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Influence of an overstorey tree (*Prosopis glandulosa*) on associated shrubs in a savanna parkland: implications for patch dynamics

Abstract The arborescent legume, honey mesquite (*Prosopis glandulosa*), appears to play a central role in patch dynamics of southern Texas savannas by modifying soils and microclimate and by facilitating the ingress, establishment and/or growth of shrubs in its understorey. As an indirect test for the occurrence and persistence of facilitation in mature shrub clusters (patches), we examined the gas exchange, water relations and production of associated shrubs growing in patches where a *Prosopis* overstorey was present and in patches where *Prosopis* had succumbed to natural mortality. Surface (0–10 cm) soils associated with shrub patches were enriched in total [N] and [C] compared to soils of neighboring herbaceous zones. However, there were no detectable differences in soil [N] or [C] in patches with and without *Prosopis*. Foliar [N] and biomass of various shrub species were also statistically comparable for patches with and without *Prosopis*. These results are in accordance with other studies that indicate the nutrient legacy associated with *Prosopis* occupation of a patch may persist for decades after its demise. In comparison to plants growing in the absence of *Prosopis*, leaf water potentials (predawn and midday), and net photosynthesis and water vapor conductance (morning and midday) of outer-canopy sunlit leaves over an annual growth cycle were comparable for two common evergreen shrubs, *Zanthoxylum fagara* and *Berberis trifoliolata*, growing in patches with a live *Prosopis*. These findings indicate that the presence of *Prosopis* was not enhancing the growth or activity of mature understorey shrubs; facilitation may, therefore,

be important only during early stages of cluster development. In addition, we found no indication that the loss of *Prosopis* has initiated a downward phase in a cyclic succession of patch initiation, growth and death. Rather, the understorey shrubs appear to be able to maintain growth and productivity in the absence of a *Prosopis* overstorey, and may, therefore, represent persistent components of woody patches on these savanna landscapes.

Key words Facilitation · Nurse plant · Photosynthesis · Primary production · Water relations

Introduction

Savanna ecosystems are characterized by a continuous layer of graminoids interrupted by sparsely-spaced trees or shrubs. These discontinuities represent patches where both the microclimate and the availability of resources have been altered in concentric zones surrounding the woody vegetation (Kellman 1979; Belsky et al. 1989; Vetaas 1992). Isolated trees can influence the growth and productivity of the understorey herbaceous layer (Belsky 1994) and are thought to serve as nuclei (i.e., nurse plants) for subsequent vegetation development in tropical, sub-tropical and temperate savanna ecosystems (Tupas and Sajise 1977; Hacker 1984; Rykiel and Cook 1986; Smith and Goodman 1987; Archer et al. 1988; Fowler 1988; McPherson et al. 1988). Through their role as nurse plants, savanna trees can thereby significantly influence long-term patterns of community structure and function, landscape heterogeneity and ecosystem processes (Archer 1995).

While the characteristics of woody patches in savannas have been widely studied, little is known of their dynamics and how patch properties change as trees establish, develop and die (Belsky and Canham 1994). In an ongoing case study in southern Texas, United States, succession from grassland to woodland has been

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shown to begin when honey mesquite (*Prosopis glandulosa*) invades and establishes in grassland sites and then facilitates the ingress, establishment and/or growth of various subordinate shrub species in its understorey (Archer et al. 1988). Over time, distinct shrub clusters (patches) thereby develop within a matrix of herbaceous grassland vegetation (Whittaker et al. 1979). Under certain conditions, shrub clusters organized around the *Prosopis* nucleus expand and coalesce to form a continuous, closed-canopy woodland (Archer 1989). For some clusters, however, the central *Prosopis* eventually dies leaving isolated patches of understorey shrubs (Archer et al. 1988).

Understanding the nature and persistence of the facilitative effects of *Prosopis* is necessary for predicting patch dynamics and future landscape states in these subtropical savannas and woodlands. If facilitation is operationally significant at latter stages of cluster development, we might expect that loss of *Prosopis* would be reflected in reduced physiological activity and/or growth of understorey shrubs. These responses should precede shifts in species composition and could, therefore, be indicative of the first stages in the downward phase in a cyclic pattern of patch initiation, growth and death (e.g., Watt 1947; Yeaton 1978; Soriano et al. 1994). On the other hand, facilitation may be critical only at the seedling stage. Following establishment, resource limitations may increase progressively as seedlings develop into adults and competitive effects might eventually outweigh the beneficial effects of habitat modification by the nurse plant (e.g., McAuliffe 1984; Franco and Nobel 1990; Aguiar et al. 1992; Aguiar and Sala 1994). In this scenario, we would expect understorey shrubs to maintain or increase their physiological activity and growth following the loss of *Prosopis*, and we would infer that shrub patches may be relatively stable and persistent components of the landscape.

