Short-Term Control of an Invasive C$_4$ Grass With Late-Summer Fire[☆],[☆☆]

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ARTICLE INFO

ABSTRACT

Yellow bluestem (*Bothriochloa ischaemum* [L.] Keng var. *songarica* [Rupr. ex Fisch & C.A. Mey] Celarier & Harlan) is a non-native, invasive C$_4$ grass common in southern Great Plains rangelands. We measured the effects of a single late-summer (September 2006) fire on yellow bluestem at two sites in central Texas (Fort Hood and Onion Creek). At Fort Hood, relative frequency of yellow bluestem in burned plots decreased from $74 \pm 4\%$ (preburn; mean ± standard error) to $9 \pm 2\%$ (2007) and remained significantly lower compared with unburned plots through 2009 (burned: $14 \pm 2\%$; unburned: $70 \pm 14\%$). At Onion Creek, yellow bluestem initially decreased from $74 \pm 5\%$ (2006) to $32 \pm 7\%$ (2007). Yellow bluestem recovered substantially by 2009 ($67 \pm 10\%$) but was still significantly lower than in unburned transects ($96 \pm 1\%$). Relative frequency of other graminoids increased significantly in burned plots (compared with preburn values) at Fort Hood (preburn: $11 \pm 4\%$; 2009: $29 \pm 7\%$) but not at Onion Creek (preburn: $24 \pm 6\%$; 2009: $22 \pm 7\%$). Frequency of forbs increased dramatically in the first growing season after fire (Fort Hood: $15 \pm 2\%$ to $76 \pm 3\%$; Onion Creek: $2 \pm 2\%$ to $45 \pm 5\%$), then decreased through the third growing season (Fort Hood: $57 \pm 6\%$; Onion Creek: $11 \pm 4\%$). Key differences between the sites include much higher biomass at Fort Hood than at Onion Creek ($8\,130\ kg \cdot ha^{-1}$ vs. $2\,873\ kg \cdot ha^{-1}$), more recent grazing at Onion Creek (ending in 2000 vs. before 1996 at Fort Hood), and higher rainfall after the Onion Creek burn (214 mm in 20 days vs. 14 mm). Late-summer fire can temporarily decrease yellow bluestem frequency, but effects vary with site conditions and precipitation. Restoring dominance by native grasses may require additional management.

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Introduction

Prescribed fire can be used to manage invasive species by burning when those species are vulnerable (DiTomaso et al., 2006). Plant vulnerability depends on individual plant characteristics, including size and reproductive state (seeds can be killed prior to dispersal), as well as fire characteristics, including intensity, frequency, and seasonality (Pyke et al., 2010). However, fire management is complicated by non-native species that share life history traits with desirable native plants because fire conditions that harm the non-native species can also harm the native species.

Tropical and semiarid grasslands around the world have been invaded by non-native C$_4$ grasses (Foxcroft et al., 2010). Like the dominant native species in these systems, many invasive C$_4$ grasses are perennial and fire adapted. Furthermore, because these grasses are often introduced for forage, they are selected to be highly tolerant of grazing and other disturbances (Wilsey and Polley, 2006; Driscoll et al., 2014). In some cases, prescribed fire can increase the abundance of these invasive species by creating bare soil for seed germination and removing competing biomass (Holzmueller and Jose, 2011).

Grasslands in the southern Great Plains are generally dominated by C$_4$ species such as big bluestem (*Andropogon gerardii* Vitman), Indian grass (*Sorghastrum nutans* [L.] Nash), little bluestem (*Schizachyrium scoparium* [Nash] E.P. Bicknell), and various grama species (*Bouteloua* spp.; Diggs et al., 1999). Many of the common non-natives in the region are also C$_4$ grasses; these include crowngrasses (*Paspalum* spp.), lovegrasses (*Eragrostis* spp.), Old World bluestems (*Dichanthium* and *Bothriochloa* spp.), and windmill grasses (*Chloris* spp.). The non-native species can be favored by common fire management practices. For example, Caucasian bluestem (*Dichanthium* [*Andropogon*] *bladhii* [Retz.] Clayton) had greater biomass than big bluestem in prairies with frequent spring burns (Reed et al., 2005).

Yellow bluestem [*Bothriochloa ischaemum* (L.) Keng var. *songarica* (Rupr. ex Fisch & C.A. Mey) Celarier & Harlan] was introduced to the

southern Great Plains from Eurasia to improve forage availability and quality, especially on marginal soils (Eck and Sims, 1984; Coyne and Bradford, 1985). This species is now widespread throughout the southern half of the United States, where it is often promoted for pasture improvement (e.g., Philipp et al., 2007). Yellow bluestem occupies a wide variety of habitats and soil types, except for sites with deep shade, and is highly tolerant of grazing (Fowler, 2002; Gabbard and Fowler, 2007). This species has many undesirable effects on native grasslands. It can decrease native plant diversity, forb cover, and arthropod biomass (McIntyre and Thompson, 2003; Hickman et al., 2006; Robertson and Hickman, 2012) as well as richness and abundance of grassland birds and rodents (Sammon and Wilkins, 2005; Hickman et al., 2006). Yellow bluestem can reduce native grass biomass and seedling survival through production of allelopathic biochemicals (Greer et al., 2014). It can also change nutrient cycling by increasing litter decomposition rates and nitrogen mineralization rates, at least on coarse-textured soils (Ruffner et al., 2012).

