

Grass effects on tree (*Prosopis glandulosa*) growth in a temperate savanna

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Abstract

The majority of studies on woody–herbaceous interactions have focused on the effects of trees on grasses; relatively few have looked at grass effects on adult trees. In a two-year study in a temperate savanna in northern Texas, tree (*Prosopis glandulosa*) basal area increased significantly following removal of associated grasses, the response being highly variable in time and space. Tree response to grass removal was strongest on shallow, clayey soils, but was evident only during the year subsequent to treatment. Low intensity surface fire enhanced growth of adult trees, but the magnitude of the response was inconsistent among sites. Clipping of grasses (proxy for grazing) had no effect on tree growth. Contrasts between the clipping and removal experiments suggest clipping may not have been frequent or intense enough to elicit a tree response; or that it is the presence/absence of grasses rather than their aboveground biomass which impacts trees. Enhanced tree growth and foliar N and P content associated with disturbance to the grass layer on shallow sites where vertical segregation of woody plant and grass roots and soil resources are constrained, may reflect reductions in competition for soil moisture and elevated soil N and P availability following fire.

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1. Introduction

Savannas are characterized by mixtures of woody and herbaceous lifeforms. Factors determining the relative abundance and productivity of these contrasting lifeforms involve interactions between climate (primarily amount and seasonality of rainfall), soils (primarily texture and depth), herbivory (grazing vs. browsing) and fire. The vast majority of studies on woody–herbaceous interactions have examined tree effects on grasses. Studies of grass effects on woody plant seedling establishment are common; but relatively few studies have examined the effect grasses might have on adult trees (Scholes and Archer, 1997), or how grazing and low intensity surface fire might modify this relationship.

The grass layer can interact directly with trees through resource competition, or indirectly through the intermediary effects of fire, which may induce tree mortality, particularly of juveniles (Menaut et al., 1990) or stressed trees (e.g. Yeaton, 1988), and benefit surviving trees by increasing soil resources post-burn (Jensen et al., 2001). Grasses, with their relatively shallow, dense, fibrous root systems, may actively compete with trees for resources (Ehleringer et al., 1991; Dawson and Pate, 1996), either directly, if they coincide with shallow tree roots in the upper soil horizons, or indirectly, by intercepting water and nutrients and reducing their percolation to deeper portions of the soil profile where tree roots may be more abundant. If this model is correct, then disturbances that reduce above and/or belowground production and resource utilization by the herbaceous layer (e.g. fire, grazing) should benefit tree growth.

Soil characteristics mediate interactions between trees and grasses. For example, the extent of grass–tree competition may be a function of soil texture, whereby the intensity of herbaceous competition is relaxed on coarse-textured soils where water and nutrients are more likely to percolate deeper into the soil profile and intensified on fine-textured soils where water is more likely to be retained in upper soil horizons (e.g. Knoop and Walker, 1985). On shallow soils where woody and herbaceous roots are confined to the same volume, grass-on-tree competition may be more intense than on deeper soils, where vertical stratification of lifeform root systems can occur. Honey mesquite (*Prosopis glandulosa* Torr.) trees in savannas of the southern Great Plains may rely heavily on shallow lateral roots, particularly where available soil volume is reduced (Ansley et al., 1990, 1991, 1992b; Cuomo et al., 1992). Herbaceous effects on tree growth may therefore be inversely proportional to soil depth.

The role of fire in maintenance of savannas ranges from one of woody plant exclusion, to one of generating a composition dominated by fire-tolerant woody and herbaceous species (Scholes and Walker, 1993). Consequently, most savanna research regarding the direct effects of fire has examined woody plant mortality and vegetative regeneration of damaged adult trees. However, individuals of larger stature often escape with minimal canopy damage, especially in low intensity surface fires (Scholes and Walker, 1993). Fire is known to enhance post-fire tree seedling establishment by increasing available nitrogen, phosphorus, potassium, calcium, and magnesium in the mineral soil (Christensen, 1977; McKee, 1982; Covington and Sackett, 1984; Schoch and Binkley, 1986; Jensen et al., 2001). Consequently, it has been proposed that low intensity understorey fires will stimulate growth in fire resistant adult trees (de Ronde et al., 1990). However, this hypothesis has not been widely tested.

P. glandulosa savannas and woodlands characterize much of the southern Great Plains in North America. There is a substantial body of work on its effects on herbaceous

vegetation, but little is known about how grasses might be influencing *P. glandulosa* production and dynamics. As a first step towards addressing this disparity, we conducted a two-year field experiment that quantified the response of adult trees to reductions in herbaceous biomass. We hypothesized that tree growth and nutrient status would be enhanced by reductions in herbaceous competition, but that the magnitude of the response would be (1) in the rank order (strongest to weakest) herbaceous layer removed > herbaceous layer burned > herbaceous layer defoliated; and (2) a function of soil depth (strongest on shallow soils; weakest on deep soils).

