
Strategies for Savanna Restoration in the Southern Great Plains: Effects of Fire and Herbicides

R. James Ansley^{1,2} and Michael J. Castellano¹

Abstract

Woody plant encroachment has degraded grassland and savanna ecosystems worldwide by decreasing herbaceous production and diversity, and altering these physiognomies toward woodlands. This study evaluated the long-term efficacy of fire and herbicide restoration strategies used in the southern Great Plains to reduce Honey mesquite (*Prosopis glandulosa*) dominance, restore a grassland/savanna physiognomy, and increase herbaceous production and diversity. Three treatments were evaluated: high-intensity winter fire, aerial spray of clopyralid + triclopyr (C + T), and aerial spray of clopyralid and were compared to untreated mesquite woodland (control). Post-treatment mesquite stand physiognomy was different between fire (low mortality, high basal sprouting), C + T (high mortality, high basal sprouting of surviving plants), and clopyralid (moderate mortality, low basal sprouting of surviving plants) treatments. From 6 to 8 years post-treatment, herbaceous production was

increased in C + T and clopyralid treatments but not in the fire treatment. Mesquite regrowth in the fire treatment exerted a competitive influence that limited herbaceous production. Herbaceous functional group diversity was increased in fire and C + T treatments due to a decrease in C₃ perennial grass dominance and an increase in C₄ perennial grasses and/or C₃ forbs. Treatments that maintained mesquite overstory (control and clopyralid) had lower herbaceous diversity due to C₃ perennial grass dominance and lower C₄ perennial grass cover. The clopyralid treatment demonstrated greatest potential for long-term restoration of southern Great Plains savanna by reducing mesquite canopy cover to historic levels, limiting mesquite basal regrowth and increasing grass production.

Key words: clopyralid, competition, fire, mesquite, prescribed burning, *Prosopis glandulosa*, species diversity, woody plant encroachment.

Introduction

Woody plants have encroached in many grassland and savanna ecosystems worldwide during recent history and continue to expand (Scholes & Archer 1997; Van Auken 2000). Woody encroachment decreases herbaceous production and diversity and may increase bare ground and soil erosion potential. Although woody encroachment occurs globally and includes many species, geographically distant ecosystems suffer similar deleterious effects (Asner et al. 2004).

Throughout the last century, the southern Great Plains of North America has been encroached by the woody legume, Honey mesquite (*Prosopis glandulosa*) (Ansley et al. 2001; Asner et al. 2003). Mesquite encroachment occurs on 38 Mha in North America and 20 Mha in Texas (Soil Conservation Service [SCS] 1984; Van Auken 2000). Currently, many regions that were once grasslands or savannas are now mesquite woodlands.

Increases in woody plant encroachment are attributed to fire suppression, enhanced seed distribution via live-

stock, and overgrazing (Van Auken 2000). Reductions or eliminations of these practices cannot restore grasslands or savannas; woody encroachment is irreversible over timescales relevant to management (Archer 1989). Therefore, a variety of mechanical, herbicidal, and pyric treatments have been employed to restore grasslands or savannas from woodland thickets. In semiarid grasslands, fire is an economical option because of its low application cost (Teague et al. 2001), but social concerns and the inability of fire to kill mesquite have limited its use. In contrast, despite relatively high application costs, herbicides have long been used for mesquite control due to their longer treatment life (Ansley et al. 2004). Indeed, similar restoration strategies use herbicide to reduce the abundance of fire-tolerant species (Wilson & Gerry 1995; Wilson & Partel 2003).

Despite the variety of treatment options, savanna restoration has met challenges from various interests whose concerns include fires' escape potential as well as herbicides' effects on human and wildlife physiology (Bureau of Land Management [BLM] 2005). But perhaps the most serious challenge is a common perception among land managers that woody cover and livestock grazing are incompatible. Accordingly, in shrub-encroached savanna, most livestock managers assume a grassland physiognomy maximizes herbaceous production and endeavor to eliminate

¹Texas Agricultural Experiment Station, Vernon, TX 76385, U.S.A.

²Address correspondence to R. James Ansley, email r-ansley@tamu.edu

all woody cover. However, grass production in a variety of shrub-encroached savannas is either increased or unaffected by light woody cover and only decreases when woody cover reaches a threshold (House et al. 2003; Ansley et al. 2004). Additionally, light woody cover benefits wildlife abundance and diversity (Fulbright 1996; Whitford 1997). Comparison of savanna restoration options that not only reduce woody plant cover but also alter its physiognomy may enhance restoration strategies' efficacy by demonstrating that limited woody cover can benefit both grass production and wildlife. This may aid various restoration strategies' social acceptability.

Here, we evaluate the long-term efficacy of two common and one novel treatment for reducing mesquite encroachment and restoring grassland/savanna. First, a widely used chemical option is a 1:1 mixture of clopyralid (3,6-dichloro-2-pyridinecarboxylic acid, monoethanolamine salt) and triclopyr (3,5,6-trichloro-2-pyridinyloxyacetic acid, butoxyethyl ester) applied aerially at 0.28 kg/ha + 0.28 kg/ha. This treatment achieves high mesquite mortality without damaging associated herbaceous species and effectively converts woodlands to a grassland physiognomy (Mitchell et al. 2004).

