Herbaceous Production and Soil Nitrogen after Mesquite Mortality in Southern Great Plains (US) Grassland

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A B S T R A C T

In the mixed C_3/C_4 grassland of the southern Great Plains, United States, the invasive woody legume, honey mesquite *(Prosopis glandulosa)*, affects grass production and composition differently beneath the canopy (subcanopy) than in spaces between trees (intercanopy) due in part to the dominant presence of C_3 Texas wintergrass *(Nassella leucotricha)* beneath the mesquite canopy and soil enrichment from N-fixation by mesquite. This arrangement, unlike most *Prosopis* systems worldwide that have C_4 grass or C_3 subshrub understories, uniquely affects grass production spatially and seasonally during mesquite expansion and possibly after anthropogenic removal of mesquite. We compared herbaceous and soil N responses in subcanopy and intercanopy microsites during the first 2 yr following a root-killing herbicide mesquite treatment. Perennial grass (PGR) and total herbaceous (THB) production were greater in treated than untreated intercanopy and subcanopy microsites at 1-yr post treatment, with Texas wintergrass comprising the largest portion of PGR. In yr 2, PGR production declined in both treated microsites with no differences between treatments. However, THB production remained greater in treated than untreated microsites due mainly to increased annual forb production that supplanted PGR production from yr 1. Increased annual forb production in treated microsites in yr 2 was likely due to high rainfall in the fall of yr 1 that stimulated forb seed germination, increased light from the loss of shading by mesquite, and soil inorganic N that increased from yr 1 to yr 2. Pretreatment spatial heterogeneity of herbaceous composition and soil N, caused by mesquite, affected post-treatment patterns of herbaceous production. The unexpected replacement of PGR by annual forbs in yr 2 revealed that grass forage production following brush control can deviate markedly from predicted models under certain conditions.

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Introduction

Woody plant invasion in grasslands and rangelands often creates a spatial mosaic of herbaceous species composition and production and soil nutrient distribution that is very different beneath than beyond woody canopies (Scholes and Archer 1997; Riginos et al. 2009). This effect is variable depending on the woody species involved, the nature of the grassland community before woody invasion, and a host of other abiotic and/or disturbance effects such as soil type, droughts, livestock grazing, and fire.

A common woody invader worldwide is mesquite (*Prosopis* spp.) (Van Auken 2000; Pasiecznik et al. 2001; Bustamante et al. 2006). Species of *Prosopis* have invaded regions of Australia, Africa, India, South America, Central America, and the south central and southwestern regions of the United States. Common observations in these regions are that, because *Prosopis* is a nitrogen-fixing legume, soil N is greater beneath than beyond the *Prosopis* canopy (Tiedemann and Klemmedson 1986; Franco-Pizana et al. 1995; Geesing et al. 2000; El-Keblawy and Al-Rawai 2007; Herrera-Arreola et al. 2007; Boutton and Liao 2010). Low densities of *Prosopis* can be beneficial to growth of some grass species beneath *Prosopis* canopies due to nutrient enrichment and ameliorating effects of the *Prosopis* canopy on air and soil temperature (Tiedemann and Klemmedson 1977; Scholes and Archer 1997; McClaran and Angell 2006). However, moderate to high *Prosopis* density and canopy cover reduces grass production, especially mid-

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sized C_4 grass species (Archer 1995; Ansley et al. 2004, 2013; Patnaik et al. 2017). Finally, most *Prosopis* species have a dimorphic root system composed of a deep taproot and lateral roots that can extend > 10 m beyond the canopy edge (Heitschmidt et al. 1988; Gibbens and Lenz 2001; Ansley et al. 2014), conferring a competitive advantage in drylands.

Honey mesquite (*Prosopis glandulosa* Torr., hereafter mesquite) is the dominant *Prosopis* species in the 368 000-km^2 Southern Great Plains (SGP) region of the United States (**Fig. S1**, available online at doi:10.5061/dryad.nzs7h44rd). Mesquite expanded in range and density in the SGP after European settlement in the late 1800s due to grassland fire suppression, overgrazing of grass by cattle, and enhanced seed distribution by cattle via endozoochory (Van Auken 2000; Ansley et al. 2017).

In the SGP there exists a unique situation of mesquite subcanopy being dominated by a C_3 midgrass, Texas wintergrass *(Nassella leucotricha),* and intercanopy microsites containing a mixture of Texas wintergrass, C_4 short grasses, and remnant patches of C_4 midgrasses that are most sensitive to mesquite expansion (Ansley et al. 2013). In contrast, *Prosopis* invasion cases elsewhere have C_4 grass (Gibbens et al. 1996; El-Keblawy and Al-Rawai 2007; Wheeler et al. 2007; Riginos et al. 2009; Getachew et al. 2012; Ndhlovu et al. 2016), or C_3 subshrub species beneath *Prosopis* canopies (Archer 1990). Mesquite understory dominance by Texas wintergrass in the SGP has resulted in an alternate stable ecological state (Westoby et al. 1989), referred to as the "*Prosopis/Nassella* association" (Ansley et al. 2019), that is unlikely to transition back to what is assumed to have been C_4 midgrass dominance (Liao et al. 2006) without significant anthropogenic inputs to remove mesquite. The loss of C_4 midgrasses is significant because these high-producing grasses are critical for gallinaceous bird habitat (Tomecek et al. 2017), cattle forage (Ansley et al. 2013), and carbon sequestration (Conant and Paustian 2002).

Herbaceous production during mesquite expansion is different in the SGP than other *Prosopis*-dominated systems because of the presence of Texas wintergrass. In many regions, understory C_4 grass production declines to near zero as *Prosopis* cover increases (Archer 1995; El-Keblawy and Al-Rawai 2007; Mohamed et al. 2011; Patnaik et al. 2017). In contrast, in the SGP, as mesquite expansion increases and canopies coalesce, Texas wintergrass remains productive in subcanopy and the progressively smaller intercanopy areas transition from a mixture of C_4 midgrasses and short grasses to Texas wintergrass and C_4 short grasses; C_4 midgrasses largely disappear. Texas wintergrass can persist under high mesquite density by avoiding direct competition with mesquite for light and soil water by growing in early spring before mesquite leaves emerge and entering a quiescent physiological state in midsummer (Hicks et al. 1990; Simmons et al. 2008). Unlike C_4 midgrasses with deeper root systems, C_4 short grasses avoid competition with mesquite for soil moisture in intercanopy because their roots occupy soil layers above the 0.5−1.5 m depth where most of the first order mesquite lateral roots reside (Ansley et al. 2014), although some second-order branches extend to near the surface (Gibbens and Lenz 2001). C_4 short grasses are also better adapted than C_4 midgrasses to withstand heavy grazing (Wood and Blackburn 1984; Teague et al. 2011).

Because mesquite resprouts vigorously after top-killing treatments such as prescribed fire or mechanical chaining, many resource managers recognize the long-term importance of root-killing treatments (Bovey and Whisenant 1991; Ansley and Castellano 2006). Aerial application of herbicides is currently the lowest-cost treatment for root-killing mesquite on large land areas and requires only a single application every 20−25 yr (Ansley et al. 2004). While several studies have quantified changes in herbaceous production following mesquite treatments in the SGP (McDaniel et al. 1982; Bedunah and Sosebee 1984), none

have recorded responses within intercanopy and subcanopy microsites and in concert with soil N measurements. Differences in C_3 and C_4 grass composition and potentially different soil N amounts between these microsites in the SGP provides a unique post-treatment dynamic compared with other *Prosopis* systems that needs further investigation to broaden our understanding of *Prosopis* invasion and management strategies in temperate climates (Bustamante et al. 2006; Riginos et al. 2009).

Some brush treatment studies have found a high forb response after treatment (Fulbright 2004). This usually occurs following mechanical woody plant treatments that disturb the soil and create favorable environments for forb seed germination (Bozzo et al. 1992; Kunst et al. 2012) or prescribed fire that temporarily increases bare ground (Engle et al. 1998; Fuhlendorf and Engle 2004). Forbs are not a prominent component of the *Prosopis/Nassella* system of the current study (Ansley and Castellano 2006; Teague et al. 2014), except for occasional rainfall-related outbreaks of annual forbs (Stanford et al. 2008).

Our objectives were to compare production of grass and forb functional groups and available soil N amounts within intercanopy and mesquite subcanopy microsites in the first 2 yr after a non−soil-disturbing mesquite root-killing treatment. We hypothesized that there would be an increase in Texas wintergrass production in soil N-enriched subcanopy to the exclusion of other grass or forb species. In addition, we expected an increase in intercanopy production of C_3 and C_4 grass species due to the loss of competition from mesquite via lateral roots that extend into intercanopy areas. We hypothesized that any short-term forb responses would occur in intercanopy but not subcanopy due to Texas wintergrass dominance in subcanopy. In addition, since our brush treatment did not disturb the soil, we expected forb production to be low relative to grass production.

