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Soil Moisture, Grass Production and Mesquite Resprout Architecture Following Mesquite Above-Ground Mortality

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Abstract: Honey mesquite (*Prosopis glandulosa*) is an invasive native woody plant in the southern Great Plains, USA. Treatments used to slow the invasion rate have either killed the plant (“root-kill”) or killed above-ground tissue (“top-kill”). Top-killing provides temporary suppression, but stimulates multi-stemmed regrowth. This study from north central Texas quantified soil moisture, grass production and mesquite resprout architecture following a mechanical clearing treatment that top-killed mesquite (cleared) compared to untreated mesquite woodland (woodland) over a 10-year period. During an extreme drought at 5 and 6 years post-clearing, soil moisture at 60-cm depth became lower in cleared than in woodland, suggesting that, as early as 5 years after top-kill, water use by regrowth mesquite could be greater than that by woodland mesquite. Perennial grass production was greater in cleared treatments than in woodland treatments in all years except the extreme drought years. Mesquite regrowth biomass increased numerically each year and was independent of annual precipitation with one exception. During the year 5 and 6 drought, mesquite stopped lateral expansion of larger stems and increased growth of smaller stems and twigs. In summary, top-killing mesquite generated short-term benefits of increased grass production, but regrowth created potentially negative consequences related to soil moisture.

Keywords: biomass; brush management; coppice; drought; leaf area index; relative growth rate; resprouting; Texas; woody plant encroachment; woody plant growth

1. Introduction

Many species of woody plants are adapted to resprout from basal meristem following disturbance or destruction of above-ground tissue [1,2]. If the disturbance occurs frequently, such as happens in fire-prone ecosystems, then woody regrowth is maintained in a state of suppression. However, if the disturbance regime is removed or reduced in frequency or intensity, the potential exists for woody regrowth to eventually dominate the landscape. Alteration of disturbance regimes can occur naturally, usually through variations in climate, but is often linked to human activities. Such is the case with many grassland ecosystems that have been invaded by woody plants.

Grasslands evolved in the Miocene under hotter and dryer climatic patterns that yielded frequent fires that maintained grass species dominance [3,4]. Woody plants in these systems survived by reseeding or resprouting [5]. Size of resprouting individuals remained small because repeated fires would continually kill above-ground tissue (hereafter: “top-kill”). Taller woody plants survived in areas such as rocky outcrops where grass fuel was low and fire rarely occurred.

If a grassland disturbance regime is reduced or removed, then the limitations to woody plant growth and recruitment are lowered, resulting in an increase in stature of individual woody plants, and possible increases in woody plant density [6]. In the southern Great Plains, USA, another factor developed after settlement by Europeans in the late 1800's. During that time, the introduction of cattle grazing not only reduced grass amounts that fueled fires, but also accelerated the dissemination of seeds of certain woody species. The best example of this is with the woody legume, honey mesquite (*Prosopis glandulosa*), a native species in the southern Great Plains and southwestern USA that has encroached to the point of ecological dominance in many grassland and savanna areas in the region [7,8]. Density of mesquite has increased primarily due to consumption of the legume "pods" (each containing 20–25 seeds) and subsequent defecation of viable mesquite seeds by cattle (i.e., endozoochory) [9]. In addition, mesquite can resprout from stem bases following top-kill, and established plants are rarely killed by fire [10,11].

There has been a long history of anthropogenic treatments to remove or suppress mesquite, with the main reason being to stimulate grass production for cattle grazing. Treatments have varied from mechanical methods (chaining, root plowing, grubbing, etc.), to use of herbicides, to application of prescribed fire [12,13]. Certain herbicides, sprayed on the foliage by aircraft, can kill (i.e., "root-kill") the majority of mesquite plants [8,14]. However, these treatments are expensive and most landowners or resource managers cannot afford to apply them on large tracts of land, even with government assistance through programs such as Natural Resource Conservation Service—Environmental Quality Incentives Program (NRCS-EQIP). Because of this, historically, there has been a continual use of less expensive treatments such as chaining, prescribed fire or general "weed" herbicides that have the effect of "top-killing" mesquite. This provides temporary suppression, but stimulates multi-stemmed regrowth that, if allowed to grow for more than a few years, can be extremely competitive with grasses and visually obstructive for livestock herding [15]. Much of the reason why mesquite has become dominant in grasslands is because these suppression treatments have not been applied at adequate frequency [16].

While anthropogenic suppression treatments have triggered mesquite into a resprouting growth form over vast regions of the southcentral and southwestern USA, it is surprising that very little research has quantified mesquite regrowth architecture and rates of wood and leaf biomass accumulation [17]. To our knowledge, no one has quantified mesquite regrowth in response to variations in annual precipitation, although a study in south Texas related annual rainfall to growth of older mesquite [18]. We also know very little about how the conversion from a few-stemmed arborescent to a multi-stemmed regrowth form affects other components of the ecosystem, such as soil moisture.

The integrated responses of mesquite regrowth, soil moisture and grass production under variable annual precipitation patterns are complex and poorly understood. For example, top-killing mature mesquite may briefly elevate soil moisture storage due to the removal of mesquite transpiration. However, this loss of mesquite competition usually stimulates grass growth [14] that may utilize most, if not all, of soil moisture made available from the temporary removal of mesquite. In time, we hypothesize that leaf mass of regrowth mesquite will exceed that of undisturbed mesquite woodland because of the multi-stemmed growth form, and this will reduce grass production and soil moisture. When and under what circumstances these transitions occur is unknown. The objective of this study is to quantify, over a multi-year period, interactions between mesquite regrowth patterns, herbaceous production, soil moisture and precipitation following the top-killing of mature mesquite plants.

2. Materials and Methods

2.1. Site Description

Research was conducted on a 6-ha area on the Smith-Walker Research Ranch located 13 km south of Vernon, in north central Texas (34°01'52" N; 99°15'00" E; elevation 372 m). Mean annual rainfall is

665 mm with monthly peaks in May (119 mm) and September (77 mm). Mean annual air temperature is 16.9 °C and mean monthly air temperatures range from an average daily maximum of 36 °C in July to an average daily minimum of −2.5 °C in January [19]. The growing season for mesquite is typically from April through September. Soils are fine, mixed, superactive, thermic Typic Paleustalfs of the Wichita series that are 1 to 2-m deep clay loams [20]. The site is on level ground.

At study initiation in 2006, the woody overstory consisted of honey mesquite with a much smaller population of lotebush (*Ziziphus obtusifolia*). Ring count data revealed that basal stems of most of the mature mesquite on the site were 25 years old. The dominant perennial grass species was the C₃ mid-grass Texas wintergrass (*Nassella leucotricha*). Other grass species that occurred on the site were C₄ perennial short-grasses, buffalograss (*Buchloe dactyloides*), and blue grama (*Bouteloua gracilis*), and C₄ perennial mid-grasses, sand dropseed (*Sporobolus cryptandrus*), vine mesquite (*Panicum obtusum*) and white tridens (*Tridens albescens*) [21]. Prickly pear cactus (*Opuntia phaeacantha*) occurred in few patches on the site. Forb production is usually sparse, although in some years there are outbreaks of common broomweed (*Amphichyris dracunculoides*) [22].

2.2. Treatment Description

Mesquite was mechanically cleared in October 2006 in four 0.5-ha plots (hereafter “cleared” treatment) using a custom-built machine equipped with a flail head rotor chopper that cut mesquite and all other vegetation to within 3 cm of the soil surface and lifted most of the mesquite debris into a collection basket which was then removed from the site. The remaining woody material (~10% of the total woody biomass) remained as a woody mulch with fragment sizes ranging from 1 to 10 cm long by 0.5 to 2 cm wide. There was no damage to the grasses or soils, and the bases of each mesquite tree were cut smooth and parallel to ground level at about 3 cm above ground. All mesquite trees subsequently resprouted from stem bases (there was zero mortality). We also established four 0.5-ha plots in untreated woodland (hereafter “woodland”) that had a dense mesquite overstory similar to what was described above. Cattle grazed in both treated and untreated plots during the study period at a stocking rate of 6 to 8 ha·AU^{−1}·year^{−1} with occasional (3–6 month) grazing deferment during droughts.

