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Restoration of C_4 grasses with seasonal fires in a C_3/C_4 grassland invaded by *Prosopis glandulosa*, a fire-resistant shrub

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Abstract

Questions: Can prescribed fire restore C_4 perennial grasses in grassland ecosystems that have become dominated by fire-resistant C_3 shrubs (*Prosopis glandulosa*) and C_3 grasses? Do fires in different seasons alter the direction of change in grass composition?

Location: Texas, USA.

Methods: We quantified short- and long-term (12 yr post-fire) herbaceous functional group cover and diversity responses to replicated seasonal fire treatments: (1) repeated-winter fires (three in 5 yr), (2) repeated-summer fires (two in 3 yr), and (3) alternate-season fires (two winter and one summer in 4 yr), compared with a no-fire control.

Results: Summer fires were more intense than winter fires, but all fire treatments temporarily decreased *Prosopis* and C_3 annual grass cover. The alternate-season fire treatment caused a long-term increase in C_4 mid-grass cover and functional group diversity. The repeated-summer fire treatment increased C_4 short-grass cover but also caused a long-term increase in bare ground. The repeated winter fire treatment had no long-term effects on perennial grass cover. Mesquite post-fire regrowth had increasingly negative impacts on herbaceous cover in all fire treatments.

Conclusions: Summer fire was necessary to shift herbaceous composition toward C_4 mid-grasses. However, the repeated-summer fire treatment may have been too extreme and caused post-fire herbaceous composition to "over-shift" toward less productive C_4 short-grasses rather than C_4 mid-grasses. This study provides some of the first long-term data showing a possible benefit of mixing seasonal fires (i.e., the alternate-season fire treatment) in a prescribed burning management plan to restore C_4 mid-grass cover and enhance overall herbaceous diversity.

Keywords: Burning; Fire ecology; Herbaceous composition; Mesquite; Prescribed fires; Savanna; Species diversity; Woody plant.

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Introduction

It has been theorized that frequent fires and possibly lower atmospheric CO_2 led to the widespread development of C_4 grasslands and savannas in Late Miocene and Early Pliocene (4–8 million yr ago) (Osborne 2008). Frequent fires cause soil nitrogen (N) deficits and high light conditions which favor N-use efficient C_4 grasses over C_3 grasses and shrubs (Reed et al. 2005).

The human-caused reduction of fire frequency, and other factors such as increasing CO_2 and increased woody seed distribution via livestock, has allowed C_3 woody plants to invade many grassland ecosystems worldwide (Trollope 1984; Van Auken 2000). In the southern Great Plains, USA, the invasion of the woody legume, *Prosopis glandulosa* (honey mesquite) combined with livestock overgrazing has led to the reduction of C_4 mid-grasses and an increase in less-productive C_3 grasses beneath *Prosopis* canopies (Ansley et al. 2004).

The prescribed reintroduction of fire is used to reduce woody plant cover and/or restore the herbaceous community in many fire-dependent grasslands and savannas worldwide (Uys et al. 2004; Fensham et al. 2005; Ansley et al. 2008). However, some woody invaders such as *Prosopis* are fire resistant and resprout following above-ground "top-kill" from fire (Ansley et al. 1998). In addition, *Prosopis* fixes N (Johnson & Mayeux 1990) which allows it to better compete in an N-depleted environment. Thus, the presence of a fire-resistant C_3 shrub may permanently limit the potential of fire alone to affect the transition of these communities from woody to herbaceous states, or from one herbaceous state to another (e.g., C_3 to C_4 grasses).

Prescribed fires are typically applied during late winter or early spring when C_4 grasses are dormant (Trollope 1984; Engle & Bidwell 2001). However, in systems invaded by woody plants, two factors limit the effectiveness of dormant season fires. First, woody plants reduce C_4 grass productivity, which serves as fine fuel for fire. Second, the C_3 grasses beneath the woody canopies are often green during these months and this retards fire intensity. Accordingly, there has been an increased interest in application of late-summer fires when C_3 grasses are not green and most C_4 grasses have entered a summer-dormant stage. These fires usually yield greater top-kill of woody plants than winter fires (Ansley et al. 2008), but there is a concern that they may damage important native C_4 grasses (Engle et al. 1998; Ansley et al. 2006).

This concern runs counter to our understanding of the historical fire regime in the southern Great Plains which likely had frequent summer fires caused by lightning (Engle & Bidwell 2001). Other fires ignited by Native Americans for hunting or fruit and grain harvest may have occurred during the autumn, early-spring or mid-summer (Anderson 1990; Stewart et al. 2002). Thus, the long-term fire pattern before European settlement may have been a continually changing mosaic of growing-season-burned and dormant-season-burned patches of widely ranging and often overlapping sizes (Bond 2001; Fuhlendorf & Engle 2004). Frost (1998) suggested the fire return interval in most of the southern Great Plains was 1–6 yr. Such a fire pattern, coupled with intense but infrequent bison grazing apparently maintained a high proportion of C_4 grasses in the herbaceous community (Knapp et al. 1998). The reduction of fire frequency and increased grazing pressure from livestock introduced by Europeans caused major shifts in herbaceous production and composition.