Methods

Research was conducted on the Smith-Walker Experimental Ranch in north central Texas (34º01′52″N; 99º15′00″E; elevation 372 m), which is near the north-south midpoint in the SGP (see Fig. S1; USDA-NRCS 2006). Mean annual rainfall (30 yr; 1981−2010) is 710 mm with peaks in June (108 mm) and September (80 mm). Mean annual air temperature is 17.1°C, and average daily monthly air temperatures range from 35.9°C in July to −2.4°C in January (NOAA-NCDC 2019). Soils are fine, mixed, superactive, thermic Typic Paleustalfs of the Wichita series and fine, mixed, superactive, thermic Vertic Paleustolls of the Tillman series; both are 1- to 2-m deep clay loams on 1−3% slopes (USDA-NRCS 2019a). Ecological site description is clay loam R078CY096TX (USDA-NRCS 2019b).

Vegetation consists of a woody overstory of multistemmed 3−5 m tall, 30- to 40-yr-old honey mesquite, 40−60% canopy cover, and a herbaceous mixture of C_3 and C_4 perennial grasses. The primary C_3 midgrass is the bunchgrass Texas wintergrass (*Nassella leucotricha* [Trin. and Rupr.] Pohl.). Common C_4 midgrasses are sideoats grama (*Bouteloua curtipendula* [Michx.] Torr.), vine mesquite (*Hopia obtusa* [Kunth] Zuloaga & Monroe), and sand dropseed (*Sporobolus cryptandrus* [Torr.] A. Gray). Common C_4 short grasses are buffalograss (*Buchloe dactyloides* [Nutt.] Engelm.), curly mesquite (*Hilaria belangeri* [Steud.] Nash), and the bunchgrass form of blue grama (*Bouteloua gracilis* [Kunth.] Lag. *ex* Griffiths). C_3 annual grasses include Japanese brome (*Bromus japonicus* Thunb. *ex* Murray) and little barley (*Hordeum pusillum* Nutt.). Perennial forbs include western ragweed (*Ambrosia psilostachya* DC.) and silverleaf nightshade (*Solanum elaeagnifolium* Cav.). Annual forbs include annual broomweed (*Amphiachyris dracunculoides* DC.) and marestail (*Conyza canadensis*), [L.] Cronquist) (Hatch and Pluhar 1993; Stubbendieck et al. 2017; USDA-NRCS 2020). Before and dur-

ing the study period, cattle freely grazed at a moderate stocking rate of 6−8 ha · animal unit^{-1} · yr^{-1}.

Herbaceous and soil nutrient responses were measured within two treatments, untreated and mesquite sprayed with root-killing herbicide (hereafter "treated"). A previous extension-oriented demonstration study established two 4-ha plots each of three different mesquite-killing clopyralid-based foliar herbicide treatments, all of which were applied on July 10, 2014. For the current study, which was conceived after these treatments were applied, we randomly selected four plots for the "treated" treatment, with the common response being that mesquite canopy cover was reduced to near zero, and there was a high percentage of mesquite with complete aboveground mortality ("top-kill") and apparent mortality ("root-kill") (formal evaluation at 2 yr post treatment found 74.5% [s.e. ± 6.5] top-kill and 66% [± 6.2] root-kill). In addition, these plots were distributed such that each plot had an adjacent ∼4-ha area of untreated mesquite. There is no indication in the literature that these herbicide mixtures (**Table S2**, available online at …) adversely affect grass or forb production. Thus, we considered the four treated plots as functionally equivalent replicates with respect to the elimination of mesquite competition.

Each pair of plots (treated, untreated) was identified as a block. Within each treatment in each block, 3 patches of 10−20 mesquite trees were randomly selected as sample areas. Within each of the three sample areas, herbaceous and soil measurements were made beneath the canopy (hereafter "subcanopy") of a single large (> 3 m tall; canopy radius > 3 m) mesquite tree and in an adjacent intercanopy area between mesquites during 2015 and 2016 (yr 1 and 2 post mesquite treatment). Subcanopy and intercanopy sites were termed "microsites." Total number of sample areas each year was 48 (2 treatments × 4 blocks per treatment × 2 microsites per treatment within a block × 3 samples per microsite). The N value for each of the four treatment-microsite combinations (intercanopy-untreated, intercanopy-treated, subcanopy-untreated, subcanopy-treated) was 12.

Herbaceous production was measured within 1-m wide × 2-m long × 1.5-m tall wire cages made of sheep fence that were randomly located in each microsite. Cages in intercanopy were located at least 2 m from the outside edge of any mesquite canopy. Cages in the subcanopy were located within the 2-m-wide band occurring at least 0.5 m away from the outer basal stems and 0.5 m inside the canopy edge of each live mesquite tree in untreated plots, or beneath standing dead stems in treated plots. During sampling, all herbaceous material was clipped to within 1−2 cm of ground level inside a 0.125-m^2 quadrat frame randomly placed in each cage, separated by species, bagged, dried at 60°C until dry, and weighed. Two clip samples were taken at different positions within each cage, one in early summer (late May or June) and the other in fall (late September or October), to account for different timing of peak production of C_3 and C_4 species. Herbaceous litter was collected in each clip sample by gathering any dead herbaceous material that was disconnected from standing grass or forbs, or determined visually to not be part of the current year's production. After oven drying, soil particles were removed from litter using a 2-mm mesh screen. All cages were moved to a different location within 2 m of the previous location in yr 2. Herbaceous data were grouped into functional groups: C_3 midgrasses (C3M), C_3 annual grasses (C3A), C_4 short grasses (C4S), C_4 midgrasses (C4M), perennial forbs, cool-season annual forbs, warm-season annual forbs, and litter (LIT). Perennial grass (PGR) production was determined by adding C_3 midgrass, C_4 short grass, and C_4 midgrass values. Total forbs (FRB) included all forb subgroups. Total herbaceous (THB) production was determined by adding all grass and forb values.

Soil samples (2-cm diameter) at 0- to 15-cm and 15- to 30-cm depth increments were collected during each herbaceous sampling period at each intercanopy (1 m north of each intercanopy clip cage) and subcanopy (1 m away from the outer basal stems and outside of the clip cages) microsite. Due to limitations in the number of laboratory samples that could be analyzed, soils from each of the three sample areas in each treatment and microsite in each block were composited (N = 4 instead of 12). Samples were mailed to the US Department of Agriculture−Agriculture Research Service Grassland Soil and Water Research Laboratory (808 E Blackland Rd, Temple, TX 76502) and analyzed for soil inorganic N (SINN; NH_4-N + NO_3-N) and water-extractable organic N (WEON) via the Haney Soil Test procedure (Haney et al. 2006, 2010). This test uses water and an organic acid extractant, H^3A (including citric, malic, and oxalic acids), which are designed to mimic plant root exudates to estimate plant-available nutrients. WEON represents the portion of organic N that is available to plants over the course of a growing season (Bavougian et al. 2019; Ward Lab 2020). For herbaceous and soil data, values from both sample periods each year were averaged.

To quantify differences in shading by mesquite canopies before and after treatment, photosynthetic photon flux density (PPFD) was measured with a Li-Cor LI-191SA Quantum sensor at ground level in intercanopy and subcanopy microsites in untreated and treated plots during a cloud-free midday period (1 050 to 1 240 h) in July 2015. Similar measurements were made in four additional plots that had similar-sized mesquite, were sprayed with the same treatments in 2013, and were located within each block that included the 2014 treated and untreated plots. These plots were not part of the herbaceous and soil response data but provided an example of subcanopy PPFD at 2 yr post treatment to account for deterioration of standing dead mesquite stems from yr 1 to yr 2. This provided a chronosequenced comparison of shade cast by untreated, 1-yr post-treated, and 2-yr post-treated mesquite in subcanopy and untreated and treated intercanopy microsites. Twenty-four PPFD measurements were made during the midday period (4 blocks × 3 treatments/block × 2 microsites/treatment; N = 4).

Statistical analysis

Effects of yr (2015, 2016); treatment (untreated, treated); microsite (intercanopy, subcanopy); and their interactions on production of herbaceous functional groups (C3M, C3A, C4S, C4M, FRB, PRG, THB, LIT) were tested using a split block linear mixed-model (Proc Mixed procedure, SAS 9.4, SAS Institute Inc., Cary, NC). There were 4 blocks and 3 samples per block (N = 12) (model: $f = B + T + M + T · M + Y + Y · T + Y · M + Y · T · M + B$, where B = Block, T = Treatment, M = Microsite, and Y = Year). Analysis of SINN and WEON was similar, except that samples in each replicate were composited (n = 4 instead of 12) (model: $f = T + M + T · M + Y + Y · T + Y · M + Y · T · M$). For PPFD, a two-way analysis of variance was performed with microsite and treatment as independent variables within each chronosequenced year (N = 4). Mean comparisons were performed using least squares at $P ≤ 0.05$. C3M, C4S, and C4M production were not normally distributed and were log10 transformed before analyses. Their actual arithmetic means and standard errors are reported in the figures.

