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Seasonal Timing of Fire Alters Biomass and Species Composition of Northern Mixed Prairie☆,☆☆

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A B S T R A C T

Fire plays a central role in influencing ecosystem patterns and processes. However, documentation of fire seasonality and plant community response is limited in semiarid grasslands. We evaluated aboveground biomass, cover, and frequency response to summer, fall, and spring fires and no fire on silty and clayey sites in semiarid, C_3-dominated grassland. The magnitude of change in biomass between years was greater than any differences among fire treatments. Still, differences existed among seasons of fire. Summer fire reduced non-native annual forb frequency (3% vs. 10% ± 2%) and *Hesperostipa comata*, reduced native annual forbs the first year, increased *Poa secunda* and bare ground, and increased *Vulpia octoflora* the second year. Fall fire increased grass biomass (1224 vs. 1058 ± 56 $kg \cdot ha^{-1}$), but fall fire effects were generally similar to those of summer fire. Spring fire effects tended to be intermediate between no fire and summer and fall fire with the exception that spring fire was most detrimental to *H. comata* the first growing season and did not increase bare ground. All seasons of fire reduced litter, forb biomass, and frequency of *Bromus japonicus* and *Artemisia* spp., and they reduced *H. comata*, *V. octoflora*, and native annual forbs the first year, but increased basal cover of C_3 perennial grasses (2.2% vs. 0.6% ± 0.4%). Fire during any season increased dominance of native species compared with no fire (6.6% vs. 2.0% ± 1.0% basal cover) and maintained productivity. Seasonal timing of fire manipulated species composition, but increased C_3 perennial grass cover and native species dominance with fire during any season indicated that using fire was more important than the season in which it occurred. In addition, fire effects on the vegetation components tended to be counter to previously observed effects of grazing, suggesting fire and grazing may be complementary.

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Introduction

Fire is becoming accepted as a vital process in ecosystems, particularly grasslands, as benefits are realized and concerns about detrimental effects are assuaged. This has resulted in considerable interest in prescribed fire as a tool to facilitate livestock production, wildlife management, conservation, and fuels reduction. The timing of fire is one of the main factors that can be controlled with prescribed fire. Changes in the seasonal timing of fire have been observed to affect ecosystem characteristics, such as productivity and species composition. Yet data are insufficient to accurately predict some of those changes. The central and southern Great Plains have long histories of fire research on grasslands. A review of seasonal fire effects on central North American prairies indicated grassland response to dormant-season fire was predictable in late-seral tallgrass prairie, but more variable for other seasons of fire or locations in the region (Engle & Bidwell, 2001). Synthesis of fire effects in the drier western Great Plains indicated fire effects on productivity were generally negative or neutral, with increased productivity only 15% of the time (Scheintaub et al., 2009). Similarly, a broader review of the Great Plains provided evidence that the variety of vegetation responses to fire seasonality limit the ability to generalize fire effects (Knapp et al., 2009). The inability to detect broad patterns is partially due to the paucity of research in some regions or vegetation types and limited testing of summer fire. In this paper, we examine the effects of summer, fall, and spring fire compared with nonburned sites in mixed prairie of the northern Great Plains.

Alterations in the timing (season) of fire correspond with changes in plant phenology and morphology (Biondini et al., 1989; Steuter, 1987; White & Currie, 1983). Fire can directly change competitive interactions within the plant community by disrupting plant developmental stages.

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Indirect fire effects, such as altered physical and chemical environment through litter removal and increased solar radiation, can be equally important (Hulburt, 1988; Old, 1969). In addition, direct and indirect fire effects often interact. For example, late-winter and early spring burns can hinder C_3 perennial grasses when substantial live tissue is exposed to fire and promote C_4 species by accelerating growth in the postfire environment (Cornell & Lawton, 1992; Howe, 1994; Steuter, 1987).

Wildfires are most prominent during summer, when the potential for ignition and fire growth is increased because of greater fuel loads and volatility combined with warmer and drier air. When these conditions coincide, fire intensities are greater than those that occur during spring or fall. Native vegetation in northern mixed prairie evolved with wildfire and associated fire intensities. Therefore plants may be less susceptible to fire damage during the historically natural fire season (summer) due to this coevolutionary exposure that has led to stored carbohydrates, reserve axillary buds, and heat or drought-induced quiescence (Johnson & Matchett, 2001; Vermeire et al., 2011). Due to perceived safety concerns and liability, prescribed burns are often conducted during spring or fall dormancy rather than summer, when the majority of lightning-ignited fires occur (Bragg, 1982). Of lightning-ignited fires in the northern Great Plains, > 73% occurred during July and August (Higgins, 1984; Westerling et al., 2003). However, firefighting resources are in greater demand during summer, so most prescribed burns are attempted outside of this period. Spring fires often produce less fire intensity with reduced flame lengths, rates of spread, and fuel consumption compared with summer fires because more active herbage results in greater fuel water content (Ford & Johnson, 2006; Steuter, 1987). Burning outside the natural fire season may have negative consequences because populations of fire-dependent species can be suppressed if timing or heating requirements for regeneration are not achieved (Odion & Tyler, 2002).