Given this history, we expect that the return of fire in any season to C_3-grass and woody-dominated areas in the southern Great Plains should increase C_4 mid-grasses relative to C_3 grasses, provided that the fires reduce woody cover. Repeated dormant-season fires have maintained C_4 tall-grass and mid-grass dominance in grasslands worldwide (Gibson & Hulbert 1987; Morgan & Lunt 1999; Fynn et al. 2004). Fewer studies have contrasted effects of fires in different seasons on herbaceous composition (Copeland et al. 2002; Towne & Kemp 2008).

Most savanna vegetation models concentrate on factors that affect tree versus grass dynamics (Archer 1989; House et al. 2003). Fire is typically identified as a disturbance variable; however, rarely are effects of seasonal fires or responses of different grass functional groups to fire disturbances addressed in detail (Fensham et al. 2005).

Our objective was to determine if fires in any season can shift ungrazed *Prosopis*/C_3 grass savannas and woodlands toward C_4 grass dominance, even acknowledging that fire will only temporarily suppress the woody component (Ansley & Jacoby 1998). Specifically, we compare effects of repeated-winter, repeated-summer or alternate-season fires on herbaceous composition over 15 yr. We hypothesized that repeated fires in any season would reduce woody canopies and C_3 grass cover, and increase C_4 mid-grass cover. The magnitude and rate of transition from one vegetative composition state to another may depend on the severity of fire, which should be greatest to least in repeated-summer, alternate-season and repeated-winter fires.

Methods

Site description

Research was conducted on a 100-ha fenced enclosure south of Vernon, Texas (33°51′ N, 99°26′ W; elev. 381 m). Mean annual precipitation is 665 mm with peaks in May (119 mm) and Sep (77 mm). Mean monthly air temperatures range from 36°C in Jul to −2.5°C in Jan. Mean annual temperature is 17°C. Soils are clay loams to 3–4 m depth, and are fine, mixed, thermic Typic Paleustolls of the Tillman series (USDA-SCS 1962).

Pretreatment overstorey consisted of *Prosopis*, 3–4 m tall, 30–50% canopy cover. The herbaceous layer consisted of a mixture of C_3 and C_4 perennial grasses dominated by the C_3 perennial mid-grass *Nassella leucotricha* and the C_4 perennial short-grass *Bouteloua dactyloides*, with several C_4 perennial mid-grass species infrequently scattered (see the Supporting Information, Appendix S1). Pretreatment herbaceous composition conducted on 10 60-m line transects at the study area found basal cover to be 26% C_3 annuals, 21% C_3 perennial mid-grasses, 15% C_4 perennial short-grasses, 3% C_4 perennial mid-grasses, 7% forbs, 27% litter and 2% bare ground. The growing season for C_4 grasses is from Apr to Sep and for C_3 grasses is from Feb to May. For this paper, reference to "growing season" means the C_4 grass growing season unless otherwise stated. Livestock grazing was excluded during the study period in order to identify effects of fire season on community composition without the confounding effects of grazing.

Fire treatments

The study had four fire treatments: (1) no-fire control, (2) repeated-winter fires in late-Jan–early

Mar in 1991, 1993 and 1995 (w91+w93+w95); (3) repeated-summer fires in Sep in 1992 and 1994 (s92+s94), and alternate-season fires in winter (Jan–Mar) 1991, summer (Sep) 1992 and winter (Jan–Mar) 1994 (w91+s92+w94). There were three replicate plots (1–5 ha each) that were randomly assigned per treatment. All fires were conducted as headfires. The original purpose of the treatments was to determine if a concentrated series of repeated fires in different seasons could increase *Prosopis* mortality and restore C_4 grass production (Ansley & Jacoby 1998). None of the plots had burned at least 30 yr prior to this study. *Prosopis* trees were in full foliage during the summer fires but were leafless during the winter fires. Each fire application period in each treatment was referred to as a "step". For example, in the repeated-winter fire treatment, w91 was step one, w91+w93 was step two, etc. Thus, in the repeated-winter fire treatment, a total of nine fires were completed (3 steps$\times$3 replications per treatment).

Air temperature, relative humidity (RH) and wind speed were measured at the site a few minutes before each fire. Herbaceous fine fuel amount (litter+grass and forb standing crop) was estimated by harvesting 15 randomly located 0.25 m^2 quadrats in interstitial spaces between *Prosopis* trees per plot. Fire temperatures were measured at 1-s intervals at six heights (0, 0.1, 0.3, 1, 2 and 3 m) at each of three to six locations per plot using thermocouples and a datalogger (Ansley et al. 2008). Fire intensity was quantified using the flame length equation of Byram (1959), $I = 5.7\,L^{2.2}$, where I = fireline intensity ($btu \cdot ft^{-1} \cdot s^{-1}$) and L = flame length (ft), and converted to $kW\,m^{-1}$.

Vegetation measurements

Fifty *Prosopis* individuals were evaluated along permanently marked line transects in each plot at the end of the second growing season following each step in each repeated fire treatment. Response variables included per cent whole-plant mortality (root-kill), per cent of trees with complete above-ground mortality (top-kill or basal-sprout only), per cent of trees partially top-killed and stand-level per cent of canopy foliage remaining relative to the original canopy.