2. Materials and methods

2.1. Study site

Experiments were conducted on the W.T. Waggoner Estate, Wilbarger County, near Vernon, TX (34°08'N, 99°18'W; elevation 381 m) (Clayton, 1993). Landscapes at the study site consisted of gently rolling hills (10–20 m elevation changes) with varying densities of *P. glandulosa*, a deep rooted, nitrogen-fixing, winter deciduous arborescent tree. Historically a grass-dominated landscape, the north Texas Rolling Plains have been extensively invaded by *P. glandulosa* since the early 1900s (Teague et al., 1997; Asner et al., 2003). *P. glandulosa* is now the dominant woody species, occurring at densities ranging from 0 to 500 trees ha⁻¹ (Ansley et al., 1995) depending on management history. The herbaceous matrix consists of C₃ (e.g. annual *Bromus* spp. and perennial *Nassella leucotricha* Trin. & Rupr.) and C₄ grasses (e.g. perennial *Buchlœe dactyloides* Nutt., *Bouteloua curtipendula* (Michx.) Torr., *Bothriochloa laguroides* DC. *Sporobolus compositus* (Poir.) Merr.). In heavily grazed 'lawn' areas the C₄ shortgrass *Buchlœe dactyloides* tends to dominate, with *N. leucotricha* and C₄ midgrasses dominating in lightly grazed areas (Teague and Dowhower, 2002). The Waggoner Ranch has generally experienced moderate cattle grazing with stocking rates of ca. 11–12 ha head⁻¹ over the last 20 years, and about 8 ha head⁻¹ prior to this (Teague et al. 1997). Soils consist of moderately deep clay-loams of the Tillman series (fine, mixed, thermic Typic Paleustoll) with 1–3% slopes overlying sandstone and shale (Daigal, 1978). The shallow-clay range sites consist of moderately fertile shallow-clays of the Vernon series (fine, mixed, active, thermic Typic Haplusteps) with 3–8% slopes.

The climate is subtropical, subhumid, characterized by hot summers and dry winters (Larkin and Bomar, 1983). Vernon, TX has a mean annual temperature of 17 °C with 30 d y⁻¹ > 38 °C. Mean monthly maximum temperature (29 °C) occurs in July; the mean monthly minimum is (4 °C) occurs in January (Bomar, 1983; National Oceanic and Atmospheric Administration, 2001). Mean annual rainfall (665 mm) is bimodally distributed with peaks in May (104 mm) and September (89 mm) (Texas Water Development Board, 2002).

Experiments were conducted in level, upland landscape pastures selected for differences in depth to underlying parent material. The shallow site (33°57'N, 99°04'W, elev. 360 m) had a soil depth of 1.0–1.2 m (Vernon series). Soils in the intermediate site (33°54'N, 99°20'W, elev. 370 m) had a depth of 2–3 m (Tillman series), and those in the deep site (33°51'N, 99°26'W, elev. 381 m) had a depth of 3–4 m (Tillman series). The fact that the shallow Vernon soils were more clayey; and the deeper Tillman soils were more loamy, would be expected to further accentuate differences in soil moisture and root distributions. These pastures were located along a 33 km line running approximately east–northeast to

west–southwest. The shallow and intermediate sites were 32 and 9 km east–northeast of deep site, respectively. Rain gauges installed at the shallow and deep sites were manually read at monthly intervals.

2.2. Data collection

To experimentally test whether the presence of the herbaceous layer affects adult tree growth, three treatments (control, herbaceous defoliation and herbaceous removal (herbicide)) were applied within a 5 m radius of randomly selected *P. glandulosa* trees 2–3 m tall (five replicates per treatment) at the deep, intermediate and shallow sites. This typically represented a treated area that extended ca. 2.5 m beyond the tree canopy dripline. An early spring burn treatment (typical for prescribed management fires in this region) was also applied at the deep and intermediate soil depth sites prior to *P. glandulosa* leaf out. Fires were conducted beneath canopies of individual trees with each burn forming a circle whose perimeter was ca. 5 m from the tree bole. There was no fire treatment at shallow soil site due to restrictions in that pasture. Surface fires beneath target trees were implemented in March 1998 and repeated again on the same trees in March 1999. Fuel loads for the burn treatments were approximately 1200 kg ha⁻¹ in 1998 and 500–700 kg ha⁻¹ in 1999. Flame lengths ranged from 0.3 to 1.0 m at both sites. The fires consumed all herbaceous vegetation beneath each tree but had no observable effects on the trees. The grass defoliation treatment, a proxy for grazing, was implemented using a hand-operated mower at a frequency necessary to maintain a 3–6 cm stubble height through the growing season. Grass ‘removal’ was achieved by backpack spraying with a glyphosate herbicide (Roundup[®]), with follow-up spot treatments applied as necessary. Response variables included soil moisture and *P. glandulosa* stem basal area growth and foliar P and N concentrations.