Fire seasonality research in mixed prairies of the northern Great Plains is limited compared with tallgrass prairie research (Howe, 1995; Launchbaugh & Owensby, 1978; Towne & Owensby, 1984) and C_4-dominated sites in southern mixed and short-grass prairies of the Great Plains (Ansley et al., 2006; Castellano & Ansley, 2007). Season of fire research in C_3-dominated sites in the northern Great Plains usually involves dormant season burning during fall or spring. White & Currie (1983) reported spring burning stimulated western wheatgrass (*Pascopyrum smithii* [Rydb.] A. Löve) and blue grama (*Bouteloua gracilis* [Willd *ex*. Kunth] Lag. *ex* Griffiths) production, and fall fire reduced threadleaf sedge (*Carex filifolia* Nutt. var. *filifolia*). Vegetation responses to early and late spring burning have been shown to be site dependent, and reductions in grass biomass production are more evident on xeric than mesic sites 1 yr after fire, with no differences between sites 2 yr after fire (Engle & Bultsma, 1984). Fall and spring fires have increased forb density in a 495-mm precipitation zone of the northern Great Plains, but responses varied with precipitation (Biondini et al., 1989). Summer fire reduced forbs and annual grasses in a 339-mm precipitation zone of the northern Great Plains (Vermeire et al., 2011, 2014). Forb production was greater following backing fires than head-fired plots in tallgrass prairie (Bidwell et al., 1990), suggesting that forbs may respond more positively to a less intense spring fire than a hotter summer fire.

Our objective was to determine aboveground biomass, cover, and frequency responses to summer, fall, and spring fires on two different ecological sites in semiarid C_3-dominated grassland. Plant community responses were examined in the first and second growing seasons after treatment to evaluate the ability to maintain productivity and species composition the second year following fire treatments. We hypothesized that 1) C_4 perennial grass abundance increases following spring fire and decreases following summer and fall fire; 2) C_3 perennial grass abundance increases following summer and fall fire and decreases following spring fire; and 3) fire in any season reduces annual grass and forb abundance.

Methods

Study Site

Research was conducted in northern mixed prairie at Fort Keogh Livestock and Range Research Laboratory near Miles City, Montana, United States (lat 46°24′N, long 105°56′W; 815 m above sea level). Mean annual precipitation is 338 mm, with a majority occurring during the mid-April to mid-September growing season. Average daily temperatures range from 23°C in July to −8°C in January, with extremes of 38°C in summer and −40°C in the winter. The frost-free growing season generally ranges from 125 to 150 d.

One silty and one clayey ecological site about 600 m apart were selected for study. Topography of the sites is gently rolling, with minimal slopes (0−4%) and is characterized as upland plains. The silty study site is dominated by Pinehill loams (fine, smectitic, frigid Aridic Haplustalfs) including a complex of Kobase clay loams (fine, smectitic, frigid Torrertic Haplustepts) and Gerdrum clay loams (fine, smectitic, frigid Torrertic Natrustalfs). The clayey site is dominated by Kobase clay loams and Absher silty clays (fine, smectitic, frigid Leptic Torrertic Natrustalfs). Vegetation is overwhelmingly composed of perennial, native C_3 species, needle-and-thread (*Hesperostipa comata* [Trin. & Rupr.] Barkworth), western wheatgrass, Sandberg bluegrass (*Poa secunda* J. Presl.) and threadleaf sedge, the C_4 species blue grama, and, to a lesser extent, buffalograss (*Bouteloua dactyloides* [Nutt.] J.T. Columbus). Annual grasses include sixweeks fescue (*Vulpia octoflora* [Walter] Rydb.), Japanese brome (*Bromus japonicus* Thunb.), and cheatgrass (*B. tectorum* L.). The primary woody species on the site are Wyoming big sagebrush (*Artemisia tridentata* Nutt. ssp. *wyomingensis* Beetle & Young) and the half shrub fringed sage (*A. frigida* Wild.). The most common annual forbs were woolly plantain (*Plantago patagonica* Jacq.), field cottonrose (*Logfia arvensis* [L.] Holub), and pale madwort (*Alyssum alyssoides* L.), and the most common perennials were scarlet globemallow (*Sphaeralcea coccinea* [Nutt.] Rydb.) and Hood's phlox (*Phlox hoodii* Richardson).

Neither clayey nor silty sites were burned in recent decades until the initiation of fire treatments during summer 2006. Sites were not grazed by cattle during the study period, but cattle had historically grazed both sites under moderate stocking rates (1 AUM ha^{-1}) until May 2003, when a large cattle grazing exclosure was built. Current-year biomass ranged from 460 to 1319 $kg \cdot ha^{-1}$ during the 10 yr preceding this study.

Study Design

Four fire treatments (summer, fall, or spring fire, and a nonburned control) were randomly assigned to 15 × 20-m plots and replicated three times on each of two ecological sites for a total of 24 experimental units. Fire treatments were a single fire randomly assigned and applied to plots 19 September 2006, 24 October 2006, or 25 April 2007 using a ring fire ignition method with a 1-m mowed line and 0.5-m wet line as a fire break. Fuel loads were 1191 ± 98 $kg \cdot ha^{-1}$ for the clayey site and 1587 ± 41 $kg \cdot ha^{-1}$ for the silty site. Summer fires were applied following summer quiescence of C_3 grasses. Fall fires were implemented following the first killing frost, after temperatures reached at least −2°C. Spring fires were applied after *B. gracilis* had initiated growth, with leaves approximately 2 cm tall, and *P. smithii* was in the 3−4 leaf stage. Prescribed fires were implemented with similar ambient weather conditions across summer, fall, and spring fires (Table 1).