Results

Precipitation and PPFD

Annual precipitation was near normal during the 2014 spray yr (yr 0) and 54% and 30% above normal in 2015 (yr 1) and 2016 (yr 2), respectively (Fig. 1). Growing season precipitation (April–September) was 11%, 59%, and 38% above normal in 2014, 2015, and 2016, respectively. May 2015 had > 3 × the normal precipitation. Precipitation in fall 2014 (October–December) before yr 1 was
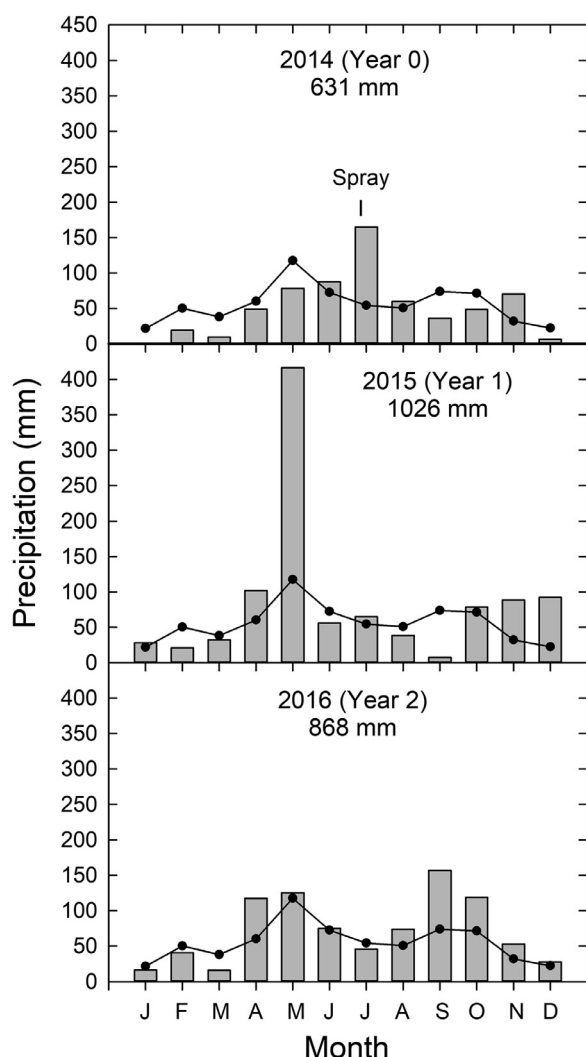
Fig. 1. Monthly and annual precipitation recorded at the study site, 2014−2016, with data collection in 2015 (yr 1) and 2016 (yr 2). Gray bars are monthly totals, and solid symbols connected by lines are 30-yr mean monthly values. Values below year label are annual precipitation totals (mean annual total 710 mm). Mesquite spray treatment was in early July 2014.

125.9 mm, close to average (125.8 mm). In contrast, precipitation in fall 2015 before yr 2 was 106% above normal at 259.8 mm.

Untreated mesquite canopies reduced subcanopy PPFD by 60.3% compared with untreated intercanopy (Fig. 2). The shading effect of standing dead treated mesquite canopies decreased from 1−2 yr post treatment (32.4−19.5%) as stems deteriorated. Untreated mesquite reduced subcanopy PPFD by 44.5% and 52.6% compared with treated mesquite at 1 and 2 yr post treatment, respectively. PPFD was similar in all intercanopy microsites.

Herbaceous and soil N responses

Thirty-seven herbaceous species (16 grasses, 21 forbs) were found over all 0.125-m^2 clipped quadrats (192 in total), with an average of 2.4 different species occurring per quadrat (**Table S3,** available online at doi:10.5061/dryad.nzs7h44rd). Texas wintergrass was the only C$_3$ midgrass species detected, and it occurred in 74% of all quadrats. Next highest percentage occurrences were warm-season annual forbs (41%), perennial forbs (37%), and C$_4$ short grasses (33%).

The mixed model revealed significant ($P \leq 0.05$) main effects of treatment, microsite, and/or year and significant year × treatment and year × microsite interactions for all herbaceous functional groups except C$_4$ midgrasses (Table 1). PGR had significant effects of year and year × treatment, while THB had significant effects of treatment and microsite with no interactions. There were significant block effects for C$_3$ annual grasses, forbs, THB, and litter.

C$_3$ midgrass (i.e., Texas wintergrass) production was 106% and 59% greater in treated than untreated intercanopy and subcanopy, respectively, and was greater in subcanopy than intercanopy in untreated and treated plots at 1 yr post treatment (Fig. 3A). C$_3$ midgrass production decreased from yr 1 to yr 2 in all but untreated intercanopy, and there were no differences between treatments or microsites in yr 2 (see Fig. 3B). C$_3$ annual grass production was not different between treatments or microsites in yr 1 but increased in untreated and treated subcanopy from yr 1 to yr 2 (see Figs. 3C and D). C$_4$ short grass production was greater in untreated and treated intercanopy than subcanopy in both years, with no change from yr 1 to yr 2 (see Figs. 3E and F). C$_4$ midgrass production was not different between treatments or microsites in either year (see Figs. 3G and H).

PGR production was 73% and 55% greater in treated than untreated intercanopy and subcanopy, respectively, in yr 1 (Fig. 4A). PGR production declined from yr 1 to yr 2 in both treated microsites and in untreated subcanopy, and in yr 2 it was greater in the untreated intercanopy than the treated subcanopy microsite (see Fig. 4B). Forb production was greater in untreated intercanopy than treated subcanopy in yr 1 (see Fig. 4C), increased in both treated microsites from yr 1 to yr 2, and was 185% and 457% greater in treated than untreated intercanopy and subcanopy microsites, respectively, in yr 2 (see Fig. 4D). Litter production was greater in subcanopy than intercanopy in both treatments in yr 1 and increased from yr 1 to yr 2 in all but untreated subcanopy (see Figs. 4E and F).

Functional group means from Figs. 3 and 4 are shown as components of THB production in Fig. 5. THB production was not different between treatments in either microsite in yr 1 (see Fig. 5A) but was greater in treated than untreated subcanopy in yr 2 (see Fig. 5B). Treated microsites were composed mostly of C$_3$ midgrasses in yr 1 and annual forbs in yr 2. THB composition in untreated intercanopy was similar in both years, but in untreated subcanopy changed from mostly C$_3$ midgrasses in yr 1 to contributions of six groups in yr 2. There were no differences in THB between years in any treatment-microsite combination.

There were significant main effects of microsite and year for SINN and year for WEON, and a significant year × treatment × microsite interaction for SINN at 0−15 cm depth (Table 2). SINN at both depths was greater in subcanopy than intercanopy in treated plots in yr 1 and in untreated plots in yr 2 and increased from yr 1 to yr 2 in treated intercanopy and untreated and treated subcanopy (Figs. 6A and 6B). WEON declined from yr 1 to yr 2 in untreated intercanopy and untreated subcanopy at 0−15 cm and in treated intercanopy, untreated subcanopy, and treated subcanopy at 15−30 cm depth (see Figs. 6C and D). There was no difference in WEON between treatments or microsites in either year or soil depth.

Discussion

The increase in PGR production following root-killing of mesquite in the first yr post treatment came mainly from the C$_3$ midgrass, Texas wintergrass, in both microsites. The percentage increase in PGR and C$_3$ midgrass production in treated subcanopy was similar due to PGR being mostly composed of C$_3$ midgrass. In contrast, the percentage increase in PGR production in treated in-
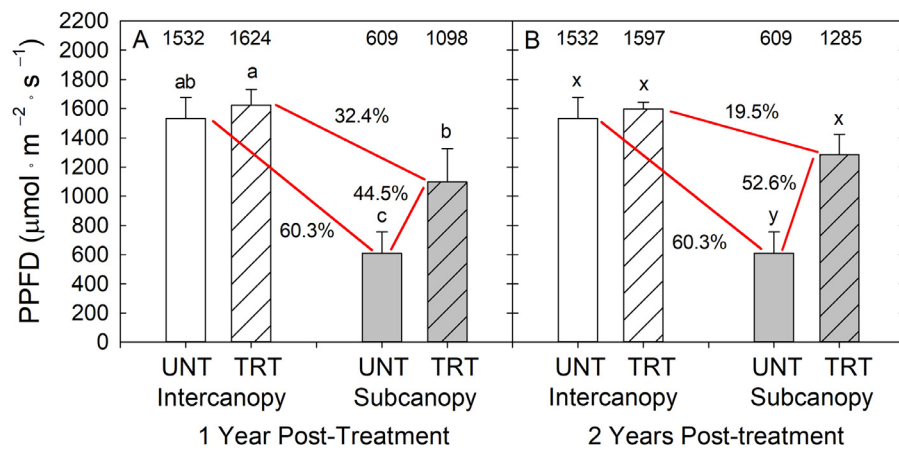
Fig. 2. A and **B,** Midday photosynthetic photon flux density *(PPFD)* at ground level on July 17, 2015 and for 1- and 2-yr post-treatment microsites. Data for untreated intercanopy and untreated subcanopy are duplicated in each "chronosequenced" year. Vertical lines are standard error ($n=4$). Actual PPFD values are shown above each bar. Percentage values represent the percent reduction in PPFD between 2 means connected by a red line. Means with similar letters within each year are not different at $P \leq 0.05$.