To test for the continued dependence of understorey shrubs on *Prosopis* and the possibility of cyclic succession in these woody patches, we compared the physiological activity and biomass production of associated shrubs growing in mature clusters containing a living *Prosopis* to those of plants growing where *Prosopis* had succumbed to natural mortality. Two of these shrub species differ in their time of arrival in cluster development [*Zanthoxylum fagara* = 10–15 years after *Prosopis* establishment; *Berberis trifoliolata* = 30–40 years later (Archer et al. 1988; Archer 1989)]. Thus, we further hypothesized that these species would be differentially affected by the loss of *Prosopis*.

Materials and methods

Studies were conducted at the Texas Agricultural Experiment Station La Copita Research Area located in Jim Wells county in the eastern Rio Grande Plains of southern Texas (27° 40' N; 98° 12' W; elevation above sea level = 75–90 m). Contemporary vege-

tation in this region has been classified as subtropical thorn woodland (McLendon 1991). Vegetation at the study site, which has been grazed by domestic livestock since the late 1800s, consists of savanna parklands in the uplands and closed-canopy woodlands in lowland drainages and playas (Archer 1995). Uplands exhibit a mosaic of herbaceous vegetation (dominated by C_4 grasses) and discrete clusters of woody plants that vary in successional age-size states (Archer et al. 1988). The overstory in upland and lowland habitats is dominated exclusively by the winter-deciduous honey mesquite [*Prosopis glandulosa* var. *glandulosa* Torr.; nomenclature follows Correll and Johnston [1979]] while the understorey woody vegetation consists of a diverse mixture of evergreen [e.g., *Zanthoxylum fagara* (L.) Sarg., *Berberis* (= *Mahonia*) *trifoliolata* Moric.], semi-evergreen (e.g., *Condalia hookeri* M.C. Johnst., *Diospyros texana* Scheele, *Celtis pallida* Torr.) and summer (drought)-deciduous [e.g., *Schaefferia cuneifolia* Gray, *Ziziphus obtusifolia* (T.&G.) Gray] shrubs. The climate of the region is subtropical with warm winters, hot summers (mean annual temperature = 22.4 °C) and bimodally distributed rainfall (mean annual precipitation = 680 mm; maxima in May/June and September). Soils on the landscapes used in our study were sandy loams underlain by a distinctive argillic (clay-rich) horizon (Loomis 1989).

Studies were conducted in several upland, savanna landscapes on discrete shrub clusters which either possessed or lacked a live *Prosopis* overstory. We restricted our sampling to "mature" clusters (approximate age = 30–60 years), in terms of successional status (Archer et al. 1988). When present, the overstory consisted of a single, central *Prosopis*. In the clusters which lacked a live *Prosopis*, there was often, but not always, remnants of a dead *Prosopis* near the cluster's center. The factors responsible for this mortality are, at present, unknown.

Surface soil samples (0–10 cm) collected from near the center of shrub patches with and without *Prosopis* and adjacent herbaceous zones were analyzed for total carbon and nitrogen by an automated (Carlo Erba NA-1500 elemental analyzer, Fisons Instruments, Saddle Brook, N.J., USA) Dumas combustion procedure (Pella and Colombo 1973). Coarse roots were removed from samples prior to grinding to a fine powder.

