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Soil moisture redistribution as a mechanism of facilitation in savanna tree–shrub clusters

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Abstract Plant–soil water relations were examined in the context of a selective removal study conducted in tree–shrub communities occupying different but contiguous soil types (small discrete clusters on shallow, duplex soils versus larger, extensive groves on deep, sandy soils) in a subtropical savanna parkland. We (1) tested for the occurrence of soil moisture redistribution by hydraulic lift (HL), (2) determined the influence of edaphic factors on HL, and (3) evaluated the significance of HL for overstory tree–understory shrub interactions. Diel cycling and nocturnal increases in soil water potential (Ψ_{soil}), characteristic signatures of HL, occurred intermittently throughout an annual growth cycle in both communities over a range of moisture levels ($\Psi_{\text{soil}} = -0.5$ to -6.0 MPa) but only when soils were distinctly stratified with depth (dry surface/wet deep soil layers). The magnitude of mean (\pm SE) diel fluctuations in Ψ_{soil} (0.19 ± 0.01 MPa) did not differ on the two community types, though HL occurred more frequently in groves (deep soils) than clusters (shallow soils). Selective removal of either *Prosopis glandulosa* overstory or mixed-species shrub understory reduced the frequency of HL, indicating that *Prosopis* and at least one other woody species was conducting HL. For *Zanthoxylum fagara*, a shallow-rooted understory shrub, *Prosopis* removal from clusters decreased leaf water potential (Ψ_{leaf}) and

net CO_2 exchange (A) during periods of HL. In contrast, overstory removal had neutral to positive effects on more deeply-rooted shrub species (*Berberis trifoliolata* and *Condalia hookeri*). Removal of the shrub understory in groves increased A in the overstory *Prosopis*. Results indicate the following: (a) HL is common but temporally dynamic in these savanna tree–shrub communities; (b) edaphic factors influencing the degree of overstory/understory development, rooting patterns and soil moisture distribution influence HL; (c) net interactions between overstory and understory elements in these woody patches can be positive, negative and neutral over an annual cycle, and (d) *Prosopis*-mediated HL is an important mechanism of facilitation for some, but not all, understory shrubs.

Keywords Argillic horizon · *Berberis trifoliolata* · Competition · *Condalia hookeri* · Hydraulic lift · Positive and negative interactions · *Prosopis glandulosa* · *Zanthoxylum fagara*

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Introduction

Woody plant clumping or aggregation is common in many arid and semiarid regions (Fuentes et al. 1984; Haase et al. 1996; Callaway and Davis 1998), particularly in the tropical and subtropical savannas (Whittaker et al. 1979a; Archer 1990; San José et al. 1991; Carter and O’Conner 1991; Mordelet et al. 1993). In certain cases, tree islands and clusters of woody vegetation arise as pioneering trees invade herbaceous patches and then facilitate the establishment of other woody plants in their understory (Archer et al. 1988). Individual trees thereby act as “nurse plants” for other species and provide “nucleation” sites for the development of woody communities (Whittaker et al. 1979b). Numerous examples of this nurse plant aspect of facilitation exist (Callaway 1995), yet the mechanisms enabling facilitation, the circumstances under which it occurs, and the

extent to which it persists beyond the seedling establishment phase remain poorly documented.

Mechanisms of facilitation vary, but generally involve direct effects on species by alterations in habitat (e.g., modification of soils or microclimate) or indirect effects involving other species (e.g., protection from herbivores or enhanced seed dispersal) (Callaway 1995). One mechanism of direct facilitation that is potentially important in tree–shrub clumps is hydraulic lift (HL; Richards and Caldwell 1987). Now being well documented in a variety of woody and herbaceous plants (Caldwell et al. 1998; Yoder and Nowak 1999; Burgess et al. 2000; Ishikawa and Bledsoe 2000; Hultine et al. 2003; Ludwig et al. 2003), HL involves the redistribution of soil moisture by plant root systems from relatively wet deep soil layers to drier surface layers. This is a passive process driven by gradients in water potential and is thought to benefit the “lifting” plant by augmenting soil moisture available for use by the plant the following day (Caldwell and Richards 1989; Dawson 1996; Ryel et al. 2002) and by enhancing nutrient acquisition in surface soils (Richards and Caldwell 1987; Matzner and Richards 1996). Nearby shallow-rooted species may also utilize this redistributed soil moisture and thus benefit from HL (Caldwell 1990). Even though studies have demonstrated that water transfer can occur between “lifting” and “non-lifting” species (Caldwell and Richards 1989), the ecological importance of HL as a general mechanism of facilitation remains unclear and poorly documented (Horton and Hart 1998).

