to be competitively excluded from the site by the plants that it initially facilitated (McAuliffe 1984; Valiente-Banuet et al. 1991a). In other cases the nurse plant and associated species appear to successfully coexist, either because of resource partitioning (Haase et al. 1996) or the development of mutualistic relationships (Pugnaire et al. 1996).

In a case study in southern Texas, succession from grassland to woodland has been shown to begin when *Prosopis glandulosa* establishes in grassland (Brown & Archer 1989, in press), and subsequently facilitates the ingress, establishment or growth of many subordinate shrub species beneath its canopy (Archer et al. 1988). Over time, distinct shrub clusters thereby develop within a matrix of herbaceous grassland. On most upland sites, these *Prosopis*-mixed shrub clusters persist as discrete entities, while in lowland, intermittent drainages and certain upland sites, the *Prosopis*-shrub clusters have expanded and coalesced to form a continuous, closed-canopy cover (Archer 1989; Scanlan & Archer 1991).

The nature and duration of the *Prosopis*-mediated facilitation of understory shrubs in these woody patches is not well understood and the factors contributing to the different pathways of cluster development remain unclear. Results from our previous studies, which examined the growth and physiology of shrubs growing in patches with and without a live *Prosopis,* indicated that the presence of a *Prosopis* canopy had little overriding positive or negative effect on associated established shrubs (Barnes & Archer 1996). This suggest that understory shrubs are not highly dependent upon *Prosopis* following their establishment. However, direct tests for facilitation in mature shrub clusters have not yet been conducted. In addition, the observation that the *Prosopis* plant has died in ca. 25 % of the clusters on the landscape (Archer et al. 1988) suggests that understory shrubs, many of which are shallow rooted (Watts, M.Sc. Thesis, Texas A&M University, 1993), may competitively exclude *Prosopis* from clusters by sequestering resources that normally percolate to deeper depths where *Prosopis* roots are concentrated. Thus, cluster dynamics and the symmetry of species interactions may shift over time from facilitation-driven and *Prosopis*-dominated, to competition-driven and understory-dominated. In the present study, we removed either *Prosopis* or the understory shrub components of woody clusters and monitored the response of the remaining plants to these manipulations to test the hypotheses that *Prosopis* continues to facilitate understory shrubs in mature woody patches, and understory shrubs compete against the founding, overstory *Prosopis*.

Methods

Study site

Studies were conducted at the Texas Agricultural Experiment Station La Copita Research Area, Jim Wells county, eastern Rio Grande Plains of S. Texas (27° 40' N; 98° 12' W; 75 - 90 m a.s.l.). The regional climate is subtropical with warm winters, hot summers (mean annual temperature = 22.4 °C) and erratic rainfall (mean annual precipitation = 680 mm with maxima in May/ June and September; C.V. = 35 %). During the study period (1988-1995), precipitation ranged from 368 - 908 mm/yr. The La Copita study site is an 1100-ha tract of rangeland grazed by domestic livestock since the late 1800s and is representative of subtropical thorn woodland habitats of southern Texas (McLendon 1991). The vegetation at La Copita consists of savanna parklands on sandy loam uplands that gradually grade (1 - 3 % slope) into closed-canopy woodlands on lowland clay loam drainages (Archer 1995). Uplands exhibit a mosaic of herbaceous vegetation dominated by C_4-grasses, interrupted by patches of woody plants that vary in successional age, size and overstory development (Archer et al. 1988). Understory woody vegetation consists of shrub species that vary in leaf habit – evergreen, summer-deciduous, winter-deciduous –, leaf longevity and time of arrival during woodland succession (Archer et al. 1988). Our studies were conducted on discrete shrub clusters underlain by a well-developed argillic (claypan) horizon (Archer 1995). Based on vegetation composition and size (Archer 1990), our shrub clusters were classified as mature, (ca. 30 - 60 yr of age), but not advanced, in terms of their successional development.

The overall goal with this paper is to characterize the nature of overstory-understory interactions. However, logistical, personnel and financial constraints prevented us from performing overstory- and understory-removal experiments simultaneously at this remote site, or from maintaining a consistent and identical level of replication and monitoring through time. Also, based on our prior studies examining the performance of shrubs growing in the presence or absence of a live *Prosopis* (Barnes & Archer 1996), we anticipated that if shrubs were to show responses to *Prosopis* removal, that changes in ecophysiological performance (gas exchange and water relations) measured over months following removal would precede changes in canopy growth or survival that may not be manifested for decades. Monitoring of understory shrub stem growth, as was done on the large, single-trunked *Prosopis* trees was not possible in these small-diameter, multi-stemmed plants. Thus, in the overstory removal experiment, we emphasized intensive physiological measurements over growth responses

of the shrubs. In contrast, our prior experience with *Prosopis* at the site indicates that leaf photosynthesis and water relations in this deep-rooted species can be less sensitive to seasonal changes or habitat differences in resource levels than that of the more shallow-rooted understory shrubs (Archer 1995; Barnes & Archer 1996; P. Barnes & S. Archer unpubl.). We were also unable to reach a similar level of the labor-intensive ecophysiological sampling in *Prosopis*. Thus, for the understory removal study, we concentrated on *Prosopis* trunk growth and reproduction responses that could be readily and inexpensively quantified, and which were known to show marked variation across the landscape (Archer 1995). Ecophysiological measurements on *Prosopis* were made when possible but are of limited extent. These differences in the time-course of measurements, levels of replication and types of response variables measured limit direct comparisons of the overstory and the understory removal experiments. Nevertheless, to best allow for an integrated assessment of overstory-understory interactions, we present the results of both experiments.

