



Fire Return Interval and Season of Fire Alter Bud Banks ^{☆,☆☆}

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ABSTRACT

Despite the importance of vegetative reproduction in annual tiller replacement, little is known about the patterns and timing of tiller recruitment from the bud bank, especially regarding fire return intervals and seasons of fire. We examined aboveground plant density, temporal patterns of tiller production, and belowground bud bank dynamics for *Bouteloua gracilis* (Willd. ex. Kunth) Lag. ex Griffiths), *Pascopyrum smithii* (Rydb.) A. Löve, and *Hesperostipa comata* (Trin. & Rupr.) Barkworth following summer, fall, and spring prescribed fires at 2-yr, 3-yr, and 6-yr fire return intervals, and their interactions. Fire treatments were initiated in 2006, and buds were assessed July 2011 through July 2013. Density and number of reproductive *B. gracilis* tillers increased in 2013 following drought during 2012, unlike *H. comata*, which decreased reproductive tiller production. Irrespective of fire treatments, *B. gracilis* produced the most buds (8–10 buds·tiller⁻¹) and *H. comata* produced the least (2–3 buds·tiller⁻¹), with *P. smithii* producing an intermediate amount (6–8 buds·tiller⁻¹). Immediate *B. gracilis* and *P. smithii* bud mortality did not occur for all season and fire return interval treatments. However, *H. comata* bud mortality increased immediately following summer and fall prescribed fires. Three-yr fire return intervals increased active buds throughout the 2013 winter and growing season for *B. gracilis* and *P. smithii* relative to control plots and 2- and 6-yr fire return intervals. Fire stimulated bud activity of *B. gracilis* and *P. smithii* relative to nonburned plots. The aboveground and belowground response of *H. comata* indicated meristem limitations following fire treatments, illustrating greater vulnerability to fire for that species than *B. gracilis* and *P. smithii*.

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Introduction

Vegetative reproduction, or stem recruitment from belowground buds, serves as the primary driver of aboveground production and growth in grasslands, producing > 99% of new tiller growth (Benson and Hartnett, 2006). Using bud banks, perennial grasses are able to respond rapidly to aboveground disturbances with tiller production, even during fluctuating environmental conditions. Periodic fire, grazing, and variable precipitation are important factors governing grassland ecosystems, with large impacts on individual species and plant community structure and function (Fuhlendorf and Engle, 2004; Archibald et al., 2005; Castellano and Ansley, 2007). Bud banks play a crucial

role in these systems by mediating effects of grazing, drought, fire, and other stresses on productivity of grassland dominated by perennial grasses (Benson et al., 2004; Benson and Hartnett, 2006; Dalgleish and Hartnett, 2009).

Dense bud banks provide a safeguard for grassland populations in response to aboveground disturbances, such as grazing, drought, fire, or a combination of these grassland processes (Dalgleish and Hartnett, 2009). In systems with less dense bud banks, meristem limitations are revealed both aboveground and belowground through decreased tillering and recruitment from the bud bank (Dalgleish and Hartnett, 2009). An improved understanding of native, dominant, grassland species responses to the timing of fire and fire return interval may elucidate mechanisms governing population processes and the potential for future tiller recruitment. Determining the links between formation, development, and maintenance of belowground meristems and aboveground processes will help explain annual growth cycles and identify periods of bud bank vulnerability and resistance (Dalgleish et al., 2008).

Despite the importance of vegetative reproduction in year-to-year replacement of tillers, little is known about the patterns and timing of tiller recruitment from the bud bank following different fire return intervals and seasons of fire. Because fire intensity varies with season

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and frequency of fire (Collins, 1992; Govender et al., 2006), plant communities can respond differently to seasonal timing of fire (Dix, 1960; Steuter, 1987; Copeland et al., 2002). For example, summer and fall fire have accelerated overwintering C₄ species bud banks, allowing maximum bud development and storage to prepare for the upcoming growing season (Russell et al., 2017). In tallgrass prairie, burned plots had greater bud bank density in perennial grasses than nonburned plots (Benson et al., 2004; Dalgleish and Hartnett, 2009). However, in the northern mixed-grass prairie, it is unclear if responses to fire and drought are mediated by the size of bud banks. Previous fire ecology research in this region typically measured aboveground vegetation response 1–2 yr post fire and did not include different seasons of fire and their interaction with fire return intervals (Engle and Bidwell, 2001; Castellano and Ansley, 2007; Vermeire et al., 2011).