Woody plants of the savanna parklands in the Tamaulipan Biotic province of southern Texas, USA, and northern Mexico are highly aggregated in distinct patches that vary in size and structure in relation to topographic patterns and successional status (Archer 1995). In upland habitats at a representative study site in southern Texas, small discrete clusters of woody plants occur on shallow, duplex soils (sandy loam surface soil overlaying clay-rich argillic horizon at 40–60 cm), whereas larger extensive groves occur on deep sandy soils lacking a well-developed argillic horizon (Stroh et al. 2001). The overstory of both these woody patch types is dominated exclusively by *Prosopis glandulosa* Torr. var. *glandulosa*, an arborescent legume that is thought to facilitate the ingress and establishment of a suite of woody understory species (Archer et al. 1988). Previous studies have shown that these local differences in soil texture discontinuities can influence available soil moisture, rooting patterns, growth and physiological performance of the overstory *Prosopis* and the understory shrubs (Watts 1993; McMurtry 1997; Midwood et al. 1998; Miller et al. 2001). Less is known about how this edaphic variation influences overstory–understory interactions. Also, it has yet to be determined whether *P. glandulosa*, which is known to be a deep-rooted facultative phreatophyte (Smith et al. 1997), is conducting HL that benefits associated understory shrubs.

Here, we examine plant–soil water relations in the context of a selective overstory/understory removal

study conducted in grove (argillic horizon poorly expressed) and discrete cluster (well-developed argillic horizon) habitats. We test the hypotheses that: (1) the overstory *Prosopis* conducts HL in these mixed species communities, but that the occurrence of HL is temporally dynamic reflecting the extreme variability in precipitation and nonseasonal growing conditions in this region; (2) relative to the shallow, duplex argillic soils, HL occurs with greater frequency and magnitude on deep, non-argillic soils where *Prosopis* plants have greater access to deeply stored soil moisture; and (3) *Prosopis*-mediated HL enhances the physiological performance of associated understory shrubs, but more so on sites with the deep soils (groves) than on sites with shallow soils (clusters).

Materials and methods

Study site

Research was conducted at the Texas Agricultural Experiment Station La Copita Research Area located in the eastern Rio Grande Plains of the Tamaulipan Biotic Province in Jim Wells County, Texas (27°40'N; 98°12'W). The climate of this region is subtropical with warm winters and hot summers (mean annual temperature = 22.4°C; Scifres and Koerth 1987). Mean annual precipitation (729 mm) is bimodally distributed (maximum in May/June and September) and highly variable (interannual C.V. = 35%; Le Houerou and Norwine 1998). Contemporary vegetation in the region is classified as subtropical thorn woodland (McLendon 1991) and is characterized by woody patches of varying sizes interspersed amongst a matrix of sparse herbaceous vegetation in uplands that grade into closed canopy woodlands in lowland drainages and playas (Archer 1995). *P. glandulosa* Torr. var. *glandulosa* is the dominant overstory woody plant at the site. The woody understory consists of a diverse assemblage of evergreen (e.g., *Berberis trifoliolata* Moric., *Condalia hookeri* M.C. Jonst., *Zanthoxylum fagara* (L.) Sarg.) and deciduous (e.g., *Celtis pallida* Torr., *Diospyros texana* Scheele) shrubs that vary in rooting depth (Watts 1993), and leaf longevity and texture (Nelson et al. 2002). Nomenclature follows Correll and Johnston (1979); hereafter, species are referred to by genus.

Soils of upland landscapes are sandy loams (Typic and Pachic Argiustolls) with a laterally extensive but discontinuous clay-rich, argillic horizon at 40–60 cm. Woody vegetation on soils where the argillic horizon is maximally developed consists of discrete tree–shrub clusters that typically possess a single small *Prosopis*. The woody communities on upland soils where this argillic horizon is minimally expressed (groves) are larger in size and consist of multiple large *Prosopis* plants together with a mixed-species woody understory community that is generally similar in species composition to that in the clusters (Archer 1995).

Experimental design and sampling protocol

A selective removal experiment was established during January–February 2001 in upland cluster and grove habitats. The presence/absence of an argillic horizon was verified by soil sampling prior to treatment imposition. Within each habitat (clusters and groves), the following treatments were established: (1) controls (intact *Prosopis* overstory + shrub understory), (2) overstory (*Prosopis*) removal (intact shrub community), and (3) understory shrub removal (intact *Prosopis* overstory). The overstory removal treatment was implemented by killing the *Prosopis* in situ by girdling the trunk near its base and then applying diesel fuel to the cut. For the understory removal treatment, all shrub stems were cut at ground level and removed from the immediate area. The treatment was maintained by regularly trimming shrub sprouts. The experiment consisted of two habitats, three treatments and four replicates for a total of 24 sampling sites; all replicates were spatially separated from one another (mean minimum distance between replicates = 120 m). For clusters, all treatments within a replicate were separated by herbaceous communities (mean minimum distance between treatments = 15 m). In groves, most, but not all treatments within a replicate were within the same contiguous grove, with individual treatments located such that the canopies of the original *Prosopis* plants associated with the various treatments did not overlap with one another (mean minimum distance between treatments = 7 m).