Overstory removal experiment

Six discrete shrub clusters possessing a single live *Prosopis* and located within the same 161-ha fenced pasture were selected in July 1992. Prior to manipulation, each cluster was characterized for overstory/understory structure and composition, light attenuation and soil chemistry. Photon flux density (PFD; 400 - 700 nm) beneath and above the shrub canopy was measured using a horizontally-placed, 1-m long quantum sensor (Model LI-191SA; Li-Cor, Inc., Lincoln, NE; 11 - 24 readings / cluster). Measurements were made under clear skies ± 1 h of solar noon. Simultaneous measurements of incoming (above-canopy) PFD were made using a point quantum sensor (Model LI-190SA; Li-Cor, Inc.) placed in a nearby clearing. Non-destructive estimates of understory leaf area index (LAI; m^2/m^2) were obtained using a plant canopy analyzer (Model LAI-2000; Li-Cor, Inc.; 45° view; 9 - 12 measurements/cluster). Soil samples (0 - 20 cm) were collected from near the center of each shrub cluster (three/cluster) and were processed and analyzed for total N and organic C (see Barnes & Archer 1996).

In three of the six selected clusters (controls) the live *Prosopis* was left intact. In the three others the aboveground part of the *Prosopis* plant was removed using a chain saw. Some basal re-sprouting of *Prosopis* occurred in one of the removal clusters, but the amount of regrowth was small – and minimized by hand pruning at ca. 6-month intervals. Because ecophysiological measurements are time-sensitive, we needed to minimize the time moving equipment from cluster to cluster. Control and removal clusters were therefore interspersed with one another

(minimum spacing between clusters = 25 m) and treatments were assigned such that control and removal clusters could be alternately sampled along a walking transect (care was taken to alter the sequence of sampling such that one cluster in the pair was not systematically sampled before or after the other cluster).

Shrub performance before and after *Prosopis* removal was assessed using a combination of physiological and growth measurements. At each sampling date, measurements of net CO_2-uptake and H_2O-loss were made on fully-expanded, outer-canopy, sunlit leaves (three/replicate; i.e. nine total leaves/species/treatment) using a closed-path, photosynthesis system (Model LI-6200, LiCor, Inc.) with a 0.25 L cuvette (Barnes & Archer 1996) for all sampling dates prior to September 1993. An open-path photosynthesis system (Model CIRAS-1; PPSystems, Inc., Haverhill, MA) was used for measurements in September 1993 and July 1994. Leaf gas exchange measurements were conducted under clear skies and ambient [CO_2] and temperature. Most sampling was conducted from 9.00 - 13.00 Central Standard Time ('midday'). Morning (7.00 - 9.00 CST) measurements were also made in July 1994, where a different subset of leaves was sampled at the morning and midday sampling periods. Following gas exchange measurements, individual leaves were collected for total (Kjeldahl) N-determinations (see Barnes & Archer 1996). Total N was also determined on oven-dried leaf tissue that was harvested from outer-canopy regions of the experimental species (4 - 15 leaves/ replicate depending on species; total leaf area collected = 40 - 100 cm^2). Predawn (ca. 1 h prior to sunrise) and midday leaf/shoot water potentials were measured using a pressure chamber (Model 3000; Soil Moisture Equip. Corp., Santa Barbara, CA) on three shoots or leaves/replicate. Samples for water potential determination were kept in a humid plastic bag prior to, and during measurement. Shoot elongation was determined by permanently marking terminal shoots (three shoots/replicate on different plants = nine total shoots/species/treatment) with aluminum bands and periodically measuring the distance from the band to the shoot apex. For each species, response data from leaves or shoots of different individuals within a cluster were averaged prior to statistical analyses (i.e. the cluster and not the plant was considered as the experimental unit such that $n = 3$ for each shrub species and all response variables).

Two shrub species, *Berberis trifoliolata* (1 - 4 plants/cluster) and *Zanthoxylum fagara* (4 - 13) were measured in all replicates of each treatment. They were not sampled with the same frequency over time; therefore their growth- and physiological data were analyzed separately using ANOVA/ANCOVA; SYSTAT MGLH; Anon. (1992). Because we were interested in exploring the possibility

of differences in short-term (days) vs. long-term (months) responses, the pre-removal and 1-day post-removal data set was analyzed separately from the longer term data set. ANOVA was used for the short-term data set (collected July 7-9, 1992) to test for a significant treatment × time interaction that would be indicative of an immediate response to overstory removal. For the long-term data set (September 1992 - July 1994), pre-treatment gas exchange and water potential data were used as covariates in each of the respective data sets to adjust for initial differences that might have existed between treatment and controls. Unless otherwise noted, pre-planned comparisons between treatment and control means were made using Fisher's least significant difference (LSD) test; differences were considered statistically significant at $P < 0.05$. As the physiological data were not consistently gathered from the same individual plants at each sampling date, the data at the various sampling dates were treated as independent samples for statistical analysis. Shoot elongation data were $\log_{10}$-transformed (Zar 1984) and analyzed using univariate repeated measures ANOVA (Anon. 1992). Number of shrubs and shrub species were subjected to square-root transformation (Zar 1984).

Understory removal experiment

This experiment was initiated in 1968, when the shrubs growing beneath *Prosopis* were hand-cleared (cut to ground level) and removed from a 14 ha portion of a large pasture as part of ranch management operations. No shrub clearing occurred in adjacent pastures with similar soils, topography and grazing history. Because the understory shrub removal treatment was initially imposed with management objectives in mind, the understory removal experiment is pseudo-replicated with respect to pasture. However, our sample units (individual woody clusters) were randomly selected (within a soil series) from throughout this 14-ha acreage and from within an adjacent non-treated pasture (ca. 70 ha). Thus, although there were inherited constraints in the experimental design at the landscape level, comparisons between individual clusters with and without a woody understory should be generally valid and robust for upland sites. Our data on *Prosopis* growth reflect a history of periodic shrub understory removal which preceded the monitoring period.

