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Original Research

Sensitivity of Different Grass Functional Groups to Honey Mesquite Encroachment: Toward Developing a Multiyear Model☆

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Introduction

abstract

Quantifying the relationship of different grass functional groups to increasing woody plant cover is necessary to better understand the effects of woody plant encroachment on grasslands. This study explored biomass production responses of three perennial grass groups based on photosynthetic pathway and potential canopy height (C_4 short-grasses, C_3 midgrasses, and C_4 midgrasses) to different percent canopy covers of the surrounding deciduous woody legume, honey mesquite (*Prosopis glandulosa*). Two methods were used to determine mesquite canopy cover, line-intercept and geospatial analysis of aerial images, and both were used to predict production of the three grass groups. Five years of grass production data were included in the mesquite cover/grass production regressions. Two yr had extreme grass production responses, one due to drought and the other to high rainfall. Of the 3 remaining yr, best-fit curves were negative linear for C_4 short-grasses and C_3 midgrasses and negative sigmoidal for C_4 midgrasses using both cover determination methods, although slopes of the curves differed between cover determination methods. C_4 midgrasses were more sensitive than the other grass groups to increasing mesquite cover. Loss of production potential when mesquite cover increased from 0% to 35% was 75.5%, 28.7%, and 23.2% for C_4 midgrasses, C_3 midgrasses, and C_4 short-grasses, respectively. Moreover, production potential of C_4 midgrasses under no mesquite cover was 3 and 6 times greater than C_3 midgrasses or C_4 short-grasses, respectively. Spatial settings of the different grass groups in relation to mesquite tree size and size of intercanopy areas provided indirect evidence that the process of mesquite encroachment in the past 50–100 yr may have negatively impacted C_4 midgrasses more than the other grass groups. Results suggest that gains in grass production following mesquite treatment would be limited if the system has degraded to where only C_3 midgrasses and C_4 short-grasses dominate.

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Woody plant expansion in savanna and grassland systems over the past century has been documented throughout the world (Scholes and Archer 1997; Van Auken 2000; Ratajczak et al. 2012; Gonzalez-Roglich et al. 2015; Axelsson and Hanan 2018). Causes include fire suppression, livestock grazing, rising atmospheric CO_2 , and introductions of non-native woody species into regions as

“ecosystem engineers” (Archer et al. 1995; Eldridge and Soliveres 2014; Ayanu et al. 2015; Ansley et al. 2017; Patnaik et al. 2017;

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Stevens et al. 2017). One of the most common examples of expansion of native woody species is with the deciduous woody legume, honey mesquite (*Prosopis glandulosa* Torr.), in the Southern Great Plains (SGP) region of the United States (Asner et al. 2003; Hughes et al. 2006).

Increasing mesquite density and canopy cover often leads to reduced grass production due to competition for water, light, and other resources (Dahl et al. 1978; Bedunah and Sosebee 1984; Laxson et al. 1997). Ansley et al. (2013) and Teague et al. (2014) identified differences in how perennial C₄ short-grasses, C₃ midgrasses, and C₄ midgrasses responded to mesquite cover, with C₄ midgrasses found to be most sensitive to increasing mesquite cover.

The current study seeks to expand findings of previous work (Ansley et al. 2013) by addressing four new objectives related to grass responses within spaces between mesquite trees (hereafter “intercanopy areas”) to different levels of mesquite cover. Our first objective was to use an alternate technique to provide a

more accurate assessment of mesquite cover on aerial images first described by Ansley et al. (2013) and then compare these results to the old aerial image classification.

Our second objective was to determine the degree to which grass production data from multiple years can be pooled into a single multiyear mesquite cover/grass production model. While we acknowledge that the mesquite cover/grass production relationship varies among years due to differences in precipitation and other growing conditions (McPherson and Wright 1990), many resource managers, agencies, or private companies that are interested in predicting grass responses to changes in woody cover would prefer to use a single cover and production model that could be applied to multiple years.

Our third objective was to compare the mesquite cover/grass production relationships using aerial image versus line-intercept methods to determine mesquite cover. A typical field-based method is to measure woody cover by line-intercept (Canfield 1941) and relate that to grass production near the line-intercept transects (Jameson 1971; Scifres et al. 1982; Nemati and Goetz 1995; Miller et al. 2000; Teague et al. 2008). While useful to provide a general idea of the relationship, the cover estimate does not account for variations in microsite conditions where grasses are sampled. A more accurate measure would be to assess woody cover immediately surrounding a particular grass sample point (Ansley et al. 2013). We know of no studies that used different techniques to measure woody cover and compare against the same grass production data.

Our fourth objective was to determine how the spatial characteristics of the intercanopy areas where grass production was measured at a set point in time might provide insights regarding historical trends (i.e., the past 50–100 yr) in grass species succession in response to mesquite encroachment and continuous cattle grazing in the SGP. As woody encroachment increases in density and canopy cover, intercanopy areas between woody plants become smaller (Mirik and Ansley 2012a; Axelsson and Hanan 2018). We hypothesize that grass groups that are more sensitive to increasing woody plant cover and density would have a higher probability of being located in larger intercanopy areas and/or surrounded by smaller mesquite trees than in smaller intercanopy areas and/or surrounded by larger trees. Therefore, we used the physical characteristics of the intercanopy area and size of surrounding mesquite trees where grass production was measured as a method to provide indirect evidence of a successional pattern among grass groups in response to mesquite encroachment (Archer 1990).

Methods

Study area

The research site is located on a 262-ha area within a fenced pasture on a cattle ranch 37 km southwest of Vernon, Texas (33°53'N, 99°21'W; elev. 380 m) in north central Texas. Mean annual rainfall (30 yr; 1981–2010) is 710 mm with peak rainfall in the months of June (108 mm) and September (80 mm). Mean annual air temperature is 17.1 °C and mean monthly air temperatures range from an average daily maximum of 35.9 °C in July to an average daily minimum of −2.4 °C in January (NOAA-NCDC 2022). Soils are Tillman series clay loams, 0–1% slopes, with C horizon beginning at ~1.6 m depth, and Ecological Site is Clay Loam R078CY096TX (USDA-NRCS 2022a).

Vegetation consists of a honey mesquite and an understory composed of a mixture of native C₃ and C₄ perennial grasses. The most abundant C₃ midgrass and C₄ short-grass species, respectively, are Texas wintergrass (*Nassella leucotricha* [Trin. and Rupr.] Pohl.) and buffalograss (*Buchloe dactyloides* [Nutt.] Engelm.). Most abundant C₄ midgrasses include silver bluestem (*Bothriochloa laguroides* [DC.] Herter. subsp. *torreyana* [Steud.]), vine mesquite (*Panicum obtusum* Kunth), sideoats grama (*Bouteloua curtipendula* [Michx.] Torr.), tall dropseed (*Sporobolus compositus* [Poir.] Merr.), and sand dropseed (*Sporobolus cryptandrus* [Torr.] A. Gray) (Stubbenieck et al. 2017). We define short-grasses and midgrasses on the basis of potential canopy

height of a species. Short-grasses have canopy heights generally < 30 cm; midgrass canopy heights are greater than short-grasses (30–70 cm) but lower than tallgrass species (Lane et al. 2000). Midgrasses are most concentrated in the mixed-grass portion of the Great Plains that occurs between the shortgrass steppe to the west and tallgrass prairie to the east (Lane et al. 2000; Stubbenieck et al. 2017).