Samples for foliar nitrogen concentration [N] and canopy biomass were obtained by harvesting all leaf tissue from within duplicate $0.3 \times 0.3 \times 0.3$ m cubes positioned in the top- (i.e., upper canopy) and bottom-most (i.e., lower canopy) regions of both *Prosopis* and shrub canopies. Samples were typically collected from 12 woody patches (6 each from clusters with and without *Prosopis*) periodically over the course of 1–2 years. Kjehldahl digestion (Nelson and Somers 1980) and autoanalysis (Lachet System 4 autoanalyzer) was used to determine total organic [N] on a subsample of harvested tissue. In addition, [N] was also determined for leaves of *Berberis* and *Zanthoxylum* used for gas exchange analysis. Because shrub species differed in their occurrence within the harvest cubes, the number of replicates per species for foliar [N] from these harvest data varied with species, canopy position and time of harvest. Canopy biomass determinations were made from harvested foliar tissue that was oven-dried (60 °C) and weighed, and these data are reported here as foliar biomass density (g/m³). Canopy height and two perpendicular diameters were measured to test for differences in shrub cluster sizes when *Prosopis* was present or absent. Studies in other ecosystems have demonstrated strong relationships between whole-shrub production and estimates derived from canopy dimensions and small quadrat samples of the canopy (e.g., Sala et al. 1989; Fernández et al. 1991). These sampled shrub clusters were also inventoried with respect to species composition and relative abundance (based on visual estimates of contribution to total canopy cover).

Measurements of net CO_2 uptake and H_2O loss were made on fully-expanded, outer-canopy, sunlit leaves from plants of *Berberis* and *Zanthoxylum* using a closed-path, portable photosynthesis system (LI-6200, LiCor, Inc., Lincoln, Neb., USA) with a 0.25-l cuvette. For most gas exchange measurements, one or several leaves were enclosed in the cuvette for 15–45 s in their natural orienta-

tion. Gas exchange measurements were taken from early-morning to late-afternoon under sunny skies. For each species, measurements taken within a 1–2 h period were pooled for statistical analysis. At a given sampling period and time interval, measurements were taken on three to six replicate plants with each replicate consisting of one to three leaves. Different shrubs were selected for measurements at each sampling date. Because most individual leaves were not sunlit at all times of the day, a different subset of leaves was usually selected for morning and midday measurements.

Leaf water potentials were measured using a pressure chamber on three to six plants per treatment for *Berberis, Condalia* and *Zanthoxylum*. Samples for water potential determination were kept in a humid plastic bag prior to, and during, measurement.

Data were analyzed using analysis of variance techniques (SAS GLM and SYSTAT for the Macintosh) for factorial treatment arrangements in a completely randomized design. Mean comparisons were made using Duncan's Multiple Range test and Student *t*-tests with differences reported as significant when $P < 0.05$.

Results

Patch composition, structure and production

With the exception of the presence/absence of *Prosopis*, the woody plant patches (= shrub clusters) inventoried were generally similar in woody species composition, canopy dimensions and total area (Table 1). When averaged over all sampling dates, the mean foliar standing crop density was significantly higher ($P < 0.05$) in upper canopy positions than lower canopy positions in both the *Prosopis* overstorey (upper canopy mean = 306 g/m^3; lower canopy = 226 g/m^3) and the shrub understorey (upper canopy mean = 265 g/m^3; lower canopy mean = 132 g/m^3). Canopy standing crop density varied seasonally in both *Prosopis* and shrubs, with peaks occurring in summer (means for combined upper and lower canopies for June to July = 331–397 g/m^3 for *Prosopis* and 225–267 g/m^3 for the shrubs) and minima occurring in winter to early spring (means for combined upper and lower canopies for January to March

= 106–157 g/m^3 for *Prosopis* and 120–160 g/m^3 for the shrubs) (Fig. 1).

There was no detectable overall effect ($P = 0.32$) of the *Prosopis* overstorey on shrub foliar standing crop density. A significant interaction of overstorey with sampling date, though, indicated that the effect of a live *Prosopis* on shrub biomass production varied with time of year. However, while shrub biomass density was correlated with the presence of *Prosopis* on two dates (November 1991, upper canopy; March 1992, lower canopy), this pattern was reversed on two other dates (June 1991 and May 1992, upper canopy for both) (Fig. 1).

Soil and foliar nitrogen

Surface (0–10 cm) soils of shrub clusters were significantly higher in both total nitrogen [N] and total carbon [C] relative to soils of herbaceous zones, but no significant differences in [N] or [C] were detected between soils from clusters with or without a live *Prosopis* (Table 2).