In 1987, 60 *Prosopis* clusters in each pasture (intact and cleared understory) were selected for monitoring. Understory shrubs which had regenerated since the last pasture-wide clearing were pruned to ground level and were re-pruned annually for the duration of the monitoring period. Seed pod production was assessed in the selected *Prosopis* plants with ($n = 60$) and without ($n = 60$) an

understory by rating pod production on a scale of 1 to 5: 1 = no pods; 2 = 1 - 5 pods/tree; 3 = 6 - 20; 4 = 21 - 100; 5 = > 100. This was done yearly in June/July (time of peak production) 1987-1990. A subsample of pods from producing trees was collected in a haphazard fashion for determination of pod length, no. of seeds/pod and air-dry seed mass. Scarcity of pods in 1990 precluded quantification of pod and seed attributes. In March 1988, subsets of these *Prosopis* plants with and without ($n = 26$ each) a shrub understory were arbitrarily selected for stem growth measurements. Dendrometer bands (Palmer & Ogden 1983) were placed around the bole of each experimental plant, ca. 10 - 15 cm above the soil surface. Because of band breakage and the death of plants, only 19 control and 20 treatment trees were included in data analysis. Dendrometer bands were read seasonally (4 - 6 dates/yr), but only annual trunk growth data are presented here. Annual growth increments are based on live plants (i.e. plants that died were excluded).

In August 1994 and 1995, leaf biomass production, and the elongation and production of the current year's stem (twig) growth was assessed in 20 arbitrarily selected control and treatment *Prosopis* plants ($n = 10$ each) by harvesting and measuring stem and foliar tissue from eight terminal shoots (two from each of the four cardinal directions on the canopy) per plant. All tissue was oven-dried (60 °C) and weighed. At the time of sampling, current-year shoots had completed elongation and leaves were fully expanded. Individual leaf gas exchange measurements were made on fully-expanded, outer-canopy, sunlit leaves using the CIRAS-1 photosynthesis system on a subset of control and treatment *Prosopis* plants in June and September, 1995 ($n = 6$ each). Leaf water potential was measured with a pressure chamber. June physiology measurements were made from 14.00 - 14.30 CST, those in September from 10.00 - 10.40 CST.

Radial trunk growth data from the dendrometer bands were analyzed using a repeated measure general linear model (GLM) with polynomial contrasts (Anon. 1988). Because of a significant time × treatment interaction, treatment effects were also tested separately for each date. Within each treatment, one-way ANOVA with least-square means was used to determine differences in annual growth among years from 1989-1993. Pearson's correlation coefficients were determined for the relationships between annual growth and annual precipitation and late winter/spring precipitation (i.e. January-June) from 1989-1992. Statistical differences in the frequency distribution of pod production classes between *Prosopis* plants with and without an understory were assessed with the SAS-Catmod procedure; pod and seed attributes were compared using SAS-GLM. Leaf/shoot production data from 1993-1995 were analyzed using a two-way ANOVA (treatment × azi-

muth position), and the physiological data were analyzed using repeated measures ANOVA.

Results

Overstory removal experiment

Prior to experimental manipulation, treatment and control clusters were statistically comparable (ANOVA; $P > 0.05$) with respect to overstory and understory canopy diameter, LAI, species composition, light attenuation, and soil nitrogen and carbon concentrations (data not shown). Plant physiological status (net photosynthesis, stomatal conductance, and leaf water potential) was also similar ($P > 0.05$) for treatment and control clusters at the start of the experiment (Figs. 1, 2). The only notable exception was in *Zanthoxylum fagara*, where plants in control clusters showed higher pre-removal photosynthesis ($P < 0.001$) and conductance ($P = 0.06$) than those in clusters slated for *Prosopis* removal. Annual precipitation was 34 % above the long-term mean in 1992 (908 mm), when the overstory removal study was initiated, and was 5 % below normal in 1994 (644 mm), when the last measurements were taken. Accordingly, midday net photosynthesis, stomatal conductances and pre-dawn water potentials of the experimental species were highest early in the study and lowest later on (Figs. 1, 2).

With the exception of changes in midday leaf water potential for *Berberis*, neither shrub species showed an immediate (1 - 3 day) response to *Prosopis* removal (Figs. 1, 2; Table 1). After adjustment for pre-removal differences, there were no detectable effects of overstory removal on midday photosynthesis, stomatal conductance and water potential in either *Berberis* or *Zanthoxylum* when averaged over the long-term (September 1992 - July 1994; Table 1). Non-significant date × treatment interaction terms (ANCOVA; $P = 0.15$ - 0.95) for these three response variables further indicated that overstory removal had no differential effect, positively or negatively, on daytime physiological activity or status during the early/wet or late/dry periods for these shrub species. Similarly, no significant ($P > 0.05$) treatment differences were detected in photosynthesis and stomatal conductance in *Zanthoxylum* or *Berberis* for a morning sampling period in July 1994 (Fig. 1; ❑, ■). In contrast to the results for midday physiological activity, plants of both shrubs in the control clusters showed significantly higher pre-dawn water potentials than removals when averaged over the long-term (Fig. 2; Table 1). For both *Berberis* and *Zanthoxylum*, the greatest treatment differences in pre-dawn water potentials were observed under the driest conditions, which occurred > 1 yr following *Prosopis* removal.
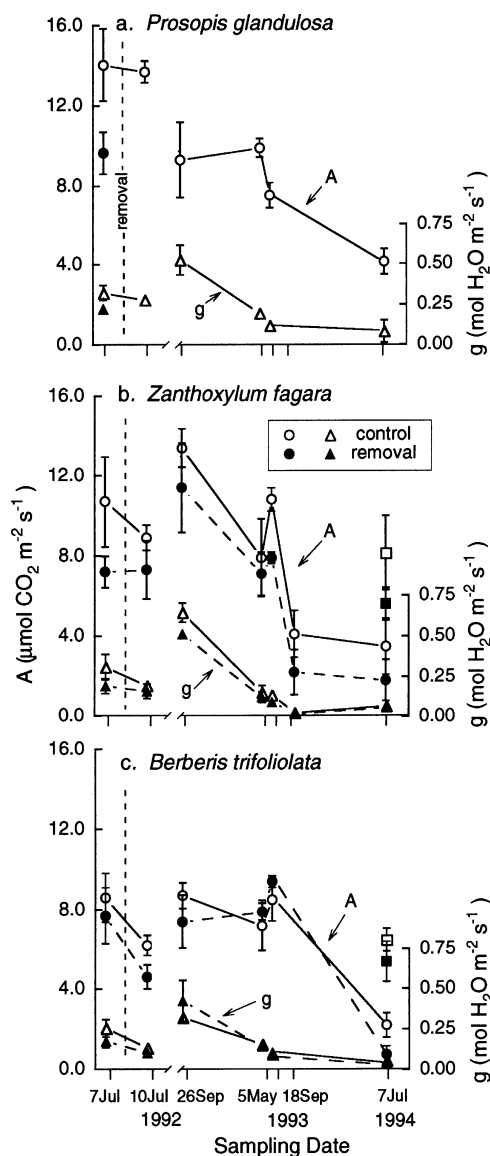

