

Tree (*Prosopis glandulosa*) effects on grass growth: An experimental assessment of above- and belowground interactions in a temperate savanna

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Abstract

Savanna trees can impose above- and belowground effects on the herbaceous layer by changing water, nutrients and microclimate. Proposed mechanisms governing savanna tree-on-grass interactions include: (1) improved fertility and structure of soils below tree crowns; (2) improved water relations of shaded plants; and (3) increased competition for light, soil moisture and nutrients. To assess the relative importance and outcome of these interacting positive and negative factors, we conducted a series of field experiments that altered the presence and absence of tree canopy and tree roots at locations both immediately under trees and in interstitial locations in a mesquite (*Prosopis glandulosa*) savanna. Basal area, tiller density and production of the dominant C₃ grass, *Nassella leucotricha*, and herbaceous layer annual net primary production (ANPP) were quantified in 1998 and 1999. Annual rainfall during these 2 years was substantially below normal and most responses to treatments were neutral. However, a significant reduction in herbaceous ANPP, largely annual C₃ grasses, indicated that belowground competition rather than facilitation was the mechanism controlling tree effects on grass in this savanna. Lower than average rainfall was a potentially overriding factor. Hence, it is possible that other tree-on-grass mechanisms might operate under average or above-average rainfall years.

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1. Introduction

Savanna trees impose both above- and belowground effects on the sub-canopy environment. Collectively, these modifications may have a net positive, neutral, or negative effects on the performance and production of herbaceous vegetation beneath tree canopies (Scholes and Archer, 1997). There are many proposed mechanisms governing tree–grass interactions, but these are variable and frequently interactive. Belsky and

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Canham (1994) attributed the differences in herbaceous productivity between inter- and below-canopy locations to three primary interacting and potentially off-setting or reinforcing factors: (1) improved fertility and structure of soils below tree crowns (Belsky, 1994); (2) improved water relations of shaded plants; (3) improved water relations of sub-canopy plants able to access soil water produced via stem flow or hydraulic lift (Ludwig et al., 2003); (4) competition between trees and understory plants for light, soil moisture and nutrients. Few studies have attempted to differentiate the relative importance of these factors (Archer et al., 2001; Scholes and Archer, 1997).

In tropical and subtropical systems where tree densities are low, herbaceous productivity under or near tree canopies can exceed that in inter-canopy areas (Belsky, 1994). In these cases, benefits associated with soil nutrient enrichment and temperature amelioration appear to outweigh reductions in photosynthetically active radiation and rainfall interception by tree canopies (Fisher, 1990). Alternatively, sub-canopy grass growth may be reduced by the presence of tree canopies, suggesting that deleterious effects associated with light attenuation and/or canopy interception of rainfall (McPherson, 1997; Scholes and Archer, 1997) outweigh positive effects. Although there is evidence for belowground resource partitioning between deeply rooted savanna trees and shallow-rooted grasses (Brown and Archer, 1990; Knoop and Walker, 1985; Soriano and Sala, 1983), there is also evidence that near-surface tree roots may actively compete with grasses for resources depending on water availability (Belsky, 1994). In many savanna trees, lateral roots extend well-beyond the canopy dripline and thus have the potential to affect herbaceous composition and production in inter-canopy as well as sub-canopy areas (Scholes and Archer, 1997). However, the combination of deep tap roots and shallow lateral roots also means hydraulic re-translocation of water from deep to shallow layers can occur (e.g., Dawson, 1993; Ludwig et al., 2003; Zou et al., 2005). The extent to which this may benefit grasses vs. the tree is unknown. At the landscape scale, the net effect of trees on grasses in savannas may also be a function of the interaction between woody plant density, basal area or cover and annual rainfall (e.g., Walker et al., 1986). For example, in *Acacia farnesiana* (L.) Willd. savannas in southern Texas, USA, herbaceous production increased as tree cover increased to ca. 25%, then declined at higher tree coverage (Scifres et al., 1982).

Little is known of the mechanics of tree–grass interactions in the *Prosopis glandulosa* (Torr.) savannas of the southern Great Plains in North America. Studies to date suggest *P. glandulosa* may have negative (Dahl et al., 1978; Heitschmidt and Dowhower, 1991; Laxson et al., 1997; McDaniel et al., 1982) neutral (Heitschmidt et al., 1986) or positive (Hughes et al., 2006) effects on herbaceous production. The extensive lateral root architecture of *P. glandulosa* (Ansley et al., 1991; Fisher, 1950; Heitschmidt et al., 1988; Tiedemann and Klemmedson, 1977) suggests that *P. glandulosa* may also affect herbaceous production of areas beyond canopy drip lines (henceforth “interstitial” locations). The objectives of this study were to determine: (a) if production of the sub-canopy herbaceous layer would be comparable to, greater than, or less than that in interstitial zones, (b) whether differences in sub-canopy vs. interstitial production (if any) were due to the modification of the aboveground (light and temperature) or belowground (water and nutrients) environment, and (c) if *P. glandulosa* competitive effects extend beyond its canopy.

