

Biogeography of woody encroachment: why is mesquite excluded from shallow soils?

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ABSTRACT

While some studies aim to generalise the attributes of woody encroachers, examining their functional differences across biogeographic regions may also be instructive. Most of Texas is encroached by *Prosopis glandulosa*, but on the eastern Edwards Plateau, a limestone plateau with thin soils, *P. glandulosa* is rare and *Juniperus ashei* is dominant. We hypothesised that *P. glandulosa* is excluded from sites where bedrock at a depth of 1 m or less restricts the development of taproots, thus rendering this normally deep-rooted species too vulnerable to drought. To test this idea, we monitored the physiological status of the two species on a site where both species were encroaching and the soil was 1.5–2.5 m deep, thus relatively deep for the Edwards Plateau region but not for regions where *P. glandulosa* dominates. Data were collected across three tree size classes from May to November 2006. Stem water potentials were similar across species and water potentials and photosynthetic rates decreased with tree size. Based on isotopic evidence, the effective rooting depth of *P. glandulosa* increased with tree size, but not in *J. ashei*. *P. glandulosa* had a higher rate of leaf gas exchange overall as expected for a drought-avoider; except for large trees during a summer drought, when species differences in photosynthesis rates diminished and the stomatal conductance for *J. ashei* exceeded that of *P. glandulosa*. We speculate that restrictions of soil depth may limit the invasiveness of *P. glandulosa* in part through negative effects on large trees, which may lower fecundity. Copyright © 2009 John Wiley & Sons, Ltd.

KEY WORDS Edwards Plateau; gas exchange; groundwater recharge; *Juniperus ashei*; *Prosopis glandulosa*; rooting depth; stable isotopes; woody encroachment

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INTRODUCTION

Woody encroachment is the expansion of woody plants into grasslands and open savannas with usually negative consequences for rangeland productivity and water resource management (Kraaij and Ward, 2006; Wilcox *et al.*, 2008). It is a world-wide phenomenon that has been occurring over the past 100–200 years (Bragg and Hulbert, 1976; Archer, 1995; Van Auken, 2000; Wilcox *et al.*, 2008). The reasons for woody encroachment are still debated. While there is wide agreement that the introduction of live stock and fire suppression aided woody encroachment in many parts of the world (Van Auken, 2000), some argue that woody encroachment would have occurred even without these facilitating factors, based on changes in climate (Reich *et al.*, 2001), increase in atmospheric CO₂ concentration (Bradley and Fleishman, 2008), landscape fragmentation (Briggs *et al.*, 2007), and a decrease in harvest rates for food and lumber by native people (Fredrickson *et al.*, 2006).

Typically, very few species out of a much larger community of woody plants become woody encroachers, while other species do not change or even decline in abundance. Thus, whatever regime change occurred a century and a half ago benefited only a small minority of species. Determining what characteristics may have

predestined these species to become woody encroachers may help us better understand the causes for woody encroachment, indicate avenues for more effective grassland management, and aid in predicting future vegetation changes.

The characteristics of woody encroachers vary substantially between biogeographic regions. Morphological and physiological features that appear to make one species a successful encroacher in one region are not necessarily the same that make another species successful in a different region. For example, large portions of the Intermountain West have been encroached by Western juniper (*Juniperus occidentalis*) at mid- to low-elevations (Miller and Rose, 1995; Weisberg *et al.*, 2007; Bradley and Fleishman, 2008), while semi-arid grasslands of the south-west at lower elevations have been encroached by velvet or honey mesquite or their hybrids (*Prosopis velutina* and *Prosopis glandulosa*; Archer *et al.*, 1988; Schlesinger *et al.*, 1990; Van Auken, 2000; Browning *et al.*, 2008). *J. occidentalis* is a drought tolerant evergreen tree with an extensive but shallow root system and no central taproot (Hall, 1952; Dealy, 1990), while members of the *Prosopis* genus are among the most deep-rooted tree species in the world (Phillips, 1963). *Prosopis* trees are winter-deciduous drought avoiders, while members of the *Juniperus* genus are evergreen drought tolerators. How can two so distinct genera be both among the most prolific woody encroachers in North America?