Mean maximum foliar [N] of tissue obtained from bulk harvests was highest in the winter-deciduous, N_2-fixing *Prosopis* (52 mg/g) and generally lowest in the evergreen species (*Zanthoxylum* = 30 mg/g; *Berberis* = 15 mg/g) (Fig. 2). Summer-deciduous (*Ziziphus* = 30 mg/g; *Schaefferia* = 35 mg/g) and semi-evergreen (*Celtis* = 37 mg/g; *Condalia* = 33 mg/g; *Diospyros* = 29 mg/g) growth forms typically had intermediate [N] values. Seasonal variation in leaf [N] was also greater in *Prosopis* and *Condalia* than in the evergreen species, *Zanthoxylum* and *Berberis*. Foliar [N] was slightly, but significantly, higher in upper canopy than in lower canopy positions in *Prosopis* (overall upper = 32 mg/g; lower = 31 mg/g) as well as the shrubs, *Berberis, Condalia* and *Zanthoxylum* (overall upper = 24 mg/g; lower = 21 mg/g).

Table 1 Composition and structure (mean ± SE; $n = 6$) of woody patches with and without a live *Prosopis glandulosa* overstorey. [*Rank* is the mean rank order of the species, where ranking was based on the species canopy cover relative to that of other woody species present (*1* most important); *F* frequency of occurrence]

Patch characteristics		Patch type				
		Prosopis Present		*Prosopis* Absent		
Prosopis structure						
Upper canopy height (m)		2.8 ± 0.2		–		
Lower canopy height (m)		1.6 ± 0.1		–		
Canopy area (m^2)		21.2 ± 3.1		–		
Basal stem diameter (cm)		23.9 ± 8.4		–		
Shrub cluster structure						
Upper canopy height (m)		1.2 ± 0.1		1.1 ± 0.1	NS	
Lower canopy height (m)		0.3 ± 0.03		0.2 ± 0.02	*	
Canopy area (m^2)		34.4 ± 8.5		27.9 ± 4.5	NS	
Number of woody species		6.3 ± 0.7		5.0 ± 0.6	NS	
Shrub cluster composition	%Cover	Rank	*F*	%Cover	Rank	*F*
Zanthoxylum fagara	41 ± 9	1.3	1.0	47 ± 12	1.3	1.0
Condalia hookeri	38 ± 8	1.7	1.0	39 ± 13	1.8	1.0
Berberis trifoliolata	4 ± 1	3.8	0.8	4 ± 1	2.5	0.5

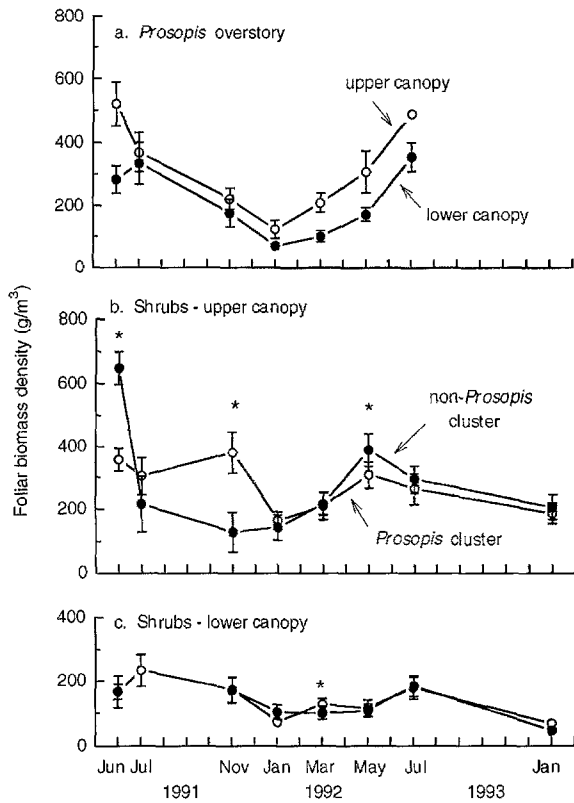*NS P > 0.05, * P ≤ 0.05*; Student *t*-tests

Fig. 1a–c Seasonal patterns of mean (± 1 SE) foliar standing crop density (g/m³) in upper and lower canopy positions of the *Prosopis glandulosa* overstorey and shrubs in clusters with and without a live *Prosopis*. For a given canopy position and date, significant differences (*P* < 0.05) in mean foliar biomass density of shrubs with and without *Prosopis* are denoted by *, as determined by Duncan's Multiple Range test. Error bars not visible are within the boundaries of the symbol. For *Prosopis*, *n* = 4–6 except January 1992 (*n* = 1–2). For the shrubs, *n* = 6 except June 1991 (*n* = 4) and July 1991 upper canopy (*n* = 2). Lower canopy shrub biomass data were not collected in July 1991

