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Vegetation Response of a Dry Mixed Prairie to a Single Spring or Fall Burn

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ABSTRACT

Climate change may make semiarid grasslands increasingly prone to wildfire. We studied fire seasonality and growing season condition effects on a semiarid grassland in Southern Alberta, Canada. Plots were hand-torched in either fall or spring. Response variables estimated included plant composition and diversity, plant height, aboveground net primary production (ANPP), and forage nitrogen quality. The experiment was replicated over three consecutive growing seasons, and each replicate was monitored for 3 yr thereafter. Drought conditions occurred during two of the six growing seasons. Fall fires appeared to be hotter than spring fires based on a greater fuel mass (standing litter) and exposed the soil surface to a longer period without the benefit of standing litter over winter. Although this grassland is resilient to fire, compared with spring-burned grasslands, the species composition, ANPP, and leaf length of grasses of fall burned communities took a longer time to recover to preburn conditions. Our results suggest that spring-burned grasslands should not be grazed for 1 year post burn to allow time for recovery of ANPP and litter. However, given that ANPP of fall-burned communities also exhibited higher nitrogen concentration that may make the forage more palatable to livestock, and that these communities were more severely impacted, it seems prudent to delay their grazing for more than 1 year to prevent overgrazing. The negative impacts of fire on ANPP may be ameliorated with above-average precipitation in June, which may be forecast during an El Niño year.

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Introduction

Fire is an ecological driver of global vegetation patterns (Bond and Keeley 2005) and helps maintain grassland ecosystems (Anderson 2006; Vermeire et al. 2011; Ratajczak et al. 2014; Valkó et al. 2018). Fire likely played a role in shaping the Great Plains ecosystems; the historical frequency, intensity, and seasonality of wildfires is unknown, but presumably they varied across locations and time (Bailey 1978; Perryman and Laycock 2000; Vermeire and Russell 2018) and were anthropogenically influenced (Stewart et al. 2002). Fire is now rarely used intentionally and instead is actively suppressed across much of the Great Plains (Morton et al. 2010), particularly in more arid parts. More recently, however, their

frequency and scale have increased significantly (Donovan et al. 2017).

There are two reasons why we need to understand how plant communities in drier parts of the Great Plains respond and recover following fire. Human-caused climate change may increase winter precipitation and summer temperatures in the Great Plains, which in turn will promote earlier spring growth and summer desiccation (Flanagan 2015). The combined impact of summer desiccation and spring fire has a greater effect on the structure and composition of a tallgrass prairie plant community than either alone (Ratajczak et al. 2019).

Second, drier rangelands are generally conservatively stocked in order to maintain abundant carryover as plant litter (Adams et al. 2013). Litter includes standing senescent and fallen partially decomposed plant material from previous growing seasons. Litter can increase forage productivity in drier grasslands (Willms et al. 1986; Willms et al. 1993; Deutsch et al. 2010) but also increases fuel load and subsequent fire intensity.

Presently, grassland fires occur primarily during the dormant season when litter is dry, with the greatest frequency in fall (Donovan et al. 2017). Wildfires are caused primarily by humans

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and by lightning strikes with most lightning strikes (73%) occurring in July and August (Higgins 1984) in the Northern Great Plains.

How plant communities are affected by fire depends on intensity and time of year, and the two may be linked. For example, fire intensity is affected by fuel mass (litter), which is greater in fall than spring because of weathering losses of litter over winter. Fire in fall may also exacerbate more droughty soil conditions by removing litter, which helps capture snow and buffers soil temperature in spring. However, this hypothesis was contradicted by Clark et al. (1947) in one of the few studies on the effects of burning in the dry mixed prairie. They reported a greater loss of production from a spring-burned (50%) compared with fall-burned (30%) grassland. Unfortunately, they did not report their protocol or pre-fire and postfire conditions.

The season and intensity of fire can have a selective effect on plant species depending on their phenological development (Ruckman et al. 2011) and the amount of fuel at the crown (Erichsen-Arychuk et al. 2002), which can influence fire intensity and, therefore, damage to the growing point (Wright 1971) and subsequently plant growth. Erichsen-Arychuk et al. (2002) suggest that the smaller mass of litter at the crown of Junegrass (*Koeleria macrantha* [Ledeb.] Schult.) makes it more tolerant of fire than needle-and-thread (*Hesperostipa comata* [Trin. & Rupr.] Barkworth), which has a greater mass. Wright (1974) suggests that fall burning favors cool-season (C3) grasses while spring burning may kill C3 bunchgrasses, which allows weedy species to colonize the range. On the dry mixed prairie the primary warm-season (C4) species is blue grama (*Bouteloua gracilis* [Willd. ex Kunth] Lag. ex Griffiths), which begins growth later in spring than C3 species and better tolerates the warmer environment that fire creates. For this reason, we hypothesize that spring burning is likely to be more damaging to cool-season grasses than blue grama.

Postfire grazing management of a grassland needs to consider the potential loss of production, as well as the increased preference by livestock for burned areas. Loss of production may be caused by shorter leaves of grasses (Clarke et al. 1947) possibly produced by drier soils or increased light at the crown (Willms 1988). Forage palatability may be increased with a higher concentration of N in the leaves (Powell et al. 2018) and by the removal of standing litter, which is unpalatable to livestock and produces a barrier effect to new growth (Willms et al. 1980). Loss of litter also enables livestock to graze nearer the crown, which can produce intense defoliation that further delays plant recovery. Therefore, burned grassland requires a period of protection from grazing for timely recovery.