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In central Texas, members of both the *Prosopis* and *Juniperus* genera are encroaching grasslands. Though elevation, longitudinal or climate gradients are not involved, *P. glandulosa* and *J. ashei* also segregate in space, suggesting that nearly identical conditions of historic regime shift, whether in land use or climate, favoured the encroachment of different woody species in different places. *P. glandulosa* has encroached large portions of west to central Texas rangelands, but on the eastern edge of the Edwards Plateau, a limestone karst in central Texas, *J. ashei* is the main woody encroacher. These regions are distinct primarily in terms of their soils. *P. glandulosa* is associated with deep prairie soils, while *J. ashei* is associated with the rocky and shallow soils of the limestone karst.

Like *J. occidentalis*, *J. ashei* is also evergreen, chiefly shallow-rooted, and extremely drought tolerant (Owens, 1996; Wayne and Van Auken, 2002; Schwinning, 2008). On sites with highly fractured bedrock, roots of this species have been found in caves 9 m from the surface (Jackson *et al.*, 1999), however, where geology prohibits the formation of deep roots, *J. ashei* appears to persist without deep taproots, relying instead on an extensive system of shallow fibrous roots (Thurow and Hester, 1997). We hypothesised that while *J. ashei* tolerates sites that prohibit the formation of deep taproots, *P. glandulosa* does not and would become too water stressed during episodic drought events.

To test this hypothesis, we selected a savanna site on the eastern Edwards Plateau where the soil is deeper than on most other sites in the region (1.5–2.5 m) and where both *P. glandulosa* and *J. ashei* are currently encroaching. We assumed that this site would be near the limit of the site tolerance for *P. glandulosa*, with a soil just deep enough for trees to establish, but perhaps causing severe drought stress in dry summers. Thus, we expected *P. glandulosa* to develop greater water stress than *J. ashei*. Over the course of one growing season, which included period of no rain for 63 days in July and August, we followed the water potentials and gas exchange rates of the two species to assess their drought responses. In addition, we collected stem samples for stable isotope analysis of stem water to make inferences about rooting depths. We collected these data for trees of different sizes, expecting that *P. glandulosa*'s disadvantage relative to *J. ashei* would increase with plant size, as larger trees of *P. glandulosa* would normally have deep taproots and perhaps depend more on deep, stable soil water sources than smaller trees, which would be relatively shallow-rooted in any species on any site.

MATERIALS AND METHODS

The study was conducted on the Freeman Ranch, a 1700 ha working ranch in the Texas Hill Country near San Marcos, TX (97°79'56" W and 29°56'56"). The climate is semi-arid to humid sub-tropical, with an annual

temperature of 20 °C, summer highs of 43 °C and winter lows near 0 °C (Dixon, 2000). Based on 30-year records from Austin ending in 1990, the area receives about 850 mm of precipitation per year. However rainfall is extremely variable and unpredictable by season (Dixon, 2000).

The study was conducted at a savanna site characterised by clusters of ash juniper (*Juniperus ashei*) and honey mesquite (*Prosopis glandulosa*) interspersed in intermittently grazed grassland composed predominantly of the C₄ species King Ranch bluestem [*Bothriochloa ischaemum* (L.) Keng.] and the C₃ species Texas wintergrass (*Stipa leucotricha* Trin. & Rupr.), along with some forbs. Tree cover is about 50%. The site is winter-grazed with an average cattle stocking rate between 12 and 15 ha per cow. The soil is a Rumble-Comfort Association dominated by Rumble gravelly clay loam (Carson, 2000). Based on excavations done at the site, the soil is 1.5–2.5 m deep above minimally fractured limestone bedrock. Both *J. ashei* and *P. glandulosa* have been increasing at this site, and there are numerous juvenile trees in both populations.