There was no significant main effect (*P* = 0.22) of *Prosopis* overstorey on bulk foliar [N] in *Berberis*, *Condalia* and *Zanthoxylum*. Mean comparisons at the various sampling dates also revealed few consistent statistically significant differences in bulk foliar [N] for these species (Fig. 2) as well as for other species at a single sampling date (September 1992: *Celtis* = 33 vs. 37 mg/g; *Diospyros* = 21 vs. 18 mg/g; *Schaefferia* = 21 vs. 21 mg/g; *Ziziphus* = 26 vs. 30 mg/g) growing with

Table 2 Mean (± 1 SE) total nitrogen and carbon concentrations (mg/g) of surface (0–10 cm) soils in upland habitats at the LaCopita study site

Patch type	*n*	Nitrogen	Carbon
Herbaceous zone	12	0.7 ± 0.2[a]	9.4 ± 1.7[a]
Prosopis shrub cluster	6	1.8 ± 0.5[b]	21.9 ± 6.8[b]
Non-*Prosopis* shrub cluster	6	1.8 ± 0.6[b]	21.7 ± 9.4[b]

Within a column, means with *different letters* denote significant differences (*P* < 0.05) according to Duncan's multiple range test
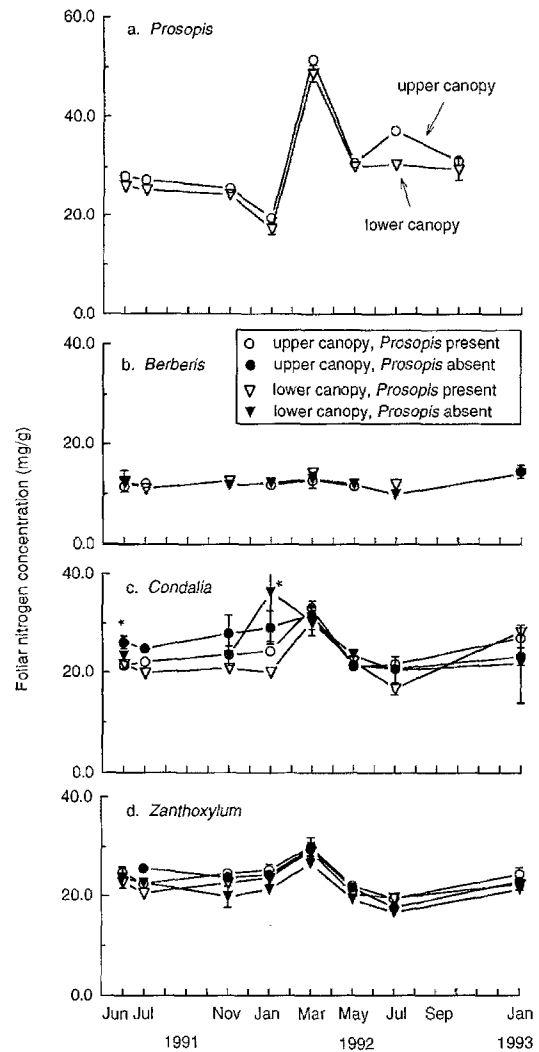

Fig. 2a–d Seasonal patterns of mean (± 1 SE) bulk foliar nitrogen concentration in upper and lower canopy positions for the *P. glandulosa* overstorey and common shrubs (*Berberis trifoliolata*, *Condalia hookeri*, and *Zanthoxylum fagara*) growing in upland woody patches in the presence and absence of a live *Prosopis*. Significant (*P* < 0.05) differences between means as determined by Duncan's Multiple Range test are denoted by *. Error bars not visible are within the boundaries of the symbol. For *Prosopis*, *n* = 6 at all dates and canopy positions except July 1991 and January 1992 (*n* = 2–4) and July 1992, lower canopy (*n* = 1). For *Berberis*, few (*n* = 1–2) or no samples were collected from upper canopy positions; for lower canopy positions, *n* = 2–4 except July 1991 (*Prosopis* present) and July 1993 (*Prosopis* absent) where *n* = 1. Lower canopy data for *Berberis* were not collected in January and May 1992 (*Prosopis* present) and July 1991 (*Prosopis* absent). For *Condalia* upper canopy positions, *n* = 3–6 except July 1991, where *n* = 1–2; for lower canopy positions, *n* = 2–3 except July 1991 (*Prosopis* present), where *n* = 1. For *Zanthoxylum*, *n* = 3–6 except June, July and November 1991 (*Prosopis* absent) where *n* = 1–2