Second, prescribed fire is widely used to reduce mesquite canopies and restore herbaceous productivity (Scifres & Hamilton 1993). Intense fires kill most mesquite canopies (i.e., top kill), but rarely achieve more than 5% whole-plant mortality (i.e., root kill) (Ansley & Jacoby 1998). As a result, nearly all mesquite resprout from stem bases and over time form a dense thicket. Little data are available concerning long-term impacts of such postfire regrowth on herbaceous production.

Third, the new and relatively little-used aerial application of a low rate of clopyralid alone at 0.28 kg/ha can modify mesquite stand physiognomy from woodland to savanna by yielding a moderate level of whole-plant mortality (20–40%) while causing partial canopy mortality of surviving mesquite. Partial canopy mortality reduces per tree leaf area, but trees maintain apical dominance and have little or no basal sprouting (Ansley et al. 2003). This feature increases treatment life because the landscape does not become dominated by basal regrowth. Therefore, this treatment may enhance multiple use options by providing screening cover for wildlife in addition to increasing herbaceous production through reduced mesquite competition with grasses. Moreover, the savanna physiognomy may facilitate other conservation goals by increasing floral and faunal diversity and thereby possibly facilitating survival of threatened species.

These three mesquite canopy disturbances will likely alter herbaceous production and diversity, depending on the degree to which mesquite canopies and stand densities are altered and basal regrowth is stimulated. We hypothesize that the clopyralid-generated savanna physiognomy will yield the greatest long-term, sustained herbaceous production and diversity compared to open grasslands

(C + T treatment), mesquite thicket (fire), and mesquite woodlands (control) (Scholes & Archer 1997).

Methods

Research was conducted in north Texas, southeast of Vernon (lat 33°53'N, long 99°02'W; elevation 352 m). Mean annual rainfall is 677 mm (National Oceanic and Atmospheric Administration [NOAA] 2001). Soils are fine, mixed, thermic Typic Paleustolls of the Tillman series, which are 3- to 4-m-deep alluvial clay loams underlain by sandstone/shale parent material (Koos et al. 1962). Primary C₃ grass species are perennial mid-grass, Texas wintergrass (*Nassella leucotricha*) and the annual grass, Japanese brome (*Bromus japonicus*). C₄ grasses include perennial mid-grasses Sideoats grama (*Bouteloua curtipendula*) and Meadow dropseed (*Sporobolus compositus*), and perennial short-grass Buffalograss (*Buchloe dactyloides*).

Prior to treatment, the site was dominated by multi-stemmed mesquite. Mean canopy cover was 49.5% (SE 5.5), and mean tree height was 2.4 m (SE 0.3). No other woody species had greater than 2% cover. Cattle grazing was continuous and stocking rate was maintained at what is considered a moderate level of 12–15 ha/cow (Teague et al. 2001) for the past 50 years.

Treatments

The study consisted of four replicates of four treatments arranged in a completely randomized design. Treatments were (1) high-intensity winter fire (fire); (2) aerial spray of 0.28 kg/ha clopyralid + 0.28 kg/ha triclopyr (C + T); (3) aerial spray of 0.28 kg/ha clopyralid (clopyralid); and (4) an untreated control. Each replicate plot was 4 ha (100 × 400 m).

Fire treatments were applied in January–February 1996. Air temperature, relative humidity, and wind speed averaged 24.8°C, 19%, and 3.9 m/s, respectively, over all fires. Preburn herbaceous fine fuel averaged 315 g/m² (SE = 23; n = 4). Fire intensity was high with flame heights 3–5 m. Postfire soil surface was completely blackened.

Herbicide treatments were applied on 2 July 1996 using fixed-wing aircraft. Total spray volume was 37.4 L/ha in a diesel-to-water emulsion ratio 1:7 (4.7 L/ha of diesel). Application occurred between 7:00 and 9:00 a.m. with air temperatures 25–31°C, wind speed 1–3 m/s, and soil temperature 29°C at 46-cm depth. Surface soil moisture was dry due to spring and summer drought, but deep moisture was plentiful.

Vegetation Measurements

Eighty to 120 mesquite were evaluated at 3 years post-treatment (1999) along two 200-m line transects that were randomly located in each plot. At every 20 m on each line all trees within a 5-m radius were evaluated. Mesquite trees exhibit one of four possible responses to treatment:

whole-plant mortality (root kill), stem sprouts only (SS), stem sprouts + basal sprouts (SS + BS), and basal sprouts only (BS). Percentage of trees per transect with each of these responses was determined. Most trees have one or two basal sprouts naturally, so a tree was not counted as having basal sprouts in response to treatment unless there were five or more sprouts (after Ansley et al. 2003). Mesquite aerial cover was quantified in 2001 and 2004 along two 30-m line transects in each plot using the line intercept method (Canfield 1941). Mesquite live height was determined in 2001 and 2004 by randomly measuring eight trees per plot.