We randomly selected individuals in three tree height classes for this study, small trees (<1m), medium trees (between 1 and 4 m) and large trees (>4 m). In March 2006, we tagged in each species five medium, five large trees and 15 small trees to avoid over-sampling. Large and medium trees were sampled repeatedly throughout the study, while the small size classes were sampled randomly with replacement in groups of five.

Physiological measurements were taken every two weeks from May to November 2006. *P. glandulosa* was in full foliage from May to Oct and started to drop leaves in November. Thus during the last sampling date, measurements were taken only on those individuals that still had leaves. Maximum daily net photosynthesis (A_{net} , $\mu\text{mol m}^{-2} \text{s}^{-1}$) and stomatal conductance (g_s , $\text{mol m}^{-2} \text{s}^{-1}$) were measured on sun adapted needles/leaves between noon and 3 pm using an open system—infrared gas analyser (LICOR-6400-02B, LICOR, Lincoln, NE, USA). Air and leaf temperatures in the chamber were maintained within 1–2 °C of ambient and leaves received saturating light levels between 1250 and 1500 $\mu\text{E m}^{-2}$ with red and blue LED lights, depending on the empirically determined light response curve at the time of measurement. Leaf gas exchange is expressed on a one-sided leaf area basis. The projected leaf area of juniper was multiplied by 1/2 π to account for the cylindrical shape of its needles (Cregg, 1991).

Pre-dawn (ψ_{pre}) and midday (ψ_{mid}) stem water potentials were measured with a PMS 1000 Pressure Chamber Instrument (PMS, OR, USA) on the same days as gas exchange. ψ_{pre} was measured from 2 h before dawn until dawn and ψ_{mid} was measured between 11 am and 1 pm.

On every other sampling date (once a month), we also took stem samples for stable isotope analysis of stem water. Suberized stems were collected below evaporative surfaces to avoid evaporative enrichment of stem water by back diffusion. Stem samples were placed in screw

capped glass vials, sealed with parafilm and frozen until cryogenic vacuum extraction (Ehleringer *et al.*, 2000). Samples were analysed at the SIRFER facility at the University of Utah on a Thermo Finnigan Delta Plus XL Isotope Ratio Mass Spectrometer along with internal standards. Hydrogen and oxygen isotope ratios were expressed in delta notation in parts per thousand (‰) relative to the V-SMOW standard (Gonfiantini, 1978):

$$\delta D \text{ or } \delta^{18}\text{O} = \left(\frac{R_{\text{sample}}}{R_{\text{standard}}} - 1 \right) \times 1 \quad (1)$$

where, $R = {}^2\text{H}/{}^1\text{H}$ or ${}^{18}\text{O}/{}^{16}\text{O}$.

Data were analysed using repeated measures analysis, multiple regression and orthogonal comparisons using the SPSS 10.0 software (SPSS Inc., Chicago, Illinois). Gas exchange, water potential and isotope data met ANOVA assumptions of normality and homogeneity of variances.

RESULTS

Precipitation and temperature

Total precipitation measured 6 km from the study area was 863 mm for year 2006 (Figure 1), thus close the 30-year average (Dixon, 2000). However, a 63-day drought period occurred from July to August at an average temperature of 27.5 °C, with an average daily high of 33 °C and an average daily low of 22.6 °C (Marcy Litvak, personal communication). The National Climate Data Center classified the month of August for the region as a 'moderate drought' based on the Palmer Z Index for short-term drought conditions.

Physiological status

Date, species, tree size and their interactions all had significant effect on plant physiological status (Figure 2, Table I). Consistent with rainfall patterns (Figure 1), A_{net} and g_s peaked in July, though seasonal trends in gas exchange were not expressed in small trees. ψ_{pre} and ψ_{mid} were maximal in late spring and fall and minimal during the 63-day drought period in July/August.