2. Methods

2.1. Site description

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 (Asner et al., 2003). *P. glandulosa* is now the dominant woody species, occurring at densities of up to 500 trees ha⁻¹ (Ansley et al., 1997) and aerial canopy cover up to 65% (Teague and Ansley, unpublished data) depending on management history. The herbaceous matrix consists of C₃ (e.g., annual *Bromus* spp. and perennial *Nassella leucotricha* Trin. and Rupr.) and C₄ grasses (e.g., perennial *Buchlœ dactyloides* (Nutt.), *Bouteloua curtipendula* (Michx.) Torr., *Bothriochloa laguroides* (DC.), *Sporobolus compositus* (Poir.) Merr.). In heavily grazed “lawn” areas the C₄ shortgrass *B. dactyloides* tends to dominate, with *N. leucotricha* and C₄ mid-grasses 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 fertile shallow-clays of the Vernon series (fine, mixed, active, thermic Typic Haplustepts) with 3–8% slopes (USDA, 1962).

The climate is subtropical, subhumid, characterized by hot summers and cold, dry winters (Larkin and Bomar, 1983). Vernon, Texas has a mean annual temperature of 17 °C with 30 d yr⁻¹ > 38 °C. Mean monthly maximum temperature (29 °C) occurs in July; the mean monthly minimum (4 °C) occurs in January (Larkin and 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). On-site rain gauges indicated precipitation the year prior to the study (698 mm, 1997) was above average, but below average in 1998 (427 mm) and in 1999 (614 mm), with wetter than usual spring weather and several consecutive dry weeks during the summer season when C₄ grasses are typically most physiologically active (Fig. 1).

2.2. Experimental design

A randomized-block experiment was established to separate the mechanisms contributing to the net outcome of facilitative vs. competitive interactions between *P. glandulosa* and the *N. leucotricha* dominated understory. A full factorial experiment of all treatments: sub-canopy vs. interstitial sites; presence or absence of tree canopy; presence or absence of tree roots, was not possible (i.e. an interstitial site with a tree canopy is not possible; Table 1). Therefore, 10 treatments were applied to plots (0.25 m²) situated under (sub-canopy) and away (interstitial) from *P. glandulosa* tree canopies, creating different combinations of the presence or absence of tree canopy and roots ($n = 8$ per treatment; Fig. 2; Table 1). The treatments were installed in December 1997 and data collection commenced in spring, 1998. For treatments minimizing *P. glandulosa* root competition, vertical trenches were excavated with a gasoline-powered trencher (Case 460) to a depth of 1 m, lined with 6-mil black polythene, then backfilled. Care was taken to avoid disturbing the soil hydrological environment by placing root barriers about 1 m from the plot perimeter. The effects of *P. glandulosa*-induced alterations of soil properties on production was assessed by comparing herbaceous biomass on plots in interstitial locations to that of plots where *N. leucotricha*, *P. glandulosa* was present or on soils from which *P. glandulosa* plants had been removed by hand. A field survey of photosynthetic photon flux density (PPFD; 400–700 nm) was conducted on 20 July 1998 with a horizontally oriented 1-m long quantum sensor (LI-191SA, LI-COR Inc., Lincoln, NE). Mean (S.E.; $n = 16$ sub-canopy and 16 interstitial zones) solar noon PPFD at the top of the herbaceous layer under *P. glandulosa* canopies ($735 \pm 44 \mu\text{mol m}^{-2} \text{s}^{-1}$) was significantly less than that at the top of herbaceous canopies in the interstitial zones ($2167 \pm 21 \mu\text{mol m}^{-2} \text{s}^{-1}$)

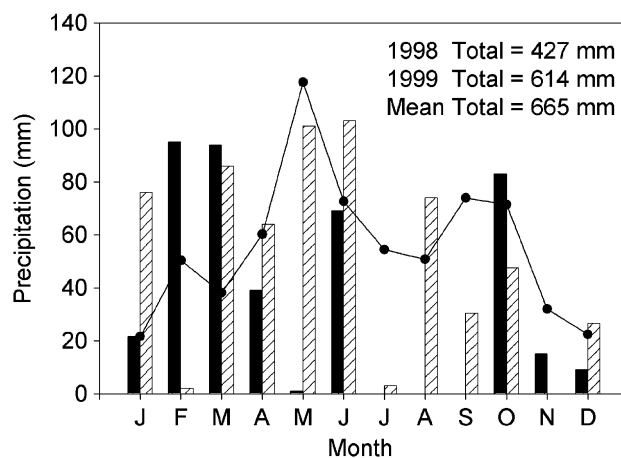


Fig. 1. Rainfall patterns during 1998 (solid) and 1999 (hatched) at the study site. Line represents local 30-year monthly mean from a gauge 32 km west.