P. glandulosa basal growth was quantified using dendrometer bands (Palmer and Ogden, 1983) on larger trees, and calipers for smaller (<5 cm basal diameter) trees at locations marked with indelible ink. Initial basal area (cm²) measurements were made in December 1997 with subsequent growth increments recorded in December 1998 and 1999. Basal area was chosen as a metric because it integrates whole plant above-ground growth and is a strong predictor of above-ground biomass on shallow and deep sites ($R^2 = 0.98$; R.F. Hughes unpublished data), such that a 5 cm² increase in basal area equates to a ca. 5–6% increase in total (leaf + wood) mass.

Foliar nutrient concentrations are a reasonable proxy for soil nutrient availability (Vitousek, 2004). Changes in *P. glandulosa* nutrient acquisition in response to grass manipulation were thus assessed by quantifying total P and N concentrations on foliage harvested in July 1999. Four subsamples (8–10 sunlit leaves from similar canopy settings in each cardinal direction) were collected from each experimental tree. The subsamples were transported to the laboratory, dried at 70 °C, ground to pass through a 1 mm mesh, acid digested, and colorimetrically analysed for N (TNT persulphate digestion method) and P (acid persulphate method) using a spectrophotometer (Hach DR/3000, Hach Company, Loveland, CO).

Soil moisture was measured to 1.5 m using neutron scattering (Model 3220 series soil moisture gauge, Troxler Electronic Laboratories, Research Triangle Park, NC) (Pearcy et al., 1996) on deep and shallow soil sites. Aluminium access tubes (5.08 cm diameter, one per tree) were situated 4 m from the tree bole. Volumetric soil moisture readings were taken

at five depths (where soil depth allowed) (probe centre at 25, 55, 85, 115, and 145 cm) through the 1999 growing season. To assess horizontal surface moisture gradients (1, 2, and 4 m from tree bole), near-surface (0–30 cm) volumetric soil moisture was quantified with Time Domain Reflectometry (TDR) (Topp et al., 1984; Topp and Davis, 1985) using paired (5 cm spacing) 4-mm steel probes.

ANOVA and repeated-measures ANOVA were used to compare leaf nutrient concentrations and changes in soil moisture with depth and time using SAS (SAS Institute, 1988) and Number Cruncher Statistical System (NCSS, Hintze, 2001). To avoid problems associated with the potential relationship between relative growth rates and initial tree size (South, 1991), treatment responses were compared using ANCOVA on absolute growth rates with initial stem size as a covariate. Unless indicated otherwise, statistical significance was set at $\alpha = 0.05$. Tukey's multiple comparison test ($\alpha = 0.05$) was used to compare means (Zar, 1999).

3. Results

Precipitation the year prior to the study (1997) was above-average. Precipitation in 1998 (504 and 427 mm on deep and shallow sites, respectively) was lower than that received in 1999 (560 and 614 mm); and both years were below the long-term average (665 mm), especially during the summer season when grasses are most physiologically active (Fig. 1). Monthly rainfall patterns were also slightly different between sites. In 1998, the shallow

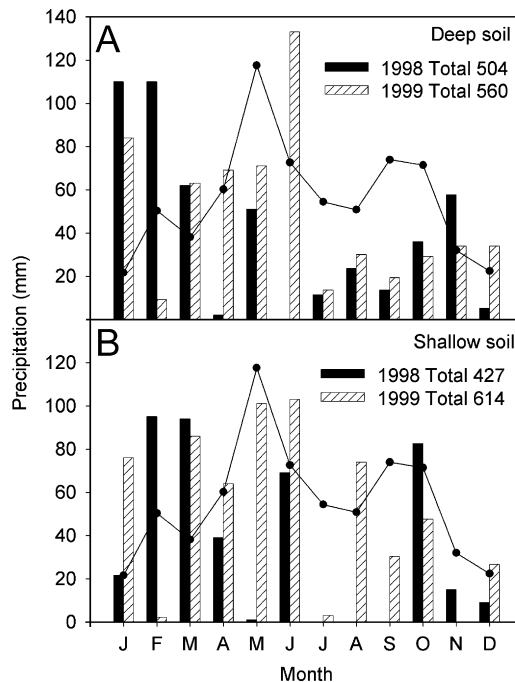


Fig. 1. Rainfall patterns during 1998 (solid) and 1999 (hatched) at deep (A) and shallow (B) soil sites. Line represents local 30-year monthly mean (Texas Water Development Board, 2002). Long-term mean annual rainfall for the area is 665 mm.

soil site received no measurable rainfall from July through September, whereas the deep soil site received 49 mm during this period; conversely, the shallow soil site received more rainfall than the deep soil site in spring and late summer 1999.