In both species, A_{net} and g_s tended to increase with tree size (Figure 2) and during the dry summer months,

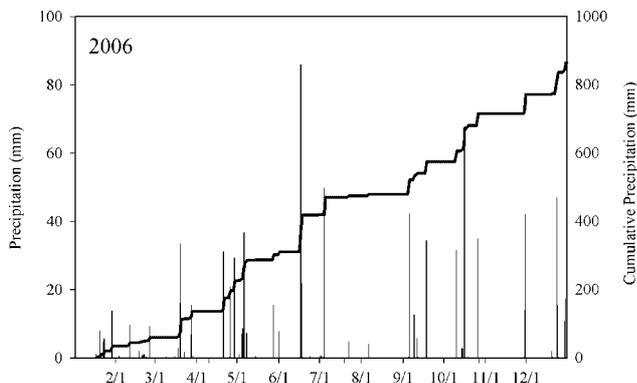


Figure 1. Seasonal course of precipitation (mm) and cumulative precipitation (mm) during the experimental year (2006).

both ψ_{pre} and ψ_{mid} were more negative in small compared to medium and large trees, suggesting that smaller trees experienced greater physiological stress than larger trees.

Averaged over all dates and size classes, *P. glandulosa* had about twice the net assimilation rate of *J. ashei*, and average stomatal conductance was 26% higher, while ψ_{pre} were very similar for the two species (Figure 2). However, over three measurement dates from July to August, and for large trees only, *J. ashei* maintained a 65% higher stomatal conductance than *P. glandulosa*. The average photosynthetic rate of *P. glandulosa* was only 30% higher than that of *J. ashei*, with a declining trend as the drought wore on.

Oxygen isotope composition

Pooling all data, stem water isotope ratios were significantly affected by date and species, but not by tree size (Table II). On all measurement dates, stem water isotope ratios plotted to the right of the local meteoric water line, indicating uptake of evaporatively enriched, and presumably shallow soil water in both species (Figure 3). In May, June and August, the stem water isotope ratios of *J. ashei* and *P. glandulosa* were clearly separated, with *P. glandulosa* having the less enriched stem water. These three measurement dates were preceded by relatively dry conditions, which would have favoured the establishment of a stable isotope gradient in the soil through evaporative enrichment (Barnes and Turner, 1998). Under such conditions, plants with deeper roots take up relatively more water from deeper soil layers and thus transport less enriched stem water compared to plants with a shallower root system. By contrast, the measurements in July and September, which were preceded by rainfall events (Figure 1), made the water sources of the two species less distinct, indicating that the species were using more similar, and presumably shallow soil water sources.

The mid-August measurement date was preceded by the largest number of dry days (52), thus we expected the stable isotope data from this date to discriminate root distributions most clearly. On this date, species, size and species*size effects on $\delta^{18}\text{O}$ values were all significant (Table III, Figure 4). For *P. glandulosa*, there was a clear trend in $\delta^{18}\text{O}$ with tree size, indicating that small trees were not as deep-rooted as medium and large trees. No trend with tree size was apparent for *J. ashei*, and it appeared to take up water from the same soil layers as small *P. glandulosa* trees.

DISCUSSION

The purpose of this study was to examine why *P. glandulosa* was rare on the eastern Edwards Plateau, despite being highly abundant almost everywhere else in surrounding regions. Since it is difficult to observe the process of species exclusion *in situ*, as a first approach, we observed *P. glandulosa* on what we considered to be a marginal site for this species, where soil depth was limited compared to that of the adjacent Blackland Prairie,