Yellow bluestem appears to benefit from cool-season fire compared with many native grasses, but sometimes decreases after warm-season fires. Yellow bluestem is twice as likely to be present in sites that have received winter burns compared with unburned sites (Gabbard and Fowler, 2007). A February burn increased yellow bluestem biomass by 16% (Pase, 1971). In contrast, repeated prescribed fires in March and April, when yellow bluestem first begins to grow, reduced end-of-season biomass by 6% to 30% depending on rainfall (Berg, 1993). In coastal prairie, yellow bluestem frequency did not change after a June prescribed fire during a drought (Twidwell et al., 2012). However, in central Texas, burning during a drought at any time from June through January decreased yellow bluestem tiller count by 32% to 64%, with the largest decrease for the June burn (Havill et al., 2015). Prescribed fires in August decreased yellow bluestem frequency by 30% to 35% on both shallow and deep soils in Texas (Simmons et al., 2007). By comparison, burns in late October and early November reduced yellow bluestem frequency by only 10% on the shallow soil, but by 28% on the deeper soil (Simmons et al., 2007). The variability in yellow bluestem response to warm-season fire suggests that factors beyond seasonality are important.

Yellow bluestem's sensitivity to warm-season fire is linked to reproductive status and seed vulnerability. Yellow bluestem is most vulnerable to fire during stem elongation, when plants begin to form flowering stems, but before they actually flower (Ruckman et al., 2012b; Havill et al., 2015). Yellow bluestem flowers throughout the growing season (approximately April–November), with flowering often triggered by rainfall (Diggs et al., 1999; Ruckman et al., 2012b). In this region, early fall rains often trigger a pulse of flowering after typically dry summers. Yellow bluestem seeds are also more vulnerable to high fire temperatures than many native grasses (Ruckman et al., 2012a).

We burned two grasslands dominated by yellow bluestem in September 2006. Our goal was to decrease the abundance of yellow bluestem and allow native grasses to become dominant.

Materials and Methods

Our two study sites are separated by about 125 km (80 miles). The experimental design and sampling methodology differed slightly between the two sites, but are similar enough that comparisons are useful. Furthermore, comparing results from similar sites burned in the same month can illustrate how fire effects vary by site.

Study Sites

The Fort Hood Site (31.151520, –97.762980; elevation: 288 m) is a 24-ha grassland located on the Fort Hood Military Reservation. Soils are Topsey clay loam, a fine-loamy, carbonatic, thermic Udic Calcuistoll. The grassland had been unmanaged and undisturbed (i.e., not grazed, mowed, burned, or affected by military training) for at least a decade.

The Onion Creek site (30.063324, –97.957149; elevation: 280 m) is a 114-ha prescribed burn unit on the City of Austin Water Quality Protection Lands and is located near Buda, Texas. Soils are the Rumple-Comfort association. Rumple soils (clayey-skeletal, mixed, thermic, Udic Argiustolls) comprise about 60% of the association; Comfort soils (clayey-skeletal, mixed, thermic, Lithic Argiustolls) make up about 20%, and other soils make up 20%. The burn unit and surrounding 703-ha tract had been unmanaged since 2000. Prior management was fairly continuous, moderate to high-intensity cattle grazing.

The climate in this region is humid subtropical. Winters are mild, summers are hot, and precipitation exhibits a bimodal (May and September or October) pattern. At Fort Hood, the average high to low temperature range is 14.4°C to 1.1°C in January and 35.2°C to 22.1°C in July. Average annual rainfall is 834 mm. At Onion Creek, average high to low temperature range is 16.6°C to 5.5°C and 36°C to 23.8°C; average annual rainfall is 870 mm.

Field Methods

At Fort Hood, we established eight adjacent 25 x 25 m plots (Fig. 1). Plots were paired and one plot in each pair was randomly selected to be burned. We established two diagonal transects per plot.

At Onion Creek, we established three pairs of 20-m long transects. Treatment transects were located within the burn unit, 25 to 60 m from the western perimeter. Control transects were located 5 to 10 m outside of the burn unit in an area that received no management. Pairs were spaced 275 to 375 m apart along the burn unit boundary. All transects were oriented north to south and were in full sun, well away from any woody canopy.

Vegetation composition was assessed by the point intercept method using a 1-m long, 10-pin point frame (Caratti, 2006). Pins were spaced 10 cm apart. The frame was always placed perpendicular to the transect. At Fort Hood, data were collected at 1-m intervals from meter 4 through meter 24 (as measured from the plot corners); data were not collect at meter 14 (the approximate midpoint) to avoid double-sampling. A total of 40 frames were sampled for each plot. At Onion Creek, data were also collected at 1-m intervals, starting at 1 m, for a total of 20 frames per transect.

At every frame sampling location, each of the 10 pins were dropped. At Fort Hood, we recorded all plant species that intercepted each pin. At Onion Creek, the uppermost two plant species were recorded. While the difference in species number per pin could influence comparisons between the sites, only 167 out of 12,800 pin drops (1.3%) at Fort Hood recorded more than two species.