End of growing season herbaceous production was quantified in 2002, 2003, and 2004 (6–8 years post-treatment) by clipping to 3-cm stubble height all standing herbaceous biomass (grasses and forbs) within 16 randomly located, 0.25-m² quadrats that were protected from grazing by cages in each replicate plot. Grass and forb components were separated in 2003 and 2004 but not in 2002. Prior to each growing season, all herbaceous growth and old standing litter within cages was clipped to 3-cm stubble height so that only current year herbaceous growth was measured.

Herbaceous composition was quantified in 2002–2003 by placing a 0.25-m² quadrat at 5-m intervals along two randomly located 60-m line transects in each plot (24 quadrats total) and visually estimating percent basal cover of each grass species, forbs as a group, bare ground, and litter. Grass species cover values were subsequently grouped into five functional groups: C₃ annuals, C₃ perennial mid-grasses, C₄ annuals, C₄ perennial mid-grasses, and C₄ perennial short-grasses. Herbaceous community diversity at the functional group level was assessed using the Shannon-Wiener Diversity Index (H') (Zar 1999). Initial evaluation of data revealed that cover of C₃ and C₄ annuals was less than 2% in any year or treatment. Therefore, these functional groups were eliminated from analyses of percent cover and diversity. Thus, H' was based on five functional groups: C₃ perennial mid-grasses, C₄ perennial mid-grasses, C₄ perennial short-grasses, forbs, and litter.

Statistical Analysis

All responses were averaged at the plot (replicate) level prior to analysis. Percentage data were subjected to arcsine transformation prior to analysis. Otherwise, data sets did not deviate significantly from the assumptions of analysis of variance (ANOVA) except for forb production where heteroscedastic data were square-root transformed prior to analysis (Zar 1999). All mesquite response variables except height and cover were analyzed using a one-way completely randomized ANOVA. Mesquite height, cover, and all herbaceous response variables were analyzed using a general linear model repeated-measures ANOVA with treatment and year as main sources of variation and four replicate plots per treatment (SPSS 2003).

If a site by year interaction was significant, differences between treatments were analyzed within each year. Means were compared using least significant difference (LSD) with Bonferroni-adjusted p values ($p < 0.05$).

Results

Precipitation

Annual precipitation was below normal during the treatment year (1996) and in 4 of the 8 years after treatment. During the 3 years grass production was measured (2002–2004), growing season precipitation (April–September) was highly variable in relation to the 30-year average (Fig. 1).

Mesquite Responses

Mesquite live height was greatest to least in the control, clopyralid, fire, and C + T treatments, respectively, in

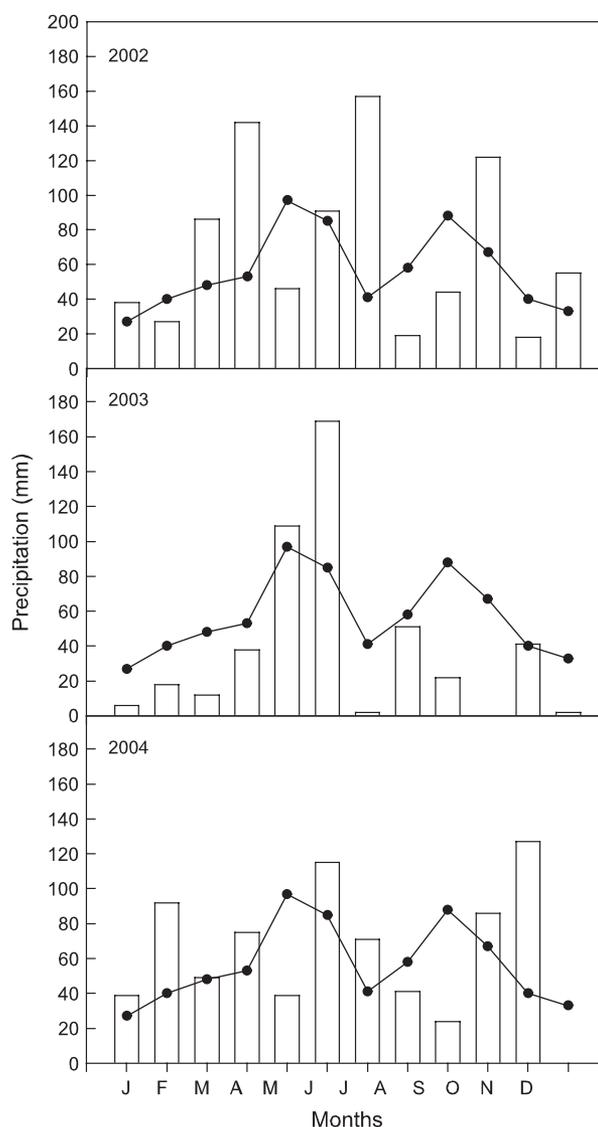


Figure 1. Monthly mean precipitation 2002–2004 (bars) compared to 30-year average monthly precipitation (line) (NOAA 2001).