In semiarid grasslands, such as northern mixed-grass prairie in the Northern Great Plains, variability in precipitation has a large effect on grass production (Vermeire et al., 2009; Wiles et al., 2011). In these systems, year-to-year variability in precipitation can have a greater effect on annual production than fire (Ansley et al., 2006). However, tallgrass prairie bud bank densities did not fluctuate due to the individual and combined effects of grazing under severe drought conditions (VanderWeide et al., 2014; VanderWeide and Hartnett, 2015). The extent to which fire season and return interval enhance or limit bud banks during dry conditions is unknown for the northern Great Plains.

This study used three growing seasons of postfire belowground and aboveground data to examine the effects of summer, fall, spring, and no-fire paired with fire return intervals of 2, 3, and 6-yr in a factorial design on aboveground and belowground dynamics. A C₄ rhizomatous/caespitose grass (*Bouteloua gracilis* [Willd. ex. Kunth] Lag. ex Griffiths), C₃ rhizomatous grass (*Pascopyrum smithii* [Rydb.] A. Löve), and C₃ caespitose grass (*Hesperostipa comata* [Trin. & Rupr.] Barkworth) were selected for study as dominant, native, perennial grasses in northern mixed-grass prairie. The objectives of this study were to quantify effects of fire seasonality and return interval on belowground bud banks and tiller emergence in relation to aboveground plant density. Previous research (Russell et al., 2015) showed fire season directly manipulated bud activity, dormancy, and mortality, and therefore, we expected summer, fall, and spring fires paired with varying fire return intervals to affect overall growth strategy and intensity of bud bank recruitment. We anticipated that differences between C₃ and C₄ species played a crucial role in magnitude and timing of tiller recruitment from the bud bank due to fire season and interval treatments. Therefore, we hypothesized that the presence of fire would increase the capacity of species' bud banks to mediate effects of subsequent fire. We expected that fall fires would stimulate *P. smithii* bud growth and spring fires would enhance *B. gracilis* bud growth. We also hypothesized that *H. comata* bud banks would decrease in productivity, illustrating bud bank vulnerability. This research is focused on population-level assessments of species-specific bud banks and will inevitably enlighten assessments of future community-level research dynamics.

Methods

Study Site

Research was conducted in semiarid mixed-grass prairie at the US Department of Agriculture (USDA)—Agriculture Research Service (ARS) Fort Keogh Livestock and Range Research Laboratory near Miles City, Montana (lat 46°24'N, long 105°56'W; 815 m elevation) from July 2011 to July 2013. Average annual precipitation for the area is 339 mm, with the majority occurring April through September. Precipitation effects on annual biomass production are typically greatest during April and May (Vermeire et al., 2008; Wiles et al., 2011). Average daily temperatures range from 23°C in July to −8°C in January, and the frost-free growing season generally ranges from 125 to 150 d (Western Regional Climate Center, Reno, Nevada, 2013).

The research area consists of native rangeland on upland plains with minimal slopes (0–4%). The 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) (USDA, NRCS Ecological Site Descriptions, 2018).