Mesquite and C₄ grass growing season is from April to September. C₃ perennial grass species grow from February through May. After May, they enter summer quiescence and may resume growth in late September and October if soil moisture is available and day-time air temperatures are cool enough.

The entire study area was commercially sprayed with 2,4,5-T [(2,4,5-trichlorophenoxy) acetic acid] in 1965 that “root-killed” about 20% of the mesquite. Remaining mesquites were “top-killed” and resprouted from stem bases. Recruitment of new mesquite plants from seed also occurred since spraying. In 1977, the area was divided into 78 large plots (each 84 × 400 m; 3.36 ha) and different plots were aerially sprayed with mesquite top-killing or root-killing herbicides in 1977, 1979, 1987, or 1988. None of these herbicide treatments damaged the soil or were harmful to the grass community (Lyons et al. 2020). Some plots were left untreated. Thus, at initiation of the study in 1998, 10 yr after the last set of herbicide treatments, the area contained a wide range of mesquite densities, canopy covers, and tree heights. A moderate, continuous cattle grazing regime had been in place since the 1970s at a stocking rate of 12 ha · cow^{−1} (30 acre · cow^{−1}) with no internal fencing in the pasture.

Twenty-five naturally growing monoculture patches, each at least 6 m² in size, of each of three perennial grass groups, C₄ short-grasses, C₃ midgrasses, and C₄ midgrasses, were identified in intercanopy areas between the mesquite trees (75 total plots) in several of the 78 large plots that were visually estimated at ground level to have light, moderate, or high mesquite canopy cover. Grass patches (hereafter “grass plot” or “plot”) were grouped in sets of three, with one representative of each grass group in each set. All C₄ short-grass plots comprised buffalograss, and all C₃ midgrass plots were Texas wintergrass. The C₄ midgrass plots were composed of either silver bluestem or vine mesquite, both having similar production potential.

After the 75 grass plots were located, thirty-two 60-m long line transects were established among the grass plots and mesquite cover was determined on each line using the line-intercept method (Canfield 1941). Mesquite canopy cover was also determined in circular rings of different radii around each grass plot using geo-referenced CIR (color infrared) aerial images (taken September 2, 2000 at a nominal scale of 1:5000 on 23 × 23 cm film) and ArcMap to generate shapefiles of four spatial zone circles (0–5 m, 0–10 m, 0–15 m, and 0–20 m radius; hereafter “spatial zone”) around each grass sample point (hereafter referred to as the “aerial image” method). An earlier version of ArcGIS was used to classify mesquite canopy cover within each spatial zone (Heaton et al. 2003). The line-intercept data determined that >98% of the woody canopy cover was mesquite. Therefore, we assumed that all woody canopies on the aerial images were mesquite trees.

Comparing aerial image techniques for mesquite cover (Objective 1)

Mesquite cover values by aerial image method reported here are different from those reported in Ansley et al. (2013). We found in our previous work that

the automated canopy cover classifications in ArcMap could not always successfully separate the shaded portions within a mesquite canopy from shade cast by the trees beyond the canopy perimeter. If intracanalopy shade was included in the automated classifications, then some shade cast by the trees into intercanopy spaces between trees was included and the cover was overestimated. The reverse was true if intracanalopy shade was not included in the classification. Others have found that canopy shadow can be problematic (Whiteman and Brown 1998; Davies et al. 2010). In addition, we used GPS coordinates taken in the field to locate the grass sample points when this technology at the time had a 5-m margin of error.

To attempt to improve classification, we combined digital and analog techniques. We re-scanned and georeferenced the original CIR images at a higher level of resolution. With the new scan we were able to visually identify the positions of the clip cages on the images instead of relying on previous GPS coordinates and thus adjusted the position of the four spatial zone shapefiles around each grass sample point. We then printed each grass plot image with red-colored spatial zone rings on paper in a muted-color tone so that shaded areas were gray instead of black and hand colored with black ink the portions within the spatial zones that included mesquite canopies. The hand-colored images were then scanned into digital format. Since they were no longer georeferenced, a native coordinate system in ArcMap 10.5.1 was used to calculate relative areas as a percentage of black (mesquite canopy) versus spatial zone. We used Maximum Likelihood Classification to create a polygon file for the total black area within each spatial zone circle and the Intersect tool and Excel to calculate the percentage of black (mesquite canopy area) in each circle.

Mesquite cover and grass production (Objectives 2 and 3)

Grass production was measured in each of 5 yr, 1998–2002. A 1 m wide × 2 m long × 1.5 m tall wire cage was placed in each grass plot to protect it from livestock grazing. In February each year, standing litter was removed from the area within and a 0.5-m border around each cage. To account for variations in precipitation patterns that might affect when peak production of each functional group occurred, two different 0.25 m² quadrat areas were clipped within each cage at different times in the growing season. The C₃ midgrass plots were clipped in late spring (early June) and midsummer (July), and C₄ short-grass and C₄ midgrass plots were clipped in midsummer and early fall (late September–early October). The highest value from the two sample periods was used to estimate peak standing crop as a proxy for annual net primary production. Cage locations were moved < 1 m within each grass plot each year to avoid excessive clipping of the same sample point.

At the end of yr 2, we noticed that mesquites near some of the plots had been damaged by herbicide spray drift from an adjacent study area, and we relocated nine plots in February 2000. We did not determine mesquite cover in 1998 and 1999 on the 9 plots that were relocated in February 2000. Thus, the sample size for relating mesquite cover from aerial image to grass production was 66 for the 1998 and 1999 data sets (21, 23, and 22 plots for C₄ short-grasses, C₃ midgrasses, and C₄ midgrasses, respectively) and 75 (25 per grass group) for the 2000 to 2002 data sets. Mesquite cover data from the two methods (aerial image and line-intercept) and grass production data from the 5 yr were used to address Objective 3.

Intercanalopy characteristics (Objective 4)

Field measurement of intercanopy area for each grass plot was determined by measuring the distance from the center point in each grass plot to the canopy edge of the nearest mesquite tree in each of four quadrants divided along north to south and east to west lines. Intercanalopy area (m²) was determined by averaging the four distance measurements and using the equation:

$$\text{Area} = \pi \cdot d^2, \quad (1)$$

where d = distance measure (m). Tree height, canopy diameter, and diameter of the largest base stem were measured for each of these four trees and averaged. Mesquite canopy volume was determined by using an inverted conic frustum equation (as a variation of Thorne et al. 2002; Sponseller and Fisher 2006):

$$\text{Volume} = ([\pi \cdot H] \cdot [\{C^2\} + \{C \cdot B\} + \{B^2\}]) / 12 \quad (2)$$

where H = tree height (m), C = canopy diameter, and B = base diameter (m). We assumed, given similar soil type and rainfall on all plots, that greater stem diameter implied older trees. Intercanalopy area and tree size were determined for each grass plot within three broad mesquite cover categories (0–24.99%, 25–49.99%, and 50–100%). In our study, mesquite canopy area + intercanopy area = 100% of the land area. Intercanalopy area included all land area from an aerial perspective that was not mesquite canopy, including grass and other herbaceous cover, bare ground, and litter.