The effects of burning on grasslands have been examined in numerous studies for the purpose of managing grasslands or understanding their impacts. However, few controlled studies have been conducted on the dry mixed prairie, possibly because fire is not seen as a tool for grassland management as it is in some more mesic grasslands. Nevertheless, wildfires are common occurrences and grazing managers need to better understand their impacts in order to better manage postfire grazing. Therefore, we conducted a study in the dry mixed prairie to 1) examine how season (fall vs. spring) of fire affects plant community composition, diversity, height, productivity, and forage quality of a dry mixed prairie site in the Northern Great Plains and 2) examine how these parameters recover over time.

Materials and Methods

Experimental site

The experiment was conducted over a 6-yr period (1997–2002) at the Onefour Agriculture and Agri-food Canada research station (–110°26'24", 49°2'58"). The site has Brown Chernozem soil (Aridic

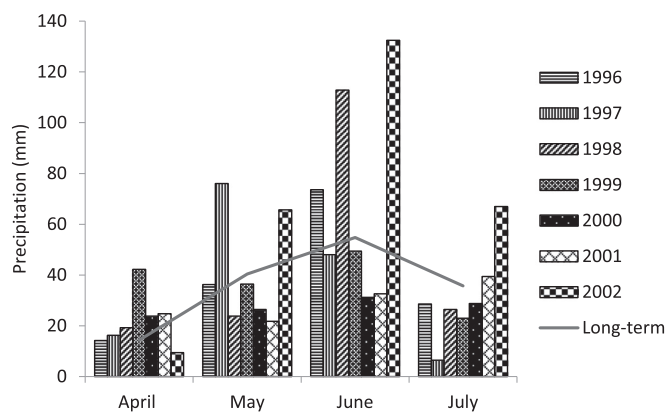


Fig. 1. Monthly precipitation from April to July for the years of the experiment from 1996 to 2002 compared to the long-term average from 1981 to 2010. Note: 2000 and 2001 were drought years.

Boroll subgroups) with loamy texture. Dominant grasses include needle-and-thread, blue grama, and Junegrass, which are common species in the dry mixed-grass natural subregion.

Vegetation productivity in southern Alberta is predominantly precipitation driven (Jiang et al. 2016). The long-term average annual precipitation (1981–2010) was 290 mm. Precipitation during the period from April to July, in the first 3 yr of the experiment (1997–1999), was 17–42% above average (Fig. 1). Precipitation was 26–28% below average for 2000–2001, while 2002 precipitation was 90% above average. Forage yields of an adjacent benchmark enclosure correspondingly varied from 53% below to 11% above average during this period.

Methods and materials

The effect of a single burn on the vegetation was examined in a split-plot experiment with four blocks where years-of-burn (YB₁, 1997/1998, YB₂, 1998/1999, and YB₃, 1999/2000) were the main plots (27 × 7 m) and season-of-burn (fall, spring or unburned control) were the subplots (9 × 7 m). The four blocks were arranged in a 2 × 2 configuration, with a 1.5-m buffer between them, and fenced to exclude livestock (60 × 50 m) before treatments began in 1997. Burning was conducted in spring between 24 March and 1 April (pregreening) or late fall between 1 September and 25 September (after plant dormancy). A propane torch was used to establish a contiguous burn line on the windward side of plots, and wet lines were used to contain burns.

The preburn fuel and community characteristics (standing and surface biomass and ground cover, classified as herbaceous, cactus, litter, manure, spikemoss [*Selaginella densa* Rydb.] green, spikemoss dead, lichen, rock, and bare ground) were sampled immediately before each burn to estimate the fuel load and other variables that might affect burn intensity. These variables were measured again immediately after burning to determine destruction. The surface biomass (surface fuel) was scraped by hand from the soil surface, and its organic content was determined by burning to correct for inorganic residue. This was necessary because scraping the soil surface would also incorporate mineral soil contaminants that would distort sample weight. The caloric content of the standing biomass was determined using an E2K bomb calorimeter system (Digital Data Systems, Randburg, Gauteng, South Africa).

Species composition and aboveground net primary production (ANPP) were sampled in 3 consecutive yr postburn after the growing season (19 August to 26 August). The first period of postburn recovery consisted of the first growing season after treatment (GS₁), which would be the growing season immediately after

spring burns and next year's growing season for fall burns. Then plant recovery was monitored for two more growing seasons, GS₂ and GS₃.

The vegetation of each burned plot was sampled along a single permanent transect (6 m) established along the center of each plot and to within 1.5 m of the edge. Twelve quadrats (50 × 50 cm) were located contiguously along the transect. Three quadrats were randomly selected without replacement for sampling before the burn and in each year postburn. Plant community composition by canopy cover classes (0–5%, 5–25%, 25–50%, 50–75%, and 75–100%) was visually assessed in smaller subquadrats (20 × 50 cm) nested within the larger. Within each subquadrat we also counted the inflorescence number of the main species (blue grama, needle-and-thread, and Junegrass) and estimated their average leaf length of current growth. This was done by selecting up to five plants of each species and measuring the length of the tallest leaf from the ground surface to leaf tip using a ruler, then arriving at a composite average for all plants of a species within the subquadrat. The quadrats were then harvested. Following harvest, the area of bare ground and ground cover of litter, moss, and lichen were visually assessed. The unburned control plots were sampled after each growing season in the same manner and time as the burned plots.

Harvested biomass was dried at 60°C for 48 h and weighed. A grab sample of harvested biomass of each quadrat was hand-sorted into green and dead (litter) portions to estimate their representation in the whole sample. Each component was ground to pass a 100-mesh screen (149 μm) and tested for nitrogen content using an automated dry combustion technique (NA-1500, Carlo Erba, Milan, Italy).