Soil water potential (Ψ_{soil}) was measured with screen-caged Peltier thermocouple psychrometers (Model PST-55-SF, Wescor, Inc., Logan, UT, USA) that were individually cleaned and calibrated using the procedures of Brown and Bartos (1982). Psychrometers were installed at soil depths of 20, 35, 50, 100 and 150 cm (2–4 psychrometers/depth) in each sampling site (336 total psychrometers) during May–June 2001. Hourly measurements of psychrometer output were obtained using nanovolt-sensitive data loggers (Model CR7, Campbell Scientific, Inc., Logan, UT, USA) enclosed in well-ventilated boxes placed in the shade. Psychrometer data were normalized to a standard temperature of 25°C. Psychrometers showing evidence of significant thermal gradients (zero offsets $> \pm 3 \mu\text{V}$) were excluded, but this was rarely the case.

Hydraulic lift was considered to have occurred when nocturnal Ψ_{soil} increased by at least 0.05 MPa. The magnitude of HL was calculated as the difference between the maximum nighttime Ψ_{soil} minus the previous day's minimum Ψ_{soil} . The frequency of occurrence of HL was computed as the fraction of the number of psychrometers that registered HL relative to the total number of functional psychrometers (a small number of psychrometers failed following installation and were excluded from calculations). The amount of water redistributed via HL in the upper 1 m of soil volume was estimated by first converting Ψ_{soil} to volumetric

moisture using soil moisture release curves derived from cluster and grove habitats at this location (Loomis 1989). These values were then multiplied by the fraction of psychrometers registering HL (i.e., frequency of HL) at each depth increment and were summed over all depths.

Plant water potential (Ψ_{leaf}) was measured at pre-dawn (0400–0600 hours CST), late morning (1000–1200 hours CST) and mid-afternoon (1400–1600 hours CST) on individual leaves (*Prosopis*, *Berberis*) or terminal shoots (*Zanthoxylum*, *Condalia*) with a pressure chamber (Soil Moisture Equipment, Inc., Santa Barbara, CA, USA) as described by Barnes and Archer (1996). Leaf net CO_2 uptake (A) was measured during morning (0800–1000 hours CST) and afternoon (1300–1500 hours CST) periods with an open-path portable photosynthesis system (Model LI-6400, LiCor, Inc., Lincoln, NE, USA) at constant saturating light levels (photon flux densities (PFD; 400–700 nm = 1,200 $\mu\text{mol m}^{-2} \text{s}^{-1}$ (shrubs) and 1,500 $\mu\text{mol m}^{-2} \text{s}^{-1}$ (*Prosopis*)) and ambient temperatures and CO_2 concentrations. Above-canopy PFD was measured with a quantum sensor (Model LI-190Q; LiCor, Inc., Lincoln, NE, USA) located in a nearby clearing; precipitation was recorded at an on-site weather station.

Owing to a limited number of data loggers, we were only able to obtain continuous measurements of Ψ_{soil} over time in a single replicate. Measurements of Ψ_{soil} in the other replicates were obtained at designated sampling dates by monitoring all treatments within the same replicate over a single 24-h period and then moving data loggers to the next replicate such that all treatments in both habitats (clusters and groves) were sampled over a 4-day period. For the data presented here, no precipitation occurred during any of these 4-day sampling periods. Similarly, we could not measure Ψ_{leaf} (one leaf/shoot per replicate) and A (two to three leaves per replicate) in all plant species and treatments in a single day. Instead, these two measurements were made in all treatments for several species in one day and then we repeated this protocol the following day for the remaining species. All measurements of Ψ_{leaf} and A for a given species and replicate were made within a 15–30 min period such that all replicates were sampled within a 2-h block. To account for any changes in leaf physiology over this 2-h measurement period, we treated the replicates as experimental blocks and statistically analyzed the data using analysis of variance (ANOVA) for a randomized block design. Preplanned mean comparisons were made using Fisher's protected LSD.