2.3. Data Collection

Soil moisture was measured using a neutron probe (CPN Model 503DR, Instrotek, Inc., Concord, CA, USA). Two 5-cm diameter aluminum tubes were established to a depth of 1.5 m in interspaces between trees in each plot. Measurements were made at 30, 60, 90 and 120 cm depth about once each month for the first 6 years, 2007–2012. Unfortunately, neutron probe measurements ceased after 2012 due to budget constraints. Precipitation was recorded on site and compared to the 30-year average [23].

Grass production was measured by clipping in the cleared and woodland treatment from 2007–2015. We did not sample grass production in 2016 (year 10). Clipping occurred twice a year, once in late spring (May or June) after the bulk of the C₃ grasses had grown, and once in the fall (October) after most C₄ grasses had grown. To protect grasses from cattle grazing, five, 1-m wide × 2-m long × 1.2-m tall wire cages were randomly located within each plot in February of each year before grasses began growing. Prior to positioning each cage, all standing dead grass litter was removed by hand from the area to be included in each cage as well as a 1-m buffer area surrounding each cage. All herbaceous material was clipped to within 2 cm of ground level within a 0.25-m² frame in each cage in late-spring and at a different location within each cage in fall. Clipped material was separated into 5 functional groups: C₃ annual grasses, C₃ perennial mid-grasses, C₄ perennial mid-grasses, C₄ perennial shortgrasses, and forbs. Samples were oven dried at 60 °C and weighed. For this paper, we report only total perennial grass (TPG) production and averaged the spring and fall data for each year.

Mesquite stand characteristics were measured in October 2006 along 3 parallel, 30-m long line transects in mesquite woodland that would be cleared and in woodland that would remain untreated.

Percent canopy cover was measured by line intercept, and tree density was measured by establishing a 5 m wide belt transect along each line and counting the number of trees within the 5 × 30 m belt. For individual mesquite tree data, height and diameter of all basal stems were measured on each of 10 randomly selected trees near the transect lines. To estimate wood weight·tree⁻¹, we used the equation:

$$\text{Stem Dry Live Wood Weight} = 0.035 x^{2.629} \quad (1)$$

For each basal stem, where x = stem diameter measured at between 5 and 20 cm above ground, then added all stem weights per tree together. This equation was based on the harvest of 160 mesquite stems (range of diameters: 2 to 25 cm) located near the study site ($r^2 = 0.97$; Figure 1). To estimate leaf weight in woodland trees, we used percentage values of 5% of total above-ground weight for 25 year old, and 4% for 30 and 35 year old mesquite, as determined by Ansley et al. [17]. Total above-ground weight·tree⁻¹ was determined by adding leaf + wood weights. At the end of the study (year 10), stand and tree characteristics were again measured (or calculated) for trees in the untreated woodland.

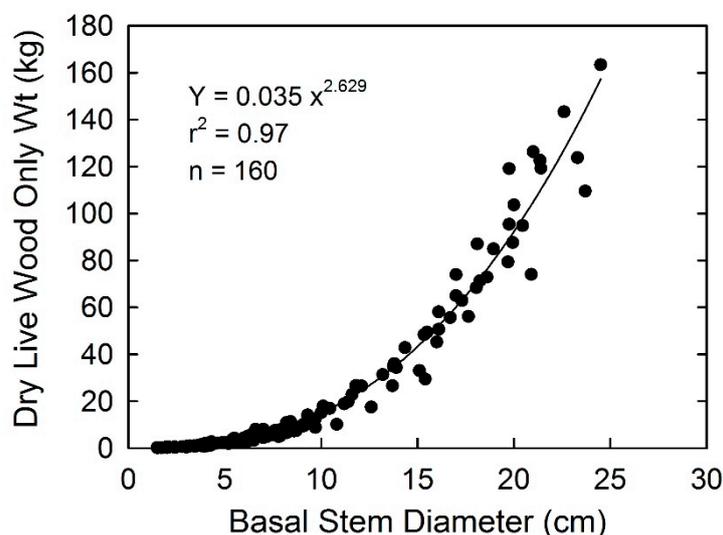


Figure 1. Relationship between mesquite basal stem diameter and oven dry live wood weight supported by that stem.

To assess architecture of mesquite regrowth in the cleared treatment, individual trees were harvested during each growing season following canopy measurements of height, diameter in two directions, and number and diameter of basal stems. Harvested material was manually separated into leaves, twigs (0–0.5 cm diameter), small stems (0.5 to 3 cm diameter) and large stems (>3 cm diameter), then oven dried at 60 °C to stable weight and weighed. A greater number of trees were harvested in early years, but as regrowth size increased, sample size was reduced due to logistic constraints. In all, 97 regrowth trees were sampled.

Leaf subsamples were collected each year to determine specific leaf area (SLA; leaf area of one side·dry weight⁻¹). Leaf area·tree⁻¹ was calculated by multiplying SLA by total leaf weight·tree⁻¹. Leaf area index (LAI) was determined by dividing leaf area·tree⁻¹ by canopy area. Tree canopy area was determined using the equation:

$$\text{Canopy Area} = \pi (D_1/2) (D_2/2) \quad (2)$$

where D_1 is canopy diameter at the widest part and D_2 is canopy diameter at 90° to D_1 .

Annual relative growth rate (RGR; expressed as $\text{kg} \cdot \text{kg}^{-1} \cdot \text{year}^{-1}$) of mesquite total tree weight was calculated using the equation:

$$\text{RGR} = (\text{Ln } W_2 - \text{Ln } W_1) / (t_2 - t_1) \quad (3)$$

where W_1 is weight in one year, W_2 is weight in the following year (kg), t_1 is the first year and t_2 is the following year [24].

2.4. Statistical Analysis

Soil moisture was analyzed within each sample date, and total perennial grass production was analyzed within each year using the analysis of variance (ANOVA) procedure (PROC) in Statistical analysis System (SAS) (Version 9.4, SAS Institute, Cary, NC, USA) with a completely randomized design model that included 4 replicate plots per treatment and two treatments: Cleared and woodland [25]. Sub-plot values were averaged to generate replicate plot values for each treatment. Percentage data were Arcsine transformed prior to analysis. Mean separation was performed using Least Significant Difference (LSD) ($p \leq 0.05$).

Mesquite regrowth architecture was analyzed using a one-way General Linear Model (GLM) analysis in SAS with regrowth age as the independent variable, structural components as the dependent variables, and trees as the replicates to determine changes in regrowth variables through time [25,26]. Mean comparisons were performed using LSD at $p \leq 0.05$. In addition, differences in weight of structural components as a percentage of total tree weight were compared within each year using Proc GLM. For this analysis, each component (leaf, twig, small stem and large stem) was established as the independent variable, with the percentage value as the dependent variable and trees as the replicates. Correlations between annual precipitation and RGR were also performed.

3. Results

3.1. Precipitation

During the 10-year post-clearing period, annual precipitation was well above average in 3 years, and well below average in 5 years (Figure 2A). Growing season (April–September) precipitation followed a similar pattern, although it was near or above average for 8 of the 10 years (Figure 2B).

The area experienced extreme drought in 2011–2012 that killed many trees and perennial grasses. Cumulative annual precipitation revealed an extended negative deviation from average from years from 2011–2015 (years 5–9) (Figure 2C).

3.2. Soil Moisture

As expected, the greatest range of soil moisture responses occurred at the 30 cm depth, followed by progressively lower ranges at lower depths for both treatments (Figure 3). Soil moisture in both treatments declined to its lowest level at 30 cm depth from July to September 2011, during a period of extreme drought (Figure 3E).