Cover was determined by placing a 0.25 m^2 quadrat at each of 15 permanently marked points in each replicate plot and visually estimating per cent basal cover of each grass species, forbs as a group, herbaceous litter and bare ground in the late-autumn season (Oct–Nov) on six sample dates (1994, 1995, 1998, 2001, 2003, 2005) that represented from 1 to 12 C_4 grass growing seasons post-fire, depending on the year of the last fire in each treatment. Sampling was conducted so that at least one C_4 grass growing season occurred between a fire step and a sample period (Appendix S2). We ensured that cover values in each quadrat added to 100%. The per cent cover of each species in each replicate plot was determined by averaging all 15 sample points. Grass species cover values were subsequently grouped into four functional groups: C_3 annual grasses, C_3 perennial mid-grasses (of which >95% was *N. leucotricha*), C_4 perennial mid-grasses and C_4 perennial short-grasses (Appendix S1). Community diversity was assessed at the functional group level using the Shannon–Wiener Diversity Index (H') (Zar 1999). The H' was based on a k value = five categories (C_3 mid-grass, C_4 mid-grass, C_4 short-grass, forbs and litter cover). The Pielou index of evenness (J') was determined by H'/H'_{max} (Zar 1999). Invasive C_3 annual grasses were not included in the diversity assessment.

Statistical analysis

All responses were averaged across sub-replicates at the plot (replicate) level prior to analysis. Percentage data were arcsine transformed before analysis to meet assumptions of normality and homoscedasticity. Fire weather and behavior were compared among fire steps within each fire treatment using a one-way completely randomized ANOVA with fire step as the independent variable ($n = 3$ per step), and by season by averaging winter and summer fire steps across all treatments and analysing using one-way ANOVA ($n = 15$ for winter, $n = 9$ for summer fire). *Prosopis* responses were first compared among fire steps within each fire treatment using a one-way completely randomized ANOVA with fire step as the independent variable ($n = 3$ per step). Responses among fire treatments were compared following the terminal fire step in each treatment, again using a one-way ANOVA ($n = 3$ replicates per fire treatment).

Herbaceous cover responses were analysed using a general linear model repeated measures analysis with fire treatment as whole plot and sample year as the split plot (three replicates per treatment). We used the replicate$\times$treatment mean square as the error term to test the effects of treatment, and the pooled error to test the effects of year and treatment$\times$year interactions. If a treatment$\times$year interaction was significant, means on each sample date were separated by LSD at $P \leq 0.05$, except where noted (SAS 2003).

Additional analyses were performed to assess short- (1–4 yr post-fire) and long-term (7–12 yr post-fire) impacts of the fire treatments by averaging, at the replicate level, functional group cover data for the first three sample periods (1994, 1995 and 1998) for short-term, and the last three sample periods (2001, 2003 and 2005) for long-term responses. These data were analysed using a 1-way ANOVA with fire treatment as the main effect. Years post-fire refers to the number of C_4 grass growing seasons (Apr–Sep) post-fire. To assess temporal peaks in herbaceous cover independent of annual variations, cover values are also reported relative to the control (% cover in each fire treatment/% cover in the control). Relative values were not analysed statistically because they represented one treatment mean divided by another.

Results

Fire conditions, fire behavior and precipitation

Air temperature, RH, herbaceous fine fuel, peak fire temperature, flame length, and fireline intensity were greater in summer than winter fires when averaged over all steps and fire treatments (Appendix S3). Annual precipitation was above or near the 30-yr average during 1991–1995 when fire treatments were applied, but was $>34\%$ below normal for four of the ten post-fire years from 1996 to 2005 (Fig. 1a). The C_4 grass growing season precipitation was above normal in 1995, but was below normal during seven of the ten post-fire years from 1996 to 2005 (Fig. 1b). The C_3 grass growing season precipitation was below normal during eight of the ten post-fire years from 1996 to 2005 (Fig. 1c).

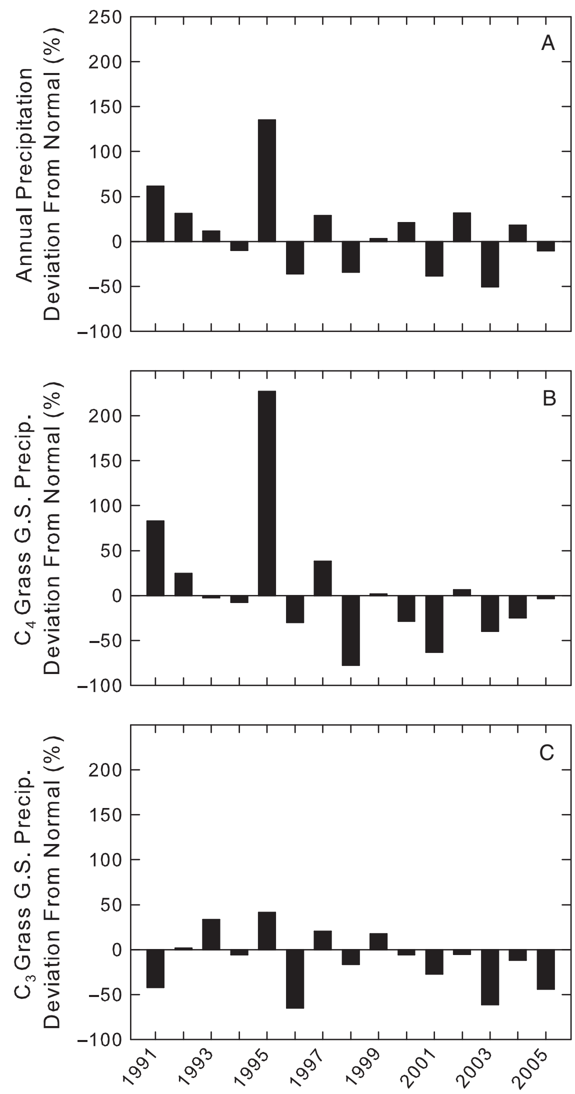

Fig. 1. Percent deviation from 30-yr average (zero line) for annual (a) total, (b) C_4 grass growing season (Apr–Sep), and (c) C_3 grass growing season (Feb–May) precipitation.