Table 1

Factorial design of treatments examining the influence of *P. glandulosa* on the herbaceous layer beneath (sub-canopy) and away (interstitial) from tree canopies showing presence (+) or absence (–) of canopy or roots within experimental layout

	Sub-canopy sites			Interstitial sites	
	Canopy	Roots		Canopy	Roots
A	+	+		n/a	n/a
B	+	–		n/a	n/a
C	–	+	G	–	+
D	–	–	H	–	–
E	+ (synthetic)	–	I	+ (synthetic)	+
F	+ (synthetic)	+	J	+ (synthetic)	–

((ANOVA) $P < 0.001$; $F = 9.12$). *P. glandulosa* canopy effects on radiant energy regimes were mimicked by using artificial shade structures consisting of colored acetate (Roscolox 66 “cool blue”) sandwiched between neutral-density window screen (1 mm × 1 mm) cloth and a structural wire mesh (e.g., Lee, 1985). Spectroradiometer (Li-COR LI-1800) measurements indicated mid-day R:FR ratios beneath *P. glandulosa* canopies and shade structures were 0.849 (± 0.171) and 0.708 (± 0.003), respectively. The artificial *P. glandulosa* canopies were orientated east-west and tilted at an angle of approximately 25° from the horizontal, dipping toward the south, such that there was maximum shade exposure to the target area below, while allowing the circulation of air and penetration of un-modified early morning and late afternoon sun (as occurs with an actual *P. glandulosa* canopy). The passage of rainfall was enabled by perforating the acetate with a grid of 1 cm holes 2.5 cm apart. This perforation also served to create some radiation “dappling” such as that which occurs in real canopies. For the second year of study, permeability of this structure to rainfall was increased by cutting the acetate with parallel slits 5–10 cm apart. The herbaceous production plots were situated within open-top wire mesh enclosures (1.5 × 1.5 × 1 m) designed to prevent small and large mammal herbivory.

For *N. leucotricha* we recorded changes in tillers per plant (%) and basal area (%) from beginning to end of the growing season and the number of reproductive and non-reproductive tillers cm⁻². Due to missing cells in the factorial experiment, statistical analyses examined contrasts between treatments whereby a suite of presence or absence of each competition element was assigned to each treatment (Table 1). For example, treatment A (Fig. 2) had the following attributes: – synthetic shade; + natural shade (canopy); + roots (no trench); + sub-canopy (tree site). All contrasts were run within a general linear model (PROC GLM; CONTRAST) using SAS (SAS, Institute 1988) with the Bonferroni correction (Keppel, 1991) applied to each comparison. To examine differences among individual treatment effects independent of contrasts, all metrics were also tested with one-way ANOVA. Canopy cover of *N. leucotricha*, annual grasses (mainly *Bromus* spp.), and forbs in plots was visually estimated at the end of each growing season (1998, 1999) and assigned a rank abundance. The Kruskal–Wallis test and associated Dunn’s multiple comparison test (Zar, 1999) was used to test similarities between rank abundances. Statistical significance was accepted at $\alpha \leq 0.05$ unless otherwise noted.

3. Results

3.1. Overview

Contrasts involving comparisons of natural and artificial shade (e.g., treatments A and E in Fig. 2) were significant in 1998 for *N. leucotricha* annual net primary production (ANPP) and for total ANPP (Table 2, contrast 17), suggesting the fabricated shade structure did not adequately simulate the effect of a natural canopy. The possibility that this was due to poor water permeability of the shade structures prompted a design modification for the 1999 season (see Section 2). During the relatively dry 1998 growing season, *N. leucotricha* experienced net reductions in tillers/plant (i.e. net tiller mortality) in both understory and interstitial settings