There were significant ($p \leq 0.05$) differences between treatments on certain dates and soil depths. In general, soil moisture was greater in the woodland than the cleared treatment at 30 cm depth on several dates in 2007 and 2008 (Figure 3A,B). However, most of the other differences during the first 4 years were due to soil moisture being greater ($p \leq 0.05$) in the cleared than the woodland treatment. During summer in 2010, soil moisture declined more rapidly at 60 and 90 cm depth in the cleared treatment following rainfall recharge (Figure 3J,P). In the last two years (2011–2012), soil moisture was remained lower in the cleared treatment than the woodland treatment at 60 cm depth on most dates (Figure 3K,L).

Figure 4 shows the difference in soil moisture mean of all growing season dates (April–September) between cleared and woodland at each depth, each year. At 30 cm depth, soil moisture was greater

in woodland in years 1 and 2, greater in cleared in years 3 and 4, and similar between treatments in years 5 and 6. At 60 and 90 cm depths, soil moisture was initially slightly greater in the cleared treatment, then progressively became greater in the woodland treatment, with the exception of year 4 (2010). The range of differences between treatments at 120 cm depth was small in all 6 years. Ecological interpretations of trends in both Figures 3 and 4 are in the Discussion section.

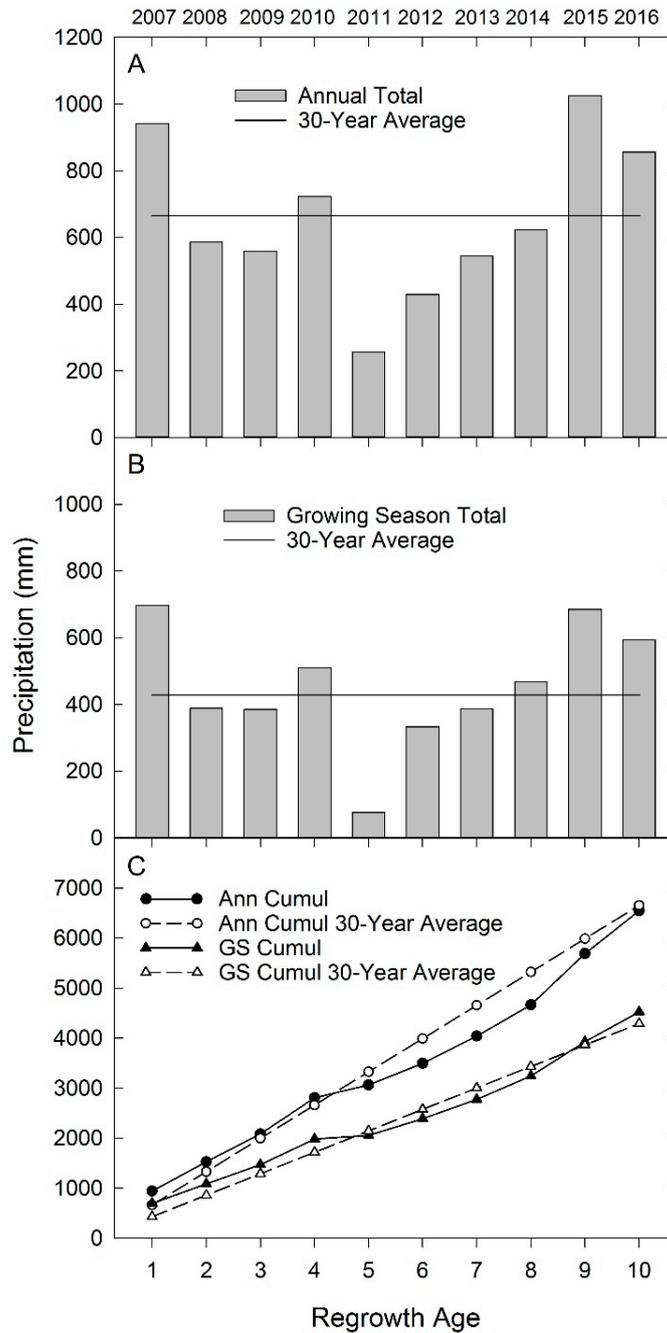


Figure 2. Annual (A) and growing season (April–September) (B) precipitation totals, and cumulative (Cumul), annual (Ann) and growing season (GS) totals (C) at the site compared to the 30-year average, years 1–10 (2007–2016).

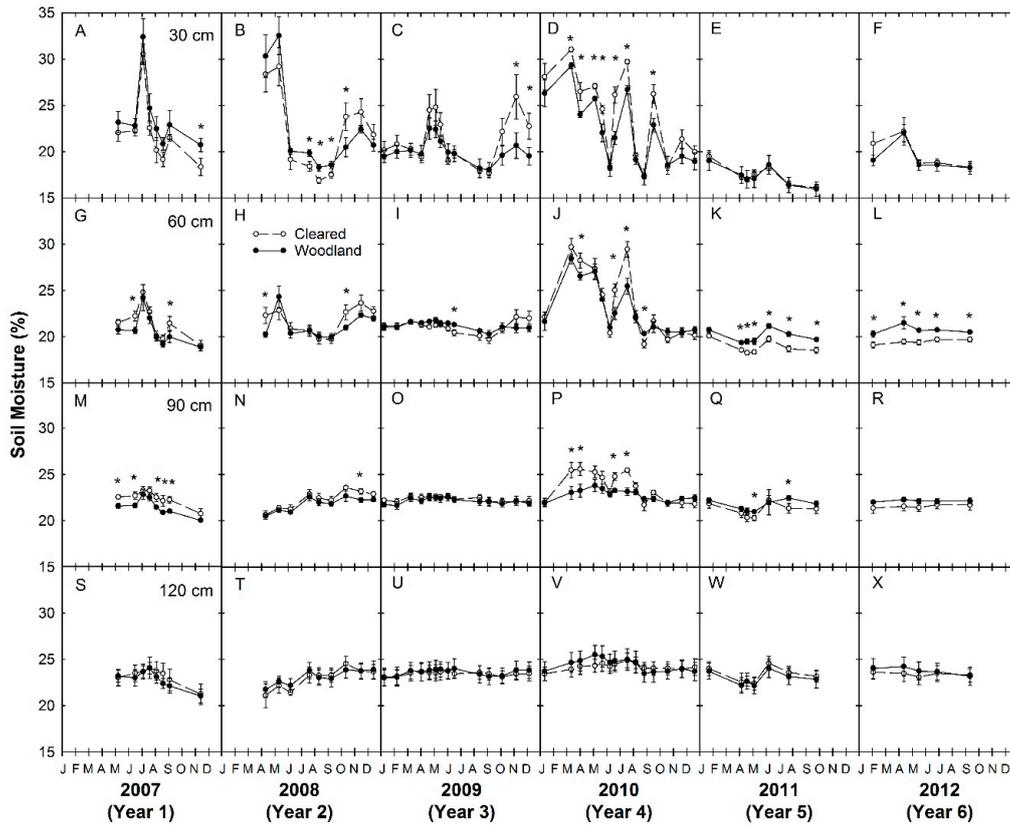


Figure 3. Soil moisture at 4 depths in cleared and woodland treatments, 2007–2012. Letters on x-axis indicate the beginning of each month and gap between hash marks is the duration of that month. Vertical bars are ±1 standard error (n = 4). Means with an asterisk above are significantly different at $p \leq 0.05$. Capital letters A through X are used to identify each panel by year and soil depth.