Table 1
Pr > F values in main model analysis of effects of treatment (T), microsite (M), and year (Y) and their interactions on annual production of C_3 midgrass (C3M), C_3 annual grass (C3A), C_4 short grass (C4S), C_4 midgrass (C4M), perennial grass (PGR), forbs (FRB), total herbaceous (THB), and litter (LIT). Values in bold and gray shade are $P \leq 0.05$.

Effect	df	C3M	C3A	C4S	C4M	PGR	FRB	THB	LIT
B	3	0.1607	**0.0074**	0.0669	0.3801	0.0859	**0.0013**	**0.001**	**<.0001**
T	1	**0.0211**	**0.003**	0.1647	0.9145	0.0895	**0.0067**	**0.0001**	0.0589
M	1	**0.0321**	0.1699	**<.0001**	0.4118	0.2318	0.0575	**0.0351**	**<.0001**
T*M	1	0.8953	0.58	0.7545	0.9194	0.8363	0.4089	0.4416	0.8357
Y	1	**<.0001**	**0.0002**	0.3853	0.0668	**<.0001**	**<.0001**	0.1543	**<.0001**
Y*T	1	**0.0055**	0.2805	0.8677	0.846	**0.0002**	**<.0001**	0.4425	0.1683
Y*M	1	**0.0218**	0.0564	0.732	0.1654	0.0835	0.2256	0.9725	0.3736
Y*T*M	1	0.9741	0.533	0.4882	0.6974	0.7991	0.958	0.6435	0.4169

Table 2
Pr > F values in main model analysis of effects of treatment (T), microsite (M), and year (Y), and their interactions on soil inorganic N (SINN) and water-extractable organic N (WEON) at 0- to 15-cm and 15- to 30-cm soil depths. Values in bold and gray shade are $P \leq 0.05$.

Effect	df	SINN 0-15	SINN 15-30	WEON 0-15	WEON 15-30
T	1	0.3676	0.4765	0.2001	0.3859
M	1	**0.0009**	**0.0058**	0.1361	0.7459
T*M	1	0.8195	0.5885	0.8429	0.8338
Y	1	**<.0001**	**<.0001**	**0.0002**	**<.0001**
Y*T	1	0.5995	0.9969	0.3591	0.4503
Y*M	1	0.3939	0.1794	0.679	0.4503
Y*T*M	1	**0.0287**	0.1206	0.7278	0.8697

tercanopy (73%) was less than the increase in C_3 midgrass production (106%) because of the low response of C_4 grasses to treatment in yr 1. Other studies in the SGP with a similar *Prosopis/Nassella* association found increases in Texas wintergrass production following mesquite treatment (McDaniel et al. 1982; Laxson et al. 1997) but did not contrast production between microsites. Increased litter in treated microsites in yr 2 was due in part to increased yr 1 C_3 midgrass production, as well as greater precipitation in yr 1 compared with the previous yr.

While most *Prosopis*-dominated systems worldwide have a C_4 grass understory, there are examples where C_3 grasses have displaced C_4 grasses beneath *Prosopis* or other woody legume species (Stuart-Hill and Tainton 1989; Rossi and Villagra 2003; Prober et al. 2005; Rauber et al. 2014). In contrast, in the subtropical region of southern Texas, *P. glandulosa* serves as a nucleus tree, facilitating the recruitment of secondary C_3 shrubs instead of C_3 grasses beneath its canopy (Archer 1990; Franco-Pizana et al. 1995) in what was C_4 grassland before mesquite invasion (Liao et al. 2006). Bustamante et al. (2006) proposed that with conspecific mesquite and similar annual precipitation in north and south Texas, the reason why C_3 subshrubs are not associated with north Texas mesquite may be due to colder winter temperatures.
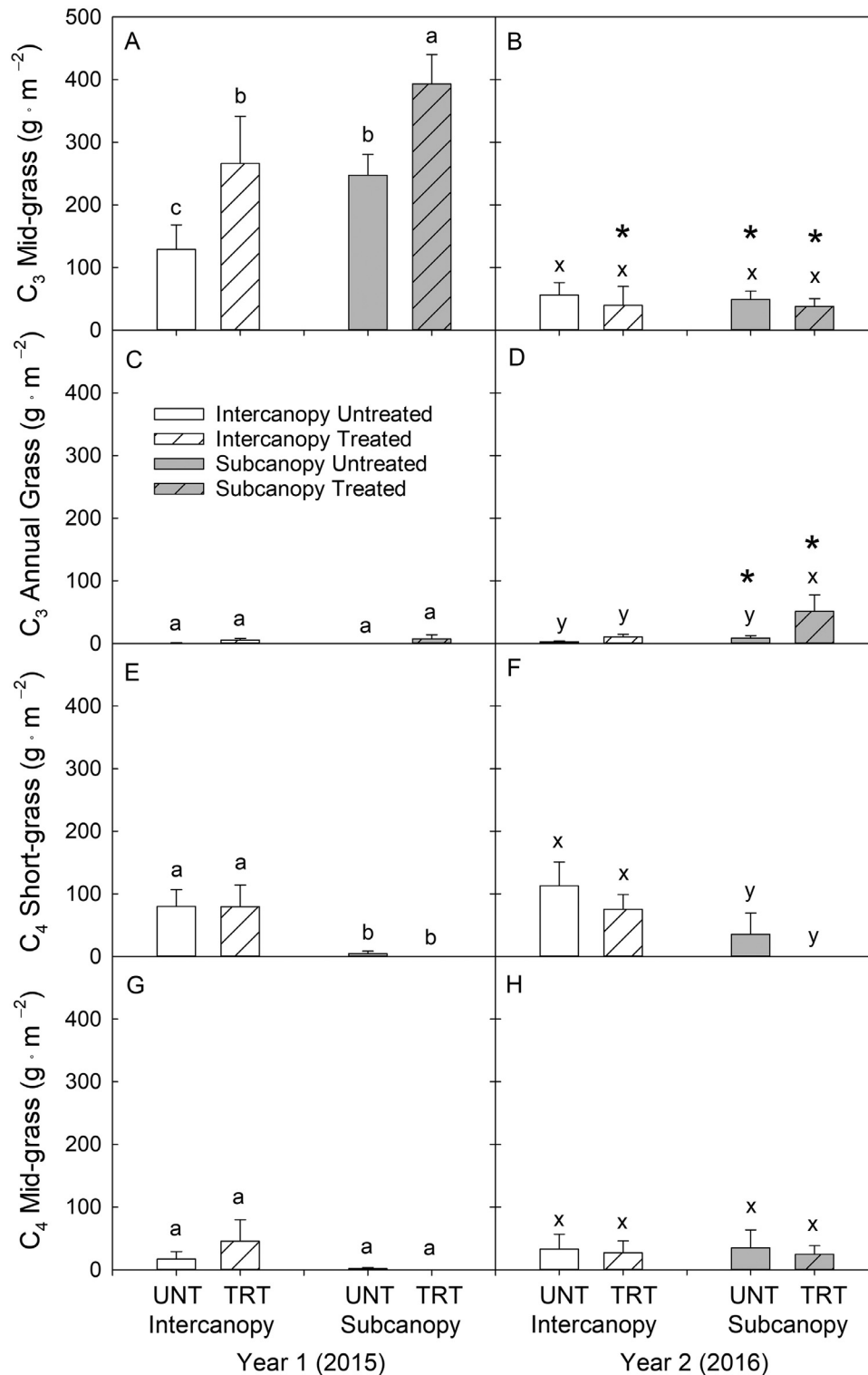
Fig. 3. A–H, Production of grass functional groups at 1-yr (2015) and 2-yr (2016) postmesquite treatment *(TRT)* compared with untreated *(UNT)* intercanopy and subcanopy microsites. Vertical lines are standard error (*n* = 12). Means with similar letters within each panel are not different at *P* ≤ 0.05. An asterisk in 2016 panels indicates a significant (*P* ≤ 0.05) difference between 2015 and 2016 within that treatment-microsite.