Mean *P. glandulosa* stem basal area was lowest on the shallow soil site ($55 \pm 4.2 \text{ cm}^2$) and higher and statistically comparable on the sites with intermediate ($206.9 \pm 20.0 \text{ cm}^2$) and deep soils ($182.7 \pm 18.7 \text{ cm}^2$). For a given site, growth rates of *P. glandulosa* control plants were statistically comparable in each year of the study, despite the fact that rainfall in year 2 exceeded that in year 1 (data not shown). Herbaceous biomass manipulations significantly affected *P. glandulosa* growth on all sites (Fig. 2; Table 1). Time (year) was significant on all sites; but there was no treatment \times year interaction. Fire enhanced

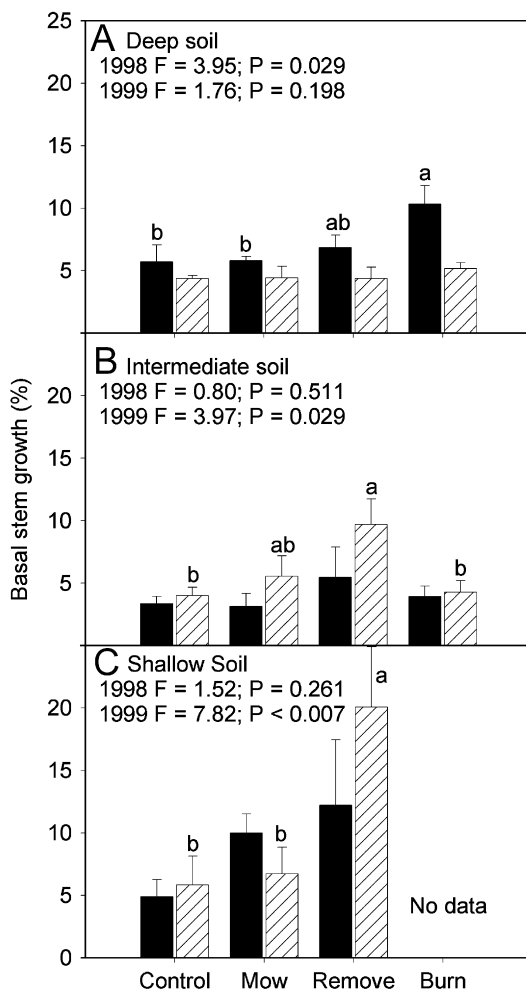


Fig. 2. Mean (\pm SE; $n = 5$) relative basal area growth (%) of *P. glandulosa* trunks in response to understorey manipulation (control = no treatment, grass mowed, grass removed, and low-intensity burn) during 1998 (solid bar) and 1999 (hatched bar) on sites with contrasting soil depths. F values represent results from ANCOVA of absolute basal areas (initial basal area as covariate) for each site and year. Bars with different letters were significantly different at $p \leq 0.05$.

Table 1

Summary of independent ANCOVA results with initial basal area as covariate, for each soil depth, year (1998, 1999), and herbaceous manipulation treatment (control, mow, herbaceous removal, burn) main effects and interactions on absolute basal area growth of *P. glandulosa*

	d.f.	F-value	p
<i>Deep soil</i>			
Treatment	3	4.47	0.0101
Year	1	7.81	0.0088
Year × treatment	3	1.28	0.2969
<i>Intermediate soil</i>			
Treatment	3	2.84	0.0541
Year	1	15.00	0.0005
Year × treatment	3	2.62	0.0682
<i>Shallow soil</i>			
Treatment	2	9.00	0.0012
Year	1	4.57	0.0433
Year × treatment	2	3.34	0.5728

Table 2

Summary of repeated measures ANOVA results for site (Shallow vs. Deep soil), depth in soil profile (5 depths, 0–115 cm), date (month of year in 1999), and treatment (control, herbaceous removal) main effects and interactions on soil moisture profiles during 1999

	d.f.	F-value	p
Site	1	0.44	0.1013
Treatment	1	24.70	<0.0001
Site × treatment	1	10.83	0.0011
Depth in profile	3	0.27	0.8485
Site × depth	3	5.13	0.0017
Treatment × depth	3	1.10	0.3507
Site × treatment × depth	3	1.25	0.2923
Date	6	41.75	<0.0001
Site × date	6	7.66	<0.0001
Treat × date	6	0.72	0.6353
Site × treat × date	6	1.68	0.1241
Distance × date	18	1.40	0.1273
Site × depth × date	18	0.66	0.8494
Treat × depth × date	18	0.15	0.9999
Site × treat × depth × date	18	0.18	0.9999

P. glandulosa growth relative to unburned controls, but only on the deep soil and only during the first growing season (1998, Fig. 2A). Growth of *P. glandulosa* plants in the grass removal treatment was significantly elevated at the shallow and intermediate soil depth sites. Mowing had no significant effect on tree growth on any site in either year.