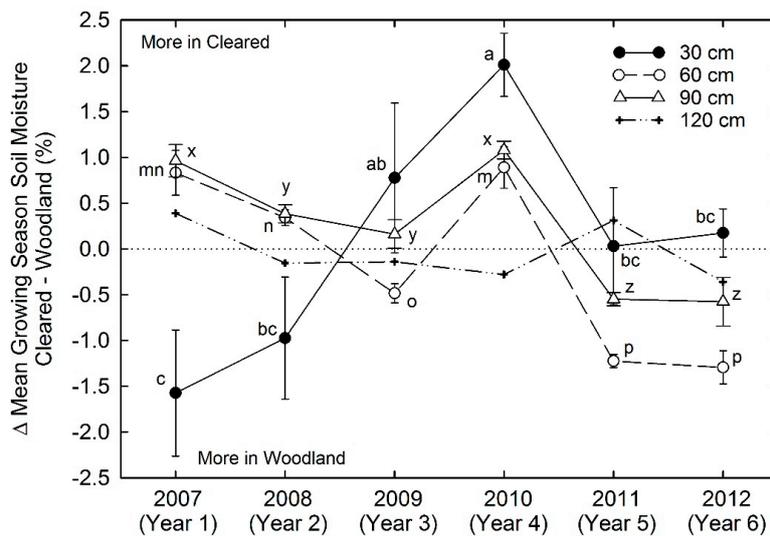


Figure 4. Difference in mean growing season soil moisture between cleared and woodland treatments at each soil depth, 2007–2012. Each point represents the mean of all growing season sample dates (April–September) in cleared minus mean of same dates in woodland. Points above zero line indicate more moisture in cleared; below more in woodland. Vertical bars are ±1 standard error (n = 4); not shown for 120 cm depth. Means with different letters within each depth are significantly different at $p \leq 0.05$ (30 cm, a–c; 60 cm, m–p; 90 cm, x–z). There were no significant differences at 120 cm depth.

3.3. Mesquite Responses

Mesquite regrowth canopy area $\cdot \text{tree}^{-1}$ increased in a linear fashion during the 10-year period (Figure 5A). Tree height also steadily increased but the rate of increase began to decline at 6 years regrowth age (Figure 5B); thus, the ratio of canopy area to tree height increased over time (Figure 5C).

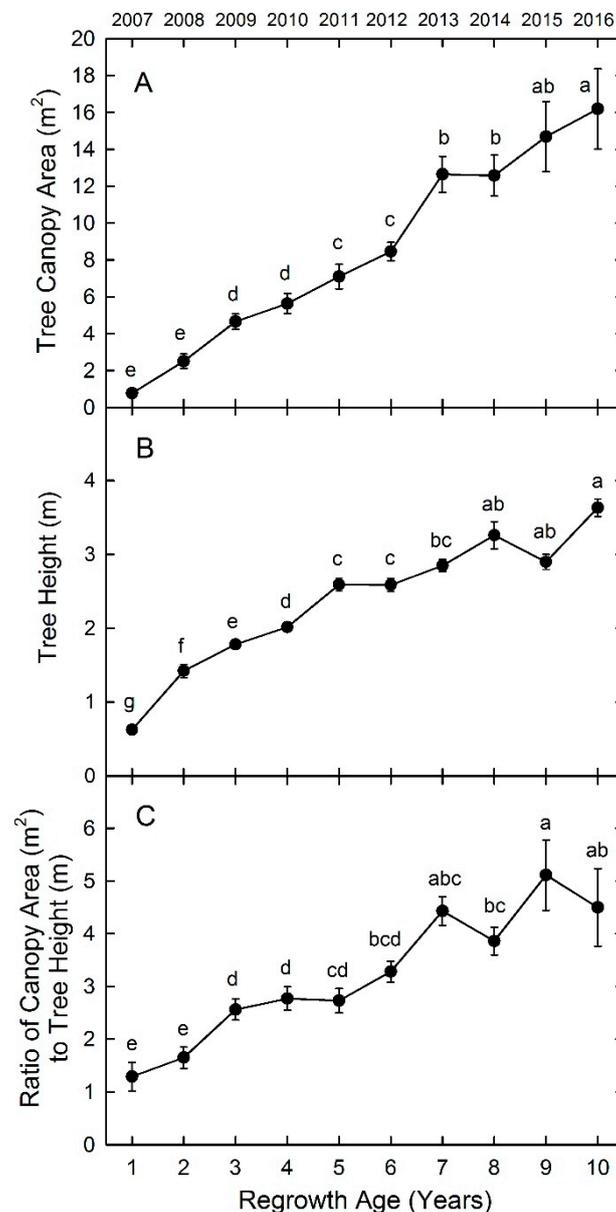


Figure 5. Mesquite canopy area (A), height (B) and ratio of canopy area to height (C) of regrowth mesquite, 1 to 10 years. Vertical bars on each mean indicate ± 1 standard error. Means with different letters within each panel are significantly different at $p \leq 0.05$.

Mesquite regrowth above-ground weight $\cdot \text{tree}^{-1}$ increased numerically each year, with significant ($p \leq 0.05$) increases occurring about every two years (Figure 6A). A linear regression predicted regrowth tree weight from regrowth age ($r^2 = 0.96$; Figure 6A). Of the regrowth structural components, the greatest biomass accumulation occurred with small stems through year 10. Large stem growth was non-existent until year 3. Substantial large stem growth occurred at a uniform rate from year 5 to 10, with the lone exception of year 6 (2012). Leaf and twig weight $\cdot \text{tree}^{-1}$ paralleled each other, with twig weight being slightly greater in 5 of the 9 years.

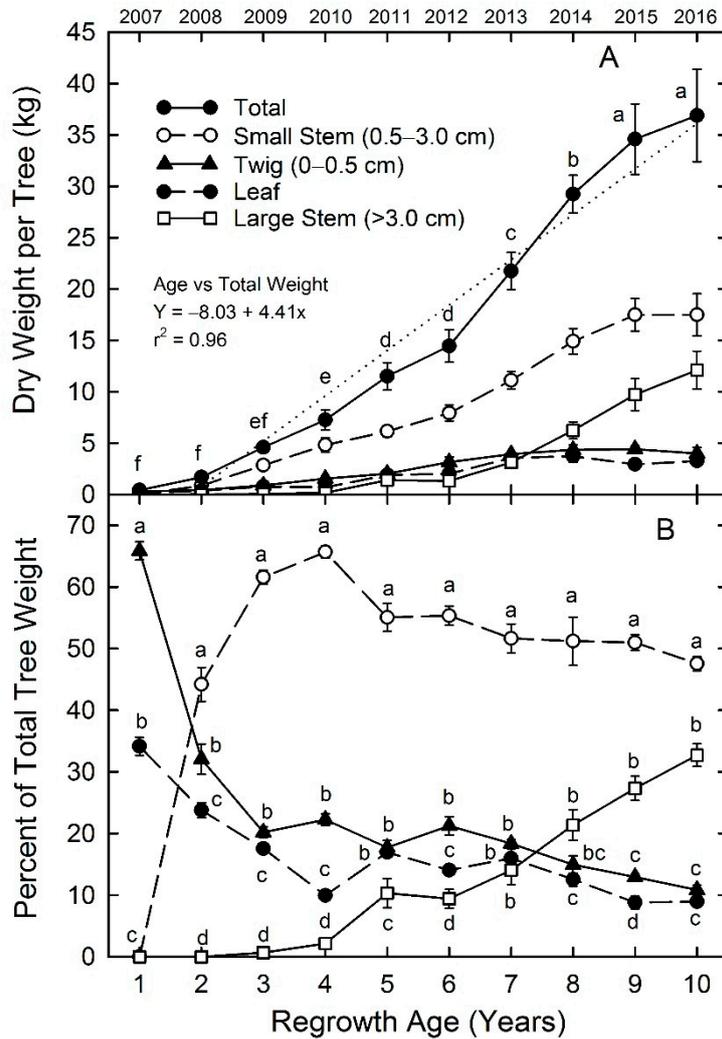


Figure 6. Canopy components in actual dry weight (A) and as a percentage of total dry weight (B). Vertical bars on each mean indicate ± 1 standard error. Means with different letters across all ages (panel A), or within each regrowth age (panel B) are significantly different at $p \leq 0.05$. Dotted line in panel A is the linear regression between age and total weight (equation shown).

When expressed as a percentage of total tree weight, leaves and twigs comprised most of the total biomass in the first year, sharply declined from year 1 to 2, and steadily declined after that until each component comprised 9–10% of the total tree weight in year 10 (Figure 6B). Small stem percentage of total weight increased from years 1–4, and slightly declined each year after that to 48% in year 10. Large stem percentage of total weight steadily increased from years 5 to 10, with the exception of year 6 (2012). By year 10, large stem weight comprised slightly over 30% of the total above-ground weight.