Results

Occurrence of HL

Diel oscillations and nocturnal increases in Ψ_{soil} , characteristic features of HL, occurred intermittently in

unmanipulated control clusters and groves during the year-long study (Fig. 1a). HL was observed in summer as well as in winter, when the overstory *Prosopis* was largely leafless. During periods of HL, the mean (\pm SE) magnitude of the diel fluctuations in Ψ_{soil} was 0.19 ± 0.01 MPa and did not differ significantly (ANOVA; $P > 0.10$) between clusters and groves. The calculated total daily amount of water redistributed by HL in the upper 1 m^3 of the soil profile was generally comparable for the two habitats (groves = 0.5 L m^{-3} ; clusters = 0.3 L m^{-3}), at least under dry-down conditions (October 2001). Day-to-day variation in the magnitude of the diel changes in Ψ_{soil} in both habitats was closely related to variation in solar radiation and hence transpirational demand (Fig. 1b).

In both woody habitats, HL was most prevalent in the shallow soil depths ($< 50 \text{ cm}$) and during periods of soil dry-down following major precipitation events that fully recharged the upper 100 cm of the soil profile (Fig. 2). This dry-down occurred more rapidly in clusters (shallow argillic soils) than groves (deep non-argillic soils), with the onset of HL in shallow soil layers occurring when Ψ_{soil} approached -0.50 MPa. Below 50 cm, the onset of HL occurred later and at slightly lower Ψ_{soil} than in shallower layers, if at all. The diel cycling in Ψ_{soil} continued throughout the soil dry-down cycle to, and likely below, the lower sensitivity threshold of the soil psychrometers ($\Psi_{\text{soil}} - 6$ MPa; data not shown). HL was coincident with the establishment of a positive Ψ_{soil} gradient between dry surface and wet deep soil layers and was nil when these Ψ_{soil} gradients were reversed (i.e., wet surface and dry deep soils; Fig. 3).

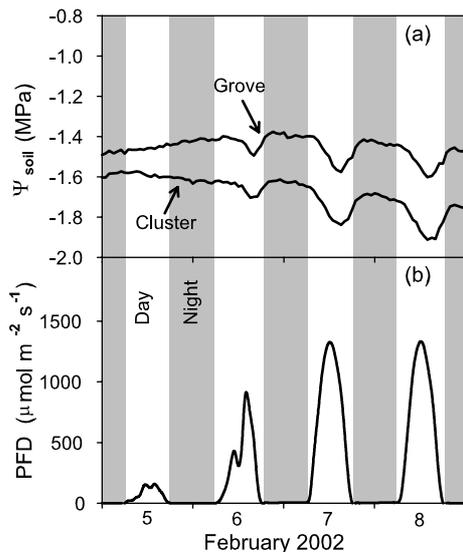


Fig. 1 Representative diel course of surface (20 cm) soil water potential (Ψ_{soil}); **a** and above-canopy photon flux density (PFD, 400–700 nm); **b** consecutive days in February in control (intact *Prosopis glandulosa* overstory and shrub understory) cluster and grove communities

Frequency of HL in different habitats and treatments

Hydraulic lift occurred more frequently in groves, where the restrictive argillic horizon was absent (mean frequent = 63% of psychrometers showing HL), than in clusters, where the argillic horizon was present (mean frequency = 43%) (Fig. 3a). Also, when totaled over the upper 50 cm, the loss of the *Prosopis* overstory or the shrub understory reduced the frequency of HL relative to controls (mean frequency = 24–27% in clusters and 30–33% in groves) (Fig. 3b). Notably, there were certain time periods (e.g., November 2001) when the frequency of HL was still 50–60% in the treatment lacking the overstory *Prosopis*.

These habitat and treatment differences in the frequency of HL were more apparent under conditions of high HL activity (October 2001) than periods of relative low activity (February 2002) (Table 1). For both dates and habitats, the loss of the understory shrubs reduced the frequency of HL in shallow depths (20 cm) to a greater extent than did the loss of the *Prosopis* overstory. In October, the removal of understory shrubs reduced the frequency of HL more in clusters than in groves, whereas removal of the *Prosopis* overstory had the opposite effect.