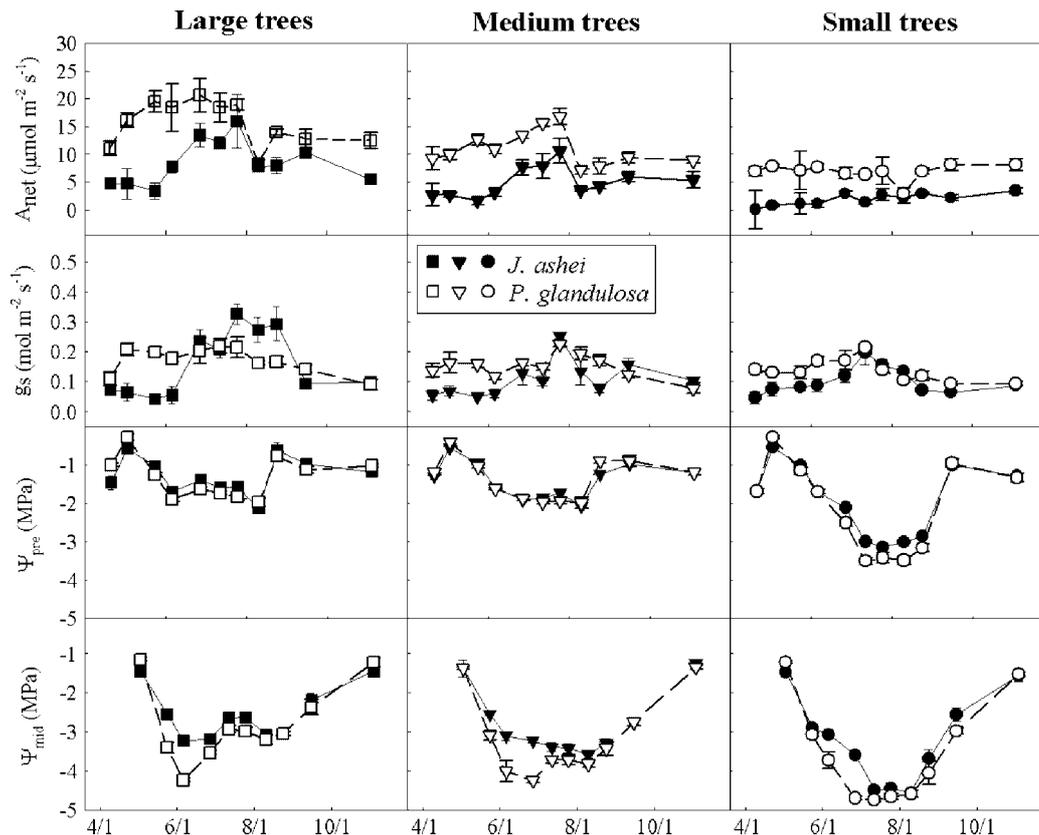


Figure 2. Seasonal course of net photosynthesis (A_{net} , $\mu\text{mol m}^{-2} \text{s}^{-1}$), stomatal conductance (g_s , $\text{mol m}^{-2} \text{s}^{-1}$), pre-dawn (ψ_{pre} , MPa) and mid-day (ψ_{mid} , MPa) water potentials with standard error bars.

Table I. Repeated measures analysis of photosynthesis (A_{net}), conductance (g_s), pre-dawn (ψ_{pre}) and mid-day (ψ_{mid}) water potentials.

Source	A_{net}		g_s		ψ_{pre}		ψ_{mid}	
	F	P	F	P	F	P	F	P
Date	1463.86	<0.001	51.59	<0.001	421.61	<0.001	679.00	<0.001
Species	74584.55	<0.001	128.08	<0.001	11.90	<0.001	184.74	0.001
Size	11189.12	<0.001	92.82	<0.001	421.39	<0.001	348.53	<0.001
Date * Species	177.04	0.003	9.71	0.003	6.96	<0.001	21.51	0.034
Species * Size	80.07	<0.001	11.20	0.694	44.85	<0.001	40.08	0.500
Date * Size	189.48	<0.001	0.36	<0.001	6.83	<0.001	4.37	0.014

Numbers in bold are significant at $p < 0.05$.

Table II. Repeated measures analyses of stem water δD and $\delta^{18}\text{O}$ (‰).