and without a live *Prosopis*, respectively. Nitrogen concentrations of individual leaves used for gas exchange measurements were also comparable for *Zanthoxylum* (July 1991: 23 vs. 22 mg/g; January 1992: 24 vs. 26 mg/g; March 1992: 24 vs. 21 mg/g) and *Berberis* (July 1991: 12 vs. 13 mg/g; January 1992: 14 vs.

14 mg/g; March 1992: 16 vs. 16 mg/g) plants growing with and without *Prosopis*.

Gas exchange and water relations

Mean maximum rates of net CO_2 uptake (A) and diffusive conductance to water vapor (g) of individual leaves were generally similar in the two evergreen species, *Zanthoxylum* and *Berberis* (c. 11 µmol CO_2 m^{-2} s^{-1}; 0.1–0.2 mol H_2O m^{-2} s^{-1}). Gas exchange activ-

ity varied little over time for either species, with the exception of a distinct period of inactivity during the summer drought (Figs. 3a, b; 4a, b). When averaged over date and species, there was no detectable effect ($P > 0.3$) of *Prosopis* on either morning (near daily maximum) or midday (near daily minimum) A and g in *Zanthoxylum* and *Berberis* and there was no indication that the presence/absence of a *Prosopis* overstorey differentially affected diurnal (data not shown) or seasonal gas exchange in these two shrub species ($P > 0.2$ for the overstorey × shrub species interaction).

Mean predawn water potentials (Ψ_L) in *Berberis* were rather constant, rarely dropping below -2 MPa, but were seasonally more variable in *Zanthoxylum*, reaching a low of -6.6 MPa in mid-summer (Figs. 3c, 4c). Seasonal minima in midday Ψ_L occurred in mid-summer for both *Berberis* (-4.2 MPa) and *Zanthoxylum* (-7.9 MPa). Presence or absence of a live *Prosopis* overstorey had no significant overall effect on either predawn or midday Ψ_L in *Zanthoxylum* and *Berberis* plants ($P = 0.8$ for main effect of *Prosopis* overstorey