Prosopis responses

Prosopis whole-plant mortality (root-kill) was $<3\%$ after each fire step in all treatments (Table 1). The repeated-winter fire treatment ultimately yielded 63% top-kill and 88% stand foliage reduction. The repeated-summer and alternate-season fire treatments ultimately yielded $>85\%$ top-kill and $>97\%$ stand foliage reduction. *Prosopis* in the no-fire control had no natural mortality or growing season foliage loss during the study period. By 2005, 10 yr post-fire, regrowth *Prosopis* in all fire treatments was >3 m tall (R.J. Ansley unpubl. data).

Herbaceous cover responses

All herbaceous functional groups had significant treatment by sample date interactions. The alternate-season fire treatment increased C_4 mid-grass cover over the no-fire control from 1998 to 2005 (Fig. 2a). The repeated-summer fire treatment increased C_4 short-grass cover over the control in 1994 and from 1998 to 2005 (Fig. 2b). The C_3 mid-grass cover was greater in the repeated-winter fire treatment than the control in 1995 and greater in the alternate-season fire treatment than the control in 1998, but was not different among treatments after 1998 (Fig. 2c). All fire treatments reduced C_3 annual grass cover in 1994 and 1995 and treatments that included summer fire continued this suppression to 1998 (Fig. 2g). The C_3 annual grass cover was greater in the repeated winter fire treatment than the control in 2001, 6 yr post-fire. All fire treatments reduced litter cover from 1994 to

Table 1. *Prosopis* responses to repeated-winter, repeated-summer or alternate-season fire treatments. Responses represent the cumulative effect of multiple fires after the first step in each treatment. All values are means ($\pm$ SE) of three plots. [1]Each fire step in each fire treatment included three replicated plots. [2]Means with similar letters (a,b) are not significantly different ($P \leq 0.05$; $n = 3$) among steps within each fire treatment. Means with similar letters (x,y) are not significantly different ($P \leq 0.05$; $n = 3$) between fire treatments following the last step of each fire treatment.

Fire treatment	Step in each fire treatment[1]	Root-killed mesquite (%)	Completely top-killed mesquite (%)	Partially top-killed mesquite (%)	Foliage reduction per stand (%)
Repeated-winter	w91	2.2 $\pm$ 1.7 a[2]	8.2 $\pm$ 5.6 b	89.6 $\pm$ 5.8 a	42.8 $\pm$ 5.3 b
	w91+w93	0.0 $\pm$ 0.0 a	57.8 $\pm$ 2.2 a	42.2 $\pm$ 2.2 b	86.0 $\pm$ 3.7 a
	w91+w93+w95	1.4 $\pm$ 0.9 a; x	63.3 $\pm$ 3.5 a; y	35.4 $\pm$ 4.2 b; x	87.5 $\pm$ 2.8 a; y
Repeated-summer	s92	0.4 $\pm$ 0.4 a	95.3 $\pm$ 2.9 a	4.4 $\pm$ 2.6 a	98.9 $\pm$ 0.9 a
	s92+s94	1.7 $\pm$ 1.3 a; x	89.2 $\pm$ 3.9 a; x	9.0 $\pm$ 2.7 a; y	98.5 $\pm$ 1.1 a; x
Alternate-season	w91	0.0 $\pm$ 0.0 a	30.3 $\pm$ 10.1 b	69.7 $\pm$ 10.1 a	54.3 $\pm$ 9.7 b
	w91+s92	0.7 $\pm$ 0.7 a	81.6 $\pm$ 2.6 a	17.7 $\pm$ 3.2 b	98.0 $\pm$ 0.6 a
	w91+s92+w94	1.4 $\pm$ 0.9 a; x	85.8 $\pm$ 6.5 a; x	12.8 $\pm$ 7.2 b; y	97.4 $\pm$ 1.6 a; x

1998 (Fig. 2h). Litter cover increased in all treatments from 1995 to 2001 and was lower in the alternate-season fire treatment than the control after 1998. Bare ground cover was greater in all fire treatments than the control in 1994 and was greater in the repeated-summer fire treatment than the control in 1995, 2003 and 2005 (Fig. 2i).

Temporally, peak post-fire cover response of perennial grasses differed with functional group. Relative to the control, peak cover of C_4 mid-grasses in all fire treatments occurred in 2001, 6–7 yr post-fire (Fig. 2d). In contrast, peak C_3 mid-grass responses occurred from 1995 to 1998, 1–4 yr post-fire (Fig. 2f). Peak responses of C_4 short-grasses was intermediate and occurred from 1998 to 2001 (Fig. 2e). Peak responses of C_3 annual grasses occurred from 2001 to 2003 (Fig. 2j).

Forb cover never exceeded 5% in any treatment or year and was not different between treatments except in the autumn of 1994 when it was greater in the repeated-summer fire treatment (4.2%) than all other treatments (<0.5%) (data not shown).