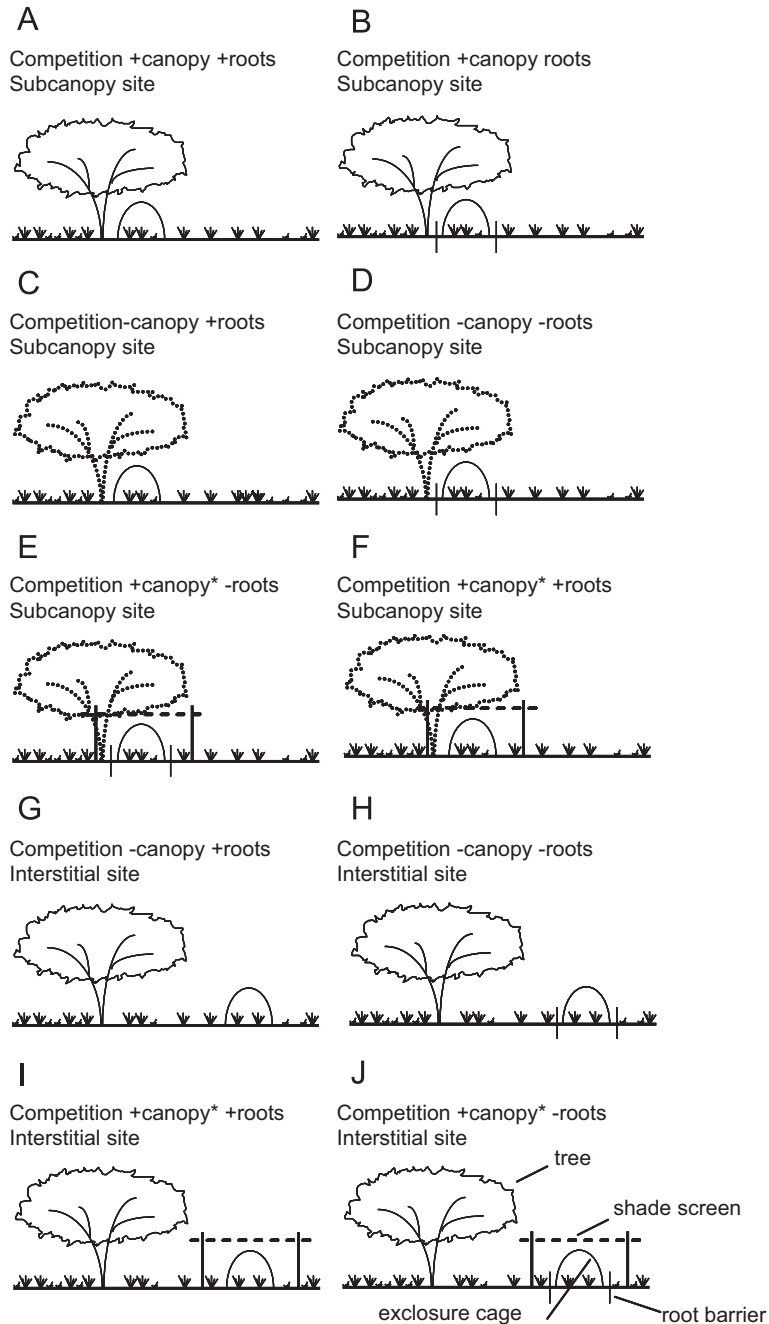


Fig. 2. Representation of experimental treatments that isolated above- and belowground competition between individual *P. glandulosa* trees and the adjacent herbaceous layer. The '*' indicates synthetic canopy treatment consisting of acetate film and neutral density shade cloth. Dashed tree outline indicates where a tree was removed. Treatments A–F were located in the sub-canopy and G–J in interstitial locations. Treatments A and G represent natural conditions.

and reductions in basal area, primarily in interstitial settings (Fig. 3c). Even so, there were no significant contrasts in total herbaceous or *N. leucotricha* ANPP or any other measured variables for *N. leucotricha* plots (Table 2). Although annual rainfall was greater in 1999, it was still below the long-term average (Fig. 1). As with 1998, *N. leucotricha* exhibited net tiller mortality and reductions in basal area in most treatments/locations in 1999 (Table 2; Fig. 4c); and its ANPP did not exhibit any significant contrast response (Table 2;

Table 2

Summary (*F*-values) of tested multiple contrasts and associated tested hypotheses of *N. leucotricha* shoot biomass; *N. leucotricha* basal area change; *N. leucotricha* vegetative tiller density; *N. leucotricha* reproductive tiller density; and plot ANPP for tree-grass competition treatments, and contrast direction

Contrast no.	Contrast description and direction (<, >)	1998					1999				
		Shoot mass	Δ Basal area	Tiller density	Reproductive tiller density	ANPP	Shoot mass	Δ Basal area	Tiller density	Reproductive tiller density	ANPP
	Model	1.54	1.22	0.76	0.99	2.22**	0.68	1.12	1.23	2.60*	2.14**
1	Sub-canopy > gap	1.14	3.33	1.86	2.14	0.77	0.03	0.62	0.08	4.47	0.85
2	+ Canopy > -canopy	0.08	0.17	0.19	0.03	3.37	1.23	0.09	0.01	16.52**	3.02
3	+ Roots < -roots	1.12	0.08	0.45	0.64	0.57	0.63	0.61	0.01	0.95	11.66**
4	+ Canopy + roots < -canopy - roots	0.74	0.03	0.45	0.22	3.99	0.06	1.01	0.07	11.91**	14.14**
5	+ Canopy + roots > -canopy + roots	0.30	2.88	0.64	0.13	0.18	0.60	1.10	0.41	11.37**	0.16
6	+ Canopy - roots > -canopy - roots	0.02	1.23	0.04	0.01	4.73	0.63	2.19	0.60	5.64	4.23
7	Sub + roots < -roots	1.22	0.01	0.14	0.01	0.01	0.00	0.03	0.61	0.87	10.62**
8	Sub + canopy > -canopy	0.69	1.35	0.18	0.87	2.12	0.57	0.04	0.74	8.14	1.30
9	Sub + canopy + roots < -canopy - roots	1.28	0.16	0.03	0.60	1.66	0.09	0.19	0.80	6.11	10.53**
10	Gap - roots > + roots	0.10	0.32	0.38	1.95	1.12	1.39	2.10	1.16	0.16	1.98
11	Gap + canopy > -canopy	0.64	0.05	0.03	0.17	1.93	0.80	0.20	1.48	6.04	2.60
12	Gap + canopy + roots < -canopy - roots	0.12	0.31	0.10	1.65	3.00	0.04	1.79	2.62	4.08	4.56
13	Sub - roots > gap - roots	0.19	2.70	1.29	3.42	0.01	0.55	0.10	0.54	1.68	1.79
14	Sub + roots > gap + roots	1.16	0.88	0.63	0.05	1.32	0.24	2.04	1.30	2.87	0.00
15	Sub - canopy > gap - canopy	0.04	3.86	0.30	2.86	0.51	0.01	0.16	0.85	0.89	0.20
16	Sub + canopy > gap + canopy	2.35	0.71	1.59	0.29	0.94	0.16	0.60	1.44	1.23	1.54
17	Natural shade = synthetic shade	8.43*	1.19	0.23	2.19	12.78**	0.06	0.72	3.28	4.27	0.43
18	Natural shade > no shade	4.61	0.17	0.41	0.72	1.03	0.97	0.11	1.29	19.43**	0.74
19	Synthetic shade > no shade	0.86	0.68	0.04	0.60	9.83**	0.84	0.39	0.68	8.22	3.44