Table 1
Ambient weather conditions during summer, fall, and spring fires

Component	Summer	Fall	Spring
Ambient temperature (°C)	19.4	15.0	21.3
Relative humidity (%)	41	41	35
1.5-m wind speed (km hr^{-1})	17	15	15

Plots were sampled during late July, near the time of peak biomass. Graminoid and forb (including *A. frigida*) biomass were obtained separately by clipping to ground level from four randomly placed 0.25-m^2 circular quadrats in each plot. Biomass samples were dried to a constant weight at 60°C and weighed to the nearest 0.01 g to estimate biomass. Biomass samples were then separated into current and past years' growth and reweighed to determine current-year biomass as an estimate of productivity. Basal cover was determined by a 10-m point-intercept transect in each plot, with points read at 10-cm intervals to determine basal cover by species, bare ground, litter, and plant frequency through all canopy layers.

All data were analyzed using SAS MIXED analysis of covariance with repeated measures to determine effects of fire seasonality. Models included the main effects of site, season of fire, and year and all possible interactions. Pretreatment data were used as the covariate when significant. Time since fire treatment was the repeated measure. Response variables were biomass, basal cover, and plant frequency. Biomass data were grass, forb, and total biomass, as well as old standing dead biomass. Only the second year after fire was analyzed for old standing dead because fire removed all old standing dead for the first postfire growing season. All biomass estimates, except old standing dead, were of current-year production. Basal cover was measured by species, but analyzed by total native species and functional groups (C_3 and C_4 perennial grasses). Frequency data were analyzed by species for graminoids and four species groups, *Artemisia* spp., perennial forbs, native annual forbs, and non-native annual forbs. Significance of tests was declared when $P < 0.05$ and interactions were followed by tests of simple effects.

Results

Precipitation and Site

Annual precipitation for the year preceding treatment through the second growing season after fire was 95% (321 mm), 89% (300 mm), and 71% (239 mm) of the 1937 − 2008 average. The year before treatment initiation (2005 − 2006), a wet fall and winter were experienced. Subsequent seasons were progressively drier, relative to seasonal averages, through the fall of 2006 (Fig. 1). Winter 2006 and spring 2007 were wet and followed by severe drought (21% of long-term average) from summer through winter, a near-average spring 2008, and a droughty summer. Many of the measured plant components varied with ecological site or year. Total current-year biomass, for example, decreased from 2007 to 2008 on both sites, but to a greater extent on the clayey (1 537 vs. 857 ± 54 kg·ha^{-1}) than silty site (1 460 vs. 1 053 ± 54 kg·ha^{-1}; $P = 0.0005$). The magnitude of change in biomass between years was greater than any differences among fire treatments. However, because our objectives focused on fire seasonality effects, site and year effects are hereafter discussed only as they interact with fire seasonality.

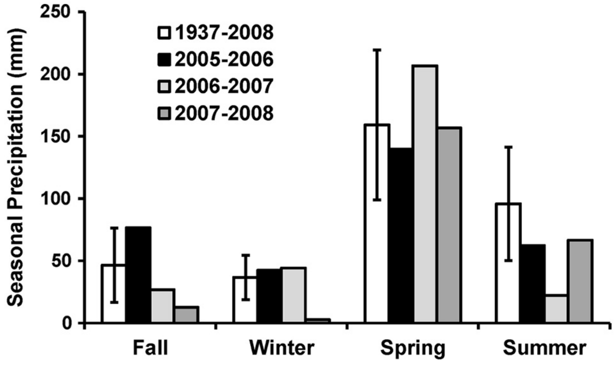

Figure 1. Fall (Oct − Dec), winter (Jan − Mar), spring (Apr − Jun), and summer (Jul − Sep) precipitation for the 72-yr mean seasonal precipitation (± 1 SD), pretreatment year (2005 − 2006), and each year of study.

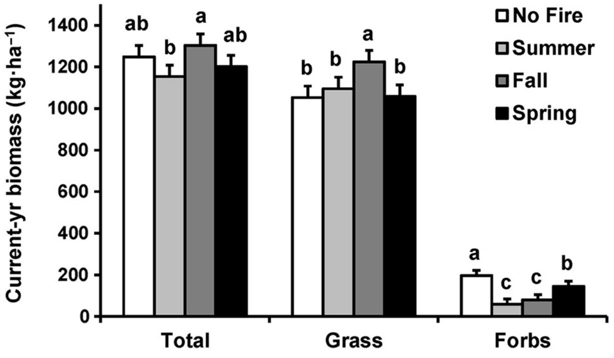

Figure 2. Total current-year biomass by fire treatments across ecological site (clayey and silty) and year (1 and 2 yr post fire) with standard errors of the comparison. Fire treatment means within a vegetation component with a common letter above bars are similar ($P > 0.05$).

Fire Effects

Biomass

Total current-year biomass was greater with fall fire than summer fire, but summer, fall, and spring fire were all similar to total biomass with no fire ($P = 0.0410$; Fig. 2). Grass biomass was greatest following fall fire, and no differences were detected across all other treatments ($P = 0.0071$). Summer and fall fire reduced forb biomass to about 30% and 40% of that in plots with no fire ($P < 0.0001$). Forb biomass after spring fire was less than that of nonburned sites and greater than that following summer or fall fire. Old standing dead biomass was eliminated by fire the first postfire growing season and was 282 ± 46 kg·ha^{-1} with no fire. By the second growing season following fire, old standing dead was similar across no fire (539 kg·ha^{-1}), summer fire (516 kg·ha^{-1}), fall fire (571 kg·ha^{-1}), and spring fire (423 ± 43 kg·ha^{-1}) treatments ($P = 0.0953$).