Data analysis

For Objective 1, we compared previous and current aerial image cover within the 0–20 m spatial zone for each grass plot via regression technique. For Objective 2, best-fit linear or curvilinear regressions between mesquite cover in each of the four spatial zones surrounding each grass plot and grass production were performed for each grass group using SigmaPlot/SigmaStat software version 14.0 (Systat Software Inc., San Jose, CA). Curvilinear regressions used a four-parameter sigmoidal curve,

$$y = y_0 + \frac{a}{1 + e^{-\left(\frac{x-x_0}{b}\right)}} \quad (3)$$

or, as displayed in the tables and figures,

$$y = y_0 + a / (1 + \exp(-(x - x_0) / b)) \quad (4)$$

where y_0 is the low-end intercept, x is the mesquite cover value, and a , b , and x_0 are coefficients. We used the sigmoidal equation instead of a power or exponential equation so that a grass production value at zero mesquite canopy cover could be predicted. The Durbin-Watson test for independent distribution, the Kolmogorov-Smirnov (K-S) test for normality, and the Constant Variance test were performed on all regressions. Grass production data from all 5 yr were initially included in each regression. Knowing that 2 of the 5 yr had very atypical weather patterns, we also developed regressions that excluded those 2 yr. Because the annual increase in mesquite cover in this region is small (Ansley et al. 2001), mesquite canopy cover values from the 2000 images were used to compare with grass production in all 5 yr. Curve-fitting was conducted for both aerial image and line-intercept cover techniques.

For Objective 3, mesquite cover determined by aerial image in the 0- to 20-m zone around each grass plot was plotted against cover determined by line-intercept values that were associated with the same grass plots. This relationship included the original 66 grass plots where cover data from each technique were available, as well as the new plots established in 2000.

For Objective 4, we used a one-point-in-time Proc Mixed analysis with unequal replicates to compare intercanopy area and mesquite size when averaged over all plots within each grass

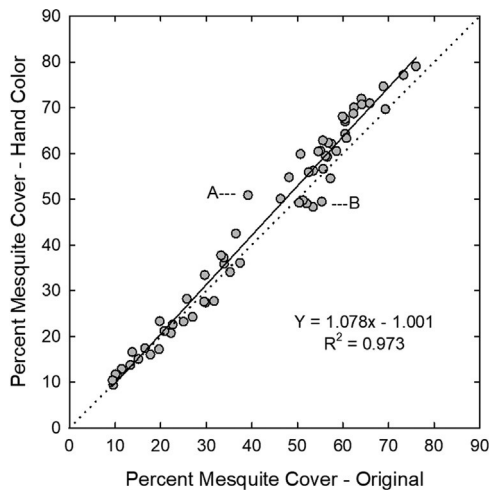


Figure 1. Comparison of mesquite cover determined by original aerial image method (from Ansley et al. 2013) to the hand-color aerial image method in the 0- to 20-m zone around each grass plot. Solid line is the regression line; dashed line is the 1:1 line. Points A and B illustrate examples of the original aerial image method either deleting too much intracanalopy shade (A) or including too much shade in inter-canalopy area as part of the mesquite cover estimate (B).

group and within the three broad cover categories described earlier (0–24.99%, 25–49.99%, and 50–100%) (SAS 2013). Means were separated using LSMEANS at $P < 0.10$.

Results

Comparing aerial image techniques for mesquite cover (Objective 1)

Regression revealed a close relationship between the original and new aerial image cover value within the 0- to 20-m zone around each grass plot ($R^2 = 0.97$; Fig. 1). However, the slope of the curve indicated that the new technique yielded higher values as cover increased. A few points deviated widely from the regression line. In these examples, the original classification either deleted too much intracanalopy shade (Fig. 1 A) or included too much inter-canalopy shade (Fig. 1 B).

Multiyear cover and production model (Objective 2)

Average air temperature was mostly above the 30-yr average in quarterly periods during the study (Fig. 2 A and B). Two important exceptions were ~2 °C deviation from average during Q4 in 2000 and Q1 in 2001. Precipitation was equal to or above average in each quarter of 1997 before study initiation (Fig. 2 C). The yr 1998 had a wet first quarter and very dry second and third quarters. The yrs 1999 and 2000 had above-average rainfall in Q1 and Q2. The yr 2000 had very high rainfall in Q4 coupled with below-average temperatures. Precipitation was well below average in Q2 and Q3 in 2001 and near or above average in each quarter of 2002.

Regressions using the aerial image method for cover and including data points from all 5 yr for each mesquite cover zone and grass group are shown in Table 1. All relationships were linear with $R^2 < 0.20$. Best-fit regressions were with the 0- to 10-m zone for C₄ short-grasses, the 0- to 15-m zone for C₃ midgrasses, and the 0- to 20-m zone for C₄ midgrasses (Fig. 3). Production of each grass group across the entire range of mesquite cover was near zero in the extreme drought yr, 2001. In contrast, each grass group had 6–10 plots with extremely high production values in the cool and wet yr, 2002.

Removing data points from 2001 and 2002 resulted in more robust aerial image cover and production relationships for each grass

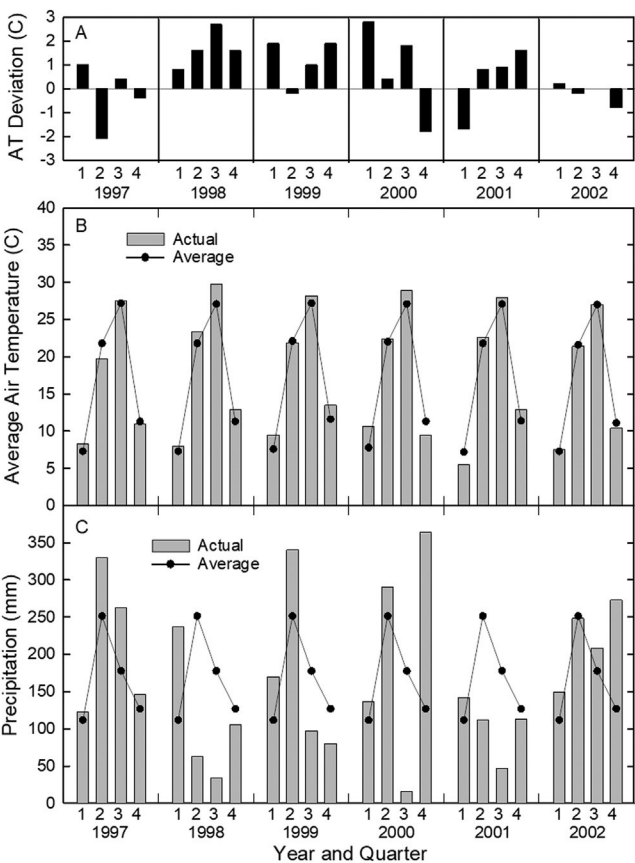


Figure 2. Quarterly deviation of actual air temperature (AT) from average (A) and actual air temperature (B) and precipitation (C) compared with the 30-yr average 1 yr before study initiation (1997) and during the 5 study yrs, 1998–2002.