Statistical analysis

Nonmetric multidimensional scaling ordinations (MJM Software Design, Gleneden Beach, OR) were used to assess plant community composition changes. Ordinations combined data collected at different times (i.e., for different years of burning: YB₁ [1997/1998], YB₂ [1998/1999], and YB₃ [1999/2000]) but were stratified for each year of recovery (GS₁, GS₂, GS₃). Burn treatment (fall, spring, or unburned control) and year of burn treatment (YB₁, YB₂, and YB₃) were fixed factors within permutational multivariate analyses of variance (perMANOVAs) to assess these effects on plant community recovery according to species composition. Indicator species analyses were used to identify species influencing compositional responses. This analysis identifies species (indicators) that distinguish between or among a priori groups of species by calculating indicator values from the product of species frequency and abundance (McCune and Grace 2002).

Univariate responses of ANPP, leaf length, inflorescence number, percent nitrogen, Shannon's diversity, and species richness and evenness were examined using the SAS/STAT software (2016, SAS Institute Inc., Cary, NC). Analyses of variance were analyzed using the mixed procedure, and the data were examined for normality and homogeneity of variance using the univariate procedure. Model fixed factors included burning treatment, year of burning (YB₁, YB₂, and YB₃), and growing season of recovery (GS₁, GS₂, GS₃) following burning. In this analysis, block nested in YB was a random factor and GS was a repeated measure. Four covariance structure matrices (autoregressive, heterogeneous autoregressive, compound symmetry, and heterogeneous compound symmetry) were tested with Akaike's Information Criterion to select the best structure.

Results

The mass of standing fuel in fall was greater ($P < 0.05$) than in spring, and the loss of surface fuel in fall after combustion was

significantly higher than in spring ($P < 0.05$; Table 1). At the same time, the caloric value per unit weight or total caloric value of standing fuel in fall was higher than that of standing fuel in spring. The difference in standing fuel from fall to spring was 27% from 1998 to 1999, 43% from 1999 to 2000, and 20% from 2000 to 2001, with an average of 30% over 3 yr (see Table 1). The organic matter remaining on the surface after burning was similar between fall and spring, although the tendency was for a smaller mass in the former.

Three-dimensional solutions were favored for all ordinations, and final stress scores ranged from 10.8 to 12.6. Treatment ($P \leq 0.02$) and year ($P < 0.01$) effects were significant with no interactions ($P \geq 0.42$) for all perMANOVA tests (Table 2). These showed that after the first growing season post burn, both spring and fall burning resulted in different plant communities based on their species composition, both from each other ($P < 0.01$) and the control ($P < 0.01$). However, these differences persisted to the third postburn growing season only between the fall-burned and control treatments.

Indicator species analyses showed that needle-and-thread was associated with controls ($P \leq 0.04$) for all three growing seasons post burning (GS₁₋₃), and spikemoss cover was associated with controls ($P < 0.01$) for the first two growing seasons post burning (GS₁₋₂) (see Table 2). The only species associated with a burn treatment (fall) was Junegrass ($P < 0.01$), and this was only in GS₁.

Ordination figures (Fig. 2) show that fall-burned communities, as opposed to spring, diverged the furthest from unburned controls. Indeed, after two growing seasons of rest, only fall-burned communities differed from controls ($P < 0.01$); spring-burned communities did not differ from fall ($P = 0.35$) or controls ($P = 0.09$) (see Table 2). The same was true after three growing seasons of recovery when fall-burned communities differed from controls ($P < 0.01$), whereas spring- and fall-burned ($P = 0.15$) and spring-burned and control ($P = 0.11$), communities again did not differ. Communities burned in different trial years always differed ($P < 0.01$) from one another for comparisons at similar stages of recovery (i.e., one, two, and three growing seasons post burn; data not shown).

The burning treatment had no effect ($P > 0.05$) on indices of species evenness or Shannon's diversity in any year or their subsequent recovery year (GS₁₋₃) while species richness was affected by the influence of burning treatment and year of burning in GS₁ only. However, each of those indices was affected ($P < 0.05$) by the year of treatment (data not shown) except for evenness in GS₃ ($P > 0.05$) and Shannon's diversity in GS₁ ($P > 0.05$). In GS₁, both fall- and spring-burned treatments showed increased species richness for plots burned in YB₁ (9.2^a and 9.8^a for fall- and spring-burned, respectively, vs. 8.0^b for the control; $P < 0.05$; means with a different superscript letter are different), whereas only spring, not fall, burning increased species richness for plots burned in YB₂ (8.2^b, 9.2^a, and 8.0^b, respectively, for fall- and spring-burned plots and the control), while burning reduced species richness for plots burned in YB₃ (7.5^b, 7.2^b, and 8.2^a, respectively, for fall- and spring-burned plots and the control).

ANPP was affected ($P < 0.05$) by the main effects of year of burning (YB), burning treatment (Trt), recovery time (growing season) after burning (GS), the interaction of YB × GS, and the interaction of Trt × GS (Table 3). The effect of burning treatment was consistent ($P > 0.05$) among the 3 yr (YB₁₋₃) and among the three postburn growing seasons (GS₁₋₃) after treatment. Burning depressed ANPP yields in GS₁ with the greatest decrease caused by fall burning (see Table 3). The effect of spring burning persisted to GS₂, and ANPP in both burning treatments had recovered by GS₃ (see Table 3).

The mass of standing litter in the average of the burned treatments was less ($P < 0.05$) than the control after each of the post-

Table 1
Characteristics of surface fuel (dead plant litter lying on the ground) and standing fuel (standing dead plant litter) of burned plots in fall and spring on a dry mixed prairie grassland.