Positive (+) and negative (-) sign refers to presence or absence of canopy or roots. Gap: interstitial site; sub: sub-canopy site. Significant effects are indicated by '*' ($P < 0.1$ with Bonferroni correction $P < 0.00526$) and '**' ($P < 0.05$ with Bonferroni correction $P < 0.00263$).

Fig. 4b). The number of tillers per plant, tiller density and basal area were unresponsive to treatments. Only *N. leucotricha* reproductive tiller production showed any significant response), with greater reproductive tillering occurring under shade conditions with and without belowground competition (Table 2; Fig. 4d).

Manipulation of above- and belowground *P. glandulosa* influences had no significant affect on *N. leucotricha* or total ANPP in the driest year. In 1999 annual grasses dominated in sub-canopy settings, but this pattern was not repeated by *N. leucotricha* or forb cover (Table 3). Plot ANPP in 1999 was greater in the absence of belowground competition and in the absence of above- and belowground competition in the sub-canopy locations (Table 2, contrasts 4, 5, 7, and 9).

3.2. Belowground competition

We saw no evidence that the presence or absence of *P. glandulosa* roots were significantly influencing *N. leucotricha* growth metrics or total herbaceous ANPP in either sub-canopy or interstitial locations in the driest year (1998; Table 1). However, in 1999, total herbaceous ANPP was significantly greater in the absence of competition from tree roots; and in the absence of above- and belowground competition in a sub-canopy (Table 2, contrasts 3, 4, 7, and 9).