Fig. 1. Midday net photosynthesis (A) and stomatal conductance (g) of *Prosopis glandulosa* **(a)** and understory shrubs, *Zanthoxylum fagara* **(b)** and *Berberis trifoliolata* **(c)**, in upland woody clusters with (control) and without an intact *Prosopis* canopy (removal). ❑, ■ in **(b)** and **(c)**: photosynthesis data collected in the morning. Data are means ± 1 SE ($n = 3$; three leaves/replicate) and show values prior to (7 July), and following *Prosopis* removal (dashed vertical line).

Total N-concentrations of gas exchange leaves were nearly two-fold higher in *Zanthoxylum*, an evergreen species with leathery leaves, than in *Berberis*, a sclerophyllous evergreen; both species showed significant variation ($P < 0.001$) in leaf-[N] over time (Fig. 3). Leaf-[N] of *Prosopis* was higher than that of the shrubs (mean ranged from 27 to 34 mg/g; data not shown). *Prosopis* removal had no significant overall effect on leaf-[N] in
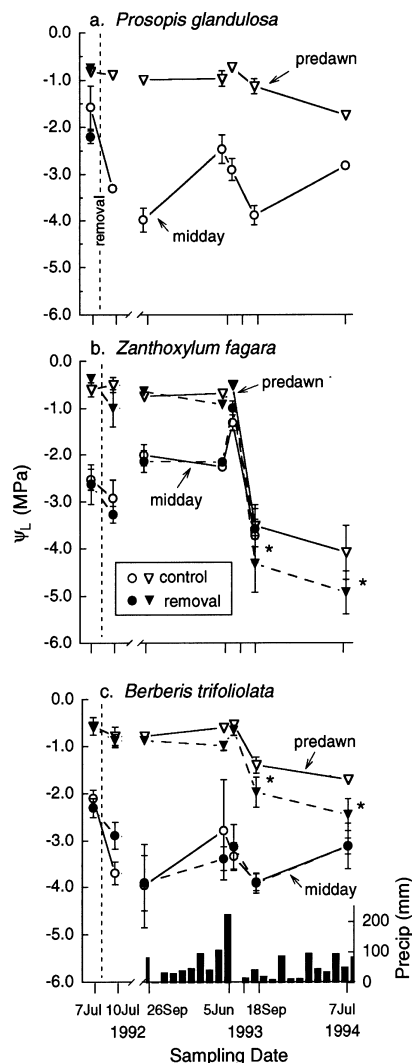
Fig. 2. Pre-dawn and midday leaf/shoot water potentials (ψ_L) of *Prosopis glandulosa* (**a**) and understory shrubs, *Zanthoxylum fagara* (**b**) and *Berberis trifoliolata* (**c**), in upland woody clusters with (control) and without (removal) an intact *Prosopis* canopy. Data are means ± 1 SE (*n* = 3; three leaves/replicate) from prior to (7 July) and following *Prosopis* removal (dashed vertical line). On-site monthly precipitation shown in (**c**). * = significant treatment differences at $P < 0.05$. Midday water potential data for *Zanthoxylum* missing for the last two sampling dates (18 September and 7 July 1994).

Fig. 3. Mean (± 1 SE; *n* = 3; three leaves/replicate) total N-concentration of gas exchange leaves of *Zanthoxylum fagara* and *Berberis trifoliolata* in woody clusters with (control) and without (removal) an intact *Prosopis glandulosa* canopy. * = $P < 0.05$.

tected in the bulk foliage samples of *Berberis* and *Zanthoxylum* collected during July and September 1992 and July 1993 (Table 1).

Mean (± SE) annual shoot elongation was greater (ANOVA; $P = 0.002$) in *Zanthoxylum* (20.1 ± 2.0 cm) than in *Berberis* (4.7 ± 1.2 cm). The shoot growth response of each species to overstory removal was similar ($P > 0.89$ for treatment × date interactions), with neither species being significantly ($P > 0.97$) affected (Fig. 4; Table 1).

Understory removal experiment

Stem biomass and length in 1994 were slightly, but significantly greater ($P = 0.04$) for *Prosopis* plants with a shrub understory than for those without an understory (Fig. 5a, b), whereas leaf and total shoot biomass were

Fig. 4. Elongation of terminal shoots of *Berberis trifoliolata* and *Zanthoxylum fagara* in woody clusters with (control) and without (removal) an intact *Prosopis glandulosa* canopy. All data (means ± 1 SE; *n* = 3; three shoots per replicate) were collected following *Prosopis* removal. Growth increment is the shoot elongation measured between dates, where the initial measurements were made on 9 July 1992.