Regarding soil N, studies in southern Texas (Franco-Pizana et al. 1995; Geesing et al. 2000; McCulley et al. 2004), Arizona (Tiedemann and Klemmedson 1986; Wheeler et al. 2007), and northern Mexico (Herrera-Arreola et al. 2007) found that soil total N and/or inorganic N were greater in *Prosopis* subcanopy than intercanopy microsites. We found similar responses with SINN in

two of the four treatment-microsite-year combinations, and it was consistent across both soil depth increments. However, greater SINN in subcanopy occurred in treated plots in yr 1 but in untreated in yr 2, so no conclusions regarding treatment effect can be drawn.
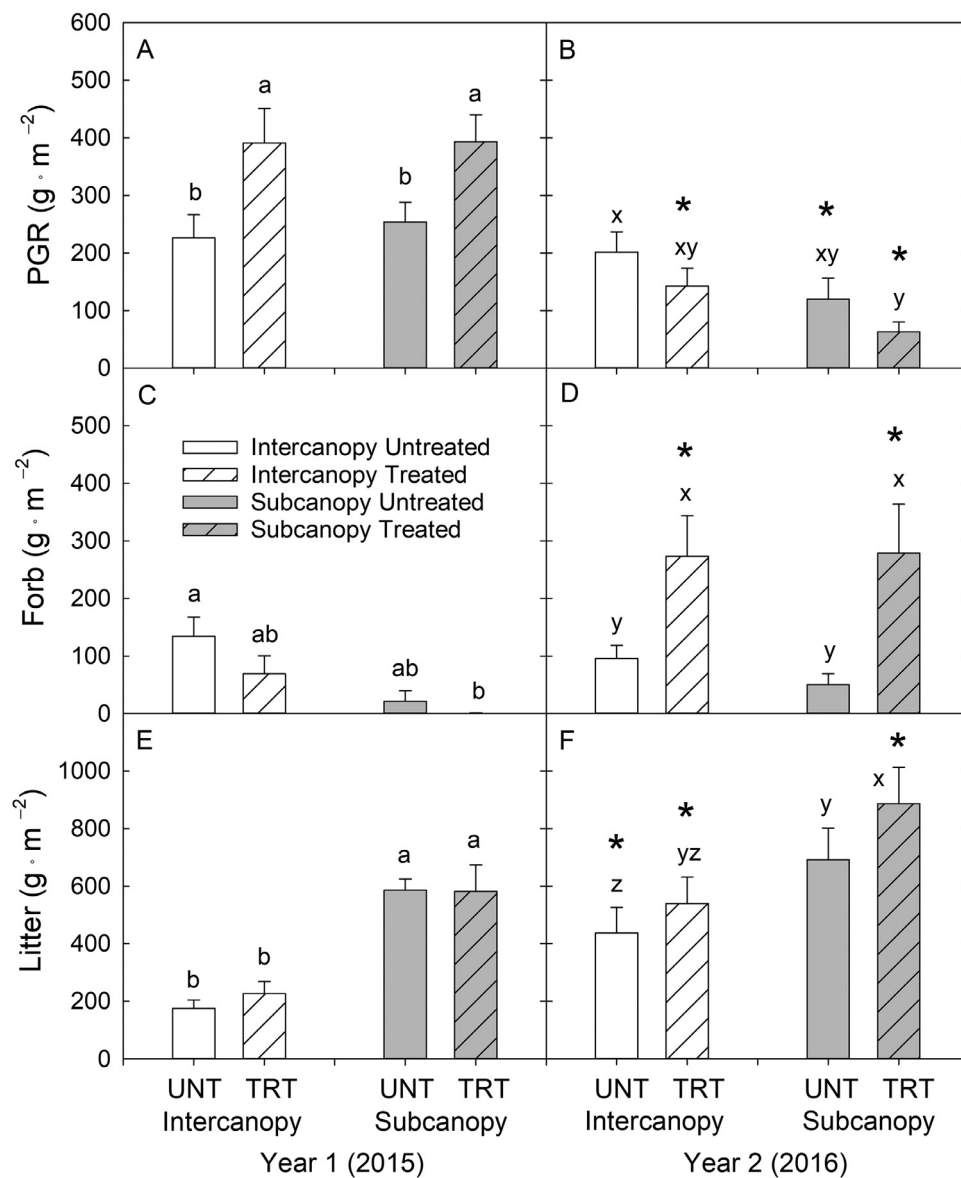
Fig. 4. **A−F**, Perennial grass *(PGR)* and forb production (annual + perennial) and litter amount at 1-yr and 2-yr postmesquite treatment *(TRT)* compared with untreated *(UNT)* in intercanopy and subcanopy. Error bars and mean comparison symbols are described in Fig. 3 caption.

SINN significantly ($P \leq 0.05$) increased from yr 1 to yr 2 in three of the four treatment-microsite combinations in both depth increments. In the other instance, untreated intercanopy, SINN increased numerically from yr 1 to yr 2, but the difference was not significant. We are uncertain as to the factors that caused SINN to increase in yr 2. Untreated intercanopy would likely have the lowest probability for the increase in SINN to be related to mesquite. The increase in SINN in the subcanopy microsites, both treated and untreated, could be related to N-fixation by mesquite. The yr 2 increase in SINN in treated intercanopy could have come from the decomposition of dead mesquite lateral roots, but other factors may have also been involved.

Soil WEON significantly decreased from yr 1 to yr 2 in five of the eight treatment-microsite-depth combinations. SINN increased from yr 1 to yr 2 in four of those five situations, but it is unknown if those two trends are related. More sample dates than used here are needed to correlate WEON with SINN.

C_3 midgrasses in untreated and treated plots in yr 1, as well as C_3 annual grasses in treated plots in yr 2, were the only functional groups that had greater production in subcanopy than intercanopy microsites within a particular treatment. However, in only one of these instances (C_3 midgrasses in treated plots) did greater grass production coincide with greater SINN in subcanopy compared with intercanopy. Other factors besides enhanced soil N must have been responsible for the increased C_3 grass production in subcanopy in the other two situations. Greater C_3 midgrass production in untreated subcanopy than untreated intercanopy may have been due to greater competition from C_4 grasses in intercanopy, or more moderate temperatures beneath the mesquite canopy that favored C_3 midgrasses (Tiedemann and Klemmedson 1977; Simmons et al. 2008). Enhanced C_3 annual grass production in treated subcanopy in yr 2 may have been the result of more propagules in subcanopy than intercanopy to begin with, a wet winter that stimulated germination, and enhanced PPFD from mesquite canopy removal.

C_4 short-grass production was greater in intercanopy than subcanopy but did not increase in treated plots within each microsite in either year. Before treatment, mesquite canopy cover was high enough (40−60%) to reduce the size of intercanopy patches
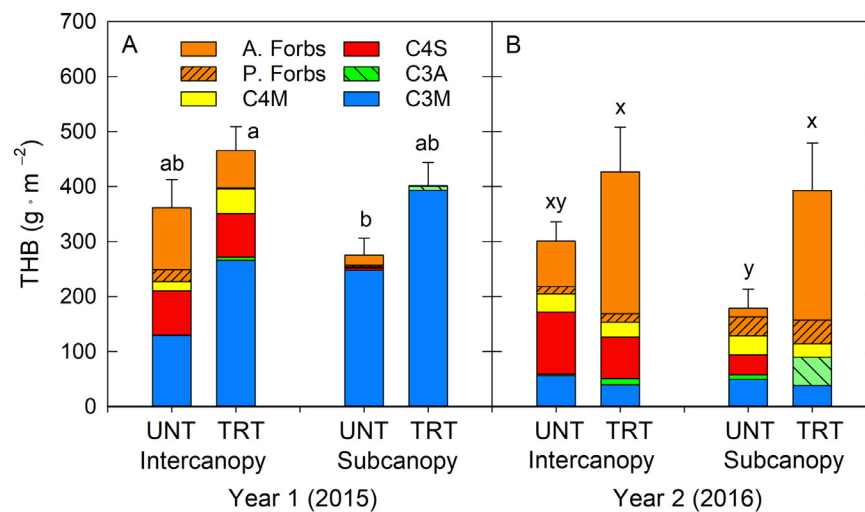
Fig. 5. A and **B,** Total herbaceous *(THB)* production comprising all herbaceous functional groups at 1 and 2 yr post mesquite treatment *(TRT)* compared with untreated *(UNT)* in intercanopy and subcanopy. Error bars and mean comparison symbols are for THB only and are described in the Fig. 3 caption. A. Forbs indicates annual forbs; P. Forbs, perennial forbs; C4M, C_4 midgrasses; C4S, C_4 short grasses; C3A, C_3 annual grasses; C3M, C_3 midgrasses.
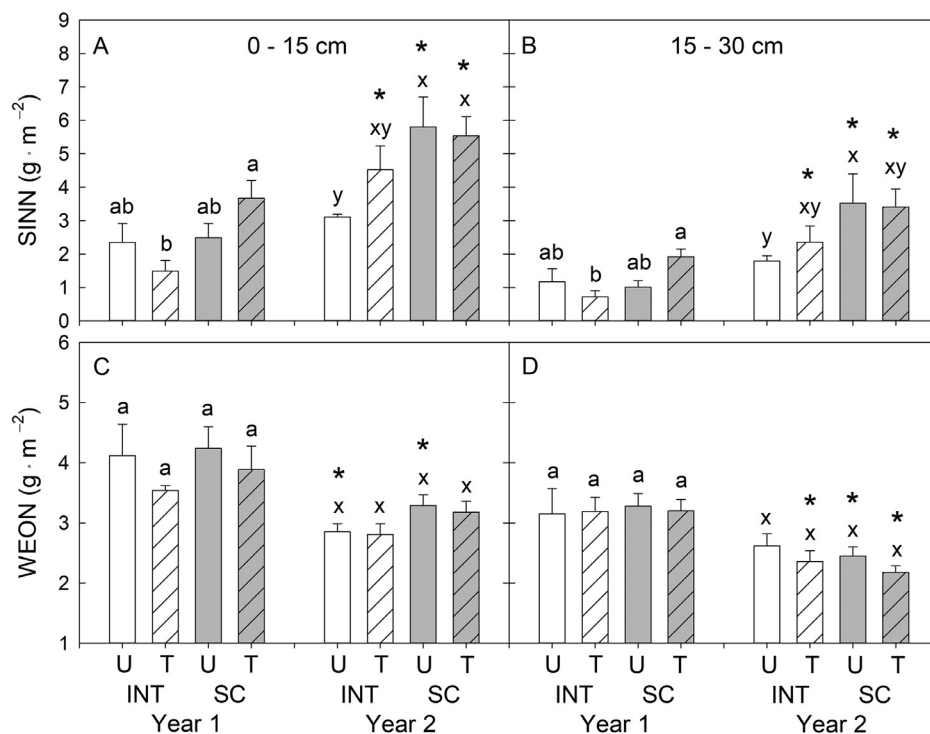