There was no overall effect of site or depth in soil profile on soil water content, but time of year (date), herbaceous treatment, and site × treatment, site × depth and site × date interactions were significant (Table 2; Fig. 3). Shallow sites exhibited more pronounced

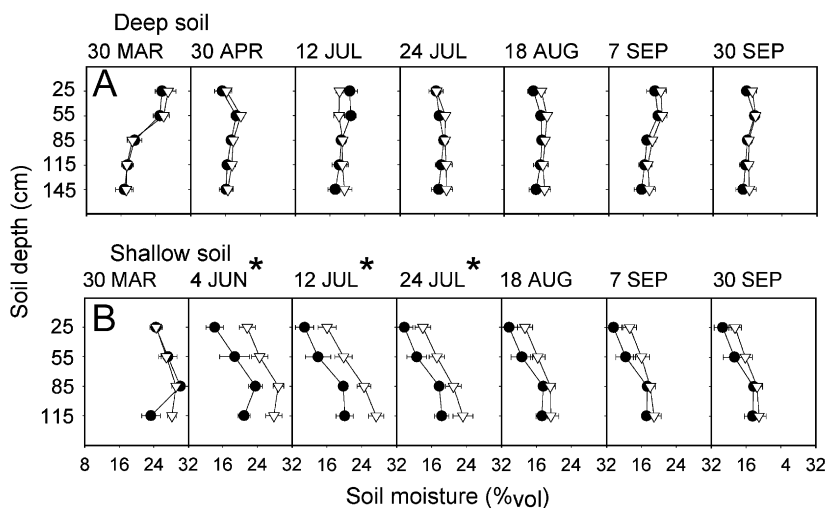


Fig. 3. Patterns of soil moisture (mean \pm SE; $n = 5$) (neutron scattering; volumetric) with depth on control plots (herbaceous layer intact; closed circles) and herbaceous removal plots (open triangles) on deep (A) and shallow (B) soils on 7 dates during the 1999 growing season. Asterisks indicate significant differences ($p \leq 0.05$) between control and removal moisture profiles. All readings were 4 m from *P. glandulosa* boles.

Table 3

Summary of repeated measures ANOVA results for site (shallow vs. deep), treatment (control, mow, herbaceous removal), distance from tree bole (1, 2, 4 m), and date (month of year, 1999) main effects and interactions on TDR-measured soil moisture (0–30 cm) during 1999

	d.f.	F-value	p
Site	1	90.81	<0.0001
Treatment	1	5.76	0.0173
Site \times treatment	1	0.01	0.9039
Distance from bole	2	4.48	0.0125
Site \times distance	2	1.19	0.3069
Treatment \times distance	2	1.74	0.1781
Site \times treatment \times distance	2	6.90	0.0012
Month	3	13.04	<0.0001
Site \times month	3	5.81	0.0008
Treat \times month	3	0.32	0.8126
Site \times treat \times month	3	0.16	0.9199
Distance \times month	6	0.39	0.8877
Depth \times distance \times month	6	0.36	0.9009
Treat \times distance \times month	6	0.28	0.9461
Depth \times treat \times distance \times month	6	0.13	0.9929

and different seasonal patterns of soil moisture stratification with depth in profile than did deep soil sites. On the deep soil site, removal of the grass layer had no significant effect on the soil moisture profile. In contrast, soil moisture on grass removal plots exceeded that on control plots during most dates in 1999 on shallow soils.