Yr-of-burn (YB)	Surface fuel (Organic matter [OM])						Standing fuel (litter)								
	Organic matter loss (g m ⁻²) ¹			Residual OM (g m ⁻²)			Biomass (g m ⁻²)			Caloric conc. (kcal g ⁻¹)			Caloric mass (kcal m ⁻²)		
	Fall	Spring	SE _m	Fall	Spring	SE _m	Fall	Spring	SE _m	Fall	Spring	SE _m	Fall	Spring	SE _m
YB ₁ ²	103.0a	11.2b	17.8	70.1b	140.3a	21.8	65.7a	47.8b	6.8	4.65a	4.36b	0.1	305a	206b	31.8
YB ₂	35.1a	25.2a	17.8	99.9a	84.8a	21.8	78.3a	44.9b	6.8	4.53a	4.22b	0.1	355a	189b	31.8
YB ₃	53.2a	-15.6b	17.8	123.6a	147.7a	21.8	72.9a	59.0a	6.8	4.25a	4.27a	0.1	312a	252a	31.8
Avg.	63.8a	6.9b	10.3	96.4a	124.7a	14.7	72.3a	50.6b	3.9	4.47a	4.28b	0.06	324a	216b	18.3
Analyses of variance															
Probability															
Source															
Season-of-burn (SB)	0.18			0.38			0.56			0.11			0.77		
YB	< 0.05			0.10			< 0.05			< 0.05			< 0.05		
SB × YB	0.08			0.11			0.17			0.29			0.16		

¹ Calculated as: OM before burning – OM after burning (sampled from different quadrats)

² YB₁ (fall, 1997; spring, 1998), YB₂ (fall, 1998; spring, 1999), and YB₃ (fall, 1999; spring, 2000)a-b indicates paired means (fall vs. spring) within a row having different letters are significantly ($P < 0.05$) different.

Table 2
Community analyses on the effects a single burn repeated in each of 3 yr (year-of-burn, YB); season-of-burn (SB, fall or spring and an unburned control); and number of growing seasons (GS₁₋₃) post burn on the species composition of a dry mixed prairie grassland, based on canopy cover, with the use of permutational multivariate analysis of variance (perMANOVA) and indicator species analysis.

perMANOVA	Growing season (GS) postburn													
	df	(P)	GS ₁				GS ₂				GS ₃			
Yr-of-burn (YB)	2	< 0.01	< 0.01				< 0.01				< 0.01			
Season-of-burn (SB)	2	< 0.01	< 0.01				< 0.01				0.02			
YB × SB	4	0.93	0.93				0.42				0.45			
Comparisons														
Fall vs. spring		< 0.01	< 0.01				0.35				0.15			
Fall vs. Ck		< 0.01	< 0.01				< 0.01				0.01			
Spring vs. Ck		< 0.01	< 0.01				0.09				0.11			
Indicator species analysis														
Species ²		(Relative abundance ¹ ; P)	Fall (%)	Spring	Control	P	Fall (%)	Spring	Control	P	Fall (%)	Spring	Control	P
Needle-and-thread			25	30	46	< 0.01	26	31	43	0.01	26	31	42	0.04
Junegrass			43	25	31	< 0.01	39	33	28	0.47	31	30	39	0.76
Blue grama			27	40	34	0.09	37	36	28	0.60	37	37	26	0.57
Sedge spp.			34	36	30	0.97	46	28	26	0.32	31	41	28	0.40
Western wheatgrass			46	14	40	0.83	28	20	52	0.24	40	28	32	0.96
Pasture sage			0	11	89	0.54	0	100	0	0.31	40	30	30	0.92
Spikemoss			19	23	58	< 0.01	17	30	52	< 0.01	18	37	45	0.11

¹ Average abundance of a given species in a treatment relative to the average abundance of that species in all plots.

² Significant indicator species and other selected species that are important in the dry mixed prairie.

Table 3
Annual net primary production in response to a single burn repeated over 3 yr (yr-of-burn, YB₁₋₃), season-of-burn (SB, fall or spring, and an unburned control), and number of growing seasons (GS₁₋₃) postburn of a dry mixed prairie grassland.

Yr-of-burn (YB)	Growing season (GS) postburn											
	GS ₁				GS ₂				GS ₃			
	Season-of-burn (SB)		Control	SE _m	Fall	Spring	Control	SE _m	Fall	Spring	Control	SE _m
	Fall	Spring										
	ANPP (g•m ⁻²)											
YB ₁ ¹	39.7	41.0	53.4	2.9	53.0	50.0	55.0	3.4	35.8	30.4	29.4	5.0
YB ₂	41.9	49.3	60.1	2.9	25.8	25.0	30.0	3.4	22.2	21.1	22.7	5.0
YB ₃	13.9	20.0	33.6	2.9	24.7	20.3	27.7	3.4	55.8	51.6	69.1	5.0
Mean	31.8c	36.8b	49.1a	1.7	34.5ab	31.8b	37.6a	2.0	37.9a	34.4a	40.4a	2.9

¹ YB₁ (fall, 1997; spring, 1998), YB₂ (fall, 1998; spring, 1999), and YB₃ (fall, 1999; spring, 2000)

² ANOVA model (Source of variation; Probability): YB, < 0.05; SB, < 0.05; YB × SB, 0.18; GS, < 0.05; YB × GS, < 0.05; SB × GS, < 0.05; YB × SB × GS, 0.70.a-b indicates SB means with different letters within a row (YB and mean) and within a subset of GS differ significantly ($P < 0.05$).

burn growing seasons. Their proportion (%) of the control over the 3 yr (YB₁₋₃) was 4, 68, and 64 in GS₁, GS₂, and GS₃, respectively.

While the effects of burning on the number of inflorescences were inconsistent among YB and during the postburn recovery period (GS₁₋₃), over a 3-yr period (YB₁₋₃) fall burning resulted in a greater ($P < 0.05$) number of inflorescences in blue grama in each growing season of postburn recovery while spring burning had no effect ($P > 0.05$; Tables 4 and 5). The inflorescence number

of Junegrass was increased with fall burning and decreased with spring burning in GS₁, but any effects were lost ($P > 0.05$) by GS₃. Inflorescences number of needle-and-thread was reduced ($P < 0.05$) by fall burning in GS₁ only.