Zanthoxylum (Table 1); however, the treatment × date interaction was significant ($P = 0.05$) and plants in clusters lacking the *Prosopis* overstory showed a significantly lower leaf-[N] relative to controls one year following overstory removal (July 1993). This treatment difference, however, was not apparent at a sampling period two months later. The removal of *Prosopis* had a small, marginally significant ($P = 0.10$), negative effect on leaf-[N] in *Berberis* (treatment × date interaction $P = 0.62$). No treatment differences in leaf-[N] were de-

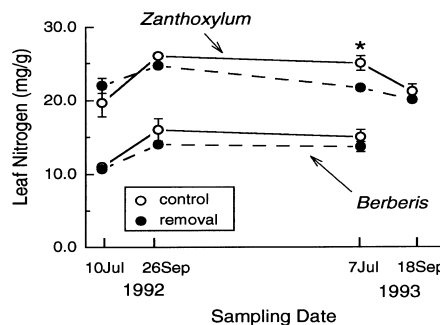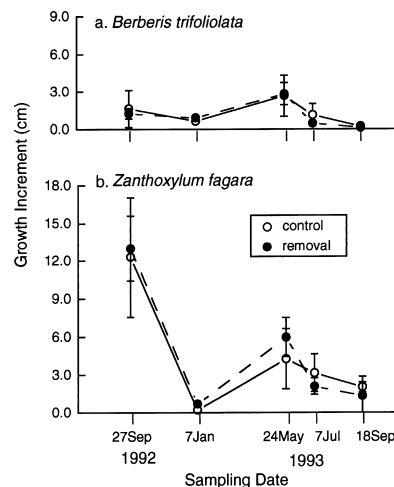comparable between treatments. None of these growth measurements varied significantly with respect to canopy azimuth position ($P = 0.13 - 0.46$). In contrast, shoot growth and production in 1995 was similar or slightly greater for *Prosopis* in the removal treatment than in the control. Understory removal had a significant overall effect ($P = 0.008$; $n = 6$) on leaf photosynthesis in *Prosopis* at two dates in 1995, with mean net CO_2 uptake rates nearly $2 \times$ higher in plants without understory than in those with an intact understory (Fig. 5c). Similar results were found for stomatal conductance ($P = 0.055$). However, the treatment effect on midday leaf water potentials differed for the sampling dates. Plants in the removal treatment showed significantly lower water potentials than controls in June, but this was reversed in September (Fig. 5d). No treatment differences ($P = 0.49$; $n = 6$) were found in pre-dawn water potentials in June.

Prosopis trunk growth was markedly enhanced by understory shrub removal (Fig. 6). The initial trunk basal diameters of *Prosopis* plants in the understory shrub removal treatment were, by chance, significantly greater (mean = 16.1 cm; range = 6.9 - 27.5 cm) than those of *Prosopis* plants in the intact understory treatment (mean = 10.2 cm; range = 3.9 - 19.1 cm). However, trunk
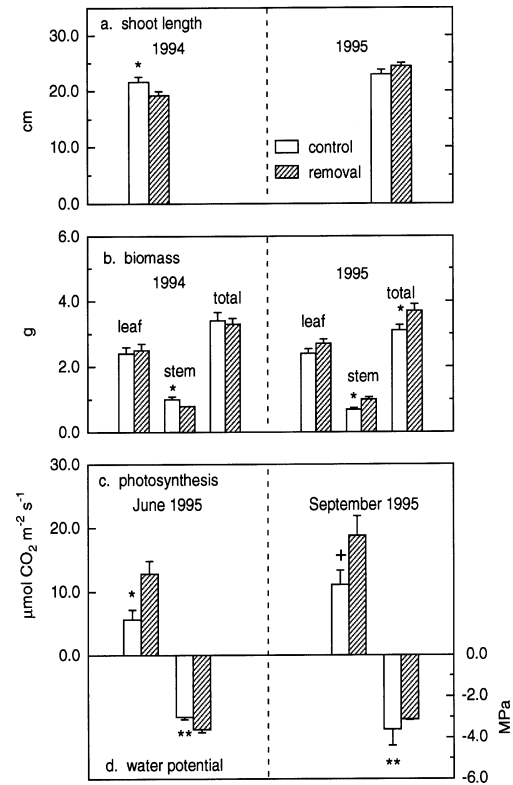
Table 1. Responses of the shrubs *Berberis trifoliolata* and *Zanthoxylum fagara* to removal of the *Prosopis glandulosa* overstory in mature, upland, woody patches. Values are ratios of control to overstory-removal treatment means (C/R, $n = 3$) and associated *P*-values for the main effect of removal treatment (Trmt) and the treatment × date interaction (Trmt*D). All short-term data and leaf-[N] and shoot elongation long-term data, were analyzed using ANOVA, whereas ANCOVA (covariate = the pre-removal value) was used to analyze long-term photosynthesis, conductance and water potential data. Short-term C/R values are from data collected 1 - 3 days after *Prosopis* removal; long-term C/R values are from data averaged over all sampling dates following overstory removal (i.e., sampling dates > 2 months post-removal). Values of C/R for water potential data are inverted to reflect the fact that absolute water potential values are negative (i.e., control means are higher (less negative) than treatment means when C/R > 1).

Response variable	*Berberis trifoliolata*			*Zanthoxylum fagara*		
	C/R	Trmt	Trmt*D	C/R	Trmt	Trmt*D
Short-term (1 - 3 days)						
Net photosynthesis[1]	1.32	0.25	0.76	1.26	0.09	0.60
Stomatal conductance[1]	1.29	0.18	0.51	1.21	0.18	0.44
Water potential[1]	0.78	0.24	0.06	1.11	0.52	0.72
Water potential[2]	1.11	0.70	0.85	2.01	0.58	0.15
Long-term (2 yr)						
Net photosynthesis[1]	1.05	0.54	0.40	0.99	0.90	0.83
Stomatal conductance[1]	0.88	0.35	0.59	1.15	0.21	0.15
Water potential[1]	1.02	0.72	0.95	0.98	0.93	0.76
Water potential[2]	1.38	< 0.01	0.22	1.36	0.02	0.41
Leaf-[N] - gas exchange leaves	1.10	0.10	0.62	1.04	0.20	0.05
Leaf-[N] - bulk samples	1.02	0.53	0.22	1.00	0.93	0.11
Shoot elongation	0.92	0.97	0.97	0.97	0.99	0.89