Fig. 3a–d Seasonal patterns of mean ($\pm$ 1 SE; $n = 3$–6) **a** net photosynthesis, **b** leaf water vapor conductance (g) and **c** leaf water potential (Ψ_L) for *B. trifoliolata* growing in woody patches with (*open circles*) and without (*closed circles*) a live *Prosopis*. Morning data were collected from 0800–1000 hours local time and midday data were collected from 1300–1500 hours local time. Predawn Ψ_L data were collected within 1–2 h before sunrise. Significant ($P < 0.05$) differences between means in the presence and absence of *Prosopis* are denoted by *, as determined by Student t-tests. **d** Mean monthly maximum (*open circles*) and minimum (*closed circles*) air temperatures at the study site with total monthly precipitation (*bars*). Error bars not visible are within the boundaries of the symbol
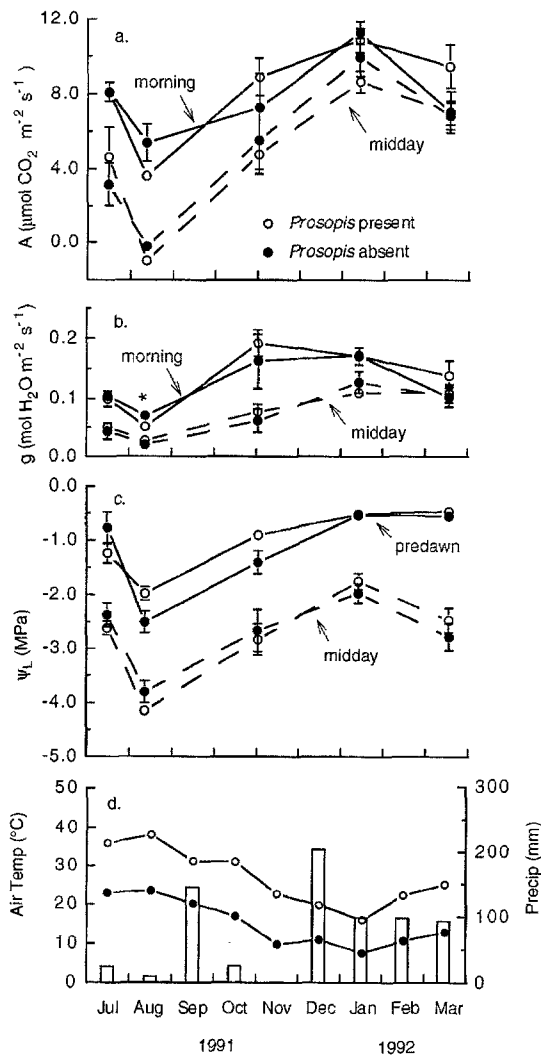
Fig. 4a–c Seasonal patterns of mean ($\pm$ 1 SE; $n = 3$–6) **a** net photosynthesis, **b** leaf water vapor conductance (g) and **c** leaf water potential (Ψ_L) for *Z. fagara* growing in woody patches with (*open circles*) and without (*solid circles*) a live *Prosopis*. The times corresponding to predawn, morning and midday are as in Fig. 3. Significant ($P < 0.05$) differences between means in the presence and absence of *Prosopis* are denoted by *, as determined by Student t-tests. Error bars not visible are within the boundaries of the symbol
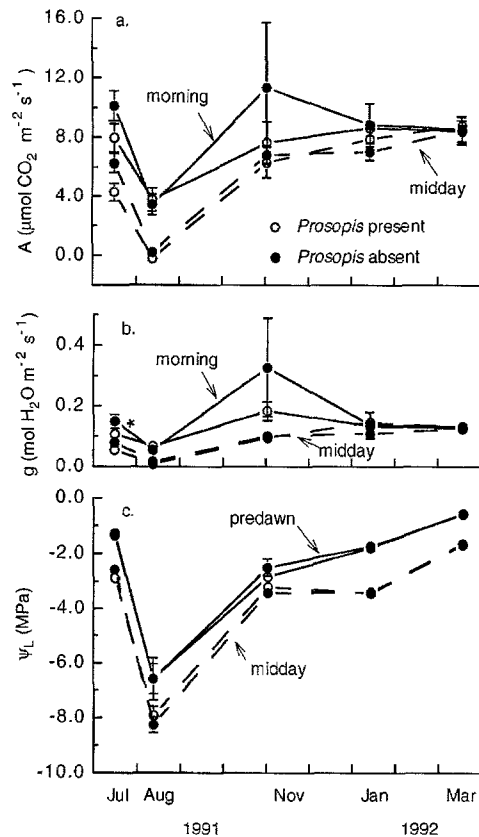
and $P = 0.3$ for the overstorey × shrub species interaction). Similarly, no statistically significant differences in predawn leaf water potentials were evident on two separate dates for *Condalia* growing in the presence or absence of *Prosopis* (August 12: $\Psi_L = -3.2$ vs. -2.9 MPa; March 19: $\Psi_L = -0.7$ vs. -0.8 MPa).

Discussion

Facilitation by *Prosopis glandulosa* is thought to be of fundamental importance in the historical and contemporary encroachment of woody plants into grasslands and savannas of southern Texas (Archer et al. 1988). The precise nature of the *Prosopis*-mediated facilitation of understorey shrubs, however, is not well understood and, indeed, the existence of facilitation has yet to be experimentally demonstrated. By providing shade and moderating air and soil temperatures beneath its canopy (Archer 1995), *Prosopis* plants may provide understorey shrubs some degree of relief from extreme high temperatures and moisture deficits that occur during summer drought periods (Fig. 3d). *Prosopis* is a known phreatophyte (Mooney et al. 1977; Nilsen et al. 1981) and plants at our study site are also deeply rooted (Midwood et al. 1993; Watts 1993). The potential therefore exists for *Prosopis* to transport and redeposit deep soil moisture to drier surface soils (i.e., "hydraulic lift"; Caldwell et al. 1991), which might then benefit shallow-rooted understorey shrubs such as *Zanthoxylum* [83–89% of root biomass in upper 40 cm (Watts 1993)]. The physiological data presented here, however, indicate that the presence of *Prosopis* did not significantly enhance the water status of associated shrubs, even during the hot, dry summer months (Figs. 3, 4). Observations that understorey shrub communities are generally circular and do not exhibit any directionality in development around the *Prosopis* nucleus (Archer et al. 1988; Scanlan 1988; Franco-Pizaña et al. 1995) further suggest that associated shrubs, as a group, are little influenced by *Prosopis*-induced modifications of the aerial environment. This is in contrast to warm deserts and some tropical savanna ecosystems where seedling establishment, species composition and production are often spatially skewed in favor of the more shaded and protected sides of nurse plants (e.g., Stuart-Hill et al. 1987; Franco and Nobel 1988).