When pooled over the first three sample dates (e.g. 1–4 yr post-fire), all fire treatments reduced C_3 annual grass and litter cover, and increased total perennial grass cover compared with the control (Table 2). The repeated-summer fire treatment increased C_4 short-grass and forb cover, while the alternate-season fire treatment increased ($P \leq 0.061$) C_4 mid-grass cover. Both the repeated-summer fire and alternate-season fire treatments increased bare ground and reduced litter to a greater degree than did the winter-fire treatment.

When pooled over the last three sample dates (7–12 yr post-fire), the repeated-summer fire treatment increased C_4 short-grass and bare ground cover, and showed a trend ($P \leq 0.09$) of decreasing C_3 mid-grass cover (Table 2). The alternate-season fire treatment increased C_4 mid-grass (520% > control) and total perennial grass cover (62% > control), and decreased litter cover. The repeated-winter fire treatment increased ($P \leq 0.052$) C_3 annual grass cover. None of the fire treatments caused a long-term reduction in cover of any perennial grass functional group compared with the control.

Fire treatments had no short-term effects on herbaceous functional group diversity (H') and evenness (J') (Table 3). Long-term (7–12 yr post-fire) diversity (H') and evenness (J') were greater in the alternate-season fire treatment than the control.

Discussion

Effects of fire season

Vegetation responses to fire in grassland and savanna ecosystems are highly variable and depend on location and ecosystem type. However, there are some general trends that can be seen worldwide. Some of the more complete data sets reveal that effects of frequently applied dormant-season (i.e. winter or early spring) fires will shift grassland communities toward C_4 grass dominance at the expense of C_3 grasses and woody plants. This has been found in the Great Plains of the USA (Gibson & Hulbert 1987; Steuter 1987; Peterson et al. 2007), and in C_4 *Themeda triandra* grasslands in South Africa (Uys et al. 2004) and Australia (Morgan & Lunt 1999; Prober et al. 2007). Our results differ from this general trend because repeated winter fires did not shift herbaceous composition toward C_4 grass dominance. Thus, we reject our hypothesis that repeated fires in any season would reduce C_3 grass cover and increase C_4 grass cover.

Regarding responses to growing-season, or "summer" fires, our results again differ from two general trends found in literature. First, studies in the northern