[1]Measured midday; [2]measured pre-dawn

Fig. 5. Mean (± 1 SE) current year's shoot length (**a**), biomass (**b**), leaf net photosynthesis (**c**) and leaf water potential (**d**) of *Prosopis glandulosa* in clusters with an intact (control) and cleared (removal) woody understory. Growth and biomass data ($n = 10$; eight shoots/plant) collected in August 1994 and 1995. Physiological measurements in June 1995 ($n = 6$; one leaf /replicate) taken ca. 14.00 CST; in September ca. 10.00 CST. ** = $P < 0.01$; * = $P < 0.05$; + = $P < 0.10$.

size was not significantly correlated with annual trunk growth rate for either group ($P > 0.46$). Thus, differences in growth rates are deemed to be treatment-induced. The annual increment of trunk growth of surviving *Prosopis* plants with understory shrubs removed was significantly greater ($P < 0.003$) than that of *Prosopis* plants with an intact understory over the entire study, and for each annual increment from 1989-1993 (Fig. 6). For *Prosopis* plants with a cleared understory, annual growth increments increased significantly from each preceding year ($P < 0.05$), except between 1990 and 1991 ($P = 0.36$). Trunk growth rates of *Prosopis* plants with intact understories were statistically comparable ($P > 0.44$) from one year to the next. As a result, there was a significant time × treatment interaction ($P < 0.0001$). During the course of our monitoring, seven *Prosopis* plants in clusters with an intact understory died, compared to two plants in clusters with the cleared understory.

Prosopis plants with a cleared understory were also more responsive to precipitation than were plants with
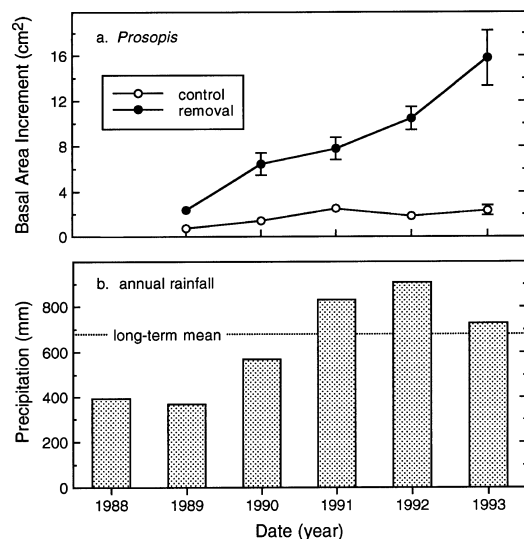
Fig. 6. Mean (± 1 SE; n = 19 - 20) annual basal area growth of *Prosopis glandulosa* plants with intact (control) and cleared (removal) woody understory (**a**), and annual precipitation at the La Copita research site (**b**). Growth increments based on live plants only.
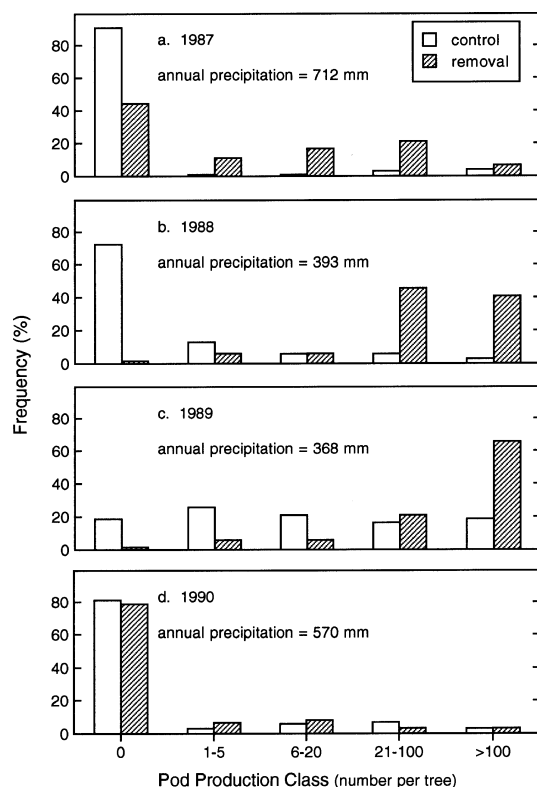

Fig. 7. Relative frequency distributions of seed pod production classes among upland *Prosopis glandulosa* plants with intact (control) and cleared (removal) woody understory. Significant treatment differences ($P < 0.01$; $n = 60$; SAS Catmod) occurred in 1987, 1988 and 1989.
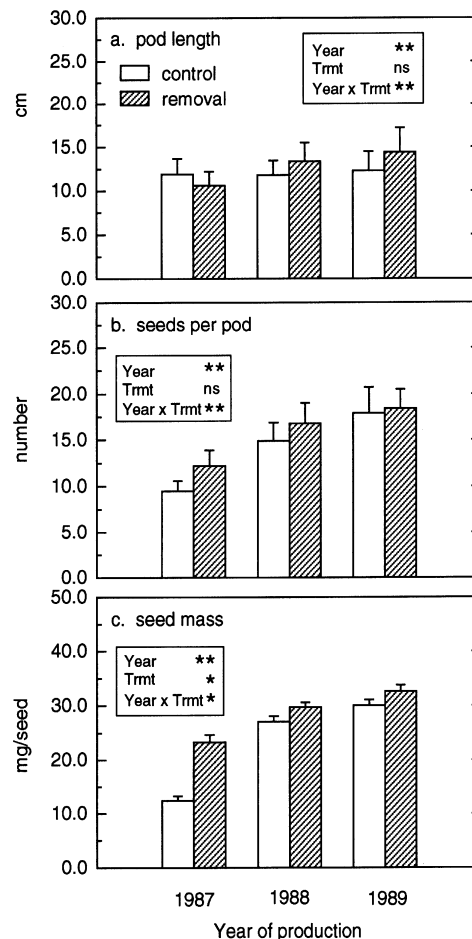

Fig. 8. Attributes (mean ± 1 SE; n = 60) of *Prosopis glandulosa* pods and seeds produced by trees with (control) and without (removal) a shrub understory. Inserts show ANOVA summaries for each variable; ** = $P < 0.01$; * = $P < 0.05$.

intact understories. Regression analysis indicated that annual and seasonal (January-June) rainfall each accounted for only 10 % of the variance in annual *Prosopis* trunk growth when understory shrubs were present. However, when understory plants were removed, the proportion of variance in *Prosopis* growth explained by annual (42 %) and seasonal (46 %) rainfall increased fourfold.