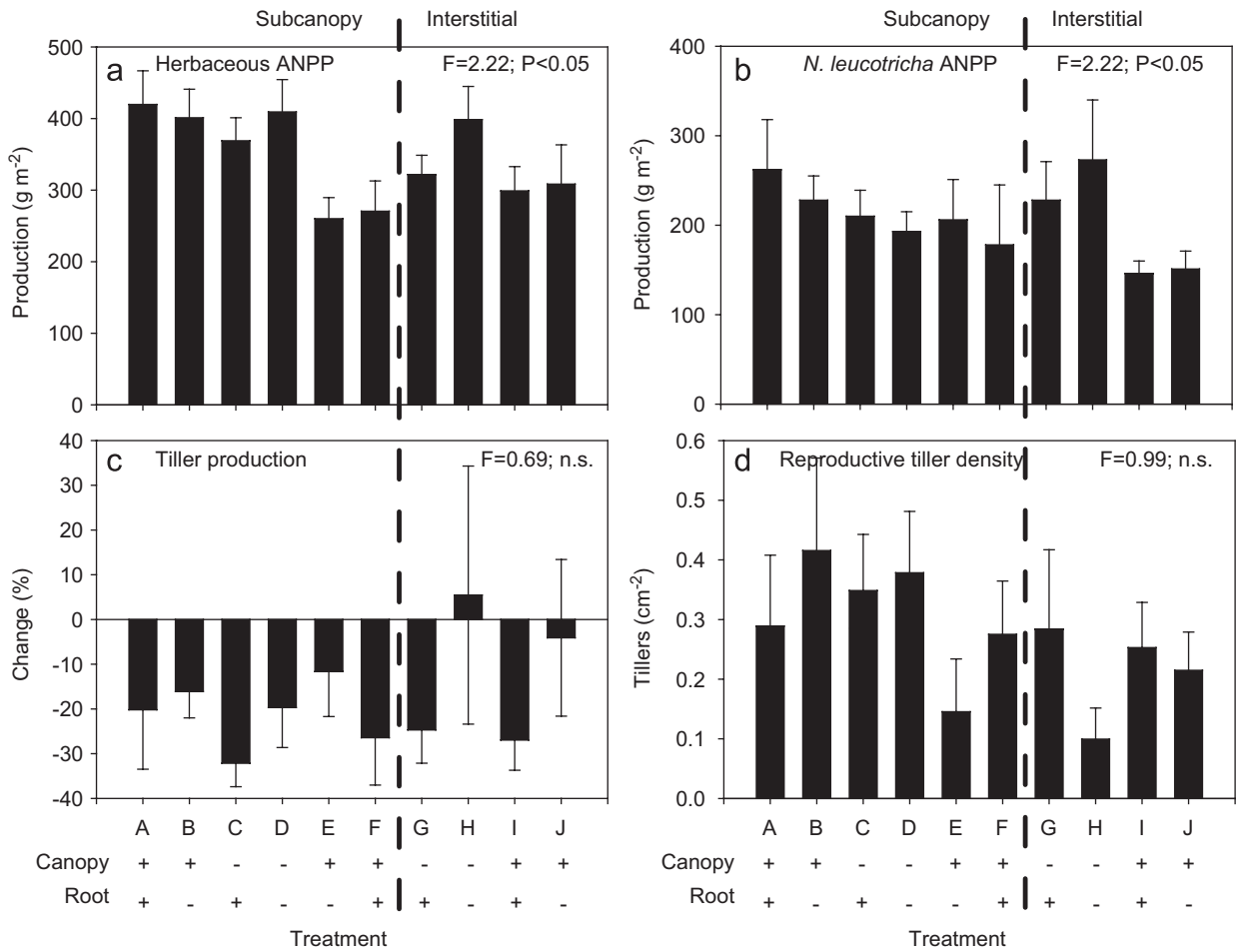


Fig. 3. Herbaceous ANPP, *N. leucotricha* ANPP, relative tiller production and reproductive tiller density, response to competitive treatments in 1998 (see Fig. 2 for treatment labels; +/- represents presence/absence of canopy or roots). Dashed line separates subcanopy from interstitial treatments.

3.3. Fertile island effect

There were no significant differences in *N. leucotricha* growth parameters or total ANPP between subcanopy and interstitial locations in either year, regardless of radiant energy levels (Table 2, contrasts 1, 13, 14, 15, and 16).

3.4. Shade effect

Shade alone did not affect any of the *N. leucotricha* vegetative growth parameters or productivity in either year, regardless of *P. glandulosa* effects on soil nutrient status (Table 1, contrasts 2, 11, 18, and 19). However, there was a greater density of *N. leucotricha* reproductive tillers under natural tree-canopy shade in 1999 (Table 2, contrasts 2, 4, 5, and 18).

4. Discussion

There were few indications of any strong or consistent competitive or facilitative tree effects on herbaceous vegetation. Apart from the facilitative effect of shade on reproductive tiller production of