The relative growth rate (RGR) of tree weight declined over time (Figure 7A). Declines in years 4 and 6 appeared to be steeper than the trend established in the other years. There was no relation between RGR and annual precipitation or growing season precipitation (data not shown). Mesquite tree weight $\cdot \text{canopy area}^{-1}$ increased over time from about 0.5 to 2.5 $\text{kg} \cdot \text{m}^{-2}$ (Figure 7B). However, mesquite LAI remained between 0.5 and 1.8 and showed no trend related to regrowth age. When plotted together, the two curves began to diverge in years 8–10.

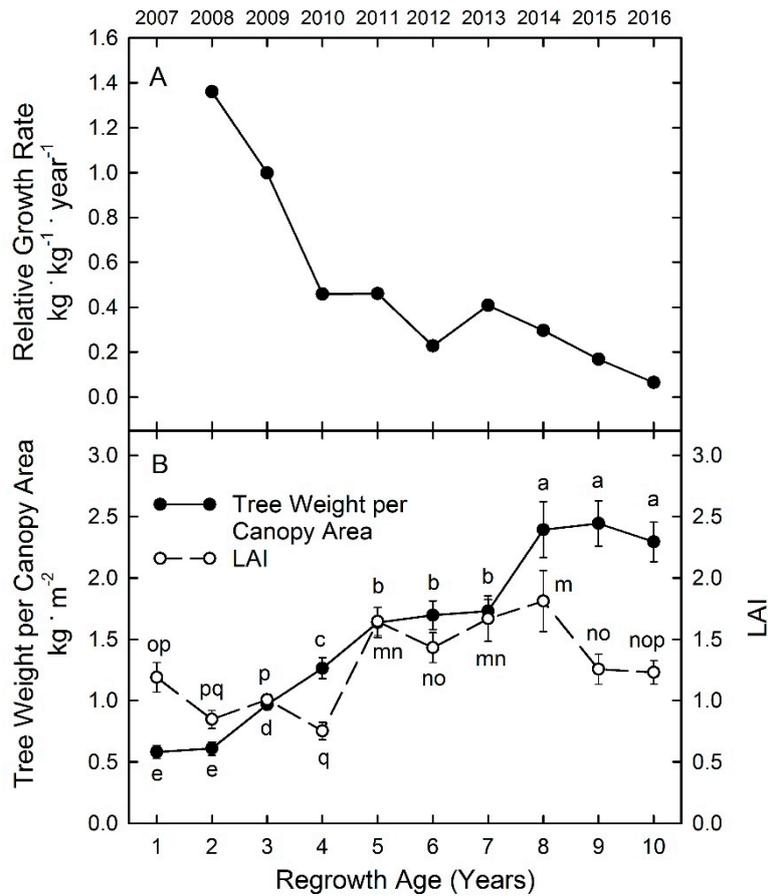


Figure 7. Regrowth age vs relative growth rate (A), and regrowth age vs mesquite tree weight per canopy area, and vs. LAI (B). Vertical bars on means in panel B indicate ± 1 standard error. Means with different letters across all ages (panel B), are significantly different at $p \leq 0.05$ for tree weight per canopy area (a–e) or LAI (m–q). Values in panel A were derived from means and have no statistical analysis.

In comparing mesquite stand data in the two treatments, prior to clearing in 2006, mesquite canopy cover, density, tree height, and wood weight·tree⁻¹ were similar between woodland-to-be-cleared and untreated woodland (Table 1). By study’s end, mesquite regrowth biomass was 36.89 kg·tree⁻¹ which was slightly lower than the pre-cleared woodland value of 39.59 kg·tree⁻¹. Untreated woodland trees had gained 13% in height and 56% in weight·tree⁻¹, and stand biomass increased by 62%. Stand canopy cover and tree density remained similar. Annual growth rate in regrowth and woodland trees was 3.69 and 2.4 kg·tree⁻¹·year⁻¹, respectively.

Table 2 compares tree and stand data in the cleared and woodland treatment at the beginning of the severe drought in 2011. Using the starting weight in 2006 and a tree growth rate of 2.4 kg·tree⁻¹·year⁻¹ (from Table 1), weight of woodland trees in 2011 was estimated to be 54.79 kg·tree⁻¹, and leaf weight, at 4% of total tree weight, was 2.19 kg·tree⁻¹. In contrast, regrowth mesquite in the cleared treatment weighed only 11.51 kg·tree⁻¹ in 2011, but because 16.95% of total tree weight was leaf tissue, leaf weight·tree⁻¹ was 1.92 kg. Using densities from pre-treatment data, mesquite stand leaf weight was 1.11 and 1.36 mg·ha⁻¹ in cleared and untreated woodland, respectively.

Table 1. Mesquite stand and individual tree data in the cleared treatment prior to clearing (2006) and at 10 years post-clearing (2016), and the untreated woodland in 2006 and 2016. Asterisk indicates a projected value, based on leaf weight being either 5% (2006), or 4% (2016) of total tree weight [17]. Means are followed by standard error in parentheses. No statistics were provided for projected values.

Mesquite Variable	Pre-cleared Woodland 2006	Cleared Regrowth 2016	Untreated Woodland 2006	Untreated Woodland 2016
Canopy cover (%)	71.1 (10.3)	No data	66.1 (7.3)	68.8 (6.6)
Density (trees·ha ⁻¹)	578 (97)	598 ¹	622 (124)	644 (146)
Tree height (m)	4.33 (0.15)	3.63 (0.12) ²	3.98 (0.12)	4.48 (0.22)
Basal Stems (#·tree ⁻¹)	4.55 (1.29)	13.11 (1.73)	4.17 (1.04)	3.42 (0.76)
Wood weight (kg·tree ⁻¹)	37.61 (7.92)	33.62 (4.17)	40.65 (6.36)	64.10 (10.24)
Leaf weight as a % of total tree weight	5 *	8.93 (0.20) ³	5 *	4 *
Leaf weight (kg·tree ⁻¹)	1.98 *	3.28 (0.35) ³	2.14 *	2.67 *
Tree weight (kg·tree ⁻¹)	39.59 *	36.89 (4.51) ³	42.79 *	66.76 *
Growth rate (kg·tree ⁻¹ ·year ⁻¹)	0	3.69 (0.45)	0	2.40
Stand leaf weight (mg·ha ⁻¹)	1.14 *	1.96 *	1.33 *	1.72 *
Stand biomass (mg·ha ⁻¹)	22.87 *	22.06 *	26.62 *	43.03 *

¹ Stand density in the cleared regrowth in 2016 was estimated based on the percent increase in density found in the untreated woodland; ² Data also shown in Figure 5B; ³ Data also shown in Figure 6.

Table 2. Mesquite stand and individual tree data of regrowth trees in the cleared treatment and woodland trees in 2011. Asterisk indicates a projected value, based on leaf weight being 4% of total tree weight. Regrowth means are followed by standard error in parentheses. No statistics were provided for projected values.

Mesquite Variable	Cleared Regrowth 2011	Untreated Woodland 2011 *
Density (trees·ha ⁻¹)	578 *	622 *
Wood weight (kg·tree ⁻¹)	9.60 (1.14)	52.37 *
Leaf weight as a % of total tree weight	16.95 (0.70) ¹	4 *
Leaf weight (kg·tree ⁻¹)	1.92 (0.21) ¹	2.19 *
Tree weight (kg·tree ⁻¹)	11.51 (1.34) ¹	54.79 *, ²
Stand leaf weight (mg·ha ⁻¹)	1.11 *	1.36 *
Stand biomass (mg·ha ⁻¹)	6.65 *	34.08 *

¹ Data also shown in Figure 6; ² Woodland tree weight in 2011 = 42.79 kg·tree⁻¹ + (2.4 kg·tree⁻¹·year⁻¹ × 5 years).