Table 1. Mesquite height and canopy cover in 2001 and 2004. Means are followed by standard error in parentheses.

Treatment	Height (m)		Canopy Cover (%)	
	2001	2004	2001	2004
Control	2.9 (0.3) a	2.9 (0.3) a	52.7 (5.3) a	60.0 (7.0) a
Fire	1.3 (0.2) b	2.0 (0.1) ab	28.5 (2.0) b	40.3 (4.3) b
Clopyralid	1.8 (0.3) b	2.3 (0.3) ab	21.1 (2.4) bc	26.4 (8.3) bc
C + T	1.0 (0.04) b	1.6 (0.1) b	9.5 (1.9) c	11.5 (1.4) c

Means within each column with similar letters are not significantly different ($p < 0.05$). Pre-treatment height = 2.4 (0.3); pre-treatment cover = 49.5 (5.5).

2001 and 2004 (Table 1). Differences in height between control and treated mesquite decreased from 2001 to 2004 as growth rate of disturbed canopies exceeded that of undisturbed canopies.

Mesquite live canopy cover was reduced to near zero in the C + T and fire treatments and was 10–15% in the clopyralid treatment the first year postfire (unquantified visual observation). Cover increased to the greatest degree in the fire treatment and was near pre-treatment levels by 2004, 8 years post-treatment (Table 1).

Mesquite stand physiognomy differed widely among treatments. Mesquite whole-plant mortality in the fire treatment was 3%; greater than 95% of surviving trees had complete aboveground mortality and basal sprouted. In contrast, the C + T treatment yielded 52% mortality, and only 40% of surviving trees had complete aboveground mortality and basal sprouted (Fig. 2). In the clopyralid treatment, roughly one-third of mesquite were killed, one-third were stem sprouted with no basal sprouting, and one-third had complete aboveground mortality and basal sprouted. The percentage of surviving mesquite with basal sprouts was significantly greater in the fire and C + T treatments compared to the clopyralid treatment.

Figure 3 illustrates landscape mesquite physiognomies of each treatment as they would appear at 8 years post-

treatment. Each panel shows physiognomy percentages (from Fig. 2) integrated with long-term growth data (from Table 1). Thus, untreated plants are shown as 3-m-tall trees, basal regrowth (BS and SS + BS trees) is 2 m, and stem sprouts (SS) occur as small patches of foliage at variable heights. Dead trees have variable rates of stem deterioration. The high percentage of basal sprout trees, coupled with basal growth, has yielded more mesquite foliage in the fire treatment than the two herbicide treatments.

Herbaceous Production

There were significant ($p < 0.05$) main effects of year and treatment and no significant treatment \times year interactions for total herbaceous (grass and forb), grass, and forb production. Despite lower annual precipitation in 2003 than 2002 or 2004, high rainfall in May and June 2003 apparently facilitated significantly greater herbaceous production in this year.

Total herbaceous production (2002–2004) was significantly greater in the C + T and clopyralid treatments than the fire or control (Fig. 4). Grass production (2003–2004) was greatest in the clopyralid treatment. In contrast, forb production (2003–2004) was significantly greatest in the C + T treatment. Analysis revealed a significant negative sigmoidal relationship between mesquite canopy cover and total herbaceous production (Fig. 5). The relationship indicated a slight decline in production between 0 and 20% mesquite cover and a more rapid decline in production between 20 and 40% mesquite cover.

Herbaceous Diversity

Cover of C_3 mid-grasses was greater in the control and clopyralid treatments than in the fire and C + T treatments (Fig. 6). Forb cover was greatest in the C + T treatment.

In general, the control and clopyralid treatments were similar and fire and C + T were similar with respect to perennial grass percent cover responses, whereas the control and fire treatments were similar and clopyralid and C + T were similar with respect to forb, bare ground, and litter cover responses.

Herbaceous functional group diversity (H') in C + T treatment was greater than in the control. Functional

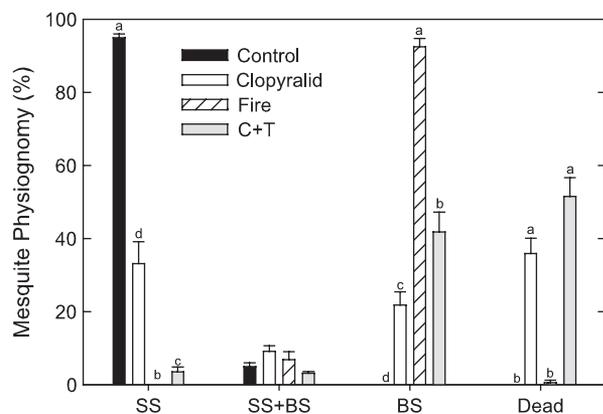


Figure 2. Mean (\pm SE) percent mesquite physiognomy/treatment (1999). Different letters among treatments within physiognomy types indicate significant pair-wise differences (LSD; $p < 0.05$). The SS + BS had a significant ANOVA but no significant pair-wise differences. Dead = complete whole-plant mortality.