The leaf lengths of all three species were affected ($P < 0.05$) by burning treatment, but these effects were not consistent in each growing season (GS₁₋₃) after burning treatments ($P < 0.05$; see Tables 4 and 6). Fall burning tended to produce shorter leaves than

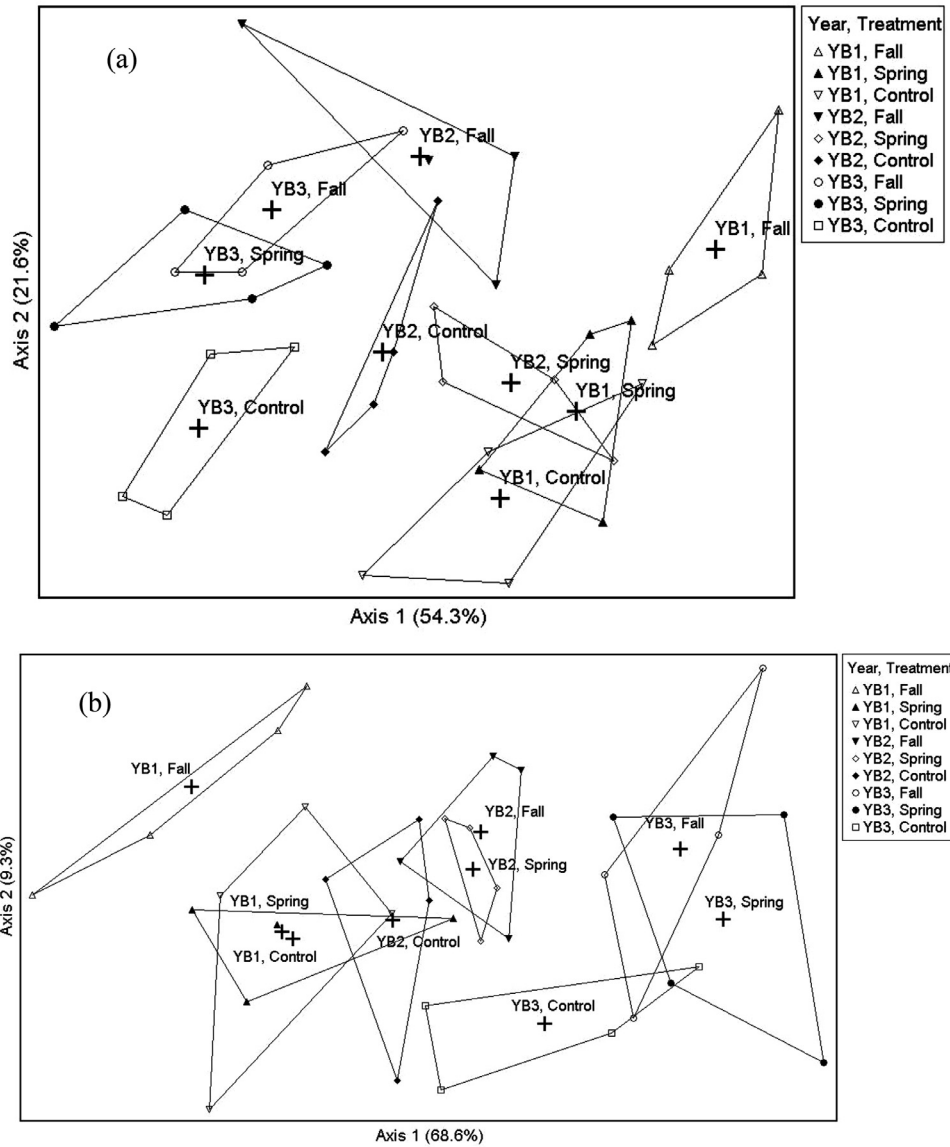


Fig. 2. NMS ordination showing burning treatment and trial years at one (a) and three (b) growing seasons postburn. Significant indicator species, plant diversity metrics, moss and lichen cover, and herbage yields are correlated with axes at a vector scaling cut-off of $r^2 > 0.20$. The axis indicate the proportion of variance accounted using the Sorenson distance measurement of all possible paired samples.

Table 4
Analysis of variance for the effects of a single burn repeated over 3 yr (years-of-burn), in fall and spring (season-of-burn with a control) and over three growing seasons of postburn recovery on the inflorescence number, leaf length, and nitrogen concentration and mass of three major species in a dry mixed prairie grassland.

Source of variation	Species	ANPP ⁴						
		B. gr. ¹ Inflorescence number	Junegr. ²	Needle. ³	B. gr. Leaf Length (cm)	Junegr.	Needle.	Nitrogen Conc.
	Probability							
Yr-of-burn (YB)	< 0.01	< 0.01	< 0.01	0.09	0.27	0.11	< 0.01	0.14
Season-of-burn (SB)	0.01	< 0.01	0.22	< 0.01	0.04	< 0.01	0.14	< 0.01
YB × SB	0.28	< 0.01	0.02	0.58	0.26	0.30	0.02	0.42
Growing season (GS)	< 0.01	< 0.01	< 0.01	< 0.01	0.18	< 0.01	< 0.01	< 0.01
YB × GS	< 0.01	< 0.01	< 0.01	< 0.01	< 0.01	< 0.01	< 0.01	< 0.01
SB × GS	0.64	< 0.01	0.03	< 0.01	0.02	< 0.01	0.02	0.09
YB × SB × GS	0.01	< 0.01	0.13	0.83	0.25	0.21	0.04	0.09

¹ Blue grama.
² Junegrass.
³ Needle-and-thread.
⁴ Annual net primary production.