Fig. 6. A–D, Soil inorganic N *(SINN)* and water-extractable organic N *(WEON)* at two depths in untreated *(U)* and treated *(T)* intercanopy *(INT)* and subcanopy *(SC)* in yr 1 (2015) and yr 2 (2016). Vertical lines are standard error (*n* = 4). Means with similar letters within each soil depth and year are not different at *P* ≤ 0.05. Asterisk in yr 2 indicates a significant (*P* ≤ 0.05) difference between years in a particular treatment-microsite combination.

sufficiently to enable Texas wintergrass to establish beyond the mesquite canopy edge. At 1 yr post treatment, Texas wintergrass may have been able to exploit mesquite mortality in intercanopy more effectively than C_4 short-grasses. By yr 2, enhanced annual forb production may have limited C_4 short-grass production in treated intercanopy.

Low C_4 midgrass production in subcanopy in yr 1 may have been a legacy effect due to the loss of C_4 midgrass propagules from prolonged dominance by Texas wintergrass, shading by mesquite, or continuous livestock grazing that caused greater detrimental effects to C_4 midgrasses (Wood and Blackburn 1984; Teague et al. 2011). Ansley et al. (2019) found that C_4 midgrass production

did not begin to displace Texas wintergrass production in intercanopy until 3 yr after a mesquite top-killing treatment. Several studies have found an allelopathic effect of *Prosopis juliflora* leaf exudates on germination of C_4 grasses (Al-Humaid and Warrag 1998; Getachew et al. 2012). It is not known if *P. glandulosa* in the SGP inhibits herbaceous production via allelopathy. If so, this may have contributed to low C_4 grass production in subcanopy in yr 1 but did not inhibit C_3 Texas wintergrass growth. Kaur et al. (2012) suggested that *Prosopis* allelopathy is more likely to occur when *Prosopis* is introduced as an exotic (e.g., *P. juliflora* native to Venezuela introduced to India). Because *P. glandulosa* is native to the SGP, it may have less of an allelopathic effect on native grasses.

Forb responses in yr 2

The most unexpected result in this study occurred with forb production on treated sites in yr 2. PGR production in treated microsites declined significantly in yr 2 compared with yr 1, yet THB production remained similar in both years due to an increase in forbs (mostly annual broomweed) and, to a lesser degree, C_3 annual grasses. Other SGP studies have shown brief periods of high forb production following chemical mesquite treatment (McDaniel et al. 1982; Bedunah and Sosebee 1984), but not in replacement of established PGR production.

Yr 2 forb response did not follow the typical postdisturbance succession pattern of initial colonization by annual forbs and grasses followed by perennial grass establishment. Nor is it similar to the increased forb production that typically immediately follows mechanical woody plant treatments that disturb the soil and create favorable microenvironments for forb seed germination (Fulbright 2004; Kunst et al. 2012). Our results are the first documentation we know of where the elimination of an invasive woody species without soil disturbance increased PGR production the first yr post treatment, yet in the second yr, forb production suppressed PGR production and accounted for nearly all of the increased herbaceous production in treated over untreated areas. These results cause us to reject our hypothesis that short-term herbaceous production increases after mesquite treatment in this *Prosopis/Nassella* system would be mostly from C_3 midgrasses.

Several factors may have been involved in increasing annual forb (and to a lesser degree C_3 annual grass) production in treated microsites in yr 2. The fall before yr 1 had average precipitation, while the fall before yr 2 had twice the average precipitation. Above-average precipitation in fall or early spring can stimulate annual forb germination and production the following growing season, especially on degraded sites (Heitschmidt 1979; Stanford et al. 2008). Annual forb growth in late winter and spring would have competed with C_3 midgrasses, and their continued growth in the summer would have competed with C_4 midgrasses, thus inhibiting PGR production. If we assume equal annual forb germination in treated and untreated intercanopy, the greater annual forb production in treated intercanopy in yr 2 may relate to loss of mesquite competition via lateral roots for water in intercanopy (Ansley et al. 2018) since PPFD was similar in the two treatments. However, yr 2 had above-average precipitation and therefore lower competition for soil moisture. Assuming equal annual forb seed germination in treated and untreated subcanopy in the fall of yr 1 or spring of yr 2, the greater annual forb production in treated subcanopy in yr 2 may have been due to greater PPFD from the removal of shading by the mesquite canopy. While 2-yr-old treated canopies, which consisted of standing dead stems and no foliage, slightly reduced (19%) subcanopy PPFD compared with intercanopy microsites, the untreated mesquite canopies reduced PPFD by 53% compared with 2-yr post-treated canopies and 60% compared with intercanopy.

The increase in SINN from yr 1 to yr 2 in treated intercanopy and subcanopy could partially explain the enhanced forb production (Berg 1995; Paschke et al. 2000). SINN also increased from yr 1 to yr 2 in untreated subcanopy microsites, but forb production did not increase, likely due to shading from the untreated mesquite canopy. Low forb production may also have been due to allelopathic effects of mesquite leaf litter (Nakano et al. 2004). However, any allelopathic effect would have had to come from mesquite litter produced in the treatment yr (2014) or yr 1 (2015). Before that, mesquite litter deposition would have been similar for untreated and treated subcanopy microsites, and treated subcanopy had high annual forb yield in yr 2. High rainfall in May and the previous fall may have accelerated the decomposition of mesquite litter and release of allelopathic compounds in untreated subcanopy in yr 2.

Despite large differences in production of individual functional groups from yr 1 to yr 2, the facts that THB production was similar in both treated microsites each year and both years had above-average precipitation suggest that site production potential at this stage of post-treatment succession occurred with different vegetation assemblages. We assume site production potential may increase in future years if C_4 midgrasses increase because they are inherently more productive than Texas wintergrass or C_4 shortgrasses (Ansley et al. 2013, 2019).

High forb production in treated plots in yr 2 was not necessarily a negative, as perceptions about the value of forbs on rangeland landscapes have changed (Fulbright 2004; Linex 2014). Forbs are important for wildlife habitat, pollinators, and multiple-use management goals (Rollins and Bryant 1986; Nolte and Fulbright 1997; Fuhlendorf and Engle 2004). Sixteen of the 21 forb species identified in this study (see Table S3) have high value as wildlife and/or livestock food or provide wildlife habitat cover (Linex 2014; Stubbendieck et al. 2019).

Functional group composition of THB production in untreated subcanopy changed from mostly C_3 midgrasses in yr 1 to a contribution from six functional groups in yr 2 including both C_4 grass groups. This response suggests that the *Prosopis/Nassella* association, with Texas wintergrass monoculture beneath mesquite canopies, may vary in composition in certain years. These changes may be related to 3 consecutive yr of above-average growing season precipitation.

Ecological and Management Implications

Our study revealed that post-treatment perennial grass production may differ between intercanopy and subcanopy microsites, especially if the woody overstory is an N-fixing legume that may facilitate C_3 over C_4 grass production beneath its canopy. Models that predict landscape scale post treatment herbaceous responses in such systems could incorporate these differences based on pretreatment woody canopy cover. Composition of total herbaceous production varied considerably in yr 2, yet mesquite removal yielded similar herbaceous production levels each year and in each microsite. Because both years had above-average growing season precipitation, site production potential may have been achieved with available propagules (i.e., without higher-producing C_4 midgrasses). There was no strong association between soil inorganic N and increased herbaceous production when compared across all treatments and microsites. This was due to low herbaceous production beneath untreated mesquite canopies where soil inorganic N was highest and high production in treated intercanopy where inorganic N was lowest. Other factors, such as increased light from mesquite canopy removal and precipitation patterns that stimulated annual forb and grass germination, had greater effect on total herbaceous production.