We also collected biomass samples from both sites to measure fuel loads. At Fort Hood, we collected biomass in 2006 and 2007 from six randomly placed quadrats (0.36 m²) in each plot. At Onion Creek, biomass was collected in 2006 and 2007 from six randomly placed 0.25-m² quadrats, with three quadrats inside the burn unit and three quadrats outside. Unfortunately, the 2006 biomass data from Onion Creek were lost. All plants were clipped to ground level; litter was also collected. Samples were dried at 60°C until the weight was constant, usually 24 to 48 hours.

Fort Hood transects were sampled 12 to 19 July 2006 (preburn); 16 to 20 July 2007; 17 to 18 July 2008; and 21 to 22 July 2009. Onion Creek transects were sampled 17 July 2006 (preburn); 15 August 2007; 16 September 2008; and 17 September 2009.

Prescribed Fire

The Fort Hood grassland, including all three treatment plots, was burned on 11 September 2006. Burn plots were ignited on the downwind side, followed by the flanking sides. When enough of the plot had burned that the fire would be contained by the burned area, the final side was lit with a head fire. Control plots were protected by mowed fire breaks and remained unburned. The air temperature varied
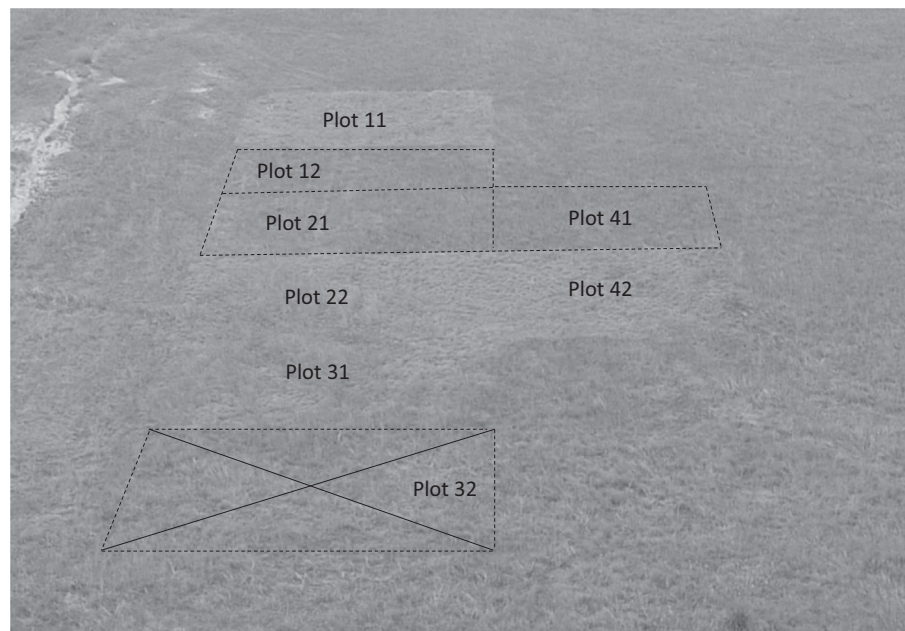
Figure 1. The Fort Hood study site in August 2008 (11 months after the prescribed fire). Approximate locations of the burned plots are shown with dashed lines (the grassland surrounding the study area was also burned). The solid lines in Plot 32 indicate the transect locations.

between 29°C and 33°C; relative humidity ranged from 46% to 66%. Wind speeds were 6 to 12 km · h^{-1}. Fire behavior was very active, with two sustained fire whirls.

The Onion Creek site was burned on 29 September 2006. Air temperature during the ignition phase increased from 29°C to 31°C and relative humidity varied between 41% and 46%. Wind was 8 to 10 km · h^{-1} out of the southeast with gusts to 14.5 km · h^{-1}. Because the treatment transects were located near the western edge of the burn unit, they were burned by backing and flanking fires.

Statistical Analyses

Our sampling unit for Fort Hood was the plot ($N = 8$; both transects combined). For Onion Creek, we used transect as the sampling unit ($N = 6$) while acknowledging that these transects are subsamples of the burn unit, which is the true (unreplicated) sampling unit (Wester, 1992). For this reason, our inference space is limited. Such pseudoreplication is a common problem in fire studies that use management burns or wildfires (Van Mantgem et al., 2001).

We calculated relative frequency for each species of interest by counting the number of pins at which that species was present in a sampling unit and dividing by the total number of pin contacts by all species for that unit. We also grouped species by growth form (forbs and graminoids excluding yellow bluestem). For growth form relative frequency, we counted how many species of each growth form contacted every pin, summed those values by sampling unit, and divided by the total number of pin contacts in that unit. These calculations express frequency as a proportion of the plant community and accounts for changes in overall plant cover with varying rainfall. Trends using relative frequency calculated as a proportion of pins sampled were similar to the results presented below.

We analyzed trends in frequency for yellow bluestem, common native grasses (Table 1), all forbs, and all graminoids (excluding yellow bluestem). Data from the two sites were analyzed separately using R 3.4 (R Core Team, Vienna, Austria). We analyzed trends in frequency with generalized linear mixed models using penalized quasi-likelihood (MASS package, Venables and Ripley, 2002). Because frequency is a binomial variable, we used the binomial family with a logit link. As fixed effects, all models included treatment, year, pair,

and a treatment by year interaction. As random effects, we included intercepts for the pair-treatment interaction. While a repeated measures study like ours should ideally account for temporal autocorrelation, our datasets were too small to include complex correlation structures.