3.4. Grass Production

Total perennial grass production (TPG) was significantly ($p \leq 0.05$) greater in the cleared than the woodland treatment from 2007 through 2011, even under slightly below average precipitation in 2008 and 2009 (years 2 and 3) (Figure 8). The extreme drought of 2011–2013 reduced TPG to below 50 g·m⁻¹ in both treatments during 2012 and 2013 (years 6 and 7). With increasing precipitation in 2014 and 2015, TPG recovered in both treatments and was again significantly ($p \leq 0.05$) greater in the cleared treatment, although by this time mesquite regrowth was 3 m tall. A high level of forb production, mainly common broomweed, occurred in 2007 and was similar in both treatments, as described previously [22].

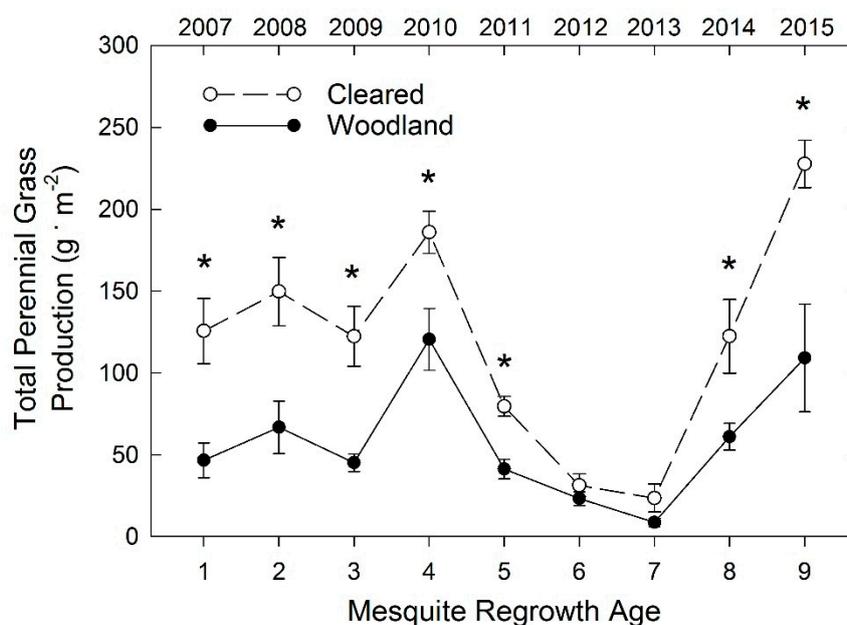


Figure 8. Total perennial grass (TPG) production, 2007–2015. Vertical bars on each mean indicate ± 1 standard error ($n = 4$). Means with an asterisk above are significantly different at $p \leq 0.05$.

4. Discussion

4.1. Soil Moisture

Soil moisture responses at 30 cm depth are likely the result of grass root activity, while responses at deeper depths are due to mesquite roots [27]. Since there was little soil moisture change at 120 cm depth (Figures 3 and 4), it appears that most of the mesquite root activity occurred at 60 and 90 cm depths.

Our goal with soil moisture measurements was to compare cleared vs woodland treatments at depths deep enough to detect mesquite root system effects. We acknowledge that our sampling frequency may not have captured the complete range of soil moisture dynamics as has been demonstrated elsewhere [28]. However, our sampling scheme was sufficient for us to draw the conclusions related to soil moisture and ecosystem responses.

In years 1 and 2 (2007, 2008), the reason soil moisture at 30 cm depth was, on average (Figure 4), greater in the woodland than the cleared treatment was because greater grass production increased soil moisture uptake in the cleared treatment. In years 3 and 4 (2009, 2010), soil moisture at 30 cm was greater in the cleared treatment due to greater gain in soil moisture during rainfall events because mesquite canopies in woodland, which were much larger than regrowth canopies in cleared, intercepted some of the rainfall, which evaporated before reaching soil. By years 5 and 6, an extreme drought caused grasses to exhaust soil moisture at 30 cm depth to low levels in both treatments.

The reason soil moisture at 60 and 90 cm depth was, on average (Figure 4), greater in the cleared treatment in years 1 and 2 was because the top-killing of mesquite greatly reduced leaf transpiration and water uptake by mesquite root systems. From years 3 through 6, soil moisture became progressively greater in the woodland treatment at these soil depths as regrowth mesquite in the cleared treatment grew and extracted more soil water. This trend reached maximum extent in drought years 5 and 6 (2011–2012). Responses were most evident at 60 cm depth, suggesting that this was the soil depth where mesquite roots were concentrated. The exception to this trend was year 4 (2010), a wet year.

Figure 4 demonstrates that under drought conditions, relatively young regrowth mesquite progressively extracted a greater amount of soil moisture than did mature woodland mesquite. However, the opposite trend occurred in wet years because the larger woodland canopies intercepted more rainfall than did the smaller regrowth canopies. Eventually regrowth canopies would grow too

similar (or possibly larger size due to more stems) than woodland canopies and the trend that favors soil moisture gains in the cleared treatment in wet years would disappear.

Since mesquite density was similar in both treatments, we must ask why regrowth mesquite in the cleared treatment extracting were more soil moisture than were woodland mesquite in years 5 and 6. Table 2 shows that when the severe drought began in 2011, regrowth mesquite in the cleared treatment weighed much less per tree than did woodland trees, but the greater percent leaf weight in regrowth trees offset most of the differences in stand leaf weight between regrowth and woodland treatments. Additionally, leaf transpiration rates may have been greater in regrowth mesquite, possibly due to younger, more efficient vascular tissue [29–31]. Root-to shoot ratios were likely greater in regrowth than woodland trees because regrowth arose from old root systems, and this may also have enhanced transpiration rates in regrowth trees.

4.2. Relation of Mesquite Regrowth to Precipitation

The high variability of annual precipitation compared to a linear gain in regrowth biomass provided evidence that mesquite regrowth in any year was independent of precipitation trends during that year. A similar lack of correlation between precipitation and growth of mature mesquite was found in south Texas [18]. The authors of Reference [18] hypothesized that this was due to deeper roots that could draw on soil moisture reserves during drought. It was not until two consecutive drought years occurred (2011–2012) that mesquite RGR declined sharply and weight·tree⁻¹ did not significantly ($p \leq 0.05$) increase in 2012.

In addition to the RGR and tree total weight responses, another aspect of mesquite regrowth that was affected by consecutive droughts was the response of large stem growth in 2012. Radial expansion of large stems ceased during the second year of extreme drought, yet twig and small stem growth continued. Many species, including mesquite, shift carbon allocation to increase production of reproductive structures during drought [32,33]. However, this study revealed that the process of activating cambial meristem to expand stem diameter was delayed during extended drought to prioritize growth of smaller woody components via apical meristem. A similar strategy was described for physiologically stressed lodgepole pine (*Pinus contorta*) [34].

4.3. Mesquite Regrowth Architecture and Biomass

Structurally, the greater expansion of canopy area relative to gain in height-maintained LAI with increasing regrowth age, and increased the potential for canopy interception of rainfall, both of which are factors that could help withstand drought.

The regrowth leaf weight value of 8.9% of total plant weight by year 10 is similar to findings by Northup et al. [35] who found that mesquite leaf weight percent (tree ages unknown) averaged 10.1. Studies of similar shrubs in Africa, Australia and India found that leaf weight percentages ranged from 3–7% [36–38]. Ansley et al. [17] found that leaf weight in 28-year old mesquite comprised 5% of total tree weight.

Twig weight remained slightly greater than leaf weight and the ratio of leaf to twig weight was maintained between 0.5 and 1.0 during all 10 years. A similar relationship was found with post-fire dogwood (*Cornus drummondii*) regrowth in Kansas [39]. In contrast, leaf-to-twig weight ratios ranged from 3–10 in white oak (*Quercus alba*) and other shrub species in the more mesic Northeastern USA [40]. It is possible that greater twig mass relative to leaf mass was needed in mesquite because of the large bi-pinnately compound mesquite leaf (even though each leaflet is small), and/or because twigs are usually the structures that support relatively heavy legume pods.