	$\delta^{18}\text{O}$		δD	
	F	P	F	P
Date	68.24	0.007	118.879	0.001
Species	41.03	0.045	73.884	0.001
Size	1.64	0.298	2.540	0.437
Date * Species	8.00	0.316	15.401	0.421
Species * Size	1.97	0.103	2.549	0.050
Date * Size	1.20	0.658	3.437	0.725

Numbers in bold are significant at $p < 0.05$.

but not as shallow as in most other sites on the eastern Edwards Plateau, where *P. glandulosa* was excluded.

We hypothesised that the site restriction on root development would lead to greater water stress in *P. glandulosa* compared to *J. ashei* during periodic drought events. Fortunately, the observation period contained a significant drought period with 63 days without effective rainfall which caused moderate drought conditions in the month of August (Figure 1), allowing us to test this hypothesis.

First, we found that throughout the observation period the pre-dawn water potentials of *P. glandulosa* and *J. ashei* remained very similar (Figure 2), suggesting that *P. glandulosa* did not have access to more stable water sources than *J. ashei*. Based on the stem water isotope ratio data (Figure 4), we inferred that large- and medium-sized *P. glandulosa* trees took up relatively more water from deeper soil layers than *J. ashei* trees in the same

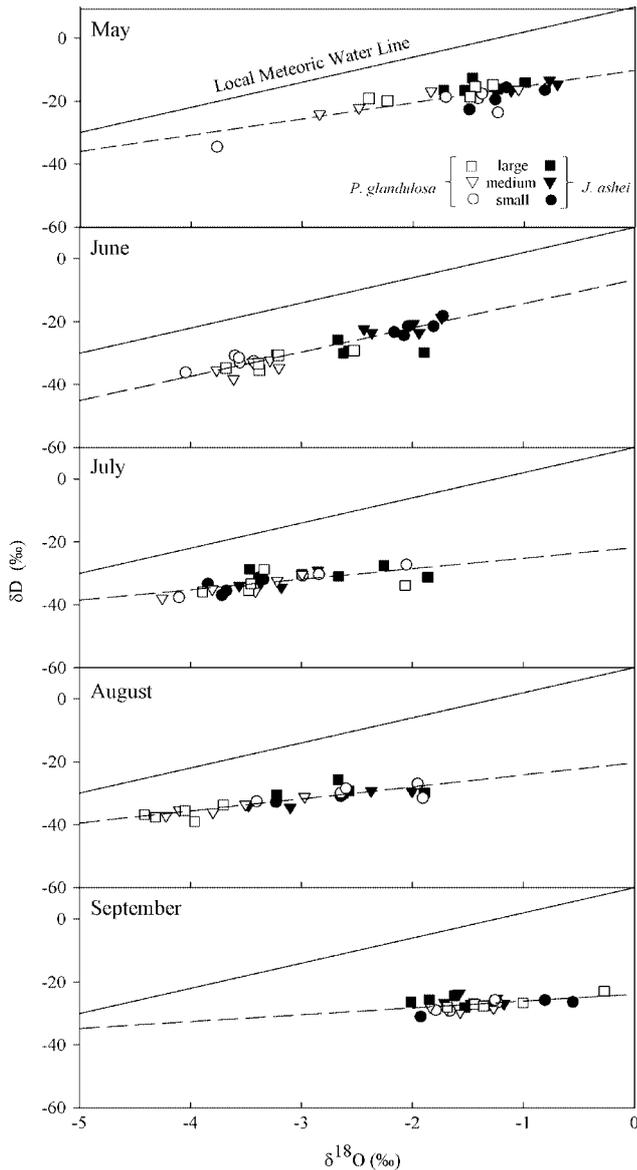


Figure 3. Hydrogen isotope ratio (δD , ‰) as a function of oxygen isotope ratio ($\delta^{18}O$, ‰) in stem water of the two study species.