Table 1
Correlation coefficient and equation for each linear or sigmoidal regression between mesquite cover in each spatial zone using the aerial image method and 5 yr of grass production² value for (1998 each –grass2002) group of each is in perennial bold. grass group. Relationship with highest R

Group	Zone	R^2	Equation
C ₄ Short-grass	0-5 m	0.06	$Y = 55.43 - 0.52 x$
C₄ Short-grass	0-10 m	0.10	$Y = 63.01 - 0.56 x$
C ₄ Short-grass	0-15 m	0.07	
C ₄ Short-grass	0-20 m	0.05	$Y = 58.22 - 0.45 x$
C ₃ Midgrass	0-5 m	0.06	
C ₃ Midgrass	0-10 m	0.12	$Y = 54.13 - 0.37 x$
C₃ Midgrass	0-15 m 0-20 m	0.15	$Y = 115.07 - 1.12 x$
C ₃ Midgrass	0-5 m	0.14	
C ₃ Midgrass	0-10 m 0-15 m	0.08	$Y = 138.33 - 1.40 x$
C ₄ Midgrass	m	0.15	$Y = 142.24 - 1.41 x$
C ₄ Midgrass	0-20 m	0.16	$Y = 141.34 - 1.35 x$
C ₄ Midgrass		0.17	$Y = 227.92 - 3.41 x$
			$Y = 302.37 - 4.02 x$
			$Y = 320.61 - 4.01 x$
			$Y = 328.77 - 3.92 x$

functional group. Best-fit regressions were with the 0- to 10-m zone for C₄ short-grasses, 0- to 15-m zone for C₃ midgrasses, and 0- to 20-m zone for C₄ midgrasses (Table 2). Relationships were negative linear for C₄ short-grasses and C₃ midgrasses and negative sigmoidal for C₄ midgrasses (Fig. 4 A–C). The negative sigmoidal function for C₄ midgrasses revealed that most of the decline in production occurred before mesquite cover exceeded 35%. C₄

midgrass yields in the aerial image method were $< 100 \text{ g} \cdot \text{m}^{-2}$ when cover was $> 35\%$.

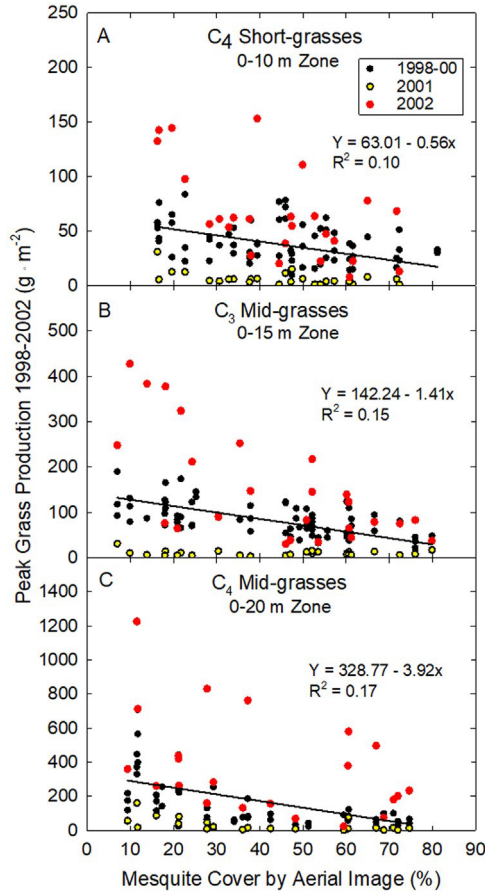


Figure 3. Relationship between mesquite cover as determined by aerial image and intercanopy production of each grass group within best-fit spatial zones over 5 yrs (1998–2002). Regressions from Table 1 determined best-fit spatial zone for each grass group. Responses in the 2 highly variable yrs are in yellow (extreme drought yr, 2001) and red (extreme wet yr, 2002).

Table 2

Correlation coefficient and equation for each linear or sigmoidal regression between mesquite cover in each spatial zone using the aerial image method and 3 yr of grass production (1998–2000) of each perennial grass group. Relationship with highest R^2 value for each grass group is in bold.

Group	Zone	r^2	Equation
C ₄ Short-grass	0–5 m	0.11	$Y = 54.29 - 0.44 x$
C₄ Short-grass	0–10 m	0.12	$Y = 55.85 - 0.37 x$
C ₄ Short-grass	0–15 m	0.07	$Y = 50.94 - 0.26 x$
C ₄ Short-grass	0–20 m	0.03	$Y = 50.94 - 0.26 x$
C ₃ Midgrass	0–5 m	0.14	$Y = 47.02 - 0.18 x$
C ₃ Midgrass	0–10 m	0.31	$Y = 106.83 - 0.84 x$
C₃ Midgrass	0–15 m	0.35	$Y = 125.49 - 1.08 x$
C ₃ Midgrass	20 m	0.31	$Y = 125.49 - 1.08 x$
C ₄ Midgrass	0–5 m	0.34	$Y = 126.91 - 1.04 x$
C ₄ Midgrass	0–10 m	0.47	$Y = 126.91 - 1.04 x$
C ₄ Midgrass	15 m	0.50	$Y = 124.43 - 0.95 x$
C ₄ Midgrass	0–20 m	0.57	$Y = 124.43 - 0.95 x$
C₄ Midgrass			$Y = 51.5 + 251.1 / (1 + \exp[-(x-8.9) / -5.3])$
			$Y = 42.3 + 277.8 / (1 + \exp[-(x-23.4) / -7.3])$
			$Y = 54.7 + 258.7 / (1 + \exp[-(x-25.6) / -4.9])$
			$Y = 56.3 + 322.5 / (1 + \exp[-(x-21.8) / -6.2])$

Comparing cover measurements as they relate to grass production (Objective 3)

In comparing the relationship between cover and production using aerial image versus line-intercept cover values, the negative response curves for C₄

short-grasses and C₃ midgrasses were steeper with aerial image than with line-intercept (Fig. 4 A, 4 B, 4 D, and 4 E). In contrast, the negative sigmoidal curve for C₄ midgrasses declined at a steeper rate between 10% and 30% cover with line-intercept than aerial image (Fig. 4 C and 4 F). Thus, the aerial image technique revealed possibly greater sensitivity of C₄ short-grasses and C₃ midgrasses and less sensitivity of C₄ midgrasses to increasing mesquite cover when compared with the line-intercept technique.

The reason for these differences is because the line-intercept method in the middle cover range (20–60%; Fig. 5) included more open spaces than what occurred with the more targeted spatial zone method that quantified mesquite cover immediately surrounding each grass production plot. This resulted in a lower cover value that flattened the linear response curves for C₄ short-grasses and C₃ midgrasses but generated a steeper reduction at lower cover values in the negative sigmoidal curves for C₄ midgrasses.