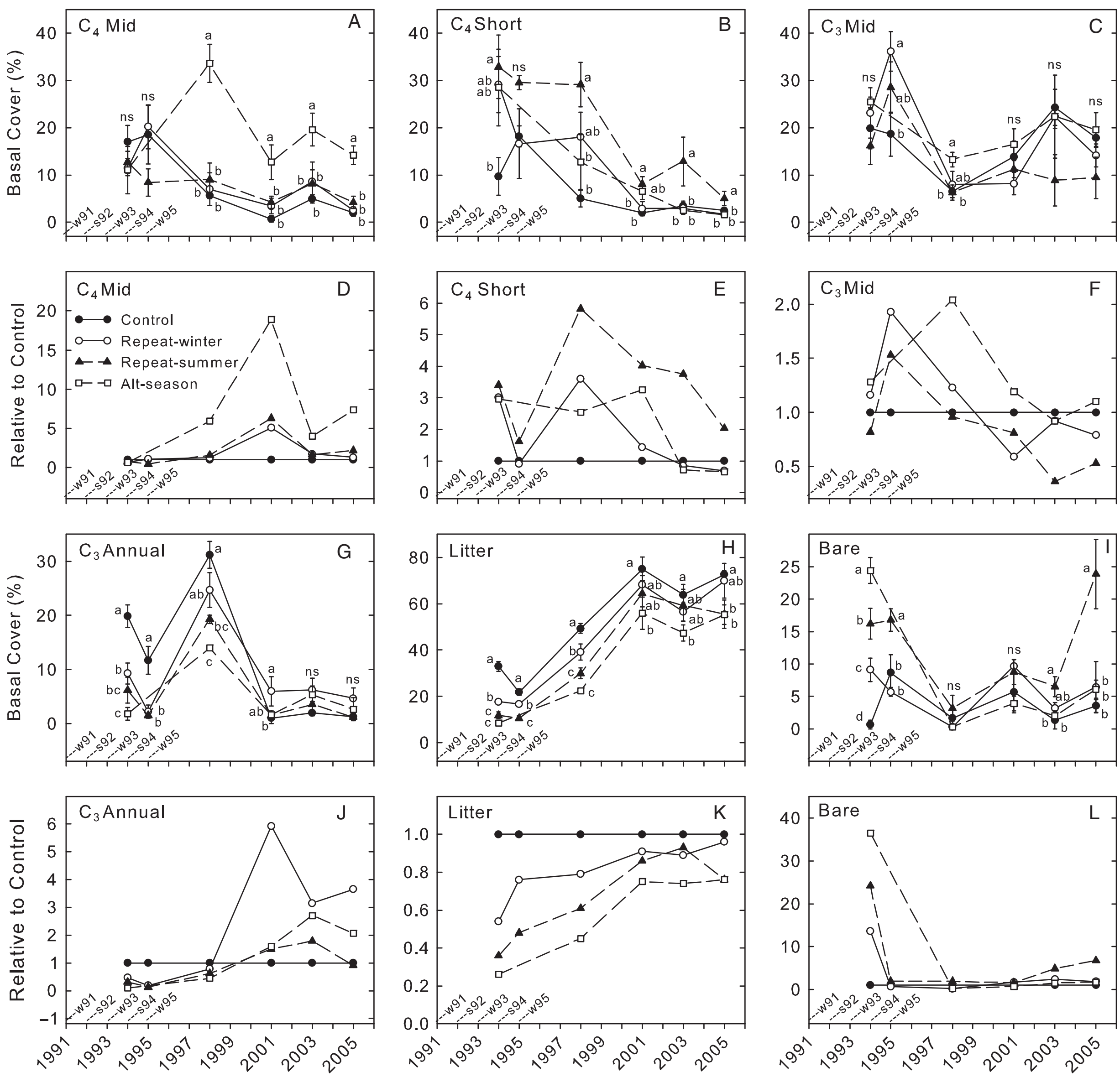

Fig. 2. Cover of each grass functional group, litter and bare ground in response to fire treatments (a-c, g-i) and relative to the control (d-f, j-l). Vertical lines are $\pm$ 1 SE ($n = 3$). Means with similar letters within each date are not significantly different ($P \leq 0.05$) (ns = no significant differences). Time of fire steps is displayed on the x-axis.

Great Plains show that summer fires will reduce abundance or productivity of C_4 grasses and favor C_3 grasses (Steuter 1987; Howe 1995). Similarly, summer fires significantly delayed post-fire recovery of C_4 *T. triandra* in South Africa (Everson et al. 1985; Trollope 1987). The second trend in the literature regarding summer fire in grassland is that they have little long-term effect on grass species production or composition. This has been found in the central Great Plains (Engle et al. 1998, 2000) and south Texas (Mayeux & Hamilton 1988; Owens et al. 2002). Different from these trends, Towne & Kemp (2008) found, in a long-term central Great Plains study, that both annual spring and biennial summer fires increased C_4 grass cover but C_4 tallgrasses *Andropogon gerardii*, *Sorghastrum nutans* and *Panicum virgatum* increased to a greater degree under spring burning, while shorter C_4 grasses *Schizachyrium scoparium* and *B. curtipendula* increased more in the summer fire treatment. Both fire treatments decreased C_3 *Poa pratensis* cover. Thus, our finding that treatments that included summer fires (repeated-summer, alternate-season) benefited C_4 grasses and had little effect on C_3 mid-grasses differs from previous studies. Treatments with summer fires were

Table 2. Short-term (1–4 yr postfire; 1994–1998) and long-term (7–12 yr post-fire; 2001–2005) functional group per cent basal cover responses to fire treatments. [1]Means ± 1 SE. Means with similar letters are not significantly different ($P \leq 0.05$; $n = 3$) in each column and postfire time. [2]Difference between control and alternate-season fire treatment is significant at $P \leq 0.061$. [3]Difference between control and repeated-winter fire treatment is significant at $P \leq 0.052$.

Fire treatment	Total perennial grass[1]	C_4 perennial mid-grass	C_4 perennial short-grass	C_3 perennial mid-grass	C_3 annual grass	Forbs	Litter	Bare ground
1–4 yr Post-fire; 1994–1998								
No-fire control	39.7 ± 0.9 b	13.7 ± 0.9 ab	10.9 ± 1.9 b	15.0 ± 3.3 a	20.9 ± 0.8 a	0.8 ± 0.3 b	34.7 ± 0.4 a	3.7 ± 0.8 b
Repeated-winter	56.5 ± 1.2 a	12.9 ± 2.8 b	21.2 ± 5.6 ab	22.4 ± 3.3 a	12.0 ± 1.3 b	1.8 ± 0.8 ab	24.5 ± 1.1 b	5.0 ± 0.5 b
Repeated-summer	57.5 ± 3.9 a	10.0 ± 1.3 b	30.5 ± 4.2 a	17.0 ± 3.6 a	9.0 ± 0.9 bc	4.1 ± 1.4 a	17.4 ± 0.3 c	12.0 ± 1.9 a
Alternate-season	62.3 ± 1.4 a	22.3 ± 4.5 a[2]	20.6 ± 6.8 ab	19.3 ± 1.3 a	7.9 ± 0.7 c	2.1 ± 0.6 ab	15.5 ± 0.9 c	12.4 ± 0.9 a
7–12 yr Post-fire; 2001–2005								
No-fire control	23.7 ± 3.4 b	2.5 ± 0.7 b	2.6 ± 0.4 b	18.6 ± 3.0 a	1.4 ± 0.4 a	0.9 ± 0.2 a	70.5 ± 3.7 a	3.5 ± 1.8 b
Repeated-winter	22.2 ± 4.2 b	4.8 ± 1.1 b	2.5 ± 0.3 b	14.9 ± 4.2 a	5.6 ± 2.1 a[3]	1.0 ± 0.5 a	64.8 ± 4.7 ab	6.4 ± 1.7 b
Repeated-summer	24.0 ± 5.2 b	5.5 ± 1.6 b	8.6 ± 2.3 a	9.8 ± 3.5 a	2.1 ± 0.8 a	1.3 ± 0.1 a	59.7 ± 5.7 ab	13.0 ± 1.3 a
Alternate-season	38.4 ± 3.4 a	15.5 ± 2.6 a	3.5 ± 0.5 b	19.5 ± 1.3 a	3.2 ± 1.1 a	1.4 ± 0.3 a	52.8 ± 2.3 b	4.0 ± 0.6 b

Table 3. Short (1–4 yr post-fire; 1994–1998) and long-term (7–12 year post-fire; 2001–2005) functional group diversity (H') and evenness (J') in each treatment. [1]Means are shown ± 1 SE. Means with similar letters are not significantly different ($P \leq 0.05$; $n = 3$) in each column and post-fire duration.