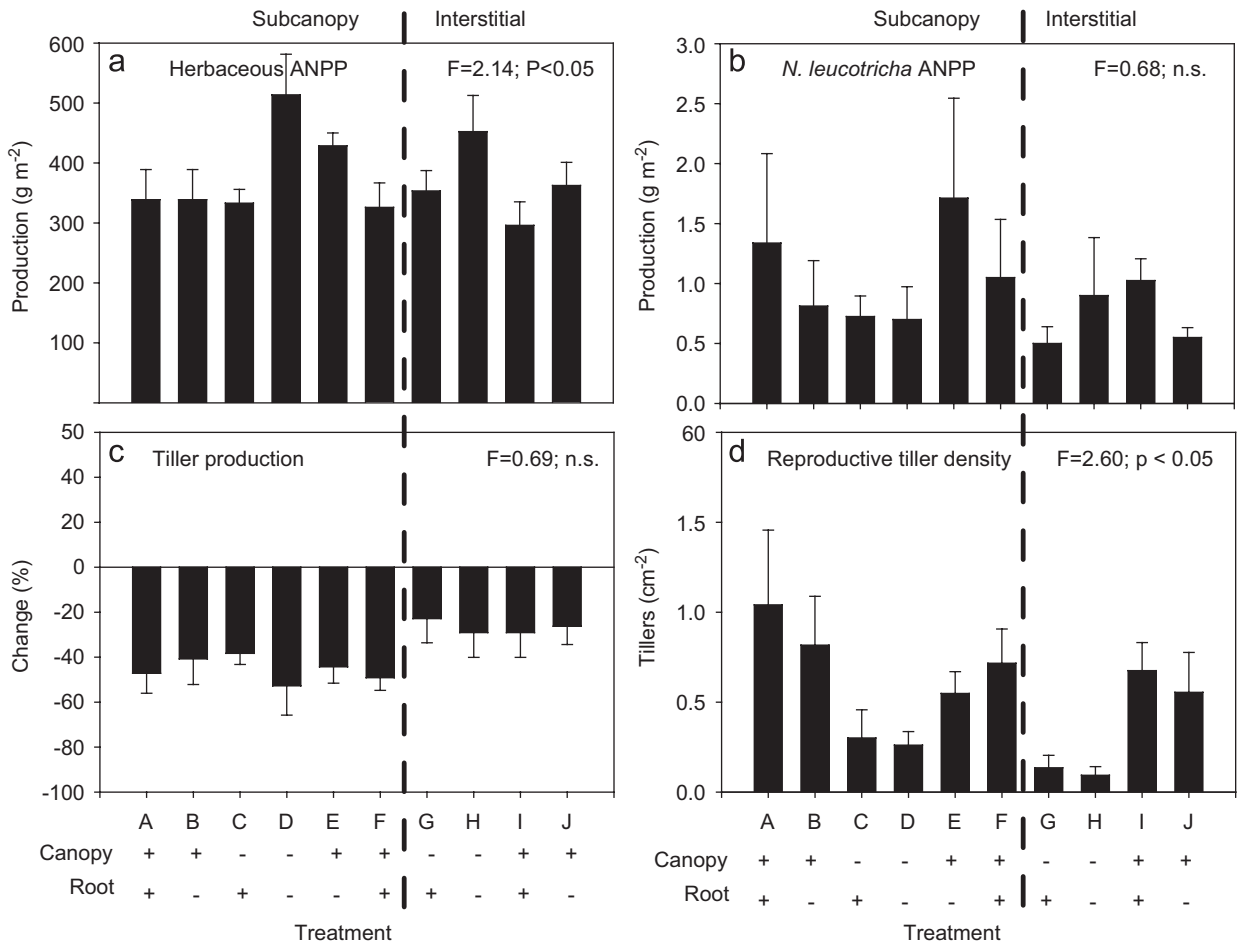


Fig. 4. Herbaceous ANPP, *N. leucotricha* ANPP, relative tiller production and reproductive tiller density, response to competitive treatments in 1999 (see Fig. 2 for treatment labels; +/- represents presence/absence of canopy or roots). Dashed line separates subcanopy from interstitial treatments.

Table 3

Mean rank abundance (estimated canopy cover; $n = 8$) of three plant groups (*N. leucotricha*; *Bromus* spp.; forbs) with 1 being most abundant and 3 least abundant (see Fig. 2 for treatment labels) at the end of 1999; +/- represents presence/absence of roots or canopy)

	A	B	C	D	E	F	G	H	I	J
Canopy	+	+	-	-	+	+	-	-	+	+
Roots	+	-	+	-	-	+	+	-	+	-
	Sub-canopy sites					Interstitial sites				
<i>N. leucotricha</i>	1.63ab	1.88abc	1.75abc	2.13bc	1.75abc	2.13c	1.13a	1.50a	1.25abc	1.75abc
<i>Bromus</i> spp.	1.50abc	1.38abc	1.25a	1.13a	1.25ab	1.13ab	2.0bc	2.5c	2.25bc	1.63abc
Forbs	2.88b	2.75b	3.00b	2.75b	3.00b	2.75ab	2.88b	2.14b	2.50a	2.62ab

Mean rank with different letter are different within each species at $P < 0.05$ level.

N. leucotricha, the main underlying mechanism emerging from this study that appeared to influence herbaceous productivity was competition rather than facilitation; and the competition component was predominantly belowground.

4.1. Above- vs. belowground competition

Tree effects on herbaceous production are a function of woody plant basal area and cover; and there are widespread reports of reductions in herbaceous production with increasing woody abundance (Scholes and Archer, 1997). In savannas of the southern Great Plains, herbaceous production declines when the *P. glandulosa* canopy cover rises above 15–20% (McDaniel et al., 1982) and when *A. farnesiana* (L.) Willd. cover exceeds ca. 25% (Scifres et al., 1982). These trends are typically ascribed to competitive effects without specifying whether the competition is above- or belowground. In our study, removing tree canopies had little effect on herbaceous plant growth and production, suggesting neither attenuation of light (competition) nor cessation of hydraulic lift by *P. glandulosa* roots (facilitation) were of much consequence. In contrast, exclusion of tree roots elicited a significant increase in herbaceous plant production. Thus, it appears that belowground competition played an overriding role in explaining tree effects on herbaceous ANPP in this climatic region. Although belowground competition was significant in sub-canopy and interstitial locations combined (Table 2, contrast 3), it appears to have been primarily associated with the sub-canopy zone (Table 2, contrast 7). Our results help explain brush management studies which have noted that stand-level increases in herbaceous production following herbicide applications to *P. glandulosa* were primarily associated with positive grass and forb responses in the sub-canopy rather than interstitial zones (Heitschmidt et al., 1986; McDaniel et al., 1982). Given that *P. glandulosa* roots often extend well beyond their canopies (Heitschmidt et al., 1988), it would be interesting to investigate why belowground competitive interactions are concentrated in the sub-canopy zone.