Vegetation is dominated by perennial, native C₃ species, including *H. comata*, *P. smithii*, and threadleaf sedge (*Carex filifolia* Nutt. var. *filifolia*), and C₄ species, *B. gracilis*, and to a lesser extent, buffalograss (*Bouteloua dactyloides* [Nutt.] J.T. Columbus). Annual grasses include sixweeks fescue (*Vulpia octoflora* [Walter] Rydb.), field brome (*Bromus arvensis* L.), and cheatgrass (*B. tectorum* L.). The primary shrub species on the site is Wyoming big sagebrush (*Artemisia tridentata* Nutt. subsp. *wyomingensis* Beetle & Young) and half shrub fringed sage (*A. frigida* Willd.). The perennial legume, silverleaf Indian breadroot (*Pediomelum argophyllum* [Pursh.] J. Grimes), and the biennial forb, yellow salsify (*Tragopogon dubius* Scop.), were also present. Annual forbs included field cottonrose (*Logfia arvensis* [L.] Holub), woolly plantain (*Plantago patagonica* Jacq.), and rough false pennyroyal (*Hedeoma hispida* Pursh.). Plant nomenclature follows the USDA PLANTS database (USDA, NRCS; PLANTS Database 2018).

Fire Measurements

Fire treatments consisted of summer, fall, spring fire, and nonburned controls with 2, 3, and 6-yr return interval treatments in a factorial design. Each treatment was replicated three times on 15 × 20 m plots for a total of 36 plots with nonburned controls. All fires were set using the ring-fire method (Wright and Bailey, 1982). Summer, fall, and spring fire treatments were initiated in 2006. Summer fires were applied following quiescence of *H. comata* and *P. smithii*, fall fires burned after the first killing frost, and spring fires implemented on green-up of *B. gracilis*. Fire treatment years consisted of 2006, 2008, 2010, and 2012 for the 2-yr treatment; 2006, 2009, and 2012 for the 3-yr treatment; and 2006 and 2012 for the 6-yr treatment, respectively. Two-yr fires did not carry through the plots during 2012 because drought and the 2-yr fire regime limited fuel mass and continuity. The 3- and 6-yr fire return interval treatments were applied with ambient temperatures 30–34°C, winds 7–10 km·h⁻¹, and relative humidity 30–36%; after the first killing frost with ambient temperatures 18–24°C, winds 8–12 km·h⁻¹, and relative humidity 37–41%; and when *B. gracilis* initiated aboveground growth with ambient temperatures 20–25°C, winds 13–20 km·h⁻¹, and relative humidity 39–43%.

We used HOBO U12 J, K, S, T Thermocouple Data Loggers (Onset Computer Corporation, Bourne, MA) with K-type Thermocouples (Omega Engineering, Inc., Stamford, CT) to create time-temperature profiles at the plot level (Table 1). Thermocouples were placed on plant litter at the

Table 1

Thermocouple measurements at the plot level for summer, fall, and spring fires at 2-, 3-, and 6-yr fire return intervals near Miles City, Montana.

	2-yr	3-yr	6-yr
Summer fire¹			
Maximum temperature (C)	240 ± 10	287 ± 12	306 ± 25
Heat duration (s)	297 ± 16	884 ± 13	438 ± 8
Heat dosage (C ● s)	10 381 ± 569	27 774 ± 621	16 878 ± 718
Fall fire			
Maximum temperature (C)	225 ± 8	240 ± 16	261 ± 11
Heat duration (s)	135 ± 16	162 ± 14	214 ± 13
Heat dosage (C ● s)	12 891 ± 426	13 428 ± 589	13 775 ± 646
Spring fire			
Maximum temperature (C)	206 ± 12	266 ± 16	186 ± 10
Heat duration (s)	268 ± 5	83 ± 9	100 ± 11
Heat dosage (C ● s)	2 789 ± 457	5 744 ± 368	4 837 ± 540

¹ Heat duration and dosage were assessed using 60°C as a base temperature. Heat duration was calculated as time (s) of heat > 60°C, and heat dosage was the sum of the degrees > 60°C for each s (degree-sec).

base of a plant's crown within 1–2 cm above the soil surface in a 10 × 10 m square within each plot (4 thermocouples·plot⁻¹) and were programmed to record temperatures at 1-sec intervals. Maximum temperature was identified by finding the greatest value for each time-temperature profile. Heat duration was calculated as time (seconds) of heat > 60°C, and heat dosage was calculated as the sum of the temperatures exceeding a base temperature of 60°C (degree-sec). These measurements were used to derive the mean maximum temperature, heat duration, and dosage of heat imposed at the plot level. Fire behavior measurements were taken during the study yr 2011 and 2012.