Significance of fixed effects were calculated using Wald Chi-square tests (car package, Fox and Weisberg, 2011). We used contrasts (multcomp package, Hothorn et al., 2008) to compare burned and unburned values within a year. We also compared postfire values with pretreatment values within a treatment (e.g., burned 2007 vs. burned 2006). Contrast significance was adjusted using the single-step method (Hothorn et al., 2008). Pretreatment biomass at Fort Hood was compared using a Welch two-sample t-test with unequal variances.

Results

Our two sites (Fort Hood and Onion Creek) were dominated by yellow bluestem before treatment. At both sites, pretreatment vegetation was dominated by yellow bluestem (Fort Hood frequency: 66 ± 7% at Fort Hood; Onion Creek: 78 ± 4%; mean ± standard error, Table 1, Fig. 2). Yellow bluestem was the only non-native grass present at Fort Hood. At Onion Creek, Johnsongrass (*Sorghum halepense* [L.] Pers.) was

Table 1
Pretreatment (2006) frequency (mean ± standard error) for yellow bluestem and other species of interest.[1]

Species or Group	Site	Control (%)	Burned (%)	z	P
Yellow bluestem	Fort Hood	57 ± 13	74 ± 4	1.60	0.54
	Onion Creek	83 ± 6	74 ± 5	2.61	0.07
Composite dropseed	Fort Hood	4 ± 2	1 ± 0.4	3.00	0.02
	Onion Creek	1 ± 1	1 ± 1	1.03	0.89
Little bluestem	Fort Hood	21 ± 8	7 ± 2	3.20	0.01
Purple threeawn	Onion Creek	6 ± 5	4 ± 2	0.63	1.00
Texas wintergrass	Onion Creek	1 ± 1	9 ± 5	5.18	<0.001
Graminoids	Fort Hood	29 ± 11	11 ± 4	2.74	0.046
	Onion Creek	17 ± 6	24 ± 6	2.40	0.13
Forbs	Fort Hood	14 ± 2	15 ± 2	0.54	1.00
	Onion Creek	1 ± 0.2	2 ± 2	1.84	0.36

[1] The values for graminoids excludes yellow bluestem. Little bluestem was not found at Onion Creek; Texas wintergrass and purple threeawn were too uncommon at Fort Hood for analysis. Significance was calculated using contrasts with the single-step adjustment.

present in one control transect throughout the study and field brome (*Bromus arvensis* L.) was found only in 2007.

Native species composition differed between the two sites. The two most common native grasses at Fort Hood were little bluestem (frequency = 14%) and composite dropseed (*Sporobolus compositus* [Poir.] Merr., 3%). The most common forb was Maximilian sunflower (*Helianthus maximiliani* Schrad., 4%). At Onion Creek, the two most common native grasses were purple threeawn (*Aristida purpurea* Nutt., 6%) and Texas wintergrass [*Nassella leucotricha* (Trin. & Rupr.) Pohl, 5%]. The most common forb was hoary false goldenaster (*Heterotheca canescens* [DC.] Shinners, 1%).

Fuel loads, as measured by biomass, also differed between the two sites. Preburn (2006) biomass at Fort Hood was $7\,600 \pm 262$ kg · ha^{-1}. The preburn (2006) biomass data for Onion Creek were lost, but 2007 biomass near control transects was much lower compared with 2007 values from Fort Hood control plots ($2\,873 \pm 46$ kg · ha^{-1} vs. $9\,479 \pm 752$ kg · ha^{-1}). The differences in species composition and biomass are related to the management histories of the sites. At Fort Hood, the most common native species (such as little bluestem and Maximilian sunflower) tended to be grazing sensitive while at Onion Creek, the most common native species (such as purple threeawn and hoary false goldenaster) tended to be grazing tolerant. Onion Creek had been grazed until only 6 years before data collection; Fort Hood had not been grazed within at least the previous decade.

Next, we confirmed that treatment and control areas within each site were similar before treatment. In 2006 (preburn), control and burned sample units did not differ in frequency of yellow bluestem or forbs at either site (Table 1, Fig. 2). At Fort Hood, pretreatment frequency of little bluestem and composite dropseed were higher in control plots (bluestem: $21 \pm 8\%$ vs. $7 \pm 2\%$; dropseed: $4 \pm 2\%$ vs. $1 \pm 0.4\%$), leading to higher graminoid frequency in those plots ($29 \pm 11\%$ vs. $11 \pm 4\%$). At

Onion Creek, control and burned transects were similar for all variables examined. Pretreatment biomass at Fort Hood was higher in the burned plots than in the control plots ($8\,130 \pm 263$ kg · ha^{-1} vs. $7\,070 \pm 254$ kg · ha^{-1}, $t = 2.9$, df $= 6$, $P = 0.03$). Because Onion Creek preburn biomass data were lost, we do not know how biomass may have differed, but control and burned transects were not visually different.

We found differences in yellow bluestem response to fire between the two sites (Fig. 2, Tables 2 and S1). At both sites, yellow bluestem frequency initially decreased after summer fire. At Fort Hood, burned plots in 2007 had very little yellow bluestem (preburn: $74 \pm 4\%$; 2007: $9 \pm 2\%$). Yellow bluestem frequency in burned plots remained significantly lower than in control plots through 2009 (burned: $9 \pm 2\%$ to $16 \pm 2\%$; control: $63 \pm 11\%$ to $70 \pm 14\%$). Yellow bluestem frequency also remained lower than pretreatment values ($74 \pm 4\%$), even as burned plot frequency increased to $14 \pm 2\%$ in 2009.