Figure 6 displays curves from Figures 4 A–4 C on the same Y-axis (i.e., grass production) scale, illustrating that C₄ midgrasses have a much greater production potential under low mesquite cover and much greater sensitivity under increasing mesquite cover compared with the other two grass groups. Using equations from Figure 6, loss of production potential when mesquite cover increased from 0% to 35% was 75.5%, 28.7%, and 23.2% for C₄ midgrasses, C₃ midgrasses, and C₄ short-grasses, respectively.

Intercanopy characteristics (Objective 4)

There was a negative power curve relationship between mesquite cover, as determined by the aerial image method within the 20-m zone, and intercanopy area (Fig. 7 A). The range of intercanopy area size was greater (8–262 m²) when mesquite cover was $< 30\%$ compared with mesquite cover $> 30\%$ (5–80 m²). Mesquite canopy volume ranged from 0.6 m³ to 86.9 m³, and base stem diameter ranged from 2.2 to 15.1 cm across all grass plots (Fig. 7 B and 7 C). Both these variables increased with increasing mesquite cover.

Mesquite cover by aerial image was similar among the three grass groups when averaged over all plots or over plots within each of the three broad cover categories (Fig. 8 A). Intercanopy area was lower in C₄ short-grass plots than in C₄ midgrass plots when averaged over all plots, or over plots within the 0–24.99% mesquite cover category with intercanopy area of C₃ midgrass plots intermediate (Fig. 8 B). Mesquite trees surrounding the intercanopy areas where grass plots were located had larger canopy volumes and larger basal stem diameters in C₄ short-grass plots than in plots of the other grass groups within the 0–24.99% mesquite cover category (Fig. 8 C and 8 D). When averaged over all three cover categories, mesquite canopy volume and stem diameter were lowest in C₄ midgrass plots.

Discussion

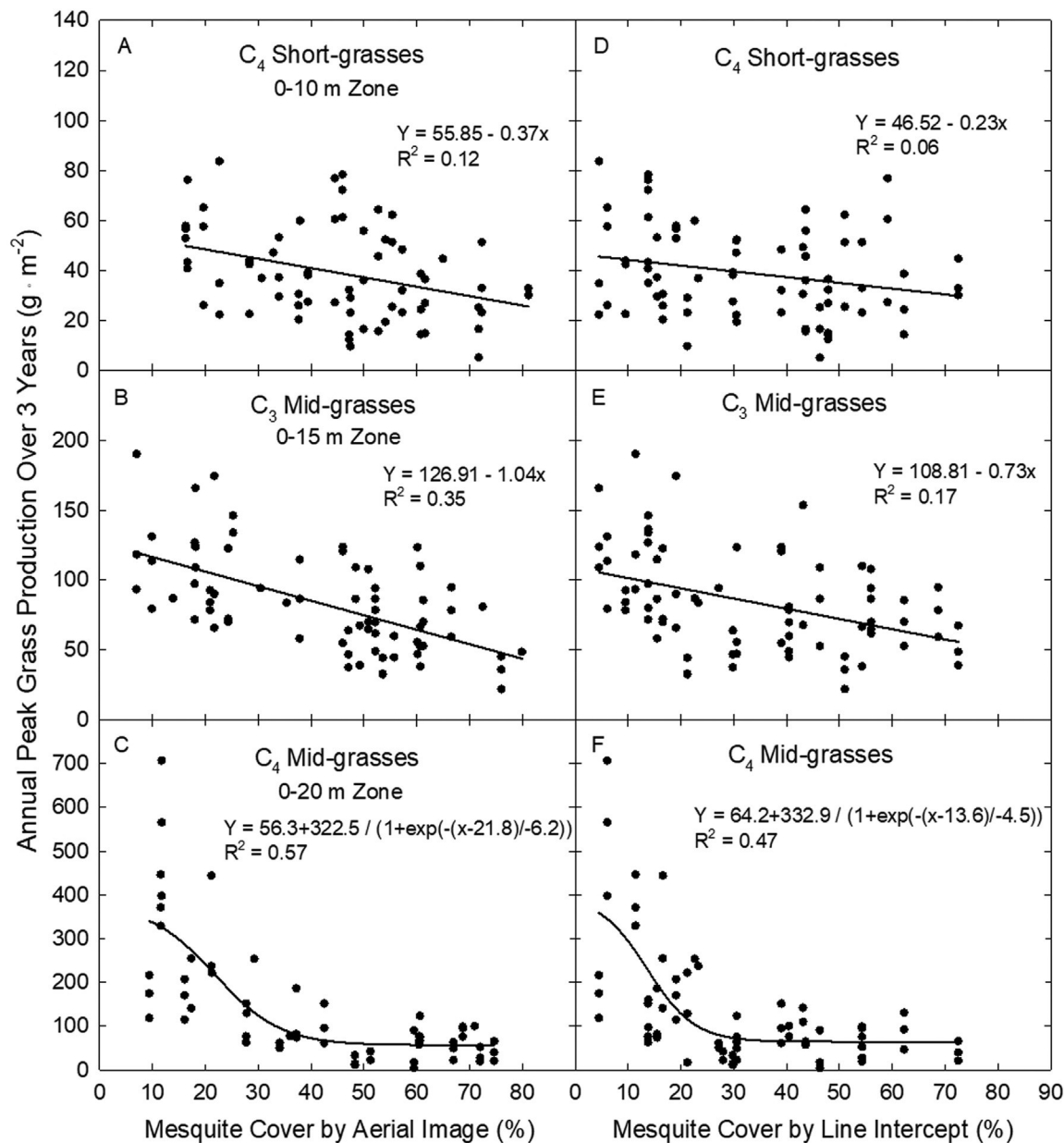
Comparing aerial image techniques for mesquite cover (Objective 1)

The close relationship between the original and new aerial image cover values reinforced previously documented mesquite cover and grass production relationships (Ansley et al. 2013). However, the current study revealed that the original automated classification underestimated mesquite cover, especially when values were $> 40\%$. This was mostly because the automated removal of colors that represented shade cast by mesquite trees into intercanopy regions also resulted in the removal of a substantial portion of shade within mesquite canopies (intracanopy shade) that should have been included in the cover assessment (Whiteman and Brown 1998; Davies et al. 2010).

Multiyear cover and production model (Objective 2)

Inclusion of all 5 yrs markedly reduced the R^2 in the mesquite cover/grass production regressions for each grass group compared

Figure 4. Relationship mesquite cover within circular zones around each grass plot as determined by aerial image (left-side panels) or line-intercept (right-side panels) and production of each grass group in intercanopy areas between mesquite over 3 yr, 1998–2000. Best-fit regression from Table 2 determined mesquite zone for each grass



group in left-side panels.

with the grouping of 3 of the 5 yrs that had more consistent responses. The greater variation in the 5-yr model was due to inclusion of an extremely wet yr and an extremely dry yr. Focusing on the 3-yr model in Figure 6, of the three grass groups studied, the mesquite cover/grass production relationships were either negative linear (C₄ short-grasses and C₃ midgrasses) or negative sigmoidal (C₄ midgrasses). Our linear relationships were similar to those found for mesquite by Mohamed et al. (2011) and Teague et al. (2014).