Cover

Summer fire created nearly seven times the bare ground as no fire the first postfire year (Fig. 3). There was less bare ground following fall fire than summer fire, but fall fire caused more than twice the bare ground observed for spring and nonburned plots, which were similar. By the second postfire year, bare ground on summer-burned plots was reduced to similar levels as on fall-burned plots, but still at least 1.6 times greater than spring or nonburned plots. Fall, spring, and nonburned plots each had similar percentages of bare ground between years. Fire in any season reduced litter cover (Fig. 3). Litter cover was similar among seasons of fire on the silty site, but summer and fall fire reduced litter considerably more than spring fire on the clayey site. Although grass biomass was similar across treatments, C_3 perennial grass basal cover was at least three times greater on burned than nonburned

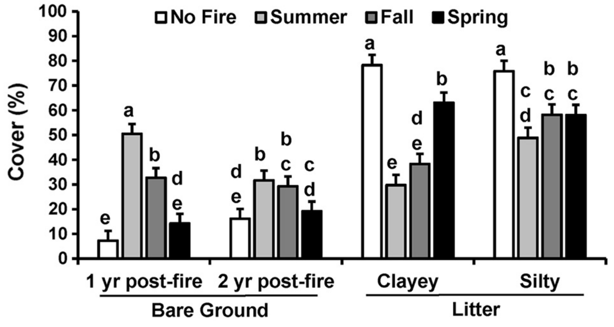

Figure 3. Bare ground (%) by fire treatment and year (1 and 2 yr post fire) across ecological sites (clayey and silty) and litter cover (%) by fire treatments and ecological site across years with standard errors of the comparison. Fire treatment means within a cover component with a common letter above bars are similar ($P > 0.05$).

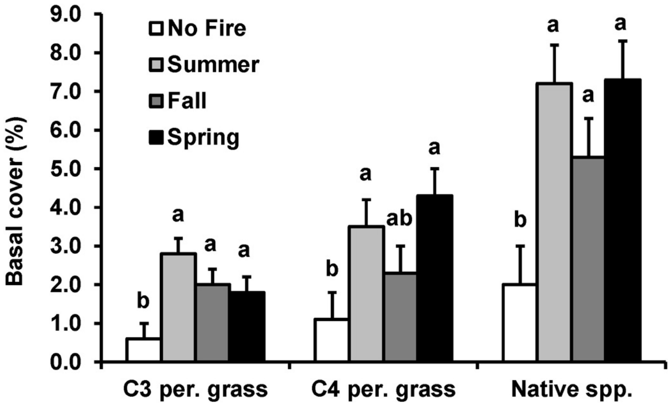

Figure 4. Basal cover (%) by fire treatments across ecological site (clayey and silty) and year (1 and 2 yr post fire) with standard errors of the comparison. Fire treatment means within a vegetation component with a common letter above bars are similar ($P > 0.05$).

Table 3
Frequency by vegetation component across yr post fire (1 and 2) with standard errors and P values for the season-of-fire x ecological-site interactions

Component	Site	Summer	Fall	Spring	No fire	SE	P value
		Frequency (%)					
Poa secunda	Clayey	20 a	17 a	3 c	5 c	2	0.0124
	Silty	14 ab	10 bc	8 bc	10 bc		
Vulpia octoflora	Clayey	11 cd	16 cd	8 d	21 bc	4	0.0004
	Silty	49 a	14 cd	17 cd	32 b		

[1]Season-of-fire x site means within component are similar when followed by a common letter ($P > 0.05$).

plots (Fig. 4). Likewise, C_4 perennial grass basal cover was about three to four times greater with summer or spring fire. C_4 perennial grass basal cover after fall fire was intermediate and did not differ from any of the other treatments. The ratios of C_3 to C_4 perennial grass basal cover were 0.80, 0.87, 0.42, and 0.55 for summer, fall, spring, and no fire, respectively. Basal cover of native species, collectively, was similar across seasons of fire and considerably greater than that on plots with no fire.

Frequency

Frequency of canopy or basal hits was similar across treatments for nearly half of the species and species groups measured (Tables 2-4). Except for *B. tectorum,* the resistant species were perennials, with perennial forbs and four prominent graminoids exhibiting similar responses across treatments. Fire during any season reduced *B. japonicus* and *Artemisia* spp. (Table 4). Summer fire reduced frequency of non-native annual forbs across years, whereas fall and spring fire yielded frequencies that did not differ from summer or nonburned plots. Native annual forbs were similarly reduced by fire in any season the first year after fire, but recovered by the second year (Table 2). The first year after fire, *V. octoflora* was reduced by fire in any season, as were most of the other annual species (Table 2). However, *V. octoflora* was unique in that frequencies on fall and spring fire plots recovered to nonburned levels the second year and frequency on summer fire plots exceeded all other treatments. The response of *V. octoflora* to fire also varied by ecological site (Table 3). On the clayey site, only spring fire reduced *V. octoflora,* whereas *V. octoflora* was reduced by fall and spring fire and increased by summer fire on the silty site. *P. secunda* frequency after summer fire was greater than that on nonburned plots the first and second years (Table 2). *P. secunda* frequency was not affected the first year after fall fire, but increased the second year to values similar to those after summer fire. Fire effects on *P. secunda* frequency also varied by ecological site (Table 3). Summer and fall fire increased *P. secunda* frequency relative to spring fire and no fire on the clayey site, but only summer fire increased *P. secunda* relative to no fire on the silty site and all other treatment pairs were similar. *H. comata* was the only perennial graminoid to indicate a negative response to fire (Table 2). Fire in any season initially reduced *H. comata* frequency. By the second growing season after fire, frequencies did not differ among burned plots and fall- and spring-burned plots had frequencies similar to nonburned plots, but *H. comata* frequency after summer fire was still about half of that with no fire.