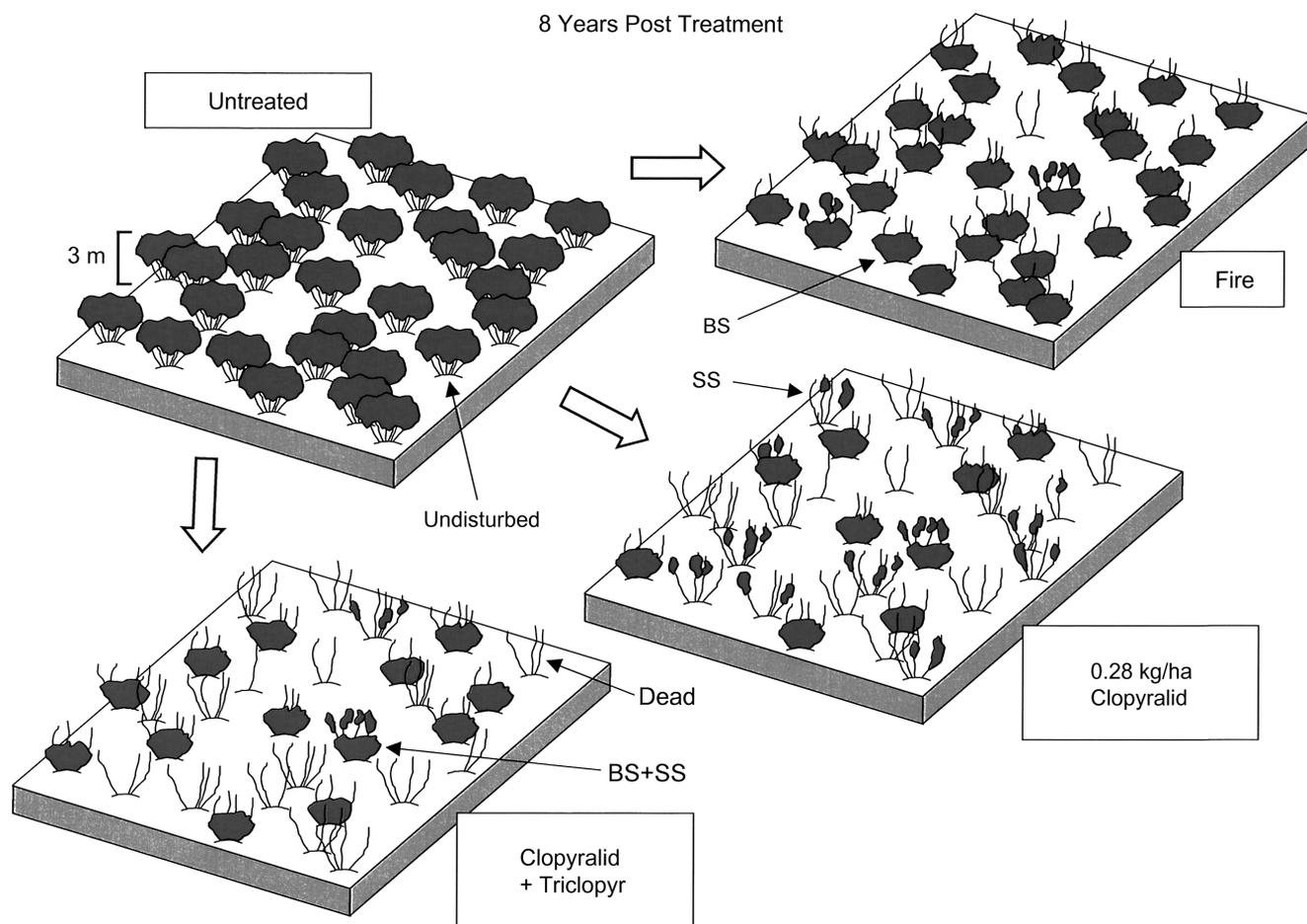


Figure 3. Conceptual illustration of mesquite landscape physiognomies 8 years after chemical or fire treatments compared to an untreated control. Percentage of each physiognomy (dead, SS, SS + BS, and BS) of 30 trees in each panel is based on Figure 2. An example of each physiognomy is identified. Mesquite foliage is green. Stems are undulating vertical lines.

group diversity in the fire and clopyralid treatments was not significantly different from any of the other treatments (Fig. 7).

Discussion

Mesquite Physiognomy Responses

The fire treatment yielded a “temporary” grassland physiognomy. High initial canopy kill but low whole-plant mortality triggered rapid mesquite basal regrowth such that, by 8 years post-treatment, mesquite canopies were approaching that of a woodland thicket (Fig. 3). Our results agree with other studies that very few mature mesquite are killed by single winter fires (Scifres & Hamilton 1993; Ansley & Jacoby 1998).