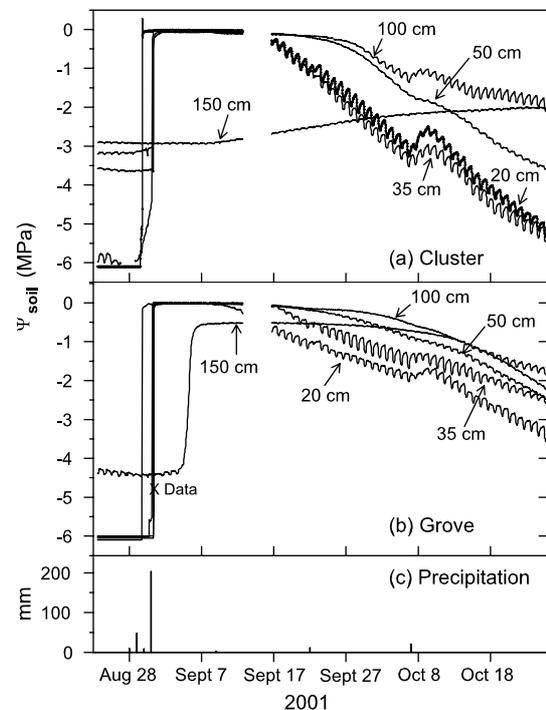


Fig. 2 Soil water potential (Ψ_{soil}) at five depths in representative control (intact *P. glandulosa* overstory + shrub understory) cluster (**a**) and grove (**b**) communities over a 2-month wetting-drying cycle. Daily on-site precipitation is shown in (**c**). At water potentials below -6 MPa, many soil psychrometers failed to register reliable data; thus, all data below this threshold are shown here as -6 MPa for simplicity. No data were collected from 13 September to 17 September

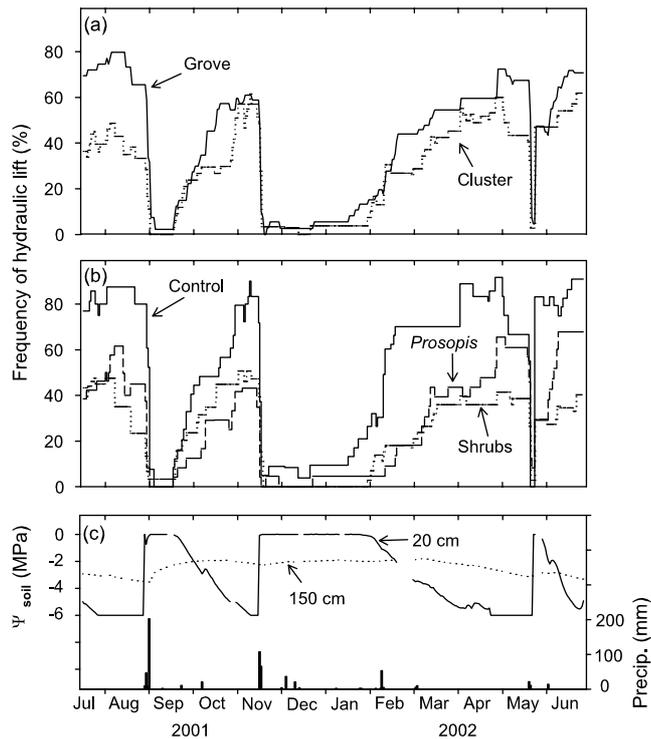


Fig. 3 Frequency of hydraulic lift (% of psychrometers exhibiting diel cycling in the upper 50 cm of the soil profile) in cluster and grove habitats (a) and in different woody plant removal treatments (b) over an annual growing cycle. Data in a are pooled over treatments while those in b are pooled over habitat (72 total psychrometers in each). Daily on-site precipitation and daily mean soil water potentials (Ψ_{soil}) at 20 and 150 cm for a representative control cluster are shown in (c). *Control* intact *P. glandulosa* overstory + shrub understory; *Prosopis* intact *Prosopis* with shrubs removed; *Shrubs* intact shrubs with *Prosopis* removed

Consequences of reductions in HL for tree–shrub interactions

The loss of a live *Prosopis* overstory had negative, positive and neutral effects on the physiological performance of understory shrubs during a period of active

HL (September–October 2001), but significant treatment effects were only detected in clusters (Table 2) and not in groves (data not shown). Specifically, removal of *Prosopis* reduced leaf/shoot water potentials (Ψ_{leaf}) and net CO_2 uptake (A) of the shallow-rooted *Zanthoxylum*, at least early in the day (LSD; $P > 0.1$ for afternoon; data not shown). In contrast, the loss of *Prosopis* increased (*Berberis*) or had no effect (*Condalia*) on predawn and morning Ψ_{leaf} in more deeply rooted shrub species (Table 2). No treatment differences in CO_2 uptake were detected for either of these two shrub species, and no treatment differences in predawn Ψ_{leaf} were detected in any species during periods when HL was minimal (late August and December, 2001; data not shown).

Removal of the understory shrub community had no detectable effect on *Prosopis* Ψ_{leaf} in either clusters (not shown) or groves (Table 2), but there was a significant increase in A in plants in the removal treatment relative to controls during the morning period in groves. No significant treatment effects (LSD; $P > 0.1$) on *Prosopis* CO_2 assimilation were detected in clusters at this time (data not shown).