Discussion

This research assessed the effects of summer, fall, and spring fire on two ecological sites for two postfire growing seasons. The magnitude of change in biomass between years was greater than that among seasons of burning. Weather was also shown to have greater influence on biomass than fire when comparing summer fire and no fire (Vermeire et al., 2011, 2014). Season of fire contributed to differences in biomass, basal cover, and species frequency, the latter emphasizing differences between native and non-native species responses. Data support hypothesized increases in C_4 perennial grass abundance following spring fires. However, summer fire similarly increased C_4 abundance. Contrary to our expectations, all seasons of fire increased basal cover of C_3 perennial grass species compared with no fire. *H. comata* was the only C_3 perennial grass species to respond negatively to fire, particularly the first year following spring fire and the second year after summer fire. As hypothesized, forb biomass decreased following summer, fall, or spring fire. However, forb reductions were much greater following summer and fall fire than spring fire. Data provided limited support for the hypothesis that fire in any season would reduce annual grasses. Fire effects on annual grasses varied by species, with reductions in *B. japonicus,* initial reductions in *V. octoflora* followed by an increase with summer fire, and no changes for *B. tectorum*. Overall, fire shifted the plant community in the opposite direction previously indicated for grazing effects

Table 2
Frequency by vegetation component across ecological sites (clayey and silty) with standard errors and P values for the season-of-fire x years-postfire interactions

Component	Yr postfire	Summer	Fall	Spring	No fire	SE	P value
		Frequency (%)					
Hesperostipa comata	1	22 b	24 b	12 cd	36 a	3	0.0263
	2	10 d	13 cd	14 cd	19 bc		
Poa secunda	1	17 a	7 b	4 b	9 b	2	0.0107
	2	17 a	20 a	7 b	6 b		
Vulpia octoflora	1	26 bc	11 d	13 d	39 a	4	0.0004
	2	33 ab	18 cd	13 d	15 d		
Native annual forbs	1	6 bc	6 bc	12 b	23 a	3	0.0030
	2	4 bc	5 bc	3 c	1 c		

[1]Season-of-fire x year-post-fire means within component are similar when followed by a common letter ($P > 0.05$).

Table 4
Frequency by vegetation component across ecological sites (clayey and silty) and yr post fire (1 and 2) with standard errors and P values for season of fire comparisons

Component	Summer	Fall	Spring	No fire	SE	P value
	Frequency (%)					
Carex spp.	5	11	7	6	2	0.1453
Pascopyrum smithii	16	20	22	20	2	0.2848
Bouteloua gracilis	19	18	19	21	1	0.3913
Bouteloua dactyloides	2	2	3	2	1	0.2449
Bromus japonicus	49 b[1]	48 b	50 b	63 a	3	0.0118
Bromus tectorum	17	15	23	22	4	0.2951
Artemisia spp.	1 b	3 b	1 b	7 a	1	< 0.0001
Perennial forbs	3	3	4	3	1	0.9443
Non-native annual forbs	3 b	6 ab	6 ab	10 a	2	0.0356

[1] Season of fire treatment means within component are similar when followed by a common letter ($P > 0.05$).

(Vermeire et al., 2008), suggesting fire and grazing may complement one another (Vermeire et al., 2018).

Native perennial grasses responded positively to fire in general, and differences between burned and nonburned sites were greater than those among seasons of fire. The response of C_4 perennial grasses to spring fire aligns with previous research, illustrating consistently high allocation of resources belowground throughout the growing season, short-shoot growth form, and high regrowth potential (Menke & Trlica, 1981). Greater C_4 perennial grass abundance following summer fire did not follow expectations based on results from others (Howe, 1995; Steuter, 1987). Typically, midsummer and late-summer fires have the potential to suppress C_4 grasses by causing direct fire damage to aboveground structures during a period of maximal growth and reproduction, thereby reducing carbohydrates and other energy sources (Howe, 1994). Research in tallgrass prairie has reported reduced C_4 perennial grass production and vigor the year following summer fire (Howe, 1994). However, our data indicate that increased basal cover with summer fire was similar to that following spring fire. The mechanism for this adaptive response is unknown. However, spring fire caused an immediate increase in active axillary buds for *Bouteloua gracilis,* the dominant C_4 grass on the study site. Summer fire immediately reduced bud activity, but increased bud activity the following two growing seasons. Active buds were unaffected immediately after fall fire, but increased by the middle of the first and second growing seasons after fire (Russell et al., 2015). Furthermore, fire effects on buds can interact with nitrogen availability (Russell & Vermeire, 2015) and fire can increase nitrogen availability (Hobbs & Schimel, 1984; Neary et al., 1999). Collectively, these data indicate increasing resource availability during a period of meristem abundance may offset or exceed the negative effects of burning photosynthetically active tissues such that summer fire could benefit C_4 grass *(B. gracilis)*. However, we also reiterate that summer fire was late in the growing season, by which time C_4 grasses have typically completed $> 90\%$ of their annual growth (Vermeire et al., 2009), and that burning earlier in the summer may be more detrimental. In addition, the increase in C_4 grass basal cover was not matched by greater frequency throughout the canopy.