From a management perspective, although this study measured responses during only the first 2 yr after treatment, it revealed an important principle that grass forage production following brush control can deviate markedly from predicted results under certain conditions. In the system studied here (dense mesquite with a Texas wintergrass understory), research and models predict an increase in C_3 Texas wintergrass production the first few years after a mesquite root-killing treatment, followed by a replacement of Texas wintergrass by more productive C_4 grasses (Teague et al. 2001; Ansley et al. 2019). The high forb production that displaced Texas wintergrass production in yr 2 was unexpected, especially with a brush treatment that did not disturb the soil or remove litter. Responses may have been linked to late fall and early spring rainfall patterns before the yr 2 growing season. While forbs are critical for certain ecosystem services, an awareness of such a pos-

sible response is important if the business model depends on increased livestock production to offset brush treatment cost.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgments

Data Accessibility

Herbaceous production and soil nutrient data will be uploaded to Dryad; doi:10.5061/dryad.nzs7h44rd.

Supplementary Materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.rama.2021.04.002.

References

Al-Humaid, A.I., Warrag, M.O.A, 1998. Allelopathic effects of mesquite *(Prosopis juliflora)* foliage on seed germination and seedling growth of bermudagrass *(Cynodon dactylon)*. Journal of Arid Environments 38, 237–243.

Ansley, R.J., Boutton, T.W., Jacoby, P.W., 2014. Root biomass and distribution patterns in a semi-arid mesquite savanna: responses to long-term rainfall manipulation. Rangeland Ecology & Management 67, 206–218.

Ansley, R.J., Castellano, M.J., 2006. Strategies for savanna restoration in the southern Great Plains: effects of fire and herbicides. Restoration Ecology 14, 420–427.

Ansley, R.J., Cooper, C., Zhang, T., 2019. Invasion promotes invasion: facilitation of C_3 perennial grass dominance in mixed C_3/C_4 grassland by an invasive C_3 woody sprouter *(Prosopis glandulosa)*. Ecology and Evolution 9, 13438–13449.

Ansley, R.J., Mirik, M., Wu, X.B., Heaton, C.B., 2013. Woody cover and grass production in a mesquite savanna: geospatial relationships and precipitation. Rangeland Ecology & Management 66, 621–633.

Ansley, R.J., Pinchak, W.E., Owens, M.K., 2017. Mesquite pod removal by cattle, feral hogs and native herbivores. Rangeland Ecology & Management 70, 469–476.

Ansley, R.J., Pinchak, W.E., Teague, W.R., Kramp, B.A., Jones, D.L., Jacoby, P.W., 2004. Long-term grass yields following chemical control of honey mesquite. Journal of Range Management 57, 49–57.

Ansley, R.J., Zhang, T., Cooper, C, 2018. Soil moisture, grass production and mesquite resprout architecture following mesquite above-ground mortality. Water 10 (9), 1243.

Archer, S., 1990. Development and stability of grass/woody mosaics in a subtropical savanna parkland, Texas, U.S.A.. Journal of Biogeography 17, 453–462.

Archer, S., 1995. Tree-grass dynamics in a *Prosopis*-thornscrub savanna parkland: reconstructing the past and predicting the future. EcoScience 2, 83–99.

Bavougian, C.M, Shapiro, C.A., Stewart, Z.P., Eskridge, K.M., 2019. Comparing biological and conventional chemical soil tests in long-term tillage, rotation, *n* rate field study. Soil Science Society of America Journal 83, 419–428.

Bedunah, D.J., Sosebee, R.E., 1984. Forage response of a mesquite-buffalograss community following range rehabilitation. Journal of Range Management 37, 483–487.

Berg, W.A., 1995. Response of a mixed native warm-season grass planting to nitrogen fertilization. Journal of Range Management 48, 64–67.

Boutton, T.W., Liao, J.D., 2010. Changes in soil nitrogen storage and δ15N with woody plant encroachment in a subtropical savanna parkland landscape. Journal of Geophysical Research-Biogeoscience 115, G03019.

Bovey, R.W., Whisenant, S.G., 1991. Control of honey mesquite with clopyralid, triclopyr or clopyralid:triclopyr mixtures. Journal of Range Management 44, 52–55.

Bozzo, J.A., Beasom, S.L., Fulbright, T.E., 1992. Vegetation responses to 2 brush management practices in south Texas. Journal of Range Management 45, 170–175.

Bustamante, M.M.C., Medina, E., Asner, G.P., Nardoto, G.B., Garcia-Montiel, D.C, 2006. Nitrogen cycling in tropical and temperate savannas. Biogeochemistry 79, 209–237.

Conant, R.T., Paustian, K., 2002. Potential soil carbon sequestration in overgrazed grassland ecosystems. Global Biogeochemical Cycles 16, 1143.

El-Keblawy, A., Al-Rawai, A, 2007. Impacts of the invasive exotic *Prosopis juliflora* (Sw.) D.C. on the native flora and soils of the UAE. Plant Ecology 190, 23–35.

Engle, D.M, Mitchell, R.L., Stevens, R.L., 1998. Late growing-season fire effects in mid-successional tallgrass prairies. Journal of Range Management 51, 115–121.

Franco-Pizana, J., Fulbright, T.E., Gardiner, D.T., 1995. Spatial relations between shrubs and *Prosopis glandulosa* canopies. Journal of Vegetation Science 6, 73–78.

Fuhlendorf, S.D., Engle, D.M., 2004. Application of the fire–grazing interaction to restore a shifting mosaic on tallgrass prairie. Journal of Applied Ecology 41, 604–614.

Fulbright, T.E., 2004. Disturbance effects on species richness of herbaceous plants in a semi-arid habitat. Journal of Arid Environments 58, 119–133.

Geesing, D., Felker, P., Bingham, R.L., 2000. Influence of mesquite *(Prosopis glandulosa)* on soil nitrogen and carbon development: implications for global carbon sequestration. Journal of Arid Environments 46, 157–180.

Getachew, S., Demissew, S., Woldemariam, T., 2012. Allelopathic effects of the invasive *Prosopis juliflora* (Sw.) DC. on selected native plant species in Middle Awash, Southern Afar Rift of Ethiopia. Management of Biological Invasions 3, 105–114.

Gibbens, R.P., Hicks, R.A., Dugas, W.A., 1996. Structure and function of C_3 and C_4 Chihuahuan Desert plant communities—standing crop and leaf area index. Journal of Arid Environments 34, 47–62.

Gibbens, R.P., Lenz, J.M., 2001. Root systems of some Chihuahuan Desert plants. Journal of Arid Environments 49, 221–263.

Haney, R.L., Haney, E.B., Hossner, L.R., Arnold, J.G, 2006. Development of a new soil extractant for simultaneous phosphorus, ammonium, and nitrate analysis. Communications in Soil Science and Plant Analysis 37, 1511–1523.

Haney, R.L., Haney, E.B., Hossner, L.R., Arnold, J.G, 2010. Modifications to the new soil extractant H3A–multi-nutrient extractant. Communications in Soil Science and Plant Analysis 41, 1513–1523.

Hatch, S.L., Pluhar, J., 1993. Texas range plants. Texas A&M University Press, College Station, TX, USA, p. 326.

Heitschmidt, R.K., 1979. Relative annual broomweed abundance as related to selected climatic factors. Journal of Range Management 32, 401–403.

Heitschmidt, R.K., Ansley, R.J., Dowhower, S.L., Jacoby, P.W., Price, D.L., 1988. Some observations from the excavation of honey mesquite root systems. Journal of Range Management 41, 227–231.

Herrera-Arreola, G., Herrerac, Y., Reyes-Reyes, B.G., Dendooven, L., 2007. Mesquite *(Prosopis juliflora* [Sw.] DC.), huisache *(Acacia farnesiana* [L] Willd.) and catclaw *(Mimosa biuncifera* Benth.) and their effect on dynamics of carbon and nitrogen in soils of the semi-arid highlands of Durango, Mexico. Journal of Arid Environments 69, 583–598.

Hicks, R.A., Briske, D.D., Call, C.A., Ansley, R.J, 1990. Co-existence of a perennial C_3 bunchgrass in a C_4 dominated grassland: an evaluation of gas exchange characteristics. Photosynthetica 24, 63–74.

Kaur, R., Gonzales, W.L., Llambi, L.D., Soriano, P.J., Callaway, R.M., Rout, M.E., Gallaher, T.J., 2012. Community impacts of *Prosopis juliflora* invasion: biogeographic and congeneric comparisons. PLoS ONE 7 (9), e44966.