The clopyralid treatment reduced mesquite stand density and canopy cover by yielding moderate whole-plant mortality and partial canopy mortality (SS or SS + BS) in most surviving trees. Additionally, live canopy height was taller in this than the other treatments because many of

the stem sprouts occurred at high positions in the canopy (Fig. 3). The combined effect of these processes yielded a savanna physiognomy that was relatively long lasting because (1) there were fewer mesquite trees that basal sprouted in this treatment than the others and (2) most surviving trees retained sufficient stem sprout foliage to maintain apical dominance and prevent basal sprouting. Although basal sprouted plants (either BS or SS + BS) become increasingly dominant over time, as found in the fire and C + T treatments, we have found in this study and another (Ansley et al. 2003) that SS trees, most common in the clopyralid treatment, maintain a fairly consistent foliage mass over time. Because many trees retained an arborescent physiognomy in the clopyralid treatment, albeit with less leaf area per tree, mesquite foliage was less prominent on the landscape than in the fire treatment (Fig. 3).

The C + T treatment yielded greater mortality than the fire or clopyralid treatments but, similar to the fire treatment, most surviving plants were top killed and basal sprouted. As a result, this treatment yielded what could be

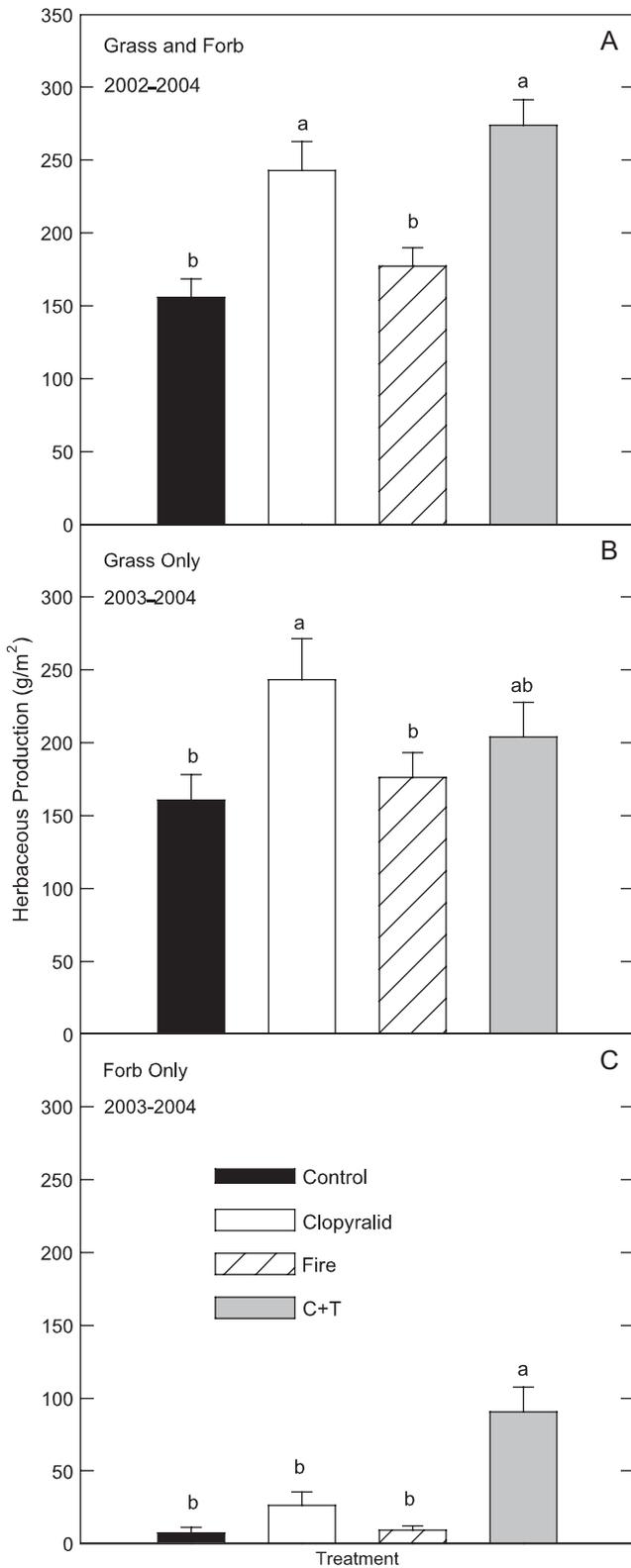


Figure 4. Mean (\pm SE) herbaceous production/treatment. Different letters among treatments in each panel indicate significant pair-wise differences (LSD; $p < 0.05$).