Near-surface soil moisture (0–30 cm) measured with TDR probes showed a third-order interaction among site, treatment, and distance from tree bole (Table 3). Mean surface

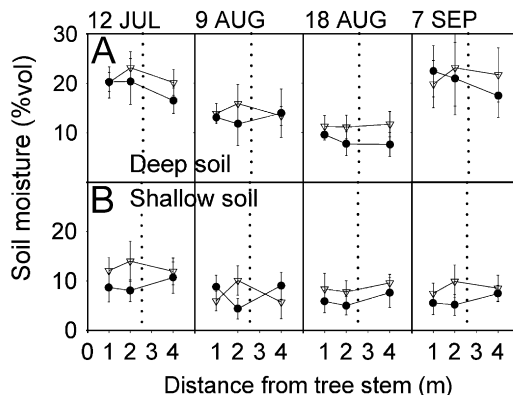


Fig. 4. Mean (\pm SE; $n = 5$) surface (0–30 cm) soil moisture (TDR; volumetric) at 1, 2, and 4 m from *P. glandulosa* stems in 1999 on deep (A) and shallow (B) soil sites where the herbaceous layer was intact (control; solid circles) or removed (open triangles). Vertical dotted lines represents average location of tree canopy drip-line.

moisture was significantly higher where the herbaceous layer had been removed, and shallow soil sites had consistently lower water content than deep soil sites independent of treatment (Fig. 4). The seasonal trends observed in the upper 30 cm of the soil profile was similar to that recorded by the neutron probe. The increase in soil moisture in September at the deep soil site reflects a rain event that occurred only at this site.

P. glandulosa leaf N and P concentrations were inversely related to soil depth, being highest on deep soils and lowest on shallow soils (Fig. 5, Table 4). Mowing and removal of the herbaceous layer elicited an increase in *P. glandulosa* leaf N concentrations at the shallow soil site, but did not affect leaf N on intermediate and deep soil sites. Fire treatments (conducted on deep and intermediate sites only) had no effect on leaf N. Differences in leaf P concentrations among sites were more pronounced and the site–treatment interaction was significant. At the deep soil site, leaf P on burned sites was greater than on control and mow treatments. However, at the intermediate soil depth site, levels of *P. glandulosa* leaf P on plots subjected to grass mowing were elevated in comparison to those of plants on control plots. At the shallow soil site, trees subjected to herbaceous removal exhibited elevated ($p < 0.01$) leaf P levels relative to controls or trees with mown understories. Leaf N:P ratios were relatively stable, ranging from 21 to 26 in eight of the 11 soil/treatment combinations (Fig. 5A). The leaf N:P ratio increased to 33 in trees on the mowed shallow sites; and dropped to 14 on the burned deep site and mown intermediate site.

4. Discussion

As a rule, root systems of dryland woody species are characterized as coarse, extensive and deep, whereas those of grasses are typically fibrous, dense and relatively shallow. These differences in root architecture and distribution are the basis for the widely accepted ‘two layer soil moisture hypothesis’ (Schimper, 1903; Walter, 1971; Breshears and Barnes, 1999; Rodriguez-Iturbe, 2000) as a mechanism of resource partitioning that could promote the co-existence of grasses and woody plants. Literature reviews substantiate the general

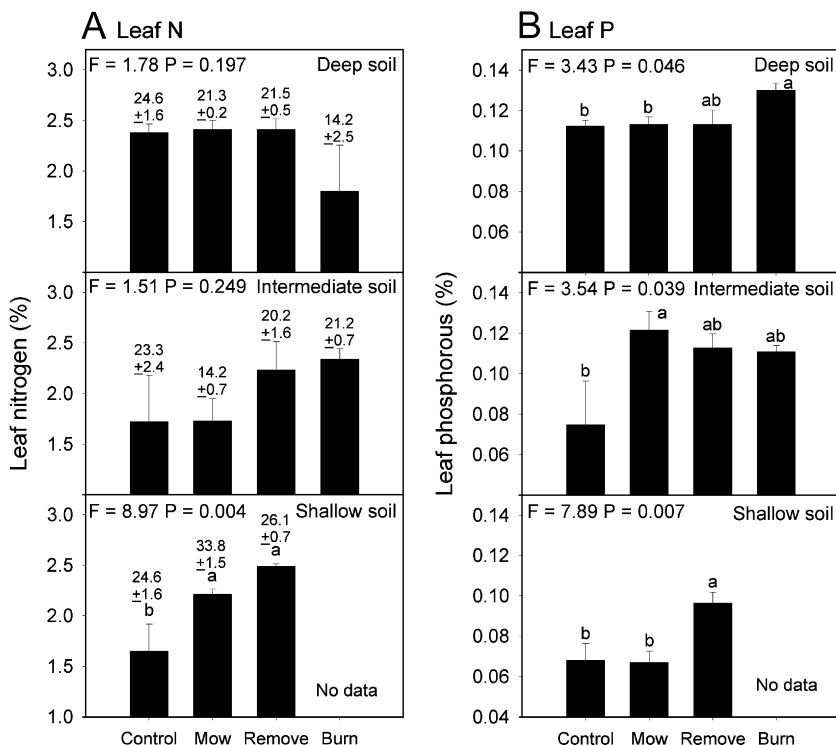


Fig. 5. Mean (\pm SE; $n = 5$) leaf N (A) and P (B) (% dry weight) of *P. glandulosa* in July 1999 in response to understorey manipulation (control = intact; mown, remove = herbicided, burned) with contrasting soil depths. Bars with different letters denote significant differences at $p \leq 0.05$. Absence of letters denotes no significant difference between bars. Numbers above bars in A indicate mean (SE) N:P ratio.