Regarding overall biomass accumulation, above-ground dry weight (wood + leaf) of 10-year-old regrowth mesquite was 36.9 kg·tree⁻¹ which is slightly greater than the 29.4 kg·tree⁻¹ found on 10-year-old regrowth mesquite at a site near the current site [17]. With an estimated density of 598 trees·ha⁻¹, the above-ground standing crop of 10-year old regrowth mesquite was 22.1 mg·ha⁻¹ (Table 1). This standing crop value is similar to that found for old growth mesquite in central Texas [41]

and southern California [42]. The weight of 10-year-old regrowth mesquite was slightly lower than that of 25-year-old mesquite in the pre-cleared and untreated woodland, respectively, at study initiation. The trajectory of regrowth biomass accumulation derived from Figure 6A ($Y = -8.028 + 4.413x$) revealed that weight of regrowth trees would equal that of pre-treatment mesquite by 12 years of age. In a different stand of mesquite located near the current study site, 14-year old regrowth trees had the same weight-tree⁻¹ as did 33-year-old trees that began as seedlings [17].

4.4. Grass Production

Grass responses agree with many other studies that found an increase in TPG production in the years immediately following the top-killing or root-killing of mesquite [13,43]. What was unusual in our study was that in the first 3 years after clearing, grass production was over twice as great in the cleared than the woodland treatment. Most studies do not show such a high level of response immediately after treatment of mesquite with such a high canopy cover of 71%. This was largely because a solid stand of Texas wintergrass existed beneath mesquite woodland canopies prior to treatment, and this grass species was able to increase production in the immediate years after mesquite clearing. In addition, growing season rainfall in those 3 years was near or above average. The range of responses seen in this study was typical for a Texas wintergrass community [8].

The severe drought from 2011–2013 removed differences in grass production between the cleared and woodland treatment in 2012 and 2013, but not in 2011. Greater grass production remained in the cleared treatment rather than the woodland treatment in 2011 because most of C₃ Texas wintergrass growth occurred in early spring before the main impact of the 2011 drought occurred. In addition, very low grass production in both treatments in 2012 and 2013 indicated that regrowth mesquite at this time were as effective as woodland mesquite at suppressing grass growth during drought.

It was unusual to find greater TPG production in the cleared than the woodland treatment in 2014 and 2015, 8 and 9 years after clearing [14,44]. Mesquite regrowth by that time was >3 m tall. The year 2014 had slightly below average annual precipitation, but had 3 times the average precipitation in July (data not shown). The year 2015, had well-above average annual and growing season precipitation, with over 400 mm occurring in May alone. A greater abundance of C₄ mid-grasses began to appear in the cleared treatment prior to the 2011–2012 drought years (data not shown), and these grasses, having greater production potential than Texas wintergrass [8], triggered greater TPG production in the cleared than the woodland treatment in response to abundant and timely rains in 2014 and 2015.

5. Conclusions

This study demonstrated that top-killing mesquite yielded greater grass growth (which has been observed in many studies), but shifted mesquite into a resprouting growth form that created potentially negative effects on soil moisture. The dynamics of soil moisture responses between woodland and cleared (i.e., regrowth) treatments were complex and depended on precipitation, soil depth, grass production, and mesquite regrowth age. In the immediate years after mesquite top-kill, increased grass production in the cleared treatment reduced soil moisture in shallow soil layers, relative to untreated woodland, but soil moisture in deeper layers increased relative to woodland because mesquite had very little transpiring tissue and minimal water uptake by remaining root systems. In wet years, woodland canopies, still larger than regrowth canopies, intercepted more rainfall, which then was lost to evaporation, resulting in soil moisture gains in the cleared treatment compared to woodland. However, in drought years, greater leaf area-tree⁻¹ and possibly greater leaf transpiration rates of regrowth mesquite reduced soil moisture in mesquite root zones (60–90 cm depth) in the cleared treatment to levels below that in woodland.

Regarding our hypothesis, we found that per tree leaf weight of regrowth mesquite exceeded that of woodland trees by 7 years after top-killing. We also found that as early as 5 years after top-killing, regrowth mesquite had a greater negative impact on soil moisture during a drought (at 60 and 90 cm depths) than did a nearly closed canopy woodland. However, we did not find that regrowth mesquite

reduced grass production below that in the woodland in any of the first 9 years after top-killing. Part of the reason for this was that years 8 and 9, when we would expect regrowth mesquite to begin to negatively impact grass growth [8,44], were exceptionally wet years. We anticipate that in future years, grass production will be lower in the regrowth than the woodland treatment.

From a rangeland management perspective, dominance of woody species like mesquite on the ecosystem is enhanced when the plant is shifted into a regrowth physiognomy. Eventually, regrowth mesquite could accelerate losses of soil moisture and grass production, which can then potentially lead to increased bare ground, soil erosion and permanent loss of livestock production potential. Managers should exercise caution before deciding to implement a treatment that causes only top-kill and not root-kill in this and similar woody invasive plants that resprout following a top-killing treatment [14].

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References

- Higgins, S.I.; Bond, W.J.; Trollope, W.S.W. Fire, resprouting and variability: A recipe for grass-tree coexistence in savanna. *J. Ecol.* **2000**, *88*, 213–229. [[CrossRef](#)]
- Bond, W.J.; Midgley, J.J. Ecology of sprouting in woody plants: The persistence niche. *Trends Ecol. Evol.* **2001**, *16*, 45–51. [[CrossRef](#)]
- Sage, R.F. Tansley review: The evolution of C4 photosynthesis. *New Phytol.* **2004**, *161*, 341–370. [[CrossRef](#)]
- Edwards, E.J.; Osborne, C.P.; Stromberg, A.A.E.; Smith, S.A. The origin of C4 grasslands: Integrating evolutionary and ecosystem science. *Science* **2010**, *328*, 587–591. [[CrossRef](#)] [[PubMed](#)]
- Bellingham, P.J. Resprouting as a life history strategy in woody plant communities. *Oikos* **2000**, *89*, 409–416. [[CrossRef](#)]
- Van Auken, O.W. Shrub invasions of North American semiarid grasslands. *Ann. Rev. Ecol. Syst.* **2000**, *31*, 197–215. [[CrossRef](#)]
- Mirik, M.; Ansley, R.J. Utility of satellite and aerial images for quantification of canopy cover and infilling rates of the invasive woody species honey mesquite on Rangel. *Remote Sens.* **2012**, *4*, 1947–1962. [[CrossRef](#)]
- Ansley, R.J.; Mirik, M.; Wu, X.B.; Heaton, C.B. Woody cover and grass production in a mesquite savanna: Geospatial relationships and precipitation. *Rangel. Ecol. Manag.* **2013**, *66*, 621–633. [[CrossRef](#)]
- Ansley, R.J.; Pinchak, W.E.; Owens, M.K. Mesquite pod removal by cattle, feral hogs and native herbivores. *Rangel. Ecol. Manag.* **2017**, *70*, 469–476. [[CrossRef](#)]
- Ansley, R.J.; Pinchak, W.E.; Jones, D.L. Mesquite, tobosagrass, and common broomweed responses to summer and winter season fires. *Rangel. Ecol. Manag.* **2008**, *61*, 588–597. [[CrossRef](#)]
- Ansley, R.J.; Kramp, B.A.; Jones, D.L. Honey mesquite (*Prosopis glandulosa*) seedling responses to seasonal timing of fire and fireline intensity. *Rangel. Ecol. Manag.* **2015**, *68*, 194–203. [[CrossRef](#)]
- McDaniel, K.C.; Brock, J.H.; Haas, R.H. Changes in vegetation and grazing capacity following honey mesquite control. *J. Range Manag.* **1982**, *35*, 551–557. [[CrossRef](#)]
- Bedunah, D.J.; Sosebee, R.E. Forage response of a mesquite-buffalograss community following range rehabilitation. *J. Range Manag.* **1984**, *37*, 483–487. [[CrossRef](#)]
- Ansley, R.J.; Castellano, M.J. Strategies for savanna restoration in the southern Great Plains: Effects of fire and herbicides. *Restor. Ecol.* **2006**, *14*, 420–427. [[CrossRef](#)]