At Onion Creek, yellow bluestem frequency also decreased, but to a lesser extent than at Fort Hood ($74 \pm 5\%$ preburn to $32 \pm 7\%$ in 2007; Table S1). Yellow bluestem frequency was significantly lower in burned than in control transects throughout the study (control: $85 \pm 5\%$ to $96 \pm 1\%$), but by 2009 frequency had recovered to pretreatment levels ($67 \pm 10\%$; $P = 0.32$).

Meanwhile, yellow bluestem frequency in control samples increased at both sites. In the unburned plots at Fort Hood, yellow bluestem frequency in 2009 ($70 \pm 14\%$) was significantly higher than in 2006 ($57 \pm 13\%$; Table S1). Similarly, at Onion Creek, yellow bluestem frequency in 2009 ($96 \pm 1\%$) was significantly higher than in 2006 ($83 \pm 6\%$).

We evaluated whether the most common native grasses increased in abundance after the fires. At both sites, composite dropseed frequency in burned plots increased. At Fort Hood, frequency in burned plots increased from $1 \pm 1\%$ to $11 \pm 4\%$ (preburn to 2009; Fig. 3, Table S1). Burned plot dropseed frequency was higher than pretreatment levels ($1 \pm 1\%$) in all
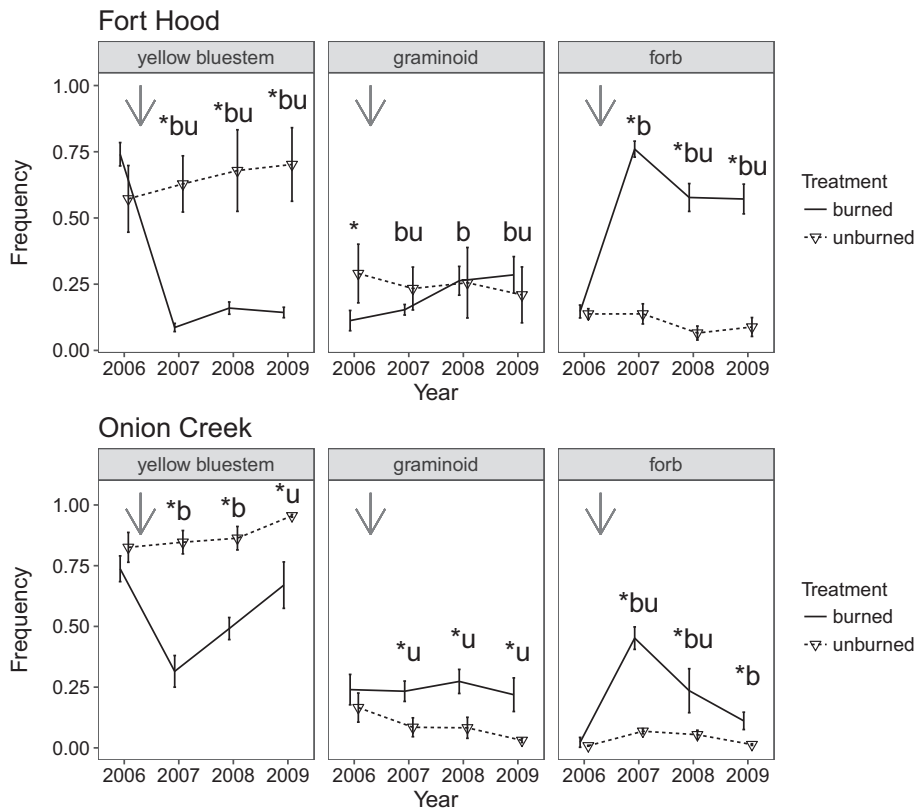
Figure 2. Relative frequency (mean ± standard error) of yellow bluestem (*Bothriochloa ischaemum*), other graminoids, and all forbs at two sites burned in September 2006 (prescribed fire timing indicated by arrow). Points are offset horizontally for clarity. * indicates significant difference between burned and control sample units within a year; *b*, burned sample unit value is significantly different from 2006 (preburn) value; *u*, unburned (control) sample unit value is significantly different from 2006 value.

Table 2
Wald Chi-square tests for fixed effects in the frequency models.[1]