Kunst, C., Ledesmaa, R., Bravob, S., Albanesic, A., Anriquezc, A., van Meera, H., Godoyaet, J., 2012. Disrupting woody steady states in the Chaco region (Argentina): responses to combined disturbance treatments. Ecological Engineering 42, 42–53.

Laxson, J.D., Schacht, W.H., Owens, M.K., 1997. Above-ground biomass yields at different densities of honey mesquite. Journal of Range Management 50, 550–554.

Liao, J.D., Boutton, T.W., Jastrow, J.D., 2006. Organic matter turnover in soil physical fractions following woody plant invasion of grassland: evidence from natural ^{13}C and ^{15}N. Soil Biology and Biochemistry 38, 3197–3210.

Linex, R.J., 2014. Range plants of North Central Texas—a land user's guide to their identification, value and management. USDA-NRCS Publication, Weatherford, TX, USA, p. 345.

McClaran, M.P., Angell, D.L., 2006. Mesquite and grass relationships at two spatial resolutions. Plant Ecology Available at: doi:10.1007/s11258-006-9220-6 (Accessed July 20, 2020).

McCulley, R.L., Archer, S.R., Boutton, T.W., Hons, F.M., Zuberer, D.A., 2004. Soil respiration and nutrient cycling in wooded communities developing in grassland. Ecology 85, 2804–2817.

McDaniel, K.C., Brock, J.H., Haas, R.H., 1982. Changes in vegetation and grazing capacity following honey mesquite control. Journal of Range Management 35, 551–557.

Mohamed, A.H., Holechek, J.L., Bailey, D.W., Campbell, C.L., DeMers, M.N., 2011. Mesquite encroachment impact on southern New Mexico rangelands: remote sensing and geographic information systems approach. Journal of Applied Remote Sensing 5, 053514.

Nakano, H., Nakajima, E., Hiradate, S., Fujii, Y., Yamada, K., Shigemori, H., Hasegawa, K., 2004. Growth inhibitory alkaloids from mesquite *(Prosopis juliflora* [Swartz.] DC leaves. Phytochemistry 65, 587–591.

Ndhlovu, T., Milton, S.J., Esler, K.J., 2016. Impact of *Prosopis* (mesquite) invasion and clearing on vegetation species composition and diversity in semi-arid Nama-Karoo rangeland, South Africa. African Journal of Range & Forage Science 2016, 1–10.

National Oceanic and Atmospheric Administration—National Climatic Data Center. 2019. Available at: https://www.ncdc.noaa.gov/cdo-web/datasets/NORMAL_MLY/stations/GHCND:USC00419346/detail. Accessed 2 February, 2019.

Nolte, K.R., Fulbright, T.E., 1997. Plant, small mammal, and avian diversity following control of honey mesquite. Journal of Range Management 50, 205–212.

Paschke, M.W., McLendon, T., Redente, E.F., 2000. Nitrogen availability and old-field succession in a shortgrass steppe. Ecosystems 3, 144–158.

Pasiecznik, N.M., Felker, P., Harris, P.J.C., Harsh, L.N., Cruz, G., Tewari, J.C., Cadoret, K., Maldonado, L.J, 2001. The *Prosopis juliflora−Prosopis pallida* complex: a monograph. HDRA, Coventry, UK, p. 172.

Patnaik, P., Abbasi, T., Abbasi, S.A., 2017. Prosopis *(Prosopis juliflora)*: blessing and bane. Tropical Ecology 58, 455–483.

Prober, S.M., Thiele, K.R., Lunt, I.D., Koen, T.B., 2005. Restoring ecological function in temperate grassy woodlands: manipulating soil nutrients, exotic annuals and native perennial grasses through carbon supplements and spring burns. Journal of Applied Ecology 42, 1073–1085.

Rauber, R., Steinaker, D., Demaria, M., Arroyo, D., 2014. Factors associated to invasion by non-palatable grasses in Argentinean semi-arid forest. Ecologia Austral 234, 320–326.

Riginos, C., Grace, J.B., Augustine, D.J., Young, T.P., 2009. Local versus landscape-scale effects of savanna trees on grasses. Journal of Ecology 97, 1337–1345.

Rollins, D., Bryant, F.C., 1986. Floral changes following mechanical brush removal in central Texas. Journal of Range Management 39, 237–240.

Rossi, B.E., Villagra, P.E., 2003. Effects of *Prosopis flexuosa* on soil properties and the spatial pattern of understorey species in arid Argentina. Journal of Vegetation Science 14, 543–550.

Scholes, R.J., Archer, S.R., 1997. Tree-grass interactions in savannas. Annual Review of Ecological Systems 28, 517–544.

Simmons, M.T., Archer, S.R., Teague, W.R., Ansley, R.J, 2008. Tree *(Prosopis glandulosa)* effects on grass growth: an experimental assessment of above- and belowground interactions in a temperate savanna. Journal of Arid Environments 72, 314–325.

Stanford, R.L., Ansley, R.J., Ransom, D., 2008. Common broomweed growth characteristics in cleared and woody landscapes. Rangeland Ecology & Management 61, 561–565.

Stuart-Hill, G.C., Tainton, N.M., 1989. The competitive interaction between *Acacia karoo* and the herbaceous layer and how this is influenced by defoliation. Journal of Applied Ecology 26, 285–298.

Stubbendieck, J., Hatch, S.L., Dunn, C.D., 2017. Grasses of the Great Plains. Texas A&M University Press, College Station, TX, USA, p. 722.

Stubbendieck, J., Coffin, M.J., Dunn, C.D., 2019. Weeds of the Great Plains. Nebraska Department of Agriculture, Lincoln, NE, USA, p. 638.

Teague, W.R., Ansley, R.J., Kreuter, U.P., Pinchak, W.E., McGrann, J.M., 2001. Economics of managing mesquite in north Texas: a sensitivity analysis. Journal of Range Management 54, 553–560.

Teague, W.R., Dowhower, S.L., Ansley, R.J., Baker, S.A., Waggoner, J.A., Ransom, R.D., 2014. Influence of increasing *Prosopis glandulosa* on herbaceous diversity and composition on two soils in southern mixed-grass prairie. Arid Land Research and Management 28, 216–231.

Teague, W.R., Dowhower, S.L., Baker, S.A., Haile, N., DeLaune, P.B., Conover, D.M., 2011. Grazing management impacts on vegetation, soil biota and soil chemical, physical and hydrological properties in tall grass prairie. Agriculture Ecosystems and Environment 141, 310–322.

Tiedemann, A.R., Klemmedson, J.O., 1977. Effect of mesquite trees on vegetation and soils in the desert grassland. Journal of Range Management 30, 361–367.

Tiedemann, A.R., Klemmedson, J.O., 1986. Long-term effects of mesquite removal on soil characteristics: I. Nutrients and bulk density. Soil Science Society of America Journal 50, 472–475.

Tomecek, J.M., Pierce, B.L., Reyna, K.S., Peterson, M.J., 2017. Inadequate thermal refuge constrains landscape habitability for a grassland bird species. Peer–J doi:10.7717/peerj.3709, Available at: https://peerj.com/articles/3709/ (Accessed April 26, 2021).

USDA-NRCS, 2006. Land resource regions and major land resource areas of the United States, the Caribbean, and the Pacific Basin. USDA Agricultural Handbook, p. 296.

USDA-NRCS, 2019a.] United States Department of Agriculture−Natural Resource Conservation Service United States Department of Agriculture−Natural Resource Conservation ServiceAvailable at: http://websoilsurvey.nrcs.usda.gov/app (Accessed 25 September 2019).

USDA-NRCS, 2019b. Ecological Site Descriptions (Texas Rangelands) Available at: https://esis.sc.egov.usda.gov/Welcome/pgApprovedSelect.aspx (Accessed September 25, 2021).

USDA-NRCS, 2020. Plants database Available at: https://plants.sc.egov.usda.gov/java/ (Accessed February 10, 2021).

Van Auken, O.W., 2000. Shrub invasions of North American semiarid grasslands. Ecology 31, 197–215.

Ward Lab, 2020. Haney Test Interpretation Guide v1.0. Ward Laboratories, Inc. Available at: https://www.wardlab.com/wp-content/uploads/2020/02/Haney-Rev-1.0-Interpretation-Guide-PDF-1.pdf .

Westoby, M., Walker, B.H., Noy-Meir, I., 1989. Opportunistic management for rangelands not at equilibrium. Journal of Range Management 42, 266–274.

Wheeler, C.W., Archer, S.R., Asner, G.P., McMurtry, C.R., 2007. Climatic/edaphic controls on soil carbon/nitrogen response to shrub encroachment in desert grassland. Ecological Applications 17, 1911–1928.

Wood, M.K., Blackburn, W.H., 1984. Vegetation and soil responses to cattle grazing systems in the Texas Rolling Plains. Journal of Range Management 37, 303–308.