Fire increased C_3 perennial grass basal cover regardless of season. Although this response was expected for summer and fall fires, spring fires coinciding with early growth of *B. gracilis* were predicted to reduce C_3 perennial grass because C_3 species would have more active tissue exposed at the time. However, the early growing season is often compressed in the region, with many C_3 perennial grasses not having substantial growth before C_4 growth begins. For example, *P. smithii* was in the $3-4$ leaf stage during spring burns. In addition, little C_4 growth occurs late in the growing season, even with favorable moisture conditions (Heitschmidt & Vermeire, 2006). Despite the unexpected changes in basal cover, ratios of C_3 to C_4 perennial grass basal cover followed predictions, with increased ratios after summer and fall fire and a reduced ratio following spring fire relative to no fire.

The positive C_3 perennial grass basal cover response had some similarity to previous research showing *P. smithii* production to more than double on burned sites 2 yr following summer fire (Vermeire et al., 2011). In the same study, *P. smithii* standing crop was 47% greater for burned than nonburned sites following a summer fire with a wet spring in the northern Great Plains. However, in our study, frequency of *P. smithii* was similar among treatments, but increases in C_3 basal cover suggest increased tillering and rhizome expansion following fire. More than 99% of perennial grass reproduction has been observed to be asexual in the Great Plains (Benson & Hartnett, 2006). Through tillering, grasses can rapidly respond to resource availability and increase basal cover. Russell et al. (2015)) observed increased bud activity for *P. smithii* following summer, fall, and spring fire. Increased basal cover of C_3 perennial native grasses was most likely due to a variety of phenological and morphological adaptations, including clonal growth form, rapid rhizome extension, and tolerance to drought; all mechanisms enhancing *P. smithii* resilience and resistance to fire (Vermeire et al., 2011).

Frequency of *P. secunda* increased after summer fire both 1 and 2 yr after fire. We suspect that *P. secunda* took advantage of increased bare ground following summer and fall fires and was able to rapidly colonize the area. *P. secunda* is well known in semiarid environments to stabilize areas quickly where fire, drought, or overgrazing have occurred (Wright & Klemmedson, 1965). This quick stabilizing effect of *P. secunda* seedlings may be due to its ability to thrive under dry conditions and its ability to compete with non-native annuals by initiating growth early and maturing quickly (Wright & Klemmedson, 1965). Greater *P. secunda* frequency on summer and fall burned plots at the clayey site support this notion because both treatments reduced litter cover considerably.

There was an exception in the response of C_3 perennial grasses to fire observed with *H. comata,* which was the only perennial graminoid to indicate a negative response to fire. Previous work has also noted this species to be sensitive to fire (Vermeire et al., 2011; Wright, 1971; Wright & Klemmedson, 1965). Caespitose grasses tend to be more vulnerable to fire than rhizomatous species because their axillary buds are elevated above the soil surface and exposed in the crown, which potentially accumulates fuel that can burn hotter and longer (Engle et al., 1998; Raunkiaer, 1934; Wright, 1971). Furthermore, the overall response of *H. comata* might be related to the carbohydrate storage levels of plants (Wright & Klemmedson, 1965). For example, bud reserves and growth from axillary buds can be limited and regrowth from these structures are less effective (Bell & Pate, 1996; Cruz et al., 2003; Russell et al., 2015; Vesk & Westoby, 2004), thus leading to decreased tillering following fire.

V. octoflora response to fire was complex and interacted with ecological site and year. Fall and spring fire reduced *V. octoflora* on both ecological sites and during the first year after fire. Summer fire was distinct in that it reduced *V. octoflora* the first year after fire, but increased *V. octoflora* on the silty site and exceeded frequencies on plots with no fire 2 yr after fire. Fire effects on *V. octoflora* in shortgrass steppe were variable as well, depending on year, season of fire, and fire return interval (Dufek et al., 2018). Although potential causes for fire-induced reductions in *V. octoflora* can be readily offered (e.g., direct mortality, seed combustion), it is less clear how summer fire may have increased *V. octoflora* on silty sites. *V. octoflora* frequency did not differ by ecological site for the other fire treatments nor between years for summer, fall, and spring fires. The primary source of change with time was a sharp reduction with no fire. Additional research is required to determine mechanisms driving fire effects on *V. octoflora*.

Except for *B. tectorum,* non-native annual species were susceptible to fire. Fire during any season reduced frequency of *B. japonicus*. Spring burning reduced *B. japonicus* density by 65% in Kansas mixed-grass prairie (Harmoney, 2007) and by 95% within the first growing season in South Dakota (Whisenant & Uresk, 1989). In addition, fire may serve as an effective ecological process to avoid invasion by exotic annual grasses, such as *B. japonicus,* that could alter fire regimes in mixed-grass prairie (Brooks et al., 2004). In our study, summer fire reduced frequency of non-native annual forbs across years, and fire during any season reduced *Artemisia* species. In addition, native annual forbs were reduced by fire the first year, but recovered by the second year. Previous research along the mesic transition zone between mixed and tallgrass prairie showed increased forb density following fall and spring burns (Biondini et al., 1989). Similarly, early dormant season burns increased native forbs, such as *Ambrosia psilostachya* (Hopkins et al., 1948). The initial reduction of native forbs and increase the second year after fire in this study demonstrate the importance of fire and the resiliency of native flora.

We observed an increase in bare ground following summer fire, which might be attributed to lack of fuel moisture and more complete combustion. Prior research showed that fire intensity and severity were greater during summer, resulting in more widespread damage and mortality to exposed surface crusts than during a spring or fall fire (Ford & Johnson, 2006). We observed that bare ground following summer fire decreased 19% between the first and second postfire years, but summer fire still had nearly twice the bare ground of nonburned sites, indicating longer exposure to potential erosion than fall or spring fires. Multiple studies have reported increased wind erosion following fire (Vermeire et al., 2005; Whicker et al., 2002; Zoebeck et al., 1989).