The negative sigmoidal response curve for C₄ midgrasses in the current study, similar to model projections by Scanlan (1992), demonstrates that this grass group was more sensitive to increasing mesquite cover in the lower range of mesquite cover values (< 40%) than were the other grass groups. Because of their greater production potential compared with the other grass groups (see Fig. 6), C₄ midgrasses provide a significant source of forage for cattle and other ecosystem services such as habitat for ground nesting birds and carbon sequestration (Rogers et al. 2014; Tomecek et al. 2017). Several studies on *Juniperus* species have found a negative exponential or “power curve” relationship between

increasing woody cover and herbaceous production or cover (Jameson 1971; McPherson and Wright 1990; Pieper 1990; Miller et al. 2000). Beale (1973) found a similar response with *Acacia aneura* in Australia. These relationships are similar to the negative sigmoidal curve we found with mesquite and C₄ midgrasses, the exception being that with denser foliage than mesquite, negative effects of *Juniperus* cover on grass production would likely occur at an earlier stage of encroachment than occurs with mesquite.

Regarding grass production responses during the 2 extreme yrs, our results demonstrate that any multiyear model may not be relevant under certain extreme abiotic or biotic conditions. The atypically high grass production in 6–10 plots in each grass group in

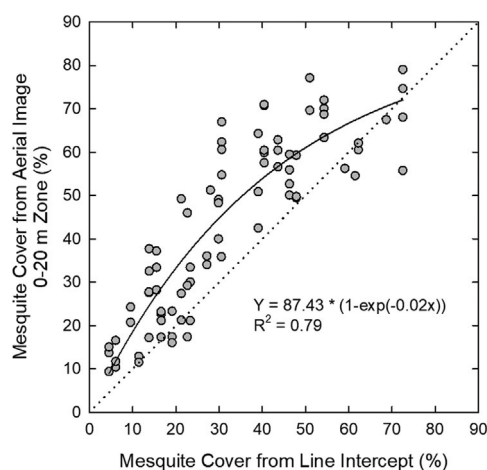


Figure 5. Comparison of mesquite cover determined by line-intercept near each grass plot versus cover determined by aerial image in the 0- to 20-m zone around each grass plot. *Solid line* is the regression line, and *dashed line* is the 1:1 line. Vertically stacked data points indicate grass plots associated with the same transect lines.

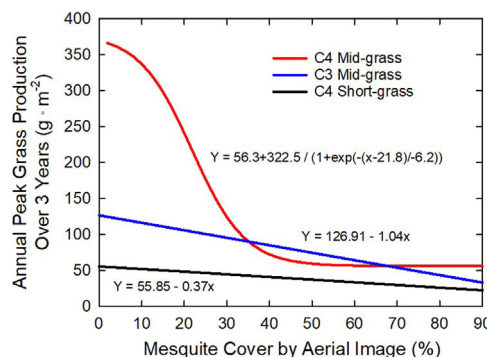


Figure 6. Comparison of the mesquite cover/grass production relationship among the three grass groups using the aerial image technique and equations from Figures 5 A–5C.

2002 (see Fig. 3) likely relates to precipitation and cooler air temperatures. The yr 2002 was the only one of the 5 yrs in which precipitation in Q3 (July–September) was above average. Moreover, most of this precipitation occurred in July, which had more than three times the average precipitation. This quarter is a critical time for C₄ grass production, but C₃ grass production can also continue under high precipitation and average or cooler-than-average air temperatures, which occurred in Q2–Q4. Under extreme rainfall, as in summer 2002, mesquite may not have depended on lateral roots for moisture and intercanopy grass growth may have been decoupled from mesquite competition for water in the high production plots (Ansley et al. 2018). We are uncertain as to why this decoupling occurred in some but not all plots as the high production plots were spatially scattered and not related to any specific area within the study site or brush cover level.

Extremely low production in all grass groups in 2001 again likely relates to precipitation and air temperature, but the interaction was more complex. Precipitation in Q2 and Q3 of this yr was < 50% of average, and this could be the sole explanation for the results except that 1998 had less precipitation in Q2 and Q3 but greater grass production than in 2001. There were differences in precipitation before Q2 and Q3 in each of these yrs that may have led to more soil moisture during Q2 and Q3 in 1998 than 2001. Rainfall in Q1 was much greater in 1998 than 2001, and there was average to above-average rainfall in all four quarters of the yr.

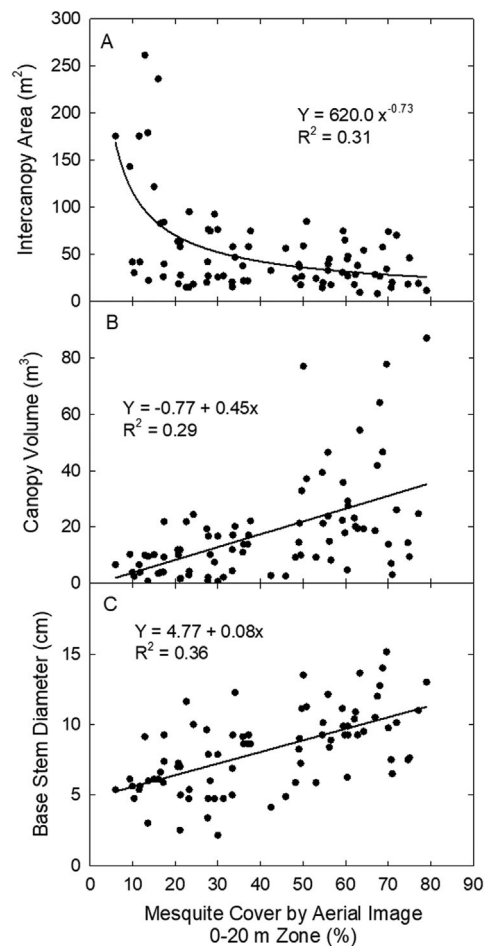


Figure 7. General relationships between mesquite cover determined by aerial image in the 0- to 20-m zone and intercanopy area (A) and canopy volume (B) and basal stem diameter (C) of mesquite trees surrounding the intercanopy areas where grass plots were located ($n = 74$; data were missing for one of the C₄ short-grass plots).

before 1998. In contrast, the yr before 2001 had extreme drought in Q3, and while there was high rainfall in Q4, much of this may have gone toward recharging depleted soil moisture from Q3. Thus, leading in to Q2, conditions were likely drier in 2001 than 1998. Air temperature may also have been a factor in lower grass production in 2001 than 1998. Q1 and Q2 in 1998 had above-average temperatures that would have favored early growth, while Q1 in 2001 had well-below-average air temperatures. McPherson and Wright (1990) with *Juniperus pinchotii* and Teague et al. (2014) with honey mesquite found similar variations in the woody cover/grass production relationship due to annual variations in climate.