Field Sampling and Laboratory Methods

Plant density was estimated at the end of the growing season for 2011, 2012, and 2013. Plant density was measured by counting individual plants rooted within a 0.25-m⁻² quadrat. *B. gracilis* was considered an individual (including rhizomes and stolons) when gaps of ≥ 3 cm were separating neighboring *B. gracilis* tillers. Each *P. smithii* tiller with a unique point of origin from the soil within a 0.25-m⁻² quadrat was considered an individual plant (including rhizomes and stolons). Individuals of *H. comata* used in plant density measurements were readily distinguished due to their bunchgrass growth form. Tiller counts were performed at the end of the 2011, 2012, and 2013 growing seasons on permanently marked individual plants with individuals defined as they were for density counts. Within each quadrat, tillers from one plant were classified as either reproductive or vegetative.

Current-yr buds and tillers were harvested from two individuals per plot for each target species immediately before and after fire and seasonally for 2 yr. Buds and tillers were harvested from randomly selected plant individuals and marked before the fire for postfire assessments. Tillers were harvested within a 10 × 10 m square within the plot, 12–24 hr before and after prescribed burns to determine immediate fire effects on bud activity and survival. Therefore, buds and tillers were assessed for immediate bud response following each fire treatment. To address seasonal fluctuations for each species' bud bank, two individuals from each plot and target species were sampled 30 July 2011, 15 March 2012, 18 July 2012, 3 November 2012, 9 January 2013, 24 February 2013, 25 March 2013, 1 May 2013, and 22 July 2013.

Buds were counted and classified using a dissecting microscope (magnification varied from 10× to 40× depending on the species) and determined to be living or dead. The numbers of active buds, dormant buds, and dead buds were confirmed using tetrazolium and Evans Blue staining procedures (Hendrickson and Briske, 1997). Tillers were submerged in tetrazolium solution at room temperature for 24 hr after initial classification. Active buds stained pink and dormant, and dead buds retained their white or yellowish color. If inactive buds were present, the tiller was submerged into Evan's Blue solution at room temperature following the tetrazolium staining for 20 min. On completion of Evan's Blue staining, dormant buds would maintain their white pigment, whereas dead buds stained dark blue.

Statistical Analysis

Vegetative tillers, reproductive tillers, and plant density (number of individuals within a 0.25-m⁻² quadrat) by species were analyzed using analysis of variance (MIXED procedure of SAS, Littell et al., 2006) to quantify aboveground plant response throughout three growing seasons after summer, fall, and spring fire at 2, 3, and 6-yr fire return intervals. The model included season of fire, fire return interval, yr, and all interactions as fixed effects with sampling date as a repeated measure, and the experimental unit was plot.

Immediate bud response was assessed after all fire treatments. Data were analyzed using analysis of variance (MIXED procedure of SAS, Littell et al., 2006). The model included season of fire, fire return interval, and their interaction as fixed effects. However, comparisons were only made within the same season of burning to avoid confounding of

seasonal and fire seasonality effects. Active, dormant, and dead buds by species were used as response variables with plot as the experimental unit. Reported standard error values were generated from the mixed model.

Bud responses after fire treatments were examined during 4 yr (October 2010–July 2013). Data were analyzed using analysis of variance (MIXED procedure of SAS, Littell et al., 2006) with sampling date as a repeated measure. The model included sampling date, season of fire, fire return interval, and their interactions. Response variables were active, dormant, and dead buds by species. For all short-term bud bank analyses, values from nonburned controls were subtracted from fire treatments and the difference was used in the models. Reported standard error values were generated from the mixed models, and statistical significance was set at $P < 0.05$ for all models.