Table 5
The effects of a single burn conducted in each of 3 yr (yr-of-burn, YB₁₋₃), in both fall and spring (season-of-burn with a control), and over three growing seasons of recovery (GS₁₋₃) post burn on the inflorescence number of major plant species in a dry mixed prairie grassland.

Plant species	Yr-of-burn (YB)	Growing seasons (GS) postburn								
		GS ₁			GS ₂			GS ₃		
		Season-of-burn (SB)								
		Fall	Spring	Control	Fall	Spring	Control	Fall	Spring	Control
		Inflorescence number								
Blue grama	YB ₁	6.3a	2.8b	2.0b	0.0a	0.2a	0.1a	0.1a	0.0a	0.0a
	YB ₂	0.0a	0.2a	0.2a	1.0a	0.1a	0.0a	5.1a	3.2ab	1.6b
	YB ₃	0.0a	0.0a	0.0a	7.6a	3.8b	1.4b	11.9a	4.8b	4.8b
	Average	2.1a	1.0ab	0.7b	2.9a	1.3ab	0.7b	5.7a	2.6b	2.2b
Junegrass	YB ₁	0.8a	0.2a	0.3a	14.1a	16.3a	4.8b	1.8a	0.6a	1.0a
	YB ₂	11.2a	2.4c	7.2b	5.3a	1.8b	0.8b	0.0a	0.2a	0.0a
	YB ₃	1.6a	0.2a	0.6a	0.0a	0.0a	0.1a	0.0a	0.0a	0.0a
	Average	4.6a	0.9c	2.7b	6.4a	6.0a	1.9b	0.6a	0.2a	0.3a
Needle-and-thread	YB ₁	0.4a	0.2a	0.5a	6.6a	4.4ab	3.8b	1.0a	0.6a	0.6a
	YB ₂	1.4b	5.2a	6.2a	0.2a	1.2a	0.9a	0.4a	0.1a	0.3a
	YB ₃	0.0a	0.6a	1.2a	0.5a	0.2a	0.5a	0.2b	0.0b	2.3a
	Average	0.6b	2.0a	2.6a	2.4a	1.8a	1.8a	0.5a	0.2a	1.1a

¹YB₁ (fall, 1997; spring, 1998), YB₂ (fall, 1998; spring, 1999), and YB₃ (fall, 1999; spring, 2000))

^{a-b}SB means with different letters within a row (YB and average) and within a subset of GS differ significantly ($P < 0.05$).

Table 6
The effects of a single burn conducted in each of 3 yr (years-of-burn, YB₁₋₃), in both fall and spring (season-of-burn with a control), and over three growing seasons of recovery (GS₁₋₃) post burn on the leaf length of major plant species in a dry mixed prairie grassland.

Plant species	Yr-of-burn (YB)	Growing seasons (GS) postburn								
		GS ₁			GS ₂			GS ₃		
		Season-of-burn (SB)								
		Fall	Spring	Control	Fall	Spring	Control	Fall	Spring	Control
		Leaf length (cm)								
Blue grama	YB ₁ ¹	3.3b	3.2b	4.7a	3.0a	3.2a	3.6a	2.9a	2.6a	3.1a
	YB ₂	2.7b	3.0b	4.1a	2.1b	2.2b	3.2a	2.6a	2.5a	2.6a
	YB ₃	1.9b	2.2b	3.2a	2.1a	2.1a	2.5a	4.6a	4.7a	4.6a
	Average	2.6b	2.8b	4.0a	2.4b	2.5b	3.1a	3.4a	3.2a	3.4a
Junegrass	YB ₁	4.9a	4.8a	6.0a	5.0a	4.6a	5.3a	7.9a	5.5a	6.8a
	YB ₂	5.0a	5.1a	5.6a	6.5a	6.6a	7.2a	4.8a	5.0a	4.3a
	YB ₃	5.3b	6.4ab	7.3a	4.3a	3.8a	4.2a	5.0ab	4.3b	5.3a
	Average	5.1b	5.4b	6.3a	5.3a	5.0a	5.6a	5.9a	4.9a	5.4a
Needle-and-thread	YB ₁	6.0c	7.1b	8.8a	8.1b	8.0b	10.5a	9.4a	9.8a	10.8a
	YB ₂	6.9b	8.0b	11.0a	7.9b	8.4b	11.6a	7.8b	8.5ab	9.5a
	YB ₃	6.4b	7.9b	12.0a	7.0b	6.8b	9.6a	12.9b	11.4b	13.5a
	Average	6.5c	7.6b	10.6a	7.7b	7.7b	10.6a	10.0b	9.9b	11.3a

¹ YB₁ (fall, 1997; spring, 1998), YB₂ (fall, 1998; spring, 1999), and YB₃ (fall, 1999; spring, 2000).a-c indicates treatment means with different letters within a row (YB and average) and within a subset of GS differ significantly ($P < 0.05$).

spring burning in GS₁, and both were shorter than those of the unburned plants (see Table 6). Leaf lengths of Junegrass were similar among treatments by GS₂, as were leaf lengths of blue grama by GS₃, while the leaf lengths of fall- or spring-burned needle-and-thread plants remained shorter than the unburned plants in the unburned control in GS₃ (see Table 6).

Burning effect on nitrogen concentration in ANPP varied by the year of burning treatment and the number of growing seasons after burning (see Tables 4 and 7). Fall burning increased ($P < 0.05$) the N concentration in GS₁, but that effect was lost ($P > 0.05$) by GS₂ (see Table 7).

The mass of nitrogen was affected ($P < 0.05$) by the main effects of burning treatment and the number of growing seasons following burning, but the effects of burning treatment were not influenced ($P > 0.05$) by the postburn period or the year when treatments were initiated (see Table 4). Nitrogen mass in the fall, spring, and control burn treatments, over the three postburn periods, was 1.3^a, 1.2^a, and 1.5^b g 0.25 m⁻² (SEm = 0.005), respectively.