4.2. Annual vs. perennial grass responses

There was some variation of the composition of the herbaceous layer with respect to tree canopy (Ludwig et al., 2004). The distribution of perennial C₃ grasses were ubiquitously distributed in sub-canopy and interstitial zones; whereas annual grasses were more generally more abundant in the sub-canopy zone and indicated generally higher abundance in competition alleviation treatments in the sub-canopy patches (Table 3). This response occurred despite limited overlap in the growth period of C₃ grass and tree growth forms. In north Texas *P. glandulosa* exhibits full leaf expansion in early May following bud break in April (Ansley et al., 1992), by which time *Bromus* spp. and *N. leucotricha* are already flowering (Diggs et al., 1999; Hicks et al., 1990). The exotic *B. japonicus*, the dominant annual grass at this site, is highly competitive and very responsive to spring rainfall (Haferkamp et al., 1998; Whisenant and Uresk, 1990); and its growth may have damped the response of other herbaceous species to *P. glandulosa* manipulation, especially in the sub-canopy. The limited contribution of warm season grasses to ANPP and their lack of response to *P. glandulosa* manipulation may reflect seasonal rainfall patterns in 1998 and 1999 that favored the exotic annuals and amplified their competitive impact on the indigenous grasses (Haferkamp et al., 1995, 1998). In any case, the annual rather than the perennial grass component largely accounted for the competitive response in the sub-canopy zone.

4.3. Fertile island effect

The lack of an herbaceous growth response to location (sub-canopy vs. interstitial), implies that if *P. glandulosa* has modified soils of sub-canopy environment as has been suggested by some studies e.g., increased soil nitrogen and organic carbon content and mineralization, etc. (Hibbard et al., 2001), then such enhancements were not sufficient to affect the growth of the dominant perennial grasses during the study period. Results from this study are consistent with findings in a separate study that found soil enrichment of C and N mass by *P. glandulosa* has been minimal at this site (Hughes et al., 2006). However, the fact that annual grass abundance was generally higher in sub-canopy zones than in interstitial zones, suggests that short-term production responses to *P. glandulosa* manipulation may not be indicative of soil fertility factors contributing to difference in the relative abundance of different herbaceous functional groups over the longer time frames (Ludwig et al., 2004).

4.4. Canopy effect

P. glandulosa plants at our study site have leaf area index values ranging from 1 to 2.2 with stems also contributing substantially to light interception (Ansley et al., 1998). The dominance of C₃ grasses in sub-canopy positions observed in this study and others in the area (Heitschmidt et al., 1986; McDaniel et al., 1982) suggests C₄ grasses, which are common in the area and in the interstitial locations (Teague and Dowhower, 2002), may more negatively influenced by *P. glandulosa* shading. PPFD levels below *P. glandulosa* canopies (e.g., 735 $\mu\text{mol m}^{-2} \text{s}^{-1}$) are similar to light saturation levels for C₃ leaves (Larcher, 1995) and the C₃ grasses that dominate the sub-canopy ground cover green up and put on substantial growth well before *P. glandulosa* canopies leaf out in the spring. Although the drought conditions during this study may have tempered understory plant responses to canopy manipulations, we saw no evidence for either positive or negative effects of *P. glandulosa* canopies on herbaceous growth. A notable exception was the increase in allocation to reproductive tillers by *N. leucotricha* under shade in 1999. Reproductive tiller production is not uncommon in grasses in shade environments (Naumburg et al., 2001) and has been attributed to low R:FR ratios under plant canopies (Ballaré and Casal, 2000). The lack of any vegetative response to the *P. glandulosa* canopy removal suggests positive ameliorative effect of shade (e.g., on water use or temperature stress) may be offset by deleterious effects associated with canopy interception of rainfall or reductions in PPFD.

4.5. Implications for savanna models

Mechanistic models predicting tree effects on grasses should take into account the fact that the relative importance of facilitation, competition and resource partitioning may vary with soil type and wood plant density, other factors held equal (e.g. Hughes et al., 2006). In this study, confined to a single soil type and *P. glandulosa* stand density, we found only inferential evidence for a fertile island effect (Belsky, 1994); and apart from a stimulation of tiller flowering, no data to support a tree-shading effect on sub-canopy production. Although soil nutrients patterns can be linked to presence and absence of trees, any related response of herbaceous growth may be masked in semi-arid climates where water availability is the more limiting resource (Ludwig et al., 2004). These responses may have been more marked if significant summer (e.g. July) rainfall had occurred, thereby providing the potential opportunity for more growth of perennial grasses. Similarly, greater than normal annual grass production, especially in 1999, may have suppressed perennial grass responses. Under conditions of below-average rainfall, any facilitative or competitive effects of *P. glandulosa* on understory plants were either antagonistic or ineffectual. However, our data do support a model that where water is limited belowground competition may be the overriding factor governing the tree–grass relationship (Sankaran et al., 2005). Furthermore, this equilibrium between these two life forms may wax and wane depending on the amount and seasonality of rainfall (e.g., Callaway, 1997; Knoop and Walker, 1985) such that under conditions of higher rainfall, belowground competition interactions may become negligible and savanna equilibrium regulated by disturbance (Sankaran et al., 2004, 2005). The largely neutral responses observed in this 2-year study, the general absence of evidence for facilitation, and the temporal variability in the presence or absence of competitive interactions observed in this study supports this theory. Under average or higher than normal rainfall, these responses may not be repeated.

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