Species or Group	Site	Variable	DF	Chi-square	P
Yellow bluestem	Fort Hood	Treatment	1	18.3	<0.001
		Year	3	379.3	<0.001
		Pair	3	6.1	0.11
		Year*treatment	3	819.4	<0.001
	Onion Creek	Treatment	1	111.2	<0.001
		Year	3	217.0	<0.001
		Pair	2	18.0	<0.001
		Year*treatment	3	111.4	<0.001
Dropseed	Fort Hood	Treatment	1	1.5	0.22
		Year	3	32.6	<0.001
		Pair	3	10.2	0.01
		Year*treatment	3	50.8	<0.001
	Onion Creek	Treatment	1	5.6	0.02
		Year	3	16.4	<0.001
		Pair	2	2.1	0.35
		Year*treatment	3	11.5	0.009
Little bluestem	Fort Hood	Treatment	1	2.9	0.09
		Year	3	79.2	<0.001
		Pair	3	39.4	<0.001
		Year*treatment	3	38.1	<0.001
Threeawn	Onion Creek	Treatment	1	0.7	0.40
		Year	3	43.7	<0.001
		Pair	2	7.4	0.02
		Year*treatment	3	5.2	0.16
Wintergrass	Onion Creek	Treatment	1	51.2	<0.001
		Year	3	40.6	<0.001
		Pair	2	62.0	<0.001
		Year*treatment	3	1.6	0.65
Graminoids	Fort Hood	Treatment	1	0.1	0.83
		Year	3	46.6	<0.001
		Pair	3	17.6	<0.001
		Year*treatment	3	103.8	<0.001
	Onion Creek	Treatment	1	35.1	<0.001
		Year	3	27.9	<0.001
		Pair	2	15.9	<0.001
		Year*treatment	3	37.0	<0.001
Forbs	Fort Hood	Treatment	1	69.9	<0.001
		Year	3	442.7	<0.001
		Pair	3	0.6	0.90
		Year*treatment	3	373.7	<0.001
	Onion Creek	Treatment	1	285.5	<0.001
		Year	3	309.9	<0.001
		Pair	2	62.1	<0.001
		Year*treatment	3	13.7	0.003

[1] Graminoid frequency excludes yellow bluestem. All models included a random intercept term for the pair-treatment interaction.

postfire years (4 ± 1% to 11 ± 4%) but was higher than in control plots only in 2009. At Onion Creek, composite dropseed frequency increased from 1 ± 1% to 9 ± 5% (preburn to 2009; Fig. 3, Table S1). Dropseed frequency in burned transects was higher than in control transects in 2007 (7 ± 3% vs. 1 ± 1%) and 2009 (9 ± 5% vs. 1 ± 1%); burned transect frequency was also higher than preburn values in all postfire years.

Little bluestem frequency at Fort Hood increased after fire from 7 ± 1% (preburn) to 15 ± 3% in 2008 (Fig. 3; Table S1). Little bluestem frequency, which was higher in control plots before the fire, remained lower in burned plots than in control plots in 2007 (5 ± 1% vs. 14 ± 6%), but increased to similar levels in 2008 and 2009 (2008: 15 ± 3% vs. 20 ± 10%; 2009: 11 ± 3% vs. 15 ± 8%). Frequency in burned plots was higher than preburn levels in 2008 and 2009.

At Onion Creek, purple threeawn frequency decreased in all transects and remained similar between control and burned transects (Fig. 3, Table S1). Compared with preburn values (5 ± 2%), purple threeawn frequency in burned transects was lower in 2008 (1 ± 1%) and 2009 (2 ± 1%). In control transects, purple threeawn frequency was lower in 2007 (1 ± 1%) and 2009 (0.2 ± 0.3%) compared with 2006 values (6 ± 5%).

Texas wintergrass frequency in burned plots at Onion Creek decreased significantly, from 9 ± 5% preburn to 0.3 ± 0.6% in 2009

(Fig. 3; Table S1). Wintergrass frequency in control and burned plots was different only in 2007 and frequency in control plots did not change (2006: 1 ± 1%; 2009: absent).

We examined the response of graminoids (excluding yellow bluestem) to test whether they became more abundant after fire. At Fort Hood, the frequency of native graminoids in burned plots more than doubled (from 11 ± 4% preburn to 29 ± 7% in 2009; Fig. 2, Table 2). After the fire, native graminoid frequency was never higher in burned plots compared with control plots (burned: 15 ± 2% to 29 ± 7%; control: 21 ± 11% to 26 ± 13%). However, in burned plots, native graminoid frequency was higher compared with pretreatment values in all years. At Onion Creek, graminoid frequency in burned plots did not change (2006: 24 ± 6%; 2007–2009: 22 ± 7% to 27 ± 5%). However, graminoid frequency was higher in burned transects compared with control transects in all postfire years because of a gradual decrease in control transects (2006: 17 ± 6%; 2009: 3 ± 1%).