15. Ansley, R.J.; Boutton, T.W.; Mirik, M.; Castellano, M.J.; Kramp, B.A. Restoration of C4 grasses with seasonal fires in a C3/C4 grassland invaded by *Prosopis glandulosa*, a fire-resistant shrub. *Appl. Veg. Sci.* **2010**, *13*, 520–530. [[CrossRef](#)]
16. Ansley, R.J.; Teague, W.R.; Pinchak, W.E.; Kramp, B.A.; Barnett, K. Integrated grazing and prescribed fire restoration strategies in a mesquite savanna: II. Fire behavior and mesquite landscape cover responses. *Rangel. Ecol. Manag.* **2010**, *63*, 286–297. [[CrossRef](#)]
17. Ansley, R.J.; Mirik, M.; Castellano, M.J. Structural biomass partitioning in regrowth and undisturbed mesquite (*Prosopis glandulosa*): Implications for bioenergy uses. *Glob. Change Biol. Bioenergy* **2010**, *2*, 26–36. [[CrossRef](#)]
18. Miller, D.; Archer, S.R.; Zitzer, S.F.; Longnecker, M.T. Annual rainfall, topographic heterogeneity and growth of an arid land tree (*Prosopis glandulosa*). *J. Arid Environ.* **2001**, *48*, 23–33. [[CrossRef](#)]
19. National Oceanic and Atmospheric Administration—National Climatic Data Center. *Climatological Data Annual Summary—Texas*; NOAA-NCDC: Ashville, NC, USA, 1997.
20. United States Department of Agriculture—Natural Resource Conservation Service (USDA-NRCS). Web Soil Survey. 2014. Available online: <http://websoilsurvey.nrcs.usda.gov/app> (accessed on 6 March 2014).
21. United States Department of Agriculture—Natural Resource Conservation Service (USDA-NRCS). Plants Database. 2014. Available online: <http://plants.usda.gov> (accessed on 6 March 2014).
22. Stanford, R.L.; Ansley, R.J.; Ransom, D. Common broomweed growth characteristics in cleared and woody landscapes. *Rangel. Ecol. Manag.* **2008**, *61*, 561–565. [[CrossRef](#)]
23. National Oceanic and Atmospheric Administration—National Climatic Data Center. *Annual Climate Normals—Texas*; NOAA-NCDC: Asheville, NC, USA, 2006.
24. Hoffman, W.A.; Franco, A.C. Comparative growth analysis of tropical forest and savanna woody plants using phylogenetically independent contrasts. *J. Ecol.* **2003**, *91*, 475–484. [[CrossRef](#)]
25. Lentner, M.; Bishop, T. *Experimental Design and Analysis*; Valley Book Company: Blacksburg, VA, USA, 1993; p. 585.
26. SAS. *Statistical Analysis Software Version 9.4 (Computer Program)*; SAS Institute: Cary, NC, USA, 2009.
27. Ansley, R.J.; Boutton, T.W.; Jacoby, P.W. Root biomass and distribution patterns in a semi-arid mesquite savanna: Responses to long-term rainfall manipulation. *Rangel. Ecol. Manag.* **2014**, *67*, 206–218. [[CrossRef](#)]
28. Molina, A.J.; Latron, J.; Rubio, C.M.; Gallart, F.; Llorens, P. Spatio-temporal variability of soil water content on the local scale in a Mediterranean mountain area (Vallcebre, North Eastern Spain). How different spatio-temporal scales reflect mean soil water content. *J. Hydrol.* **2014**, *516*, 182–192. [[CrossRef](#)]
29. Schafer, J.L.; Breslow, B.P.; Hollingsworth, S.N.; Hohmann, M.G.; Hoffmann, W.A. Size-dependent enhancement of water relations during post-fire resprouting. *Tree Physiol.* **2014**, *34*, 404–414. [[CrossRef](#)] [[PubMed](#)]
30. Cooper, C.E.; Aparecido, L.M.T.; Muir, J.P.; Morgan, C.L.S.; Heilman, J.L.; Moore, G.W. Transpiration in recovering mixed loblolly pine and oak stands following wildfire in the Lost Pines region of Texas. *Ecohydrology* **2018**, in press.
31. Ansley, R.J.; Dugas, W.A.; Heuer, M.L.; Kramp, B.A. Bowen ratio/energy balance and scaled leaf measurements of CO₂ flux over burned *Prosopis* savanna. *Ecol. Appl.* **2002**, *12*, 948–961.
32. Felker, P.; Clarke, P.R.; Osborn, J.F.; Cannell, G.H. *Prosopis* pod production—Comparison of North American, South American, Hawaiian, and African germplasm in young plantations. *Econ. Bot.* **1984**, *38*, 36–51. [[CrossRef](#)]
33. Lee, S.G.; Felker, P. Influence of water/heat stress on flowering and fruiting of mesquite (*Prosopis glandulosa* var. *glandulosa*). *J. Arid Environ.* **1992**, *23*, 309–319.
34. Waring, R.H.; Pitman, G.B. Modifying lodgepole pine stands to change susceptibility to mountain pine beetle attack. *Ecology* **1985**, *66*, 889–897. [[CrossRef](#)]
35. Northup, B.K.; Zitzer, S.F.; Archer, S.; McMurtry, C.R.; Boutton, T.W. Above-ground biomass and carbon and nitrogen content of woody species in a subtropical thornscrub parkland. *J. Arid Environ.* **2005**, *62*, 23–43. [[CrossRef](#)]
36. Meneaut, J.C.; Cesar, J. Structure and primary productivity of Lamto savannas, Ivory Coast. *Ecology* **1979**, *60*, 1197–1210. [[CrossRef](#)]

37. Werner, P.A.; Murphy, P.G. Size-specific biomass allocation and water content of above- and belowground components of three Eucalyptus species in a northern Australian savanna. *Aust. J. Bot.* **2001**, *49*, 155–167. [[CrossRef](#)]
38. Singh, G.; Mutha, S.; Bala, N. Effect of tree density on productivity of a Prosopis cineraria agroforestry system in northwestern India. *J. Arid Environ.* **2007**, *70*, 152–163. [[CrossRef](#)]
39. McCarron, J.K.; Knapp, A.K. C₃ shrub expansion in a C₄ grassland: Positive post-fire responses in resources and shoot growth. *Amer. J. Bot.* **2003**, *90*, 1496–1501. [[CrossRef](#)] [[PubMed](#)]
40. Whittaker, R.H.; Woodwell, G.M. Dimension and production relations of trees and shrubs in the Brookhaven Forest, New York. *J. Ecol.* **1968**, *56*, 1–24. [[CrossRef](#)]
41. Whisenant, S.G.; Burzlaff, D.F. Predicting green weight of mesquite (*Prosopis glandulosa* Torr.). *J. Range Manag.* **1978**, *31*, 396–397. [[CrossRef](#)]
42. Felker, P.; Cannell, G.H.; Clark, P.R.; Osborn, J.F.; Nash, P. Biomass production of *Prosopis* species (mesquite), *Leucaena*, and other leguminous trees grown under heat/drought stress. *For. Sci.* **1983**, *29*, 592–606.
43. Laxson, J.D.; Schacht, W.H.; Owens, M.K. Above-ground biomass yields at different densities of honey mesquite. *J. Range Manag.* **1997**, *50*, 550–554. [[CrossRef](#)]
44. Ansley, R.J.; Pinchak, W.E.; Teague, W.R.; Kramp, B.A.; Jones, D.L.; Jacoby, P.W. Long-term grass yields following chemical control of honey mesquite. *J. Range Manag.* **2004**, *57*, 49–57. [[CrossRef](#)]



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