Prosopis glandulosa is capable of symbiotic N_2-fixation (Virginia et al. 1984; Johnson and Mayeux 1990) and *Prosopis* roots have been found to nodulate readily when grown under laboratory conditions in soils from our study site (S. Zitzer, S. Archer and T. Boutton, unpublished work). ^{15}N analysis of plants at this site indicate that this species acquires approximately 50% of its nitrogen via symbiotic fixation (T. Boutton, S. Zitzer, S. Archer and L. Cifuentes, unpublished work). Accordingly, *Prosopis* has been shown to enhance soil N and overall fertility on this site (Archer

1995; Table 2 this study) and others in the southwestern United States (Virginia and Jarrell 1983; Tiedemann and Klemmedson 1986). Thus, we expected that shrubs associated with *Prosopis* might display elevated leaf [N] and consequently greater light-saturated photosynthetic rates (Field and Mooney 1983) than shrubs not associated with *Prosopis*. We found, however, no evidence for this. The similarity in soil and foliar [N] between clusters with and without *Prosopis* (Table 2; Fig. 2) suggests that the nitrogen legacy of *Prosopis* can persist and may still benefit the remaining vegetation for some time after its disappearance. *Prosopis* removal experiments in Arizona, United States, indicate these residual soil effects may last decades (Klemmedson and Tiedemann 1986; Tiedemann and Klemmedson 1986).

The present study was undertaken to provide an initial, albeit indirect, assessment of the degree to which the nurse tree, *Prosopis*, influences the physiology and growth of mature associated shrubs. Because we sampled from among the existing patches available on the landscape, we were unable to completely control for patch age and species composition. The composition and successional history of shrub clusters as well as the proximity and identity of immediate shrub neighbors within a cluster are all factors that could potentially affect individual shrub performance. These confounding factors might have obscured subtle effects of *Prosopis* on understorey shrubs. Also, in clusters without *Prosopis*, we do not know to what extent, if any, the loss of positive, facilitative effects of *Prosopis* were countered by the simultaneous reduction of negative, competitive effects between the shrubs and *Prosopis* (e.g., Franco and Nobel 1990; Aguiar et al. 1992; Callaway 1992). Nevertheless, based on the physiological and whole-community production data presented here, we found no clear-cut indication that the presence of a *Prosopis* canopy had an overriding and positive net effect on associated mature shrubs. It is possible that facilitation by *Prosopis* occurs only during the dispersal or seedling establishment phases and/or the early stages of cluster development (Archer 1995).

The significance of the loss of *Prosopis* with respect to subsequent patterns of shrub cluster development is not known and therefore cannot be taken into account in models of patch dynamics or landscape succession (Scanlan and Archer 1991). We found no indication in the present study that the loss of *Prosopis* has initiated a downward phase in a cyclic succession of patch initiation, growth, and death. Rather, our data on plant performance of early- and late-arriving species indicate that the adult shrubs in these patches are able to maintain growth and productivity in the absence of the *Prosopis* overstorey. These findings, together with field data of population size class structure (Archer et al. 1988), rapid vegetative regeneration following massive canopy die-back after extended drought (Carter 1964)

or rare frost (Lonard and Judd 1985), and experimentally imposed whole plant (Flinn et al. 1992) and whole-cluster disturbance treatments (Scanlan 1988), suggest that these shrub clusters will remain as persistent features of the landscape. Changes in shrub patch composition during the decades following mortality of N_2-fixing *Prosopis* plants may, however, depend on the extent to which soil nitrogen availability is altered.

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