Post-fire duration	Fire treatment[1]	H'	J'
Short-term (1–4 yr post-fire)	No-fire control	0.56 ± 0.01 a	0.81 ± 0.02 a
	Repeated-winter	0.62 ± 0.01 a	0.89 ± 0.02 a
	Repeated-summer	0.60 ± 0.03 a	0.87 ± 0.04 a
	Alternate-season	0.61 ± 0.02 a	0.88 ± 0.02 a
Long-term (7–12 yr post-fire)	No-fire control	0.33 ± 0.02 b	0.48 ± 0.03 b
	Repeated-winter	0.35 ± 0.04 b	0.51 ± 0.06 b
	Repeated-summer	0.41 ± 0.05 ab	0.58 ± 0.07 ab
	Alternate-season	0.49 ± 0.01 a	0.70 ± 0.02 a

slightly more effective than the repeated winter fire treatment in suppressing C_3 annual grass cover.

The reasons for the positive C_4 grass responses to summer fires in our study may relate to the temporary removal of the *Prosopis* overstorey that increased light available to C_4 grasses. However, this does not explain why we did not see a similar C_4 grass response in the repeated-winter fire treatment that had essentially the same effect on the *Prosopis* overstorey. The initial greater increase in bare ground and removal of litter afforded by treatments that included summer fire may have provided more opportunities for C_4 grass recruitment than occurred in the repeated-winter fire treatment.

The lack of C_3 mid-grass response by any of the fire treatments may result from extreme summer temperatures that limited C_3 grass growth following removal of the *Prosopis* overstorey by fire. The primary C_3 grass species, *Nassella*, is associated with *Prosopis* canopies and benefits from shading and cooling effects provided by the trees (Ansley & Castellano 2006). Most studies that show a positive C_3 grass response to summer fires were conducted in the northern Great Plains USA with milder summer temperatures (Steuter 1987; Howe 1995).

Our finding that none of the fire treatments increased forb cover in the long-term may result from increased grass cover or a lack of forb propagules, consistent with other studies (Copeland et al. 2002; Fynn et al. 2004).

Fire severity and state-and-transition thresholds

Our results suggest that there are two thresholds of responses to fire severity in this semi-arid ecosystem. We define fire severity here as the long-term impact of each repeated fire treatment on the ecosystem (Bond 2001). A minimum threshold of fire severity appeared to be necessary to simultaneously reduce *Prosopis* cover and subsequently cause a shift in herbaceous composition away from C_3 mid-grasses and toward C_4 mid-grasses. The repeated-winter fire treatment (three fires in 5 yr) temporarily reduced *Prosopis* cover but was not of sufficient severity to shift perennial grass composition. The alternate-season fire treatment (two low-to-moderate intensity winter fires and one intense summer fire in 4 yr) met this minimum threshold and caused a substantial long-term increase in C_4 mid-grass cover and functional group diversity (H') without reducing C_3 mid-grass and C_4 short-grass cover.

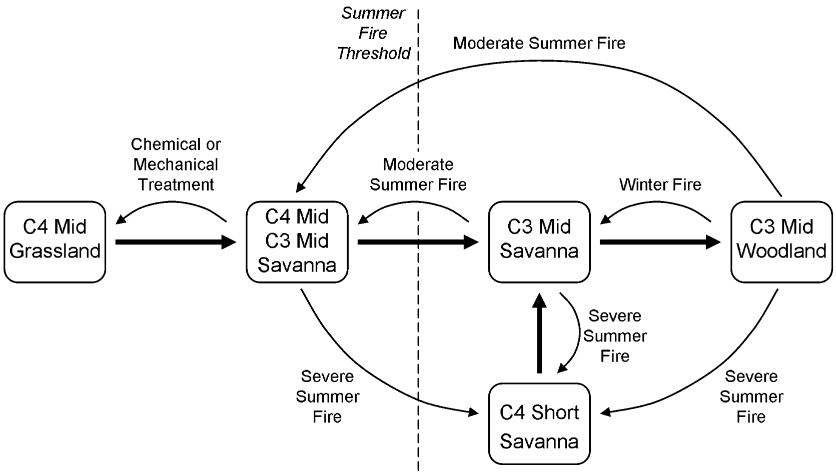

Fig. 3. Hypothetical vegetation transitions with seasonal fire disturbances. Boxes indicate vegetation states. Heavy lines depict herbaceous and woody composition transitions without fire disturbance. Curved arrows depict transitions caused by fire or other disturbances. The dashed vertical line represents a "summer fire threshold" where summer fire is necessary to shift composition back to C_4 mid-grass dominance. Chemical or mechanical treatments are necessary to remove fire-resistant *Prosopis* and return the ecosystem to true grassland.

Thus, overall perennial grass cover increased by 62%. The reasons for this are not known but inclusion of summer fire appears crucial in triggering C_4 mid-grass growth.