Table 4

Summary of ANOVA results for site (shallow, intermediate and deep soil) and treatment (control, mow, herbaceous removal) main effects and interactions on *Prosopis glandulosa* leaf N and P measured in 1999

	d.f.	F-value	p
<i>Leaf N</i>			
Site	2	4.07	0.0155
Treatment	2	3.81	0.0319
Site \times treatment	4	0.32	0.2835
<i>Leaf P</i>			
Site	2	13.59	<0.0001
Treatment	2	5.26	0.0101
Site \times treatment	4	3.36	0.0198

differences in root depth distributions between grasses and woody plant lifeforms, but also illustrate that roots of both lifeforms are most abundant in shallow soil layers, decreasing exponentially with depth (Jackson et al., 1996). Given the substantial overlap in root distributions, it seems reasonable to expect that competition for near-surface water and

nutrients may be a significant facet of woody–herbaceous interactions; and that grasses, with their dense, fibrous root networks may affect woody plant performance by extracting near surface resources and by preventing their percolation to deeper soil depths. *P. glandulosa*, the dominant woody plant in savannas of the southern Great Plains is typically characterized as a phreatophyte able to extract deep soil moisture via taproots. However, this species also relies on an extensive network of shallow lateral roots to access water delivered by small rainfall events that may only wet upper soil horizons (Heitschmidt et al., 1988; Ansley et al., 1990, 1991, 1992a). Thus, there is reason to expect that *P. glandulosa* should be responsive to the competitive status of the herbaceous layer.

4.1. Tree response to grass removal

The effects of grasses on trees were temporally variable and strongly influenced by soil depth (Figs. 2 and 5). *P. glandulosa* responded to grass removal on sites with shallow (1–1.2 m) and intermediate (2–3 m) soil depths, but only in the second year of the study. It is not clear whether this temporal variability represented a lag in the manifestation of treatment effects (as would occur if resource uptake in woody plants is uncoupled from growth, storage or biomass; Chapin et al., 1990) or the fact that rainfall in year 1 of the study was substantially lower than that in year 2 (Fig. 1). Given that growth rates of *P. glandulosa* control plants for a given site did not vary significantly from 1998 to 1999 despite these differences in rainfall, we infer that grasses were sufficiently drought-stressed in year 1 so as to have had no effect on *P. glandulosa* growth; and that in year 2 when rainfall was higher, grasses were more physiologically active and thus constrained *P. glandulosa* growth when present. While the removal of grasses enhanced *P. glandulosa* growth on the shallow sites, soil moisture levels also increased (Figs. 3B and 4B). This suggests *P. glandulosa* was not utilizing soil moisture resources as effectively as grasses on these sites.

Water and nutrients are tightly coupled and often act to co-limit productivity (Chapin et al., 1987; Chapin, 1991a,b; Schimel et al., 1997). That may well be the case in this setting, as trees in the grass removal treatment also demonstrated elevated concentrations of leaf P and N at the shallow soil site (Fig. 5) suggesting woody and herbaceous plants may compete for nutrients as well as water. Increases in soil moisture in the 0–30 cm zone resulting from grass removal (Fig. 4) may have elevated mineralization rates and nutrient availability. *P. glandulosa* is also capable of N₂-fixation (Zitzer et al., 1996); so elevated leaf N may reflect enhanced N₂-fixation brought about by increases in water and phosphorus availability resulting from grass removal. Conversely, the death of herbaceous tissue caused by the treatment could have released nutrients that *P. glandulosa* then acquired.

The grass effects on *P. glandulosa* growth did not occur on deep sites. From this we infer that in cases where soil depth exceeds ca. 3 m, opportunities for vertical soil resource and lifeform root biomass compartmentalization may be sufficient to shift grass-on-tree interactions from one of competition to resource partitioning. On the shallow and intermediate sites, grass ANPP may have been facilitated to the point where it is now having an influence on tree growth during years when resource levels are above some critical minimum threshold. If such feedback mechanisms are in place, we would predict that tree basal area would have the potential to increase on deep sites, and stabilize or perhaps even decrease on shallow sites.