Results from Figure 6 also suggest that potential for increased grass production following mesquite treatment is greater if the land area of a site has more C₄ midgrasses than C₄ short-grasses or C₃ midgrasses. For example, if a treatment reduced mesquite cover from 50% to zero, grass production gains could potentially increase by > 500% with C₄ midgrasses but only 70% for C₃ midgrasses and 50% for C₄ short-grasses. Absolute gain would be 310, 52, and 19 g · m⁻², respectively. These results reinforce the concept that grass production following brush treatment is largely dependent on the condition and composition of the grass community before treatment (Archer et al. 2011). Loss or diminution of C₄ midgrasses would severely limit gains in grass production following mesquite treatment and generate potential for hysteresis in post-treatment vegetation trajectories (Collins et al. 2021).

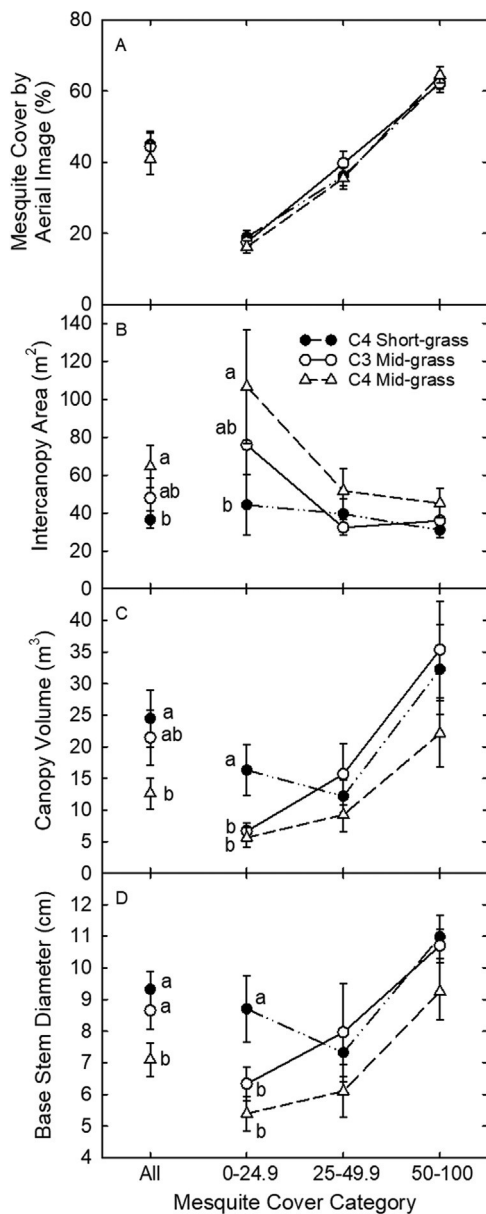


Figure 8. Mesquite cover in the 0- to 20-m spatial zone (A), intercanopy area size (B), canopy volume of surrounding mesquite (C), and basal stem diameter of surrounding mesquite (D) when averaged over all cover values (All) and within the 3 broad cover categories in each grass group. Vertical lines are $\pm$ standard error. Means with similar letters are not significantly different ($P < 0.10$) within each cover category (no letters = no significant differences).

Comparing cover measurements as they relate to grass production (Objective 3)

The curvilinear deviation from the 1:1 line between line-intercept versus aerial image mesquite cover values (see Fig. 5) was not found by Davies et al. (2010), who found a linear relationship where the line-intercept method slightly overestimated *Juniperus occidentalis* cover at $< 40\%$ cover and a remote sensing method overestimated cover at $> 60\%$ cover. Mirik and Ansley (2012b) studying mesquite at a different north Texas site than the current study site found a similar linear relationship and same deviations as Davies et al. (2010). The curvilinear deviations between the techniques in the current study occurred because we were attempting to link both cover estimation methods to the same set of grass production plots. The line-intercept transect lines were nearby but not located exactly where the aerial image cover values were quantified.

The two methods of measuring mesquite cover (aerial image and line-intercept) were remarkably similar in how they predicted production of each grass group with increasing mesquite cover (see Fig. 4). This lends support to other studies that used line intercept data to estimate cover and apply to grass production (Jameson 1971; Scifres et al. 1982; Nemati and Goetz 1995; Miller et al. 2000; Teague et al. 2008). There were, however, important differences that could affect management decisions regarding timing of when to apply mesquite control treatments. For example, the aerial image method predicted a more gradual decline in C_4 midgrass production from 10% to 30% mesquite cover compared with the line-intercept method. If mesquite cover increases by about 2 percentage points each yr in this region (as per Ansley et al. 2001), the aerial image method suggests one would have an additional 5–6 yr before C_4 midgrass production reached the low end, compared with the line-intercept method. Conversely, with respect to the other grass groups, the line-intercept method potentially underestimated the long-term negative effects of mesquite encroachment on C_4 short-grasses and C_3 midgrasses compared with the aerial image method. We assume the relationship between mesquite cover and grass production was more accurate using the aerial image method because mesquite cover was determined immediately surrounding each grass sample point.

Intercanopy characteristics (Objective 4)

Three observations of our data provide indirect evidence of a successional pattern of changing grass composition from C_4 midgrasses to C_3 midgrasses to C_4 short-grasses as mesquite encroachment increased over the past 50–100 yr. First, intercanopy area was larger in C_4 midgrass plots compared with C_4 short-grass plots (Fig. 8 B). Second, mesquite trees surrounding the intercanopy areas where C_4 short-grass plots were located were larger (greater canopy volume and base stem diameter) than trees surrounding intercanopy areas where C_3 midgrass and C_4 midgrass plots were located (Fig. 8 C and 8 D). Third, the spatial zone that yielded the best-fit cover and production regressions in the 3-yr models (see Fig. 5 A–5C) declined in size from 0 m to 20 m for C_4 midgrasses, to 0 m to 15 m for C_3 midgrasses, to 0 m to 10 m for C_4 short-grasses. Our conclusions are based on the assumption that mesquite encroachment in this portion of the Southern Great Plains steadily advanced from low cover to nearly a closed canopy as demonstrated by Ansley et al. (2001) and Hughes et al. (2006), and with this advancement the grass community shifted from midgrasses to short-grasses, as described by Archer (1990).

The process of woody encroachment in some savanna regions may generate different results. In some of these regions, there may be an upper limit to woody encroachment due to low mean annual precipitation (MAP) and other resource limitations (Goslee et al. 2003; Sankaran et al. 2005; Browning et al. 2008; Axelsson and Hanan 2018). For example, Staver et al. (2011) found that tree cover in African, Australian, and South American savannas does not expand beyond 40% until MAP exceeds 600 mm. Sankaran et al. (2005) found the 40% cover limit to occur in Africa at MAP < 400 mm. Browning et al. (2008) found an upper limit of 35% *P. velutina* cover on sandy uplands in Arizona (MAP 370 mm). Goslee et al. (2003) found an upper limit of 43% honey mesquite cover in New Mexico (MAP 230 mm). Isolated trees in lower densities accumulate nutrients in soil beneath their canopies and generate islands of fertility that can be beneficial for grass growth near the tree canopies (Schlesinger et al. 1990; Belsky et al. 1993; Rossi and Vil-lagra 2003; Riginos et al. 2009; Eldridge et al. 2011). In contrast, in our study area (MAP 710 mm) mesquite cover can increase to 70–80% (see Fig. 5), similar to findings in Africa by Sankaran et al. (2005) and Axelsson and Hanan (2018). We note that this increase may be facilitated via distribution of mesquite seed by cattle and wildlife (Ansley et al. 2017).