Discussion

Fuel properties

Fire intensity is affected by fuel load. Fuel load differences between fall and spring were likely influenced by weathering losses

of senesced herbage over winter. Willms et al. (1996) reported biomass losses from fall to spring on a fescue grassland ranging from 24% to 56%. Moreover, fire can affect the plant directly through heat damage to the meristematic tissue (Bogen et al. 2002) and indirectly through the removal of litter. The effects of both are a function of fire intensity and duration (Bogen et al. 2002). Fire intensity was expected to be greater with fall burning than with spring burning based on greater caloric mass and generally lower soil and fuel moisture. It appears that greater fire intensity in fall was associated with a differential shift in the species composition of the plant community, with shorter leaf lengths in grass species and a greater reduction in ANPP.

Fire effects on the plant community

The effect of burning on this plant community was to reduce the ground cover of needle-and thread and spikemoss. The former plant is a canopy-dominant, late-seral perennial grass in Alberta's dry mixed prairie. As such, this grass contributes disproportionately to plant community productivity (Coupland 1961) and is an indicator of healthy rangelands in this region (Adams et al. 2013). Spikemoss is a small-statured perennial forb that often functions as a ground cover species in edaphically limited ecological sites and is therefore an important structural component of the plant

Table 7

The effects of a single burn conducted in each of 3 yr (years-of-burn, YB₁₋₃), in both fall and spring (season-of-burn with a control), and over three growing seasons of recovery (GS₁₋₃) post burn on the nitrogen concentration (estimated in late August) and nitrogen mass of annual net primary production in a dry mixed prairie grassland.

Yr-of-burn (YB)	Growing seasons (GS) postburn								
	GS ₁			GS ₂			GS ₃		
	Season-of-burn (SB)								
	Fall	Spring	Control	Fall	Spring	Control	Fall	Spring	Control
	Nitrogen concentration (%)								
YB ₁ ¹	1.46a	1.22b	1.31ab	1.13b	1.30a	1.28ab	1.33a	1.39a	1.24a
YB ₂	1.32a	1.27a	1.24a	1.27b	1.22b	1.36a	1.83a	1.78a	1.93a
YB ₃	1.50a	1.37ab	1.23b	1.87a	1.92a	1.59b	1.70a	1.72a	1.56a
Average	1.43a	1.29b	1.26b	1.42a	1.48a	1.41a	1.62a	1.63a	1.58a
	Nitrogen mass (g • 0.25 m ⁻²)								
Average	0.11a	0.12a	0.16b	0.12a	0.11a	0.13a	0.15a	0.14a	0.16a

¹ YB₁ (fall, 1997; spring, 1998), YB₂ (fall, 1998; spring, 1999), and YB₃ (fall, 1999; spring, 2000). a-b indicates SB means with different letters within a row (YB and average) and within a subset of GS differ significantly ($P < 0.05$).

community. Given that both of these plants play important ecological functions, fire may disproportionately alter plant community function even if changes in plant community composition are relatively subtle.

Burning affected the composition of the plant community by selectively impacting species through mortality or altering their morphology, and these effects were greatest with fall than spring burning. In our study, needle-and-thread, Junegrass, and spikemoss defined the primary shifts in composition. Of these, spikemoss appeared to be killed by fire in either fall or spring and its cover was reduced by about 64% after the first growing season. Rowe (1969) reported a loss of 58% cover with a single burn and 85% with a second burn. Dix (1960) indicated that the frequency of spikemoss in a burned site was only 9% that of a paired unburned site after 4 yr.

Of the grasses that defined compositional shifts, needle-and-thread may also be vulnerable to heat damage as it is the largest and most productive caespitose species in the study area, which could lead to higher heat intensity near the crown; however, this impact was not monitored. On the other hand, the composition of needle-and-thread appears to be at least partly related to the effect of burning that resulted in shorter leaves. The arching leaves of needle-and-thread suggest a direct effect on canopy cover, which would be exaggerated with longer leaves. In our study, leaf length of needle-and-thread never recovered until after the third growing season post burn when its composition was still greatest in the unburned treatment. It is unclear what the dominant factors were that influenced the composition of Junegrass, which had both the greatest composition and the shortest leaves in the first growing season after fall burning. This species has mostly erect leaves so that a change in their lengths would have little effect on canopy cover. Another response variable that can affect canopy cover is inflorescences, which were significantly greater in the first growing season after fall burning than in the control and both were significantly greater than in the spring-burned treatment.

Results of this study indicate that fall, as opposed to spring, burning had both greater and more prolonged effects on community composition. This was true regardless of individual growing season conditions. Reasons for this may be that most plants better tolerate fire when actively growing (early season) and there is opportunity for immediate recovery during the growing season following burning. Despite these composition shifts, there were no clear and consistent plant diversity responses that suggest, along with a lack of indicator species, composition shifts were likely due to changes in abundance of a few consistently present plants.

The year of burn is important because weather is different from year to year and significantly influenced by the El Niño Southern Oscillation (Flanagan and Adkinson 2011). In our study, drought

conditions in 2000–2001 occurred during La Niña years that corresponded to the final growing season (GS₃) of the 1997/1998 (YB₁) burning treatments, the final two growing seasons (GS₂ and GS₃) of the 1998/1999 (YB₂) burning treatments, or first two growing seasons (GS₁ and GS₂) of the 1999/2000 (YB₃) burning treatments. Although drought conditions over the 6-yr experimental period may account for differences in plant community composition at the same stage of recovery, it isn't clear which plant responses caused these changes given that species weren't consistently associated with the drier yr (2000 and 2001), nor were species consistently associated with particular trial yr over time. However, leaf length and, concomitantly, ANPP show clear reduction during the drought years and were considerably greater in 2002, which corresponds to an El Niño year and represents the third growing season post burn (GS) of the 1999/2000 (YB₃) burning treatments.