4.2. Tree response to grass defoliation

Grazing of the herbaceous layer is often implicated as a factor that has promoted the proliferation of woody plants in grasslands and savannas (reviewed in Archer, 1995; van Auken, 2000). In our study, defoliation of the herb layer (as a proxy for grazing) had no demonstrable effects on adult tree growth and few consistent effects on leaf nutrient concentrations on any of the sites. These results, in concert with those from the removal experiment, are consistent with the results of other grass–shrub competition experiments which found that growth of competing grasses and shrubs was significantly influenced by the presence/absence of neighbours, but not neighbour shoot or root biomass (Peltzer and Kochy, 2001).

The lack of a significant adult tree response to defoliation of the herbaceous layer has been observed elsewhere (Stuart-Hill and Tainton, 1989). Given that complete grass removal did result in increased tree growth at the shallow and intermediate soil depth sites, it can be envisaged that more frequent and/or intense defoliation of the herbaceous community on our site may be required to elicit a tree growth response. In the longer term, intensification of defoliation (grazing) may shift the herbaceous community to a composition of plants that are less productive and less effective competitors with *P. glandulosa*; conversely, relaxation of defoliation may produce a shift in composition to an assemblage that more effectively competes with *P. glandulosa* (Archer, 1995).

4.3. Tree response to surface fire

Fires are known to elevate soil nutrient availability via ash deposition and increased mineralization (Valmis and Gowans, 1961; Christensen and Muller, 1975; Hobbs and Schimel, 1984; de Ronde et al., 1990; Kauffman et al., 1994). These processes can enhance growth of vegetatively regenerating woody shoots and roots (Haase and Sackett, 1996) and stimulate flowering (Hodgkinson, 1998). We therefore predicted that *P. glandulosa* trees not damaged by low intensity surface fires would respond by increasing their growth and foliar nutrient concentrations. Growth enhancement occurred only on the deep site, where burning stimulated *P. glandulosa* growth following the first post-fire growing season (1998), but not the second (Fig. 2A), despite the fact that 1999 was slightly wetter than 1998 (560 vs. 504 mm, respectively). Although leaf phosphorus was elevated in *P. glandulosa* plants on the burned deep sites there were no measurable differences in leaf N. The hypothesized benefits of surface fire on uninjured trees was thus site-specific and transient. In this study, fires were of small size and duration, and consequently of low intensity. Therefore, observed plant responses may not reflect the effects of normal prescribed burn or wildfire conditions.

4.4. Implications for savanna models and future research

Species interactions are not static; they change in space and time. In savannas, annual environmental conditions may fluctuate to accentuate or mitigate grazing effects, such that the effects of grasses on woody plants are significant in normal to above-normal rainfall years, but of little consequence in drier years (e.g. Knoop and Walker, 1985). Projecting how spatio-temporal variability in grass-on-tree effects might ultimately influence the landscape-scale population dynamics and community structure of long-lived woody plants

will require spatially-explicit, dynamic simulation modelling (e.g. Jeltsch et al., 1996). Parameterization and testing of such models will, in turn, require information and data.

The design of experiments to parameterize and test models of grass effects on established woody plants poses numerous challenges. The large size of mature woody plants (above- and below-ground) makes controlled environment and field studies logistically difficult. In our experiments, reductions in herbaceous biomass were confined to a zone within 5 m of tree boles (ca. 2.5 m beyond canopy drip lines (Fig. 4)). Given that shallow lateral roots of *P. glandulosa* extend an average of 8–11 m beyond their canopies (on deep and shallow sites, respectively; Simmons, 2003) widening the sphere of treatment influence to better approximate stand-scale grazing and fire effects may have elicited stronger *P. glandulosa* growth responses than those observed in this study.

What variables should be manipulated? In our experiment, we had no control over precipitation. Annual rainfall was below the long-term average in both years of our study. As a result, the observed effects of grasses on tree growth may have been dampened relative to what might be expected in years of average to above-average rainfall (e.g. Knoop and Walker, 1985). Thus, it would be desirable to manipulate the amount, timing and pulsing of rainfall (e.g. Huxman et al., 2004). Grass species composition may also affect the outcome of grass-on-tree competition, so experimental manipulations of herbaceous composition would be useful next steps. Our results also suggest it would be useful to experimentally tease apart grass mediation of water vs. nutrient effects on tree growth, particularly that of phosphorus in systems dominated by woody legumes.

Ecologists have long explored the question of what controls the abundance of woody plants in dryland ecosystems (Walker, 1985); and in recent decades this question has taken a new urgency as woody plant cover has increased markedly areas that were historically grasslands, savannas and open woodlands (Archer et al., 2001). Additional field and modelling experiments are needed to ascertain the conditions and settings under which the dynamics of woody cover and productivity in drylands may be contingent on the dynamics of the herbaceous layer and its influence on soil water balance and nutrient availability. Such insights are necessary if we are to correctly assess how ecosystem net primary production changes with changes in grass–woody plant abundance (House et al., 2003).

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