Discussion

Our results confirm the existence of soil moisture redistribution by HL in these subtropical savanna tree–shrub woody patches. The selective removal experiments indicate that the arborescent *P. glandulosa* and one or more of the understory shrub species were conducting HL. Various species of mesquite (*Prosopis* spp.) are known to function as phreatophytes in certain habitats (Smith et al. 1997), and have been implicated in plant-mediated redistribution of soil moisture (Mooney et al. 1980). Recently, Hultine et al. (2004) confirmed that *P. velutina* conducts hydraulic redistribution in desert streamside habitats; our findings indicate that *P. glandulosa* redistributes soil moisture in drier savanna uplands as well. *P. glandulosa* has roots that occur at depths of up to 10 m in the uplands at our study site

Table 1 Frequency (%) of hydraulic lift with soil depth (cm) for different woody plant removal treatments in cluster and grove communities

Date	Depth	Control		Shrubs		<i>Prosopis</i>	
		Cluster	Grove	Cluster	Grove	Cluster	Grove
October 2001	20	19.6	17.8	14.6	15.0	2.2	4.7
	35	17.4	24.4	19.5	22.5	22.2	23.3
	50	21.7	24.4	19.5	20.0	13.3	23.3
Total		58.7	66.7	53.7	57.5	37.8	51.2
February 2002	20	12.1	13.3	22.6	4.3	4.3	4.9
	35	9.1	8.9	3.2	6.5	13.0	9.8
	50	6.1	6.7	12.9	4.3	10.9	7.3
Total		27.3	28.9	38.7	15.2	28.3	22.0

Values indicate the percent of functional psychrometers at each depth showing diel soil water potential oscillations > 0.05 MPa (16 psychrometers/depth/treatment/habitat). *Control* intact *Prosopis*

glandulosa overstory + shrub understory; *Shrubs* intact shrub understory with *Prosopis* removed; *Prosopis* intact *Prosopis* overstory with shrubs removed

Table 2 Influence of selective woody plant removal treatments on mean (\pm SE) leaf/shoot water potentials (Ψ_{leaf}) and light-saturated net CO_2 exchange (A) of understory shrub species (*Zanthoxylum fagara*, *Berberis trifoliolata*, *Condalia hookeri*) and the overstory *Prosopis glandulosa*

Species/response variable	Treatment		<i>P</i>
	Control	Overstory removal	
<i>Z. fagara</i>			
Ψ_{leaf} predawn (MPa)	-5.4 ± 0.1	-6.2 ± 0.2	<0.01
Ψ_{leaf} morning (MPa)	-6.5 ± 0.1	-6.9 ± 0.2	0.10
A morning ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	14.9 ± 0.8	10.4 ± 1.8	0.09
<i>Berberis trifoliolata</i>			
Ψ_{leaf} predawn (MPa)	-2.9 ± 0.2	-2.1 ± 0.3	0.07
Ψ_{leaf} morning (MPa)	-4.5 ± 0.05	-3.8 ± 0.1	<0.01
A morning ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	12.8 ± 1.3	9.8 ± 6.1	0.68
<i>Condalia hookeri</i>			
Ψ_{leaf} predawn (MPa)	-2.4 ± 0.1	-2.5 ± 0.2	0.77
Ψ_{leaf} morning (MPa)	-3.3 ± 0.3	-3.2 ± 0.1	0.79
A morning ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	14.6 ± 3.2	10.2 ± 1.9	0.79
<i>Prosopis glandulosa</i>			
	Control	Understory removal	
Ψ_{leaf} predawn (MPa)	-1.6 ± 0.1	-1.5 ± 0.1	0.92
Ψ_{leaf} morning (MPa)	-3.3 ± 0.3	-2.9 ± 0.3	0.34
A morning ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	13.8 ± 2.7	23.2 ± 1.9	0.05

Control intact *Prosopis* overstory + shrub understory; Overstory removal intact shrub understory; Understory removal intact *Prosopis* overstory. Data for shrubs are from plants growing in discrete clusters; data for *Prosopis* are from plants in groves. Water potential data are from predawn (0400–0600 hours CST) and late

morning (1000–1200 hours CST) periods of 26–27 October 2001. Gas exchange data are from morning (0800–1000 hours CST) periods of 12 September 2001. *P* values as determined by pre-planned Fisher's LSD tests ($n=4$ for all cases except *Berberis* and *Condalia A*, where $n=2$)

(Hubbard et al. 1997). *P. glandulosa* can, therefore, access a persistent source of very wet (saturated or near-saturated) soils known to occur at depths of 2–5 m on this site (Midwood et al. 1998; Boutton et al. 1999). This deep soil moisture is presumably what keeps predawn Ψ_{leaf} of *P. glandulosa* high and rather constant over much of the growing season (Barnes and Archer 1996, 1999) and is the likely source of water redistributed by this species. The ability of *P. glandulosa* to tap into these deep moisture reserves would also explain our observations of HL at depths ≥ 1 m during periods when these soil depths were, themselves, moderately moist ($\Psi_{\text{soil}} = -1$ to -2 MPa; Fig. 2).