Forb frequency at both sites increased dramatically for the first year after fire (Fort Hood: 15 ± 2% to 76 ± 3%; Onion Creek: 2 ± 2% to 45 ± 5%; Fig. 2, Table 2). The most frequently encountered forb species in burned plots at Fort Hood were narrowleaf marsh elder (*Iva angustifolia* Nutt. ex DC.), white heath aster (*Symphyotrichum ericoides* [L.] G.L. Nesom), Maximilian sunflower, and smartweed leaf-flower (*Phyllanthus polygonoides* Nutt. ex Spreng). At Onion Creek, the most abundant forb species in burned transects were snakeweeds (*Gutierrezia* spp.), prairie tea (*Croton monanthogynus* Michx.), hoary false goldenaster, and black-eyed susan (*Rudbeckia hirta* L.).
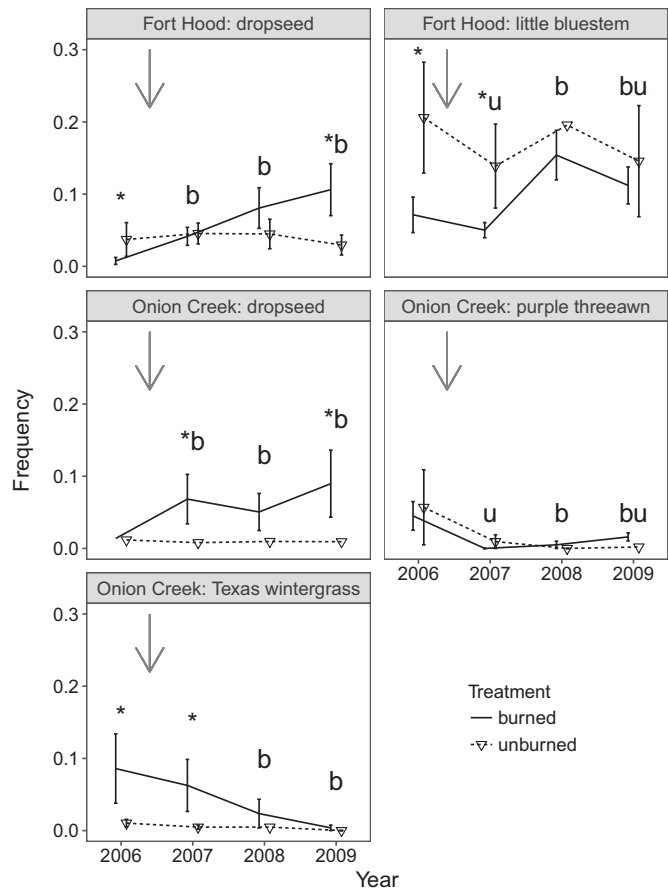
Figure 3. Relative frequency (mean ± standard error) for composite dropseed (*Sporobolus compositus*), little bluestem (*Schizachyrium scoparium*), purple threeawn (*Aristida purpurea*), and Texas wintergrass (*Nassella leucotricha*) at two sites burned in September 2006 (prescribed fire timing indicated by arrow). Points are offset horizontally for clarity. * indicates significant difference between burned and control sample units within a year; b, burned sample unit value is significantly different from 2006 (preburn) value; u, unburned (control) sample unit value is significantly different from 2006 value.

At Fort Hood, forb frequency in burned plots remained high through 2009 (57 ± 6%) and was higher compared with control plots (7 ± 3% to 14 ± 4%) and pretreatment values (15 ± 2%) in all postfire years. Similarly, at Onion Creek, forb frequency in burned transects was higher than in control transects in all postburn years (control: 1 ± 0% to 7 ± 1%; burned: 45 ± 5% to 11 ± 4%); forb frequency was also higher than pretreatment frequency (2006: 2 ± 2%). However, by 2009, forb frequency had decreased dramatically to 12 ± 4%.

Discussion

Warm-season (September) prescribed fire greatly reduced the frequency of yellow bluestem in both sites, but the effect was temporary at one site. Common warm-season native grasses responded positively or neutrally to the fires, but did not become dominant even where yellow bluestem abundance remained low. Forb frequency peaked during the first postfire growing season and then decreased in proportion to the regrowth of yellow bluestem.

Several factors could explain the much greater reduction in yellow bluestem at Fort Hood (relative frequency decreased from 74% to 9%) compared with Onion Creek (frequency decreased from 74% to 31%). Precipitation before and after the fires was considerably lower at Fort Hood. Rainfall before and after a prescribed fire influences all plants, but yellow bluestem appears to be more vulnerable to fire during dry periods than native grasses. Indeed, yellow bluestem tiller number decreased by 50% to 74% after prescribed fires during a drought in 2011, with burns conducted from June through November (Havill et al., 2015). Effects on little bluestem tiller count varied from positive to negative (42% to –38%), but the negative effects were smaller than for yellow bluestem (Havill et al., 2015). In contrast, yellow bluestem and little bluestem frequency did not change after June burn in drought-stressed coastal prairie (Twidwell et al., 2012). The coastal burn was followed by 82 mm of rain, suggesting that adequate rainfall after a fire can counteract preburn drought. In our study, very little rain fell for 20 days before or after the Fort Hood fire (21 mm and 14 mm, respectively), while the Onion Creek site received abundant rainfall (88 m before and 214 mm after). Prescribed burns targeting yellow bluestem should be planned, when possible, during dry months.

The phenological state of yellow bluestem may also have influenced outcomes. Plants are most vulnerable to loss of biomass when root reserves of carbon and nitrogen are low. For perennial grasses, reserves are lowest while plants are producing flower stalks (stem elongation) (White, 1973). In yellow bluestem, reserves begin to recover after flowering (Coyne and Bradford, 1987); in the closely related Caucasian bluestem, postelongation trends vary (Coyne and Bradford, 1987; Villanueva-Avalos, 2008). Photos taken during the prescribed fire at Fort Hood show that at least some of the yellow bluestem was already reproductive; photos taken during the Onion Creek burn indicate little, if any, yellow bluestem reproduction. Yellow bluestem has previously been shown to be most vulnerable to fire when fewer than half of the culms were reproductive (Ruckman et al., 2012b). Yellow bluestem can flower year-round, depending on rainfall, but most seed production occurs during spring and fall (Coyne and Bradford, 1985; Diggs et al., 1999), suggesting that fall burns would often target the species during a vulnerable period.