size categories. While the effective rooting depths of *P. glandulosa* appeared to increase with tree size, this trend was absent in *J. ashei*, although the lower pre-dawn water potentials of small *J. ashei* trees did indicate a difference in rooting depth that was not picked up by the stem water isotope data. During an excavation study conducted in 2007 at the same site (unpublished data), we were able to observe directly that mature trees of both species had roots extending down to the bedrock layer. However, *P. glandulosa* had thicker and more roots at depth than *J. ashei*. In general, the large structural roots of *P. glandulosa* extended downwards at a steeper angle than those of *J. ashei*. Thus, while both species likely explored the entire available soil depth, *P. glandulosa* trees appeared to have a larger capacity for taking up water from the deepest soil layers. Taken together, these observations suggest that the root systems, especially of large *P. glandulosa* trees, were indeed constrained at

Table III. Analysis of variance for plant xylem water $\delta^{18}O$ (‰).

Date	Source	$\delta^{18}O$ (‰)	
		F	P
5/3/2006	Species	8.644	0.084
	Size	0.183	0.487
	Species * Size	0.670	0.425
6/6/2006	Species	199.157	<0.001
	Size	0.047	0.102
	Species * Size	2.067	0.170
7/12/2006	Species	0.211	0.664
	Size	1.610	0.792
	Species * Size	2.758	0.144
8/10/2006	Species	11.498	0.003
	Size	4.549	0.022
	Species * Size	6.829	0.005
9/15/2006	Species	0.000	0.996
	Size	0.059	0.861
	Species * Size	3.120	0.065

Numbers in bold are significant at $p < 0.05$.

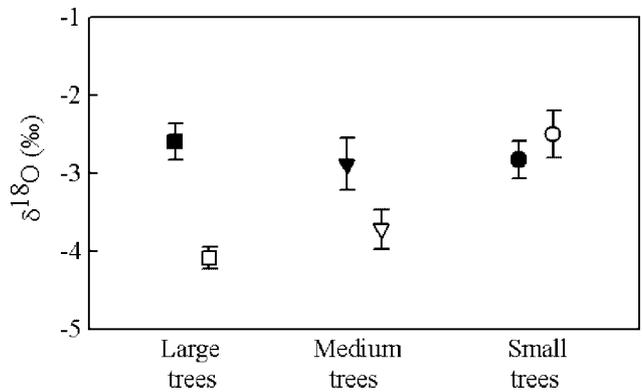


Figure 4. Stem water $\delta^{18}O$ (‰) as a function of tree size class on 10 August, 2006, the date of maximal observed water stress. Closed symbols: *J. ashei*, open symbols: *P. glandulosa*.

the site, and would have extended much deeper had it not been for the largely unfractured bedrock layer at 1.5–2.5 m depth. In *J. ashei*, the lack of a tendency to increase capacity for water uptake from deeper soil layers with tree size indicates that this species was much less constrained by soil depth.

But what was the evidence that the limited rooting depth had negative effects on *P. glandulosa*? Our initial hypothesis that *P. glandulosa* would become more water stressed than *J. ashei* during drought was not supported. However, we did find that *P. glandulosa*'s overall higher photosynthetic rate was minimised for large trees during the driest part of the summer and stomatal conductance of large *P. glandulosa* trees even dropped to levels below those of large *J. ashei* trees (Figure 2). Thus, the usually clear physiological distinction between a drought avoider (*P. glandulosa*) and a drought tolerator (*J. ashei*) during drought was not fully realized on this soil-depth restricted site.

It is often found that the water status and leaf gas exchange rates of large trees in water-limited environments are more buffered against precipitation variability

than those of small trees of the same species. One explanation is that older, larger trees have access to deeper, moister soil layers (e.g. Otieno *et al.*, 2005; Potts *et al.*, 2008). But even when rooting depth does not substantially increase with age or size, larger, older trees can maintain higher leaf conductance than smaller, younger trees if they have a more extensive root system, greater hydraulic conductivity of sapwood and/or more stored water in relation to their total leaf area (e.g. Phillips *et al.*, 2002; England and Attiwill, 2007).