Elucidation of the additional source(s) of HL in the tree–shrub communities of our savanna parkland site was not possible, as the mixed-species woody understory was removed in its entirety. Analyses of relationships between predawn Ψ_{leaf} and Ψ_{soil} (C. Zou and S. Archer, unpublished data) as well as the isotopic composition of plant and soil water at this study site (Midwood et al. 1998) indicate that two common understory shrubs, *Condalia* and *Berberis*, routinely utilize deep (> 1.5 m) soil moisture; and for *Berberis*, excavations indicate that its roots can exceed depths of 2 m on non-argillic soils (Watts 1993). Thus, it is possible that one or both of these species were also conducting HL. It seems less likely that the dominant understory shrub, *Zanthoxylum*, which is predominantly shallow-rooted (83–89% of root biomass in upper 40 cm; Watts 1993), is an important contributor to HL in these woody communities, though there are reports of HL in relatively

shallow-rooted herbaceous species (Caldwell 1990; Wan et al. 1993). Although we do not know with certainty which of these shrub species are conducting HL, it does appear that, in some cases, the woody understory actually plays a greater role than the *Prosopis* overstory in the redistribution of soil moisture to surface depths (e.g., 20 cm).

The climate of the subtropical savannas of southern Texas and northern Mexico is characteristically non-seasonal with a high degree of inter- and intra-annual variability in precipitation (Le Houerou and Norwine 1988; Archer 1989). In contrast to many tropical savannas, wet and dry seasons are not well defined in this subtropical region. At our study site, surface soils were frequently much drier than deeper soils; but there were many other periods when this pattern was reversed, with near-surface soils being much wetter than subsurface depths. Consequently, we found woody plant mediated–HL in these savannas to also be nonseasonal with HL occurring anytime during the year (summer or winter) when soil moisture profiles were distinctly stratified with depth (i.e., dry surface \rightarrow wet deep). As has been reported for tropical savannas (Ludwig et al. 2003), we also found evidence of HL when surface soils were extremely dry ($\Psi_{\text{soil}} < -5$ MPa). During these drought periods, the onset of HL, as indicated by diel patterns of Ψ_{soil} , occurred earlier in the day and prior to sunset. Mid-day stomatal closure is common in the woody plants in this system, and we routinely observe increases in plant water potential in mid-to-late afternoon (McMurtry 1997). Thus, we attribute these shifts in the

timing of HL to be the result of drought-induced reductions in transpiration later in the day, which then leads to earlier establishment of the requisite root–soil water potential gradients for water efflux from surface roots. Because there are times during the year when surface soils are considerably wetter than subsurface soils, and because some of the deeply rooted species such as *P. glandulosa* also possess considerable shallow root biomass (Watts 1993), there is also the possibility that some of these woody species may be conducting “inverse” HL (i.e., redistributing water from surface to deep soil layers; Burgess et al. 1998; Schulze et al. 1998).

The distribution of woody plant growth-forms in savannas and desert shrublands is often strongly correlated with soil texture (Johnson and Tothill 1985; Knoop and Walker 1985) and the depth to restrictive soil horizons (San José and Montes 1991; McAuliffe 1994). Subsurface discontinuities can influence the patterns of soil moisture availability and woody plant performance (Smith et al. 1995; Hamerlynck et al. 2000), but their influence on HL has not been widely investigated. The two woody communities that we examined occur on soils that either possess (clusters) or lack (groves) a well-developed clay-rich (argillic) layer beginning at 40–60 cm (Stroh et al. 2001). These soil types strongly influence the degree of the *Prosopis* overstory development (clusters = single, small *Prosopis*; groves = multiple, large *Prosopis* plants; Archer 1995) and woody plant rooting patterns (rooting density more concentrated in shallow depths (<80 cm) in clusters than in groves; Watts 1993; Midwood et al. 1998). We therefore hypothesized that HL would be greater in magnitude and frequency in groves (deep sandy soils) than clusters (shallow duplex soils). Whereas we found that the frequency of HL was indeed greater in groves than in clusters, we did not detect any differences in the magnitude of diel change in Ψ_{soil} between these two habitats. The calculated quantity of water redistributed by HL was also rather similar in clusters and groves under dry-down conditions. Thus, while the presence of the argillic horizon appeared to influence the prevalence of HL, it was not a barrier to HL. Similarly, Dawson (1993) showed that a subsurface clay-pan did not prevent HL from occurring in a deciduous forest if some tree roots were able to penetrate this subsurface horizon. Such appears to be the case for woody plants at our study site as well. We did not find any indication that HL was restricted to the shallow depths above the argillic horizon, as predicted by Hamerlynck et al. (2000). Rather HL occurred at depths ≥ 40 cm, which were well within the argillic layer, indicating that active roots were present in this subsurface clay-rich region.