Biomass at Fort Hood was almost three times greater than at Onion Creek (8 130 kg · ha⁻¹ in burned plots vs. 2 873 kg · ha⁻¹) and much greater than biomass in many other yellow bluestem studies. This high fuel load likely generated higher fire intensity that could have severely damaged or even killed more yellow bluestem plants. However, we and most other authors did not directly measure mortality. Davis (2011) found that yellow bluestem density increased by 14% to 31% after burns in July and September with low fuel loads (~2 223 kg · ha⁻¹).

Other authors' measures of yellow bluestem response (including frequency, tiller density, and biomass) vary with fuel load, showing decreases of 4% to 35% after burns with less than 2 500 kg · ha⁻¹ biomass (Simmons et al., 2007; Twidwell et al., 2012; Ruckman et al., 2012b) and greater decreases of 50% to 74% after burns with higher biomass (7 500 kg · ha⁻¹; Havill et al., 2015). Yellow bluestem response to fire is strongly related to soil temperature at 1 cm depth, suggesting that it has relatively shallow bud banks (Havill et al., 2015). Furthermore, yellow bluestem seeds are less heat tolerant than native grass seeds (Ruckman et al., 2012a). When planning burns to target yellow bluestem, grasslands should receive long-term rest from grazing or other disturbances that could decrease fuel loads.

At least at Onion Creek, a single burn did not provide long-term control of yellow bluestem. After an early-season fire with two herbicide treatments can decrease yellow bluestem cover for at least one growing season (Robertson et al., 2013). Repeated warm-season prescribed fires may also provide better control. Three sites near our Onion Creek study area have received two summer burns between 2010 and 2014. Vegetation data show a decrease in yellow bluestem frequency from 32% (preburn) to 16% in the first growing season after the second burn (Student's t test, P = 0.04; W. M. McCaw, 2016, unpublished data). Combining multiple treatments and repeating summer fires may provide better long-term control of yellow bluestem compared with a single burn.

Native grasses did not become dominant at either site. Native graminoid frequency in burned plots more than doubled at Fort Hood, but remained low (29%). At Onion Creek, graminoid frequency remained similar to preburn values (23%). Responses by individual grass species varied: frequency of the warm-season grasses composite dropseed and little bluestem increased after fire, while frequency of the cool-season Texas wintergrass and the warm-season purple threeawn decreased. Other studies have also found small responses to fire by native grasses in sites dominated by yellow bluestem. In burned coastal prairie, native grass frequency (proportion of quadrats) changed by only –3% to 3% 1 year after fire (Twidwell et al., 2012). In central Texas, changes in native grass frequency (point intercept) 1 year after fire ranged from –4% (Texas wintergrass) to 13% (silver bluestem [*Bothriochloa laguroides*] and Texas grama [*Bouteloua rigidiseta*]; Simmons et al., 2007). Our results and the literature suggest that native grasses do not become dominant in the short-term (1–3 years) after a single burn, even if yellow bluestem abundance is greatly reduced.

The rate of native grass increase may be limited by low seed availability. Many native perennial grasses, including little bluestem, do not form long-term seed banks (Abrams, 1988; Robertson and Hickman, 2012). Given the low abundance of native grasses before the fires, seed production in the burned areas would be too low for a rapid increase in abundance. Restoring native grass dominance in these sites will require additional management, such as seeding or planting.

Native grass recovery could also be suppressed by residual allelopathic characteristics of yellow bluestem. Leachate from yellow bluestem litter inhibited germination, growth, and survival of little bluestem (Greer et al., 2014). Yellow bluestem also appears to alter the association of arbuscular mycorrhizal fungi with little bluestem, reducing its growth (Wilson et al., 2012). Legacy effects on the soil microbial community could have inhibited recolonization of native grasses and their ability to compete with yellow bluestem.

In contrast to native grasses, forb frequency at both sites increased dramatically during the first year after fire (Fort Hood: 61%; Onion Creek: 43%; Fig. 2; Table 1). Such an increase in forb abundance is a common response after summer fire in grasslands, especially when the fire suppresses the dominant grasses (Copeland et al., 2002; Towne and Kemp, 2008; Howe, 2011; Twidwell et al., 2012). In many cases, the forb response is temporary, with forb cover decreasing as the dominant grasses and their thatch recover (Copeland et al., 2002). Indeed, forb cover at Onion Creek decreased to 12% by 2009. However, at Fort Hood, forb cover remained relatively high, likely because the previously dominant yellow bluestem had not recovered after the fire. Many of the most abundant forbs at our burned sites are important nectar plants for bees and monarch butterflies. Thus, late-summer fire can be used to

increase nectar availability for native pollinators, at least for one or two growing seasons.

Implications

Late-summer (September) fire successfully reduced relative frequency of yellow bluestem in our two sites, with effects lasting at least three growing seasons at one site. Factors that increased long-term control of yellow bluestem included dry conditions before and after the fire and very high fuel loads; burns should also be scheduled when yellow bluestem is preparing to flower. Our fires greatly increased forb abundance for a year or two, supporting local populations of pollinators. Common warm-season grasses responded positively or neutrally to September fire, but overall frequency of grasses other than yellow bluestem remained low at both sites for 3 years. Restoring dominance of native grasses in yellow bluestem-invaded grasslands will require additional management, such as repeated fires or seeding.

Supplementary data to this article can be found online at https://doi.org/10.1016/j.rama.2018.07.009.

Acknowledgments

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