Potts *et al.* (2006, 2008) also found for *P. velutina* populations in southern Arizona, that pre-dawn water potentials increased with tree size in riparian and upland habitats, although the riparian population had markedly higher water potentials than the upland population in the dry pre-monsoon season. Larger trees were probably deeper-rooted and, not surprisingly, more water was available at the rooting depth of large trees in the riparian zone. In the pre-monsoon season at the upland site, A_{net} and g_s of small and large trees maintained a constant offset, with small trees having the lower rates, but medium-sized trees started the dry season with gas exchange rates more similar to large trees and ended it with rates more similar to small trees, indicating that the moisture supply to medium trees worsened as the dry season wore on (Potts *et al.*, 2008). Something very similar may have happened to both medium and large trees in our study. However, lacking a direct comparison of *P. glandulosa* on shallow and deep soils, we can only speculate that large trees would have been able to maintain higher gas exchange rates in a deep prairie soil, given the same precipitation history. Thus, our original hypothesis that the spread of *P. glandulosa* populations on the eastern Edwards Plateau is foiled by shallow bedrock that constrains the development of sufficiently deep roots in mature trees remains plausible, even though we cannot claim conclusive evidence at this stage.

It should be noted that although many sites on the eastern Edwards Plateau prevent the formation of deep roots, at other sites, where the limestone bedrock is highly fractured, roots can be quite deep. For example, roots have been observed in caves at a depth of 20 m or more (Jackson *et al.*, 1999). These sites typically have skeletal soils and *P. glandulosa* is generally absent. Thus, the apparent exclusion of *P. glandulosa* from most sites of the eastern Edwards Plateau is probably not only matter of impossibility to grow deep roots, but may also involve the inability of *P. glandulosa* to establish on skeletal soils and develop a root system in a matrix of fractured bedrock.

In recent years the discussion of woody encroachment has focused primarily on the importance of the establishment phase. The line of thought is that the historically less grazed grasslands were very effective at suppressing woody plant establishment, presumably by preempting near-surface soil water and overtopping (Van Auken and Bush, 1997). Present-day grasslands, due to a century or more of overuse and soil erosion, may have lost the ability to suppress woody plant establishment, and a species

like *P. glandulosa*, characterised by fast growth and rapid tap root elongation, is now able to establish even in drier than average years (Brown and Archer, 1999). Once matured, *P. glandulosa* becomes very resistant to drought and fire (Owens *et al.*, 2002) and persists as a continuous seed source for an expanding population. However, our observations on the Edwards Plateau suggest that some site conditions suppress the invasiveness of *P. glandulosa* primarily through negative effects on mature trees: on a similarly managed site adjacent to our study area, which appears to be a stable grassland on 1 m deep soil, we found only small and medium *P. glandulosa* while large trees were entirely missing. This suggests that the ability to establish highly reproductive adults is an integral part of the woody encroachment phenomenon.

Several recent synthesis articles have explored the relationships between woody plant cover and ground water recharge (e.g. Huxman *et al.*, 2005; Jackson *et al.*, 2005; Wilcox *et al.*, 2006) highlighting the potential complexities of this issue. The expansion of deep-rooted trees like those in the genus *Prosopis* and *Tamarix* have demonstrably reduced groundwater resources and stream-flow, predominantly in riparian zones (e.g. Stromberg *et al.*, 2007; Scott *et al.*, 2008). By contrast, shallow-rooted species such as members of the genus *Juniperus*, by most accounts, have very little if any effect on groundwater recharge or stream-flow (Belsky, 1996; Wilcox *et al.*, 2005). Independent of the species involved, outside of riparian zones or where there is no rapid subsurface flow, impacts of woody plants on groundwater may also be small (Huxman *et al.*, 2005; Wilcox *et al.*, 2006). Consistent with the conclusions of Seyfried and Wilcox (2006), this study suggests that, independent of subsurface flow condition, which can be substantial in karst regions, even 'deep-rooted species' should have a negligible impact on recharge on sites that constrain their deep root development.

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