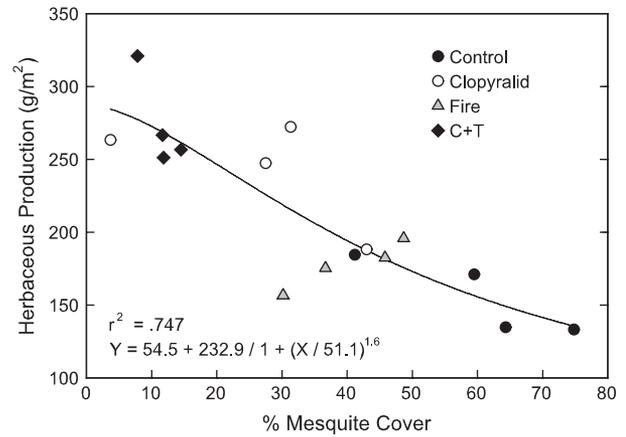


Figure 5. Relationship between mesquite canopy cover (2004) and mean annual herbaceous production (2002–2004). Each point represents a replicate plot value averaged over all 3 years ($n = 16$).

better described as a “sparse savanna” rather than a grassland. Because most surviving mesquite are basal sprouters, these plants will likely eventually have more foliage than the SS trees in the clopyralid treatment, as shown in Fig. 3.

Mitchell et al. (2004) found in 18 other studies that applied the C + T treatment that average mesquite mortality was 70 %. Thus, our mortality (52%) was lower than expected. Changing five of the BS plants to dead plants in Fig. 3 would depict a more “typical” C + T physiognomy with 70 % mortality.

Herbaceous Responses

Herbaceous production was not quantified during the first 5 years post-treatment, but studies on similar soils in the region have found short-term increases in herbaceous production in response to mesquite treatment with fire or herbicides (Bedunah & Sosebee 1984; Teague et al. 2001). Six to 8 years post-treatment, the C + T treatment increased herbaceous production and functional group diversity. The fire treatment increased diversity but not production, whereas the clopyralid treatment increased herbaceous production but not diversity. Herbaceous production increases were due either to mesquite mortality (C + T and clopyralid treatments) or to partial canopy mortality of surviving mesquite (clopyralid treatment) that reduced the competitive impact of mesquite.

Fire failed to increase long-term herbaceous production due to mesquite basal regrowth that exerted a significant competitive influence by the time herbaceous data were collected. Although fire is known to increase short-term herbaceous production, in ecosystems where the woody component sprouts vigorously following fire, this effect likely lasts less than 5 years as there was no difference in herbaceous production between the fire treatment and the control at 6–8 years post-treatment. In contrast, herbaceous production increases in the C + T and clopyralid treatments were long lasting; differences

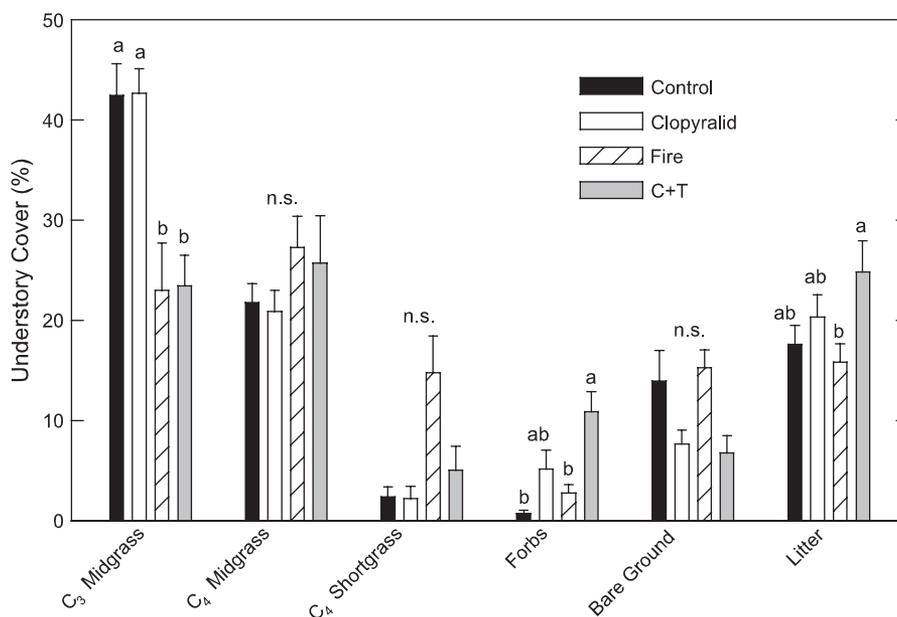


Figure 6. Mean (\pm SE) (2002–2003) percent understory basal cover/treatment. Different letters among treatments within groups indicate significant pair-wise differences (LSD; $p < 0.05$).

between these treatments and the control were clear 6–8 years post-treatment.