Fire effects on production

The reduction of ANPP with burning was expressed in shorter leaf lengths of grasses, which is closely linked to litter removal either by burning or mechanically harvesting. Litter captures and retains moisture, and its mechanical removal during the dormant season reduced ANPP by 60% on a mixed prairie grassland (Willms et al. 1993), as well as resulting in shorter leaves in plains rough fescue (*Festuca hallii* [Vasey] Piper) and rough fescue (*F. campestris* Rydb.) (Willms et al. 1986). Plant height is a sensitive indicator of environmental stress (Willms 1988) and a good predictor of ANPP when applied as a function of plant volume (Axmanova et al. 2012). Consequently, its response to burning followed a similar trend as ANPP, although recovery relative to the control was species dependent, with needle-and-thread recovery lagging beyond three growing seasons.

In our study, more organic matter was removed by fall burning than with spring burning, although that was not necessarily reflected in reduced residual organic matter after burning. Therefore, this does not appear to be a factor in explaining the greater loss of ANPP and leaf length in the first growing season after fall burning than spring burning. Instead, we propose two possible explanations for this observation: one lies in either a more intense fire in fall that caused more damage to plants or, alternatively, the loss of standing litter and with it greater environmental exposure over winter and reduced ability to capture snow. This observation seemed to be corroborated with a similar treatment response each year. Production on the mixed prairie is water limited, and when litter is removed, plant recovery is more dependent on rainfall during the growing season.

Fire can increase standing crop (Anderson and Menges 1997; Jensen et al. 2001; Augustine et al. 2010) and forb biomass (Valkó

et al. 2018) of grassland ecosystems. These positive effects, however, may be limited to only two subsequent growing seasons (Gates et al. 2017). Still, other research suggests that precipitation may play a larger role than fire in influencing plant community productivity after burning (Vermeire et al. 2011; Suazo et al. 2018). This study found that although moisture strongly influenced inter-annual productivity, fire (regardless of season) reduced productivity only in the first growing season.

Fall burning produced the greatest effect on inflorescence development in the three species examined in this study but with a contrasting response, with their number increasing in blue grama and Junegrass and decreasing in needle-and-thread. The difference is likely to have a physiological explanation as these species were all subject to the same environmental stresses. Similarly, contrasting responses to litter removal were reported for plains rough fescue and porcupinegrass (*Hesperostipa spartea* [Trin.] Barkworth) where inflorescences increased for the latter and decreased for the former following clipping or burning (Willms et al. 1986; Gerling et al. 1995).

Fire can affect nutrient translocation during tissue senescence (Lü et al. 2011), but it did not affect nutrient concentrations and stoichiometric ratios in green leaves after fire treatments were applied for 2 yr (Lü et al. 2012). The same consideration regarding litter is necessary to interpret forage quality responses at the end of the growing season in this study. Here, fire had little influence on percent nitrogen (quality) within the green portion. Quality was not ascertained for the nongreen portion, but due to senescence and subsequent weathering losses; litter is by nature low-quality forage. Fire increased the percent green portion in this study to essentially 100%, suggesting that litter was largely eliminated and overall forage quality for the sward would increase. Without further defoliation, the proportion of litter in the burned plants increased but had not reached the level of the unburned plants by the third year after treatment. This suggests that even by the third year after burning, the plants could be more attractive to herbivory than unburned plants.

Some evidence suggests that there was an additive effect of fire and drought on forage quality. Drought occurred during the first two growing seasons for the third trial year. Fire would indeed exacerbate these drought effects given litter was also eliminated. Distinctive responses for this trial include both higher forage quality and percent green portions two growing seasons post burning (in 2001). This suggests that drought conditions actually enhance forage quality and reduce litter accumulation. The latter result likely occurred because drought conditions resulted in less vegetation production in the first postburn growing season. The former result perhaps suggests that plants ameliorated low yield during drought by concentrating chlorophyll (the primary use of nitrogen) within a smaller shoot.

Implications

Despite arid conditions over several years of the study, the species composition and productivity of our dry mixed prairie study site recovered within one or two growing seasons after burning, although communities burned in fall were slower to recover than those burned in spring. This suggests that greater care in grazing management needs to be given to grasslands burned in fall than spring.

However, species composition and production, while important, are not the only criteria for determining grazing readiness, which also needs to consider livestock grazing behavior in selecting burned and unburned sites and the potential for overgrazing burned areas. Standing litter tends to be avoided by cattle so that it produces a barrier to grazing new growth (Willms et al. 1980), but by removing litter, burning not only increases the nitrogen concen-

tration of new growth but also exposes it to heavy grazing intensity. Therefore, grazing management might require fencing to exclude livestock from burned sites or destocking to avoid excessive grazing pressure. The management options chosen would depend on the proportion of area burned, the phenology of the grasses, and the number of years since burning. This recognizes that differences in palatability diminish between burned and unburned plants as they senesce within a season and that litter accumulation in burned plants will eventually reach equivalency over years with the unburned plants. The time required to reach equivalency is not certain, and the grazing managers need to remain vigilant until palatability discrepancies are no longer a factor.

Fire events on the dry mixed prairie are usually unplanned, but once they occur it is useful to predict the severity of their impact and expected postburn recovery. Results from this study indicate that fall fires have invariably more severe effects than spring fires while the recovery phase is largely dependent on postburn rainfall. Fall burning was associated with more intense fire attributed to greater fuel mass while higher precipitation in June can be expected during an El Niño event (Flanagan and Adkinson 2011), which can be predicted up to 12 months in advance. Nevertheless, the science of postburn grazing management is not exact and any prescription applied needs to be made judiciously with the maintenance of grassland health as the primary goal.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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