The number of seed pods produced by *Prosopis* plants with a cleared understory was significantly greater ($P < 0.01$) than that of uncleared controls in three of the four years monitored (1987, 1988 and 1989; Fig. 7). In 1990, few pods occurred in either treatment. The effects of understory removal on pod production varied with year and precipitation, with the greatest treatment differences occurring in the driest years (1988 and 1989). *Prosopis* plants without understory shrubs generally had slightly greater pod length, seeds per pod and mass per seed than did *Prosopis* plants with an intact understory (Fig. 8). However, the magnitude of differences be-

tween treatments varied significantly from year to year (year × treatment interactions; significant at $P < 0.05$).

Discussion

Prosopis effects on understory shrubs

Despite the apparent positive effects of the *Prosopis* (Archer et al. 1988; Fulbright et al. 1995; Franco-Pizaña et al. 1996) nurse plants on the germination and recruitment of other woody species in these savannas, results from our overstory-removal experiment indicate few persistent or strong beneficial effects of *Prosopis* on established understory shrubs . This is consistent with findings from an earlier study which revealed little difference in soils or performance of shrubs in clusters with intact, live *Prosopis* plants and those found in clusters where the *Prosopis* had naturally died (Barnes & Archer 1996). This study, which collected data over the days, weeks and years immediately following experimental *Prosopis* removal, suggests there would be no substantive short-term, transient period of physiological adjustment among understory shrubs following loss of *Prosopis*.

Although removal experiments have been used to probe for the existence of competition and facilitation between plants (Aarssen & Epp 1990), few studies have attempted to separate the immediate (short-term) effects of neighbors on resource availability from the longer-term effects associated with the exploitation of space previously occupied by the other species. We examined both the immediate and longer-term effects of *Prosopis* removal on shrub performance and, with few exceptions, found no clear differences between the two. Our assessment of shrub performance in this experiment was largely based on several ecophysiological attributes. Because field measurements of some of these attributes are logistically difficult and time-consuming, replication was limited. Even so, we consider our field sampling of these variables intensive and robust. Others have found leaf gas exchange and water potential to be sensitive indicators of neighbor removal in arid environments (e.g. Fonteyn & Mahall 1981; Ehleringer 1984). In our previous study examining shrubs growing in the presence and absence of *Prosopis* (Barnes & Archer 1996), replication was higher and we measured canopy foliar biomass production in addition to these leaf parameters. Thus, we suspect that if undetectable treatment differences did occur in the present study, they would still be relatively small in magnitude.

When beneficial effects of *Prosopis* were detected (i.e. pre-dawn water potentials and leaf-[N]), they were most pronounced under the drought conditions that occurred 2 yr after overstory removal (Fig. 2). This is in agreement with other studies that have shown facilitative effects to vary depending on precipitation and temperature (e.g. Greenlee & Callaway 1996) and support the more general hypothesis that facilitation is of greatest importance under conditions of high abiotic stress (Bertness & Callaway 1994). Maybe the higher pre-dawn water potentials of the relatively shallow-rooted shrubs growing in association with a live *Prosopis* was the result of *Prosopis*-mediated nocturnal transport of deep soil moisture to drier surface layers ('hydraulic lift', Caldwell et al. 1998). Indeed, *Prosopis glandulosa* has been characterized as a facultative phreatophyte (Nilsen et al. 1981; Ansley et al. 1990) and root excavations (Watts 1993) indicate plants at our study site are deeply rooted. While no studies have yet demonstrated hydraulic lift of *Prosopis* at this site, measurements of δ^2H and $\delta^{18}O$ in soil and plant xylem water by Midwood et al. (1998) indicated convergence in isotopic signatures between *Prosopis* (deep-rooted), *Zanthoxylum* (shallow-rooted) and deep soil water. Regardless of the mechanism resulting in higher pre-dawn water potentials in shrubs associated with *Prosopis*, we found no indication that this resulted in higher rates of photosynthesis, midday water potentials or shoot growth.

Prosopis glandulosa is a species capable of symbiotic N_2-fixation (Zitzer et al. 1996) and enhances soil fertility (Archer 1995) and N-mineralization (Hibbard 1995) at the La Copita site, as well as other sites in the southwestern USA (Virginia & Jarrell 1983; Tiedemann & Klemmedson 1986). So, the loss of *Prosopis* from clusters could depress N-cycling and N-availability. Indeed, we found some indication of a decline in leaf-[N] following removal of *Prosopis* in the individual leaves of *Berberis* and *Zanthoxylum* sampled for gas exchange measurements. But these effects were small and not evident in bulk leaf samples collected from outer canopy positions. Selective removal experiments such as ours typically leave below-ground tissues in place, and this may ultimately increase nutrient available to remaining plants as decomposition occurs. Possibly decomposition of *Prosopis* roots provided enough additional soil nitrogen to offset the loss of inputs from symbiotic N_2-fixation. Overall, the lack of an appreciable decline in leaf-[N] in shrubs following removal of *Prosopis* is in agreement with our previous study (Barnes & Archer 1996). Similarly, Hibbard (1995) found no differences in N-concentrations, N-mass, or N-mineralization rates in soils of clusters with and without *Prosopis*. The studies from La Copita are in accordance with experiments in hot desert ecosystems, which indicate that nutrient enhancements associated with *Prosopis* occupation of soils may persist for decades following *Prosopis* removal (Klemmedson & Tiedemann 1986; Tiedemann & Klemmedson 1986).