We expected similar amounts of litter cover among seasons of fire, as was observed on the silty site. Interestingly, summer and fall fires reduced litter cover considerably more than spring fire on the clayey site. Spring fires had less complete combustion than summer and fall fires on the clayey site, likely due to the combined effects of lighter fuel load on the clayey site than the silty site and proportionally more live material during spring than summer and fall.

Preserved productivity and increased native species cover across seasons of fire indicate that for the integrity of the studied system, it is more important to ensure fire occurs than to focus on a particular seasonal timing of fire. There are numerous reasons for grouping species in rangeland assessments, including the facts that a majority of rangeland species often comprise a small fraction of total biomass and animals often select diets that are biased toward one functional group over the others. However, the species-specific responses to fire we observed with *H. comata* and annual grasses show risks in trying to group responses purely by functional group.

Implications

Fire in any season tended to favor perennial grasses and native species while maintaining productivity across ecological sites. Therefore, the inclusion of fire in northern mixed prairie is more impactful than the particular season in which it occurs. Furthermore, increased native species cover in burned plots indicates fire is important for maintaining the integrity of these grasslands. However, timing of fire affected species composition and could be used to shift plant communities. Summer and fall fire reduced annual grasses and forbs to a greater extent than spring fire. Fire effects on litter and bare ground are likely related to fuel and fire weather rather than seasonal timing per se, but the odds of more complete combustion are greater with the generally dry summer conditions than what is often observed during spring. Species within functional group often responded differently to fire treatment, indicating results cannot be predicted simply on the basis of functional group response. Finally, this study examined seasonal effects of a single fire. Repeated fire effects may manifest differently and need to be investigated to determine how fire seasonality and frequency may interact.

References

Ansley, R.J., Castellano, M.J., Pinchak, W.E., 2006. Sideoats grama growth response to seasonal fires and clipping. Rangeland Ecology & Management 59, 258–266.

Bell, T.L., Pate, J.S., 1996. Growth and fire response of selected *Epacridaceae* of south-western Australia. Australian Journal of Botany 44, 509–526.

Benson, E.J., Hartnett, D.C., 2006. The role of seed and vegetative reproduction in plant recruitment and demography in tallgrass prairie. Plant Ecology 187, 163–178.

Bidwell, T.G., Engle, D.M., Claypool, P.L., 1990. Effects of spring headfires and backfires on tallgrass prairie. Journal of Range Management 43, 209–211.

Biondini, M.E., Steuter, A.A., Grygiel, C.E., 1989. Seasonal fire effects on the diversity patterns, spatial distribution and community structure of forbs in northern mixed prairie. Vegetatio 85, 21–31.

Bragg, T.B., 1982. Seasonal variations in fuel and fuel consumption by fires in a bluestem prairie. Ecology 63, 7–11.

Brooks, M.L., D'Antonio, C.M., Richardson, D.M., Grace, J.B., Keeley, J.E., DiTomaso, J.M., Hobbs, R.J., Pellant, M., Pyke, D., 2004. Effects of invasive alien plants on fire regimes. BioScience 54, 677–688.

Castellano, M.J., Ansley, R.J., 2007. Fire season and simulated grazing differentially affect the stability and drought resilience of a C4 bunchgrass, C3 bunchgrass and C4 lawngrass. Journal of Arid Environments 69, 375–384.

Cornell, H.V., Lawton, J., 1992. Species interactions, local and regional processes, and limits to the richness of ecological communities: a theoretical perspective. Journal of Animal Ecology 61, 1–12.

Cruz, A., Pérez, B., Moreno, J.M., 2003. Plant stored reserves do not drive resprouting of the lignotuberous shrub *Erica australis*. New Phytologist 157, 251–261.

Dufek, N.A., Augustine, D.J., Blumenthal, D.M., Kray, J.A., Derner, J.D., 2018. Dormant-season fire inhibits sixweeks fescue and enhances forage production in shortgrass steppe. Fire Ecology 14, 33–49.

Engle, D.M., Bidwell, T.G., 2001. Viewpoint: the response of central North American prairies to seasonal fire. Journal of Range Management 54, 2–10.

Engle, D.M., Bultsma, P.M., 1984. Burning of northern mixed prairie during drought. Journal of Range Management 37, 398–401.

Engle, D.M., Mitchell, R.L., Stevens, R.L., 1998. Late growing-season fire effects in mid-successional tallgrass prairies. Journal of Range Management 51, 115–121.

Ford, P.L., Johnson, G.V., 2006. Effects of dormant vs. growing-season fire in shortgrass steppe: biological soil crust and perennial grass responses. Journal of Arid Environments 67, 1–14.

Harmoney, K.R., 2007. Persistence of heavily-grazed cool-season grasses in the central Great Plains. Forage and Grazinglands 6, 51–60.

Heitschmidt, R.K., Vermeire, L.T., 2006. Can abundant summer precipitation counter losses in herbage production caused by spring drought? Rangeland Ecology & Management 59, 392–399.

Higgins, K.F., 1984. Lightning fires in North Dakota grasslands and in pine-savanna lands of South Dakota and Montana. Journal of Range Management 37, 100–103.

Hobbs, N.T., Schimel, D.S., 1984. Fire effects on nitrogen mineralization and fixation in mountain shrub and grassland communities. Journal of Range Management 37, 402–405.

Hopkins, H.F., Albertson, F.W., Riegel, A., 1948. Some effects of burning upon a prairie in west-central Kansas. Transactions of the Kansas Academy of Science 51, 131–141.