There also appears to be an upper threshold, above which fire severity is too extreme and can stress the ecosystem, as has been documented in northern Australian savannas (Williams et al. 2003). The repeated-summer fire treatment (two intense fires in 3 yr) appears to have exceeded that threshold by causing post-fire herbaceous composition to "over-shift" toward less productive C_4 short-grasses rather than C_4 mid-grasses. This treatment also caused a long-term increase in bare ground cover. Our results support the "intermediate disturbance hypothesis" (Connell 1978; Collins 1992) if we assume that the repeated-winter, alternate-season and repeated-summer fire treatments represent low, intermediate and high disturbances, respectively.

Figure 3 presents a hypothetical state-and-transition model for herbaceous and woody composition shifts in response to seasonal fire disturbances based on data from this study. In the absence of fire, composition shifts from C_4 mid-grass grassland, to *Prosopis* savanna stages and finally to C_3 mid-grass/*Prosopis* woodland (Archer 1989). We originally hypothesized that fire in any season would reduce C_3 grass cover and increase C_4 mid-grass cover. However, this proved not to be the case and Fig. 3 represents an adjustment to our hypothesis. Winter fire can only shift C_3 mid-grass woodland back to C_3 mid-grass savanna. Summer fire is necessary to shift communities back toward C_4 mid-grasses (i.e. the "Summer Fire Threshold"). However, without anthropogenic chemical or mechanical inputs that root-kill fire-resistant *Prosopis* (Ansley et al. 2004) summer fire can only temporarily shift the community to a C_4/C_3 mixed-grass savanna. Severe summer fires (represented by the repeated-summer fire treatment) can trigger undesirable transitions to C_4 short-grass savanna. All savanna types will ultimately shift back to C_3 mid-grass woodlands without additional fire disturbances. Our study provides an example of how variations in fire disturbance patterns alone can transition understorey vegetation into multiple states (House et al. 2003).

Importance of time since fire

This study highlights the importance of time since fire for several reasons. First, the most pronounced increases in C_4 mid-grass cover relative to the control occurred several years after the last fire in a particular treatment. This suggests that an effective fire return interval for promoting shifts in herbaceous composition toward C_4 mid-grass dominance may be at least 3–5 yr (Ansley et al. 2006). More frequent fires may slow the ability of this functional group to assert dominance. This longer fire return interval contrasts with annual or biennial burning schedules reportedly needed to maintain C_4 grass dominance of the Tallgrass prairie in the USA (Peterson et al. 2007; Towne & Kemp 2008), or a fire return interval of ≤ 5 yr that was necessary to maintain the competitiveness of *Themeda triandra* in Australia (Morgan & Lunt 1999). In contrast, a study in South Africa showed that while annual burning favored *Themeda* abundance, taller C_4 grasses such as *Cymbopogon* and *Eragrostis* were more responsive to less frequent burning (Fynn et al. 2005).

Also related to time since fire were three factors that collectively decreased herbaceous cover in all treatments over time. First, severe post-fire droughts limited grass production in all treatments. Second, multi-stemmed regrowth from top-killed *Prosopis* became increasingly more competitive with grasses over time. Third, the post-fire accumulation of herbaceous litter in all treatments may have reduced grass basal cover by attenuating solar radiation necessary for grass growth or grass seed germination (Bond 2001). Similar responses were found following >10 post-fire years of litter accumulation in one southeastern Australian *Themeda* grassland (Morgan & Lunt 1999), but not in another (Prober et al. 2007).

Applied relevance of the study

The fire treatments in this study were designed to increase *Prosopis* mortality and restore C_4 grass productivity. The fire sequences imposed theoretically could have occurred naturally in the southern Great Plains prior to European settlement as the historical fire return interval is assumed to be 1–6 yr (Frost 1998). However, current commercial livestock grazing operations in the region that utilize prescribed fire as a management tool typically burn every 10–20 yr. Grass production and precipitation are not sufficient to both maintain livestock and burn annually or biennially as is found in the tallgrass prairie USA (Knapp et al. 1998) or *Themeda* grasslands in Africa (Fynn et al. 2005). Thus, long-term (decadal) post-fire response data are relevant to management operations in this region.

The alternate-season fire treatment was most effective at increasing C_4 mid-grass cover but optimum responses occurred 3–5 yr after the last fire in this treatment. This treatment was also most effective at increasing functional group diversity by generating a better balance in basal cover among the three perennial grass functional groups. Historical fire regimes likely included a mixture of summer and winter season fires and this may have been important for the maintenance of C_4 perennial mid-grasses in these ecosystems. This study provides some of the first long-term data showing a possible benefit of mixing seasonal fires (i.e. the alternate-season fire treatment) in a prescribed burning management plan to restore C_4 mid-grass cover and enhance overall herbaceous diversity.

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Supporting Information

Additional supporting information may be found in the online version of this article:

Appendix S1. List of grass species (scientific name followed by common name) found at the research site and their classification into functional groups. Species are listed in order of abundance within each functional group. All species are native except *Bromus*.

Appendix S2. Herbaceous cover sampling schedule in relation to fire steps in each fire treatment. Each cell shows the latest fire step in each treatment before sampling (top), the number of C_4 growing seasons (gs; Apr–Sep) between the last fire step in a fire treatment and a particular sample year (middle), and the number of months (m) between the last fire step in a fire treatment and a particular sample year (bottom).

Appendix S3. Weather, herbaceous fine fuel and fire behavior of each fire step in each repeated fire treatment. Except for the last two rows, all values are means (± SE) of three plots.

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