Treatments that maintained a mesquite overstory (control and clopyralid) had lower functional group diversity due to C₃ perennial grass dominance and a trend toward lower C₄ perennial grass cover. Increases in diversity in the fire and C + T treatments were the result of a decline in C₃ grasses and a trend toward greater C₄ perennial midgrass and forb cover. Although H' assessed relative diversity among functional groups, it did not address the overall impact of functional group diversity at the landscape level because H' only accounted for relative abundance. For example, a plot that had 90% bare ground and 2% cover

of each of the five functional groups would yield the same H' value as a plot that had 20% cover of each functional group and no bare ground. Obviously, the impact of each functional group would be greater on the landscape in the latter than in the former example.

Although the C + T treatment generated the highest levels of diversity and total herbaceous production, this was due to increased forb and not grass growth. Alternatively, increased herbaceous production in the clopyralid treatment, which created a savanna physiognomy, was due to increased grass and not forb growth. Mesquite canopies, either as intact large canopies in the control, moderate-sized multistemmed regrowth in the fire treatment or as partially killed canopies in the clopyralid treatment, had the effect of limiting forb growth. The contrasting grass and forb responses in open grassland versus savanna physiognomies support the argument that herbaceous production temporal stability is greater in savanna than open grassland if, in some years, forb growth is sufficient to inhibit grass production in open grassland (Smit 2004).

In addition, this study demonstrated that, long-term grass production was greatest, although not significantly, in the clopyralid treatment (mesquite savanna). This finding is consistent with other studies in semiarid ecosystems that indicate woody cover can increase to $\approx 20\%$ before herbaceous production begins to decline (Scifres et al. 1982; Belsky 1994; Warren et al. 1996; Ansley et al. 2004). In some ecosystems, woody plant canopy cover of up to $\approx 20\%$ may facilitate grass production by reducing environmental stresses and increasing water and nutrient availability (Smith & Schmutz 1975; Weltzin & Coughenour 1990; Scholes & Archer 1997; House et al. 2003).

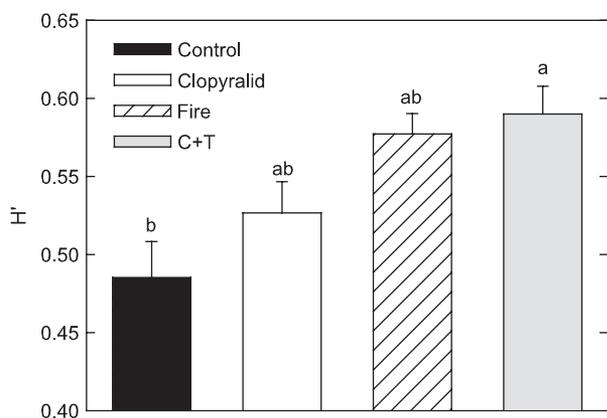


Figure 7. Mean (\pm SE) (2002–2003) functional group diversity/treatment. Different letters among treatments within years indicate significant pair-wise differences (LSD; $p < 0.05$).

Restoration Implications

The novel treatment of aerial spraying clopyralid at 0.28 kg/ha may provide a long-term solution for restoring the historical mesquite savanna physiognomy to the southern Great Plains (Asner et al. 2003) and may provide greater economic and ecological benefits compared to the fire or clopyralid + triclopyr treatments. Ecologically, an increase in spatial heterogeneity and vegetative structural complexity can augment floral and faunal abundance and diversity (MacArthur & MacArthur 1961; Schoener 1974; Fulbright 1996; Whitford 1997). This may lead to a greater potential for conservation of endangered species. From a land use perspective, a savanna physiognomy facilitates multiple-use management of livestock and wildlife by providing habitat cover for wildlife (Fulbright 1996) and increasing grass production for forage (Smit 2004). A variety of resource managers with one or more long-term goals (e.g., restoration, conservation, wildlife management, livestock production) will be well suited to employ this restoration strategy.

Our results are likely less applicable in mixed shrub communities such as in south Texas, where subsidiary species have followed the encroachment of one pioneer encroacher (e.g., Archer 1989), unless several of these subsidiary species have a similar physiognomic responses to a particular treatment. This would likely occur following an intense fire. However, a more variable response would be expected following herbicide treatments as responses are often species specific (Mitchell et al. 2004).

The partial canopy mortality response of mesquite to low rates of clopyralid have not yet been documented with other shrub species. However, restoration strategies that thin woodland thickets by other means, such as mechanical extraction, have found a similar herbaceous response to a low level of woody plants (i.e., a sparse savanna). The consistent positive or lack of a negative effect of less than 20% woody cover on grass production in other ecosystems worldwide (Weltzin & Coughenour 1990; Belsky 1994; Warren et al. 1996; Scholes & Archer 1997) suggest that our results may be broadly applicable if (1) a chemical treatment has a similar effect on other woody species as clopyralid does with mesquite or (2) other tree thinning strategies are employed.

Commercial costs are \$15, \$42, and \$62 per hectare for fire, clopyralid, and C + T treatments, respectively (Teague et al. 2001). Thus, although fire is a less expensive option, one must consider long-term effects of altering woody physiognomy from an arborescent structure to multistemmed regrowth that may become more competitive with understory species than before treatment.

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