The larger intercanopy size associated with C_4 midgrasses compared with C_4 short-grasses (with C_3 midgrasses intermediate) suggests that the initial source of competition between mesquite and this grass group is root based rather than through shading by mesquite canopies. Mesquite lateral roots can

extend > 10 m from the tree center, and most are located at 0.5–1.0 m soil depth (Heitschmidt et al. 1988). C_4 midgrass roots extend to these depths more than do the other grass groups and thus are most likely to be the first group to encounter mesquite lateral roots that compete for soil water in intercanopy areas as mesquite encroachment advances (Scholes and Archer 1997; Ansley et al. 2014).

As intercanopy size declined and mesquite tree size increased, the combined effect of root competition and shading likely reduced the presence of C_4 midgrasses from the landscape. We did find a few patches of C_4 midgrasses in higher mesquite cover areas, so they were not completely eliminated in even the densest mesquite stands, but their production was very low. Soil isotope studies in the region (Dai et al. 2006; Liao et al. 2006) suggest that C_4 grasses were dominant before mesquite encroachment. However, the historical proportion of C_4 midgrasses and C_4 short-grasses in the SGP is unknown. Recent prescribed fire studies that have reduced mesquite cover and increased C_4 midgrass production and basal cover suggest there was a greater abundance of C_4 midgrasses than what is currently found in areas heavily encroached by mesquite (Ansley et al. 2021).

Regarding C_4 short-grasses, intercanopy areas were bordered by larger and older mesquite than occurred with the other grass groups and the best-fit cover and production regressions for this grass group occurred in the smallest circular zone of 0–10 m (see Fig. 5 A). These results suggest that mesquite competes with C_4 short-grasses mostly by shading rather than root competition because mesquite trees had to be close before they had the greatest negative effect on C_4 short-grass production. Mesquite lateral roots in intercanopy areas would mostly track beneath the shallow C_4 short-grass root system and thus not compete directly for soil moisture (Ansley et al. 2014). This suggests a variation of Walter's (1971) two-layer hypothesis, where shallow-rooted rhizomatous short-grasses may be better adapted than taller grasses with deeper roots to co-exist with woody plants.

The C_3 midgrass group was composed exclusively of Texas wintergrass, which is native to the SGP (Stubbendieck et al. 2017; USDA-NRCS 2022b). We assume it was present in small amounts in predominantly C_4 midgrass grasslands before mesquite encroachment and advanced after mesquite advanced (Laxson et al. 1997; Murray et al. 2021). Texas wintergrass can coexist with taller C_4 midgrasses in open areas as most growth occurs before sufficient leaf area has developed in C_4 midgrasses (Ansley et al. 2019). With the best-fit zone for C_3 midgrasses being intermediate between C_4 short-grasses and C_4 midgrasses (see Fig. 5 B), competition from mesquite likely came from lateral roots, as well as shading. Shading from mesquite could inhibit Texas wintergrass production in wet and cool summers when growth extends beyond its normal cycle and into early summer. Another important factor in the persistence of Texas wintergrass under increasing mesquite encroachment is that it grows beneath mesquite canopies due in part to greater soil N from N-fixation by mesquite (Geising et al. 2000; Dai et al. 2006) that favors C_3 over C_4 grasses (Wedin and Tilman 1993).

After herbicide treatment of mesquite, C_4 midgrasses are often observed growing among the standing dead mesquite stems (Jacoby et al. 1982; McDaniel et al. 1982), but this rarely occurs beneath live mesquite in the SGP; C_3 Texas wintergrass or C_3 annual grasses dominate most mesquite subcanopy areas, especially under high mesquite cover and density (Laxson et al. 1997; Ansley et al. 2019; Murray et al. 2021). In south Texas, response to mesquite encroachment is different. In these ecosystems, mesquite serves as a pioneer woody plant, gaining in size and then facilitating establishment of other C_3 shrub species beneath the mesquite canopy (Archer et al. 1988). This process does not occur in the SGP. Thus, the indirect evidence we provide here pertains to a process of succession in a mesquite dominant system where mesquite cover can potentially increase to ~80% and slowly cause the elimination of the more productive C_4 grasses. This process of continued encroachment woody species to the point where C_4 tall and midgrasses are displaced by either C_3 grasses or other C_3 shrub species have been found elsewhere in Africa (Roques et al. 2001; Riginos et al. 2009; Shackleton et al. 2015), Australia (

Prober et al. 2007), South America (Kunst et al. 2012), and North America (Ratajczak et al. 2012; Connell et al. 2020).

Management Implications

Two of the 5 yrs in this study were extreme with regard to grass production on native C_3/C_4 mixed grassland invaded by honey mesquite. These years were important in demonstrating the potential range of grass responses but were less useful when developing a multiyear mesquite cover/grass production model for each of three grass functional groups: C_4 midgrasses, C_3 midgrasses, and C_4 short-grasses. When the models incorporated the remaining 3 yrs, cover and production response curves were negative linear for C_3 midgrasses and C_4 short-grasses and negative sigmoidal for C_4 midgrasses. C_4 midgrasses had a vulnerable inflection between 10% and 40% mesquite cover, where production declined at a much steeper rate than occurred with other grass groups. This fact should be considered when planning mesquite management strategies because the highest-producing component of the grass-land matrix is the most vulnerable to increases in woody cover and this component provides essential ecosystem services (e.g., forage availability, nesting habitat, carbon sequestration) that the other grass components are less able to provide.

In this ecosystem with > 700 mm MAP, mesquite has the potential to increase on clay loam soils to 80% canopy cover, thus shrinking intercanopy spaces between mesquite to 20% of total land area. Under this level of mesquite encroachment, the spatial settings of the different grass groups in relation to mesquite tree size, size of intercanopy areas, and the spatial dynamics of the best-fit mesquite cover/grass production regression relationships provided indirect evidence that mesquite encroachment in the past 50–100 yr negatively impacted C_4 midgrasses to a greater extent than the other grass groups. These results suggest that mesquite encroachment is partially responsible for the loss of C_4 midgrasses in this ecosystem. Because of inherent differences in production potential, the relationships between mesquite cover and grass production from this study suggest that gains in grass production following mesquite treatment would be severely limited if the ecosystem has degraded to the level where only C_3 midgrasses and C_4 short-grasses dominate. While our study focused on woody encroachment effects on grasses in one ecosystem, results reinforce that management of woody encroachment in any mixed-grass ecosystem should consider that different grass species may have markedly different sensitivities to woody encroachment.

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.

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Data Accessibility

Data can be found at Dryad; Data available at: <https://doi.org/10.5061/dryad.83bk3j9x1> (TBD).

Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi: [10.1016/j.rama.2023.04.004](https://doi.org/10.1016/j.rama.2023.04.004).

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