Richards and Caldwell (1987) hypothesized that hydraulically lifted water (HLW) could be utilized by shallow-rooted neighboring plants, and HL could thereby serve as an important mechanism of facilitation between plants. Caldwell et al. (1991) further speculated that HL could contribute to the common phenomenon of plant clumping in dryland ecosystems. Using

deuterated-water, Caldwell and Richards (1989) confirmed that HLW was transferred between neighboring plants. On the basis of the results from a mixing model incorporating differences in the natural abundance of O and H isotopes in plant and soil water, Dawson (1993) estimated that up to 60% of the water used by some plants in the understory of *Acer saccharum* was derived from HL conducted by the tree. By comparison, Ishikawa and Bledsoe (2000) found that HL by blue oak (*Quercus douglasii*) occurred too late in the growing season to benefit understory annual grasses. In an East African savanna, Ludwig et al. (2003) reported that, for understory grasses, competition for surface soil moisture outweighed the beneficial effect of HL by the overstory tree *Acacia tortilis*. Thus, to date, there is conflicting evidence in support of the hypothesis that HL is a significant and general mechanism of facilitation, and the role that HL plays in the origin, structure and maintenance of dryland vegetation clumps has yet to be elucidated.

The development of multispecies woody assemblages in the subtropical savannas in southern Texas begins with the establishment of *Prosopis*, which then facilitates the establishment and growth of understory shrubs beneath its canopy (Archer et al. 1988). This facilitation appears to involve enhancement of seed dispersal (Huebotter 1991), amelioration of understory microclimate (Archer 1995; Fulbright et al. 1995) and enrichment in soil fertility (Hibbard et al. 2001). Findings from our study provide experimental evidence that HL is also an important aspect of this facilitation. Specifically, we found that removal of the *Prosopis* overstory decreased the frequency of HL and this coincided with reductions in Ψ_{leaf} and A in the dominant, shallow-rooted understory shrub *Zanthoxylum fagara*. Similar responses to overstory removal have been documented for *Zanthoxylum* in a previous study (Barnes and Archer 1999). It is conceivable that removal of *Prosopis* could have reduced the physiological performance of *Zanthoxylum* by mechanisms other than reductions in HL (e.g., changes in microclimate leading to increased photoinhibition, temperature stress, and evaporative losses of soil water). However, we found that overstory removal resulted in a decrease in predawn Ψ_{leaf} of *Zanthoxylum* only during those times of the year when HL was evident. Also, preliminary results from a shading experiment intended to mimic the effects of the *Prosopis* canopy on understory microclimate show little evidence of shade-induced improvement of predawn Ψ_{leaf} in *Zanthoxylum* (P. Barnes and S. Archer, unpublished data). These findings therefore provide strong circumstantial evidence for a beneficial role of *Prosopis*-mediated HL. Our findings that the beneficial effects of *Prosopis* were most evident early in the day suggest that the HLW used by *Zanthoxylum* was rapidly absorbed and transpired. Similar responses have been observed when these shrubs are provided with supplemental water via surface irrigation (McMurtry 1997). Under drought-stres-

sed conditions, leaf gas exchange activity in *Zanthoxylum* and in other shrubs typically peaks 2–4 h after sunrise and then declines for much of the rest of the day (McMurtry 1997; P. Barnes unpublished data). Consequently, enhancement of gas exchange early in the day represents a significant increase in the daily carbon gain for this species.

In contrast to *Zanthoxylum*, *Berberis* and *Condalia*, two co-occurring species in these tree–shrub patches, showed positive or neutral responses to *Prosopis* removal. Similarly, removal of the entire shrub community resulted in increases in gas exchange in *Prosopis*, at least in the groves. Thus, in some situations, there are net competitive effects between overstorey and understorey while in others it appears that resource partitioning predominates. Both *Berberis* and *Condalia* are more deeply rooted than *Zanthoxylum* (Watts 1993) and thereby have access to water at depths utilized by *Prosopis* under drought conditions (C. Zou and S. Archer, unpublished data). Therefore, for some of the shrub species, competitive effects appear to override any interspecific facilitative effects of HL (e.g., Ludwig et al. 2003). We suspect that the higher surface rooting densities and lower Ψ_{leaf} maintained by *Zanthoxylum* enable this species to rapidly monopolize any HLW redistributed by *Prosopis* or other plants in these mixed-species assemblages. Higher rooting densities of *Zanthoxylum* in clusters than in groves (Midwood et al. 1998) may also explain why this species benefited more from HL in cluster habitats. Thus, the importance of HL as a mechanism of facilitation between trees and shrubs in this savanna ecosystem appears to be not only temporally dynamic and influenced by underlying edaphic factors but also species-specific.

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