Howe, H.F., 1994. Managing species diversity in tallgrass prairie: assumptions and implications. Conservation Biology 8, 691–704.

Howe, H.F., 1995. Succession and fire season in experimental prairie plantings. Ecology 76, 1917–1925.

Hulburt, L.C., 1988. Cause of fire effects in tallgrass prairie. Ecology 69, 46–58.

Johnson, L.C., Matchett, J.R., 2001. Fire and grazing regulate belowground processes in Tallgrass Prairie. Ecology 82, 3377–3389.

Knapp, E.E., Estes, B.L., Skinner, C.N., 2009. Ecological effects of prescribed fire season: a literature review and synthesis for managers. US Department of Agriculture, Forest Service, Pacific Southwest Research Station, Albany, CA, USA 80 pp.

Launchbaugh, J.L., Owensby, C.E., 1978. Kansas rangelands. Kansas Agricultural Experiment Station Bulletin 622, Manhattan, KS, USA 56 pp.

Menke, J.W., Trlica, M.J., 1981. Carbohydrate reserve, phenology, and growth cycles of nine Colorado range species. Journal of Range Management 34, 269–277.

Neary, D.G., Klopatek, C.C., DeBano, L.F., Ffolliott, P.F., 1999. Fire effects on belowground sustainability: a review and synthesis. Forest Ecology and Management 122, 51–71.

Odion, D., Tyler, C., 2002. Are long fire-free periods needed to maintain the endangered, fire-recruiting shrub *Arctostaphylos morroensis* (Ericaceae)? Conservation Ecology 6, 4–15.

Old, S.M., 1969. Microclimate, fire and plant production in an Illinois prairie. Ecological Monographs 39, 355–384.

Raunkiaer, C., 1934. The life-forms of plants and statistical plant geography. Oxford University Press, London, England 632 pp.

Russell, M.L., Vermeire, L.T., 2015. Fire and nitrogen alter axillary bud number and activity in purple threeawn. Rangeland Ecology & Management 68, 65–70.

Russell, M.L., Vermeire, L.T., Ganguli, A.C., Hendrickson, J.R., 2015. Season of fire manipulates bud bank dynamics in northern mixed-grass prairie. Plant Ecology 216, 835–846.

Scheintaub, M.R., Derner, J.D., Kelly, E.F., Knapp, A.K., 2009. Response of the shortgrass steppe plant community to fire. Journal of Arid Environments 73, 1136–1143.

Steuter, A.A., 1987. C3/C4 production shift on seasonal burns: northern mixed prairie. Journal of Range Management 40, 27–31.

Towne, G., Owensby, C., 1984. Long-term effects of annual burning at different dates in ungrazed Kansas tallgrass prairie. Journal of Range Management 37, 392–397.

Vermeire, L.T., Wester, D.B., Mitchell, R.B., Fuhlendorf, S.D., 2005. Fire and grazing effects on wind erosion, soil water content, and soil temperature. Journal of Environmental Quality 34, 1559–1565.

Vermeire, L.T., Heitschmidt, R.K., Haferkamp, M.R., 2008. Vegetation response to seven grazing treatments in the northern Great Plains. Agriculture, Ecosystems and Environment 125, 111–119.

Vermeire, L.T., Heitschmidt, R.K., Rinella, M.J., 2009. Primary productivity and precipitation-use efficiency in mixed-grass prairie:a comparison of northern and southern US sites. Rangeland Ecology & Management 62, 230–239.

Vermeire, L.T., Crowder, J.L., Wester, D.B., 2011. Plant community and soil environment response to summer fire in the Northern Great Plains. Rangeland Ecology & Management 64, 37–46.

Vermeire, L.T., Crowder, J.L., Wester, D.B., 2014. Semiarid rangeland is resilient to summer fire and postfire grazing utilization. Rangeland Ecology & Management 67, 52–60.

Vermeire, L.T., Strong, D.J., Waterman, R.C., 2018. Grazing history effects on rangeland biomass, cover and diversity responses to fire and grazing utilization. Rangeland Ecology & Management 71, 750–755.

Vesk, P.A., Westoby, M., 2004. Funding the bud bank: a review of the costs of buds. Oikos 106, 200–208.

Westerling, A.L., Gershunov, A., Brown, T.J., Cayan, D.R., Dettinger, M.D., 2003. Climate and wildfire in the western United States. Bulletin of the American Meteorological Society 84, 595–604.

Whicker, J.J., Breshears, D.D., Wasiolek, P.T., Kirchner, T.B., Tavani, R.A., Schoep, D.A., Rodgers, J.C., 2002. Temporal and spatial variation of episodic wind erosion in unburned and burned semiarid shrubland. Journal of Environmental Quality 31, 599–612.

Whisenant, S.G., Uresk, D.W., 1989. Spring burning Japanese brome in a western wheatgrass community. Journal of Range Management 43, 205–208.

White, R.S., Currie, P.O., 1983. Prescribed burning in the northern Great Plains: yield and cover responses of 3 forage species in the mixed grass prairie. Journal of Range Management 36, 179–183.

Wright, H.A., 1971. Why squirreltail is more tolerant to burning than needle and thread. Journal of Range Management 24, 277–284.

Wright, H.A., Klemmedson, J.O., 1965. Effect of fire on bunchgrasses of the sagebrush-grass region in southern Idaho. Ecology 46, 680–688.

Zoebeck, T.M., Fryrear, D.W., Pettit, R.D., 1989. Management effects on wind-eroded sediment and plant nutrients. Journal of Soil and Water Conservation 44, 160–163.