Prosopis is also known to alter temperature, light and soil moisture conditions beneath its canopy (Archer 1995; Fulbright et al. 1995), and in upland shrub clusters at this study site, its canopy attenuates midday light levels by about 40 % (P. Barnes & S. Archer unpubl.). However, the maximum average PFD at the top of the shrub canopy underneath *Prosopis* during summer is still ca. 1200 μmol m^{-2} s^{-1}, which is well above the light saturation point for leaf photosynthesis in these C$_3$-understory species (C. McMurtry & P. Barnes unpubl.). Thus, the shading provided by the *Prosopis* overstory likely had little direct effect on canopy photosynthesis in these shrubs, though there could have been some indirect benefits associated with reduced leaf temperatures and heat stress. In more arid systems, the alteration of radiant energy regimes and the redistribution of intercepted rainfall can lead to preferential recruitment and growth on certain sides of the nurse plant (Franco & Nobel 1989; Valiente-Banuet et al. 1991b). However, directional (azimuth) development is not evident in mature *Prosopis*-mixed shrub clusters (Archer et al. 1988; Scanlan 1988; Franco-Pizaña et al. 1995). These observations, together with the fact that physiological performance of understory shrubs was largely maintained after overstory removal, suggest that *Prosopis*-induced modifications of microclimate may have little influence on the dynamics of well-developed clusters.

Overall, our findings suggest that, while *Prosopis* may continue to facilitate established understory species under certain conditions, the associated shrubs are not highly dependent upon *Prosopis*. Over the course of this study (2 yr), we observed no mortality of shrubs in either control or removal treatments. These shrubs are capable of vegetative and seedbank propagation and rapid growth following disturbances which destroy above-ground biomass (Scanlan 1988; Flinn et al. 1992). Together, results imply that the loss of *Prosopis* from shrub clusters will not initiate a 'downgrade phase' in a cyclic succession of cluster initiation, development and death as has been proposed for other shrub cluster systems (e.g. Yeaton 1978). Rather, the shrubs associated with *Prosopis* will likely persist in the landscape long after the plant which facilitated their ingress and establishment is gone.

Understory shrub effects on Prosopis

Whereas the effects of the overstory *Prosopis* plants on established understory shrubs were neutral or positive, the woody understory species had strong negative effects on *Prosopis* photosynthesis, growth and reproduction. Competition between *Prosopis* and understory shrubs is therefore highly asymmetrical. Our data showing enhanced bole growth of *Prosopis* following understory shrub removal are in agreement with that of Cornejo-Oviedo et al. (1992) and support the hypothesis that intense competition from understory shrubs may lead to, or at least hasten, the demise of *Prosopis* in clusters and prevent its regeneration. For example, of the 110 clusters sampled by Archer et al. (1988), none contained *Prosopis* seedlings or saplings and 25 % possessed a dead *Prosopis*; where *Prosopis* was alive, its canopy often appeared sparse and poorly developed. During the course of our study, more *Prosopis* plants died in clusters with an intact understory died than in clusters with cleared understory. Lack of *Prosopis* recruitment in clusters probably reflects a combination of decreases in seed production over time and unsuitable conditions for seedling establishment. *Prosopis* is a heliophyte, and PFD at ground level in clusters (100 - 200 μmol m^{-2} s^{-1}; P. Barnes & S. Archer unpubl.) is well below that required for seedling growth (Bush & van Auken 1987) and survival (Scifres et al. 1973). In addition, field observations of discrete clusters show no evidence of 'gap formation' as occurs in forest stands. If such gaps occur, they are apparently quickly occupied by understory shrubs which have a substantial 'seedling bank' (Archer et al. 1988).

It is likely that these competitive effects are the result of differential rooting patterns and depths of woody species in these clusters. The dominant understory shrubs are relatively shallow-rooted (Watts 1993) and apparently extract moisture and nutrients that might otherwise percolate to deeper depths where *Prosopis* roots are concentrated. This is consistent with the fact that seasonal or annual rainfall accounted for only ca. 10 % of the variance in *Prosopis* trunk growth when understory shrubs were present, as compared to 42 - 46 % when understory shrubs were absent. The hypothesis of differential utilization of soil moisture with depth is also in agreement with findings which showed understory shrubs to be much more responsive to surface irrigation than were *Prosopis* plants (C.R. McMurtry and J.A. Nelson, M.Sc. Theses, SW Texas State University,1997).

Spatial variation in overstory-understory interactions?

The presence of restrictive soil horizons is of fundamental importance to plant distributions in savannas (Johnson & Tothill 1985; San José & Montes 1991) and shrublands (McAuliffe 1994). The interpretation of tree-shrub interactions presented here is based on discrete woody patches underlain by a well-developed argillic (B$_t$) horizon (zone of clay accumulation) at 40 - 100 cm. This horizon acts to create a relatively shallow soil for these species by restricting root development (Watts 1993) and the percolation of water and nutrients. However, tree-shrub patches at this site also develop on portions of the uplands where this horizon is absent and soils are coarse-textured

throughout the profile. These patches tend to support high densities of *Prosopis* plants whose canopies intersect to form extensive groves. The *Prosopis* plants in these upland groves are larger (basal diameter, canopy area, height), produce more seed and exhibit higher growth rates than those in nearby discrete clusters (Archer 1995). Photosynthesis and water potentials of understory shrubs are lower in groves than in clusters (C. McMurtry & P. Barnes unpubl.). On coarse-textured, deeper soils, the intensity of stress induced by competition of understory woody species with overstory *Prosopis* may be relaxed. This could result in contrasting successional trajectories for discrete cluster and grove patches. The extent to which species interactions and vegetation change in this landscape is mediated by this subsurface heterogeneity is the focus of ongoing study.

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