Results

Growing conditions during the spring of 2011 (April–June) were extremely wet, with a record amount of precipitation (250% of average; Fig. 1). The following winter, spring, and summer were dry with drought conditions occurring most of the spring and summer (34% below average). Spring 2012 was the second driest on record, and drought conditions persisted throughout eastern Montana and the northern Great Plains (Western Regional Climate Center, Reno, Nevada, 2013). Spring of 2013 (two growing seasons post fire) brought near-average spring and summer precipitation enabling growth of cool- and warm-season grasses after severe drought of 2011–2012. Spring precipitation (April–June) is considered to be a major driver of aboveground productivity in the northern Great Plains (Heitschmidt and Vermeire, 2005; Wiles et al., 2011). Because time since fire varied throughout the study depending on fire return interval treatments, accumulations of fuel based on above-average precipitation years (e.g., 2011) may have resulted in varying recruitment strategies from the bud bank among fire treatments and years.

Aboveground Response

Plant densities on nonburned plots were similar among years for *B. gracilis* ($P = 0.21$) and *H. comata* ($P = 0.26$), but *P. smithii* density decreased by 70% during the 2012 drought and rebounded to 138% the following year ($200, 60, 275 \pm 3$ plants·m⁻²; $P < 0.01$). In general, burning nearly doubled *B. grama* plant density estimates by the end of the study regardless of fire interval or season compared with nonburned controls (6, 4, 12 vs. 5 ± 1 plants·m⁻²; $P < 0.05$). In contrast, burning decreased *H. comata* density steadily each study yr ($5, 2, 1 \pm 0.5$ plants·m⁻²; $P < 0.01$). Two-yr fire intervals had the greatest impact on *H. comata* plant density (2 ± 1 plants·m⁻²; $P < 0.01$) compared with 3- and 6-yr fire

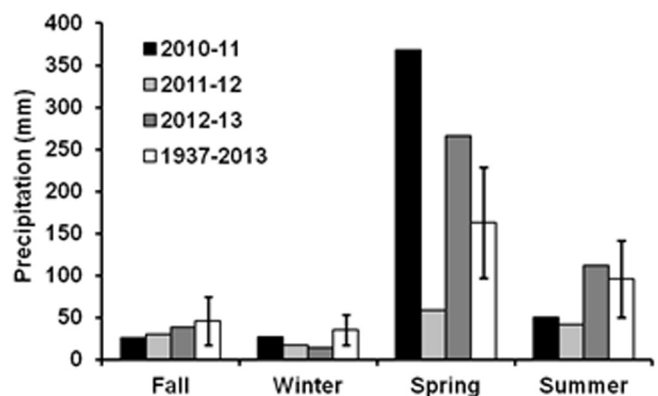


Figure 1. Study site 76-yr mean seasonal precipitation, fall (Oct–Dec), winter (Jan–Mar), spring (Apr–Jun), and summer (Jul–Sep) precipitation yr (Oct–Sep) near Miles City, Montana.

return intervals (5 and 7 ± 1 plants·m⁻², respectively). Interestingly, reduction relative to the control of *P. smithii* plant density during the driest yr (2012) was much less on both 2- and 3-yr fire return intervals relative to controls (55 and 40 vs. 10 ± 6 plants·m⁻², respectively).

B. gracilis vegetative and reproductive tillers·plant⁻¹ were similar throughout 2011 and 2012; however, in 2013, spring burns every 3 yr tripled the number of reproductive tillers·plant⁻¹ compared to the other fire treatments (14 ± 1 tillers·plant⁻¹; $P < 0.01$). *P. smithii* vegetative tillers·plant⁻¹ in plots burned every 2 or 3-yr during the summer or fall increased by 63% or more ($14, 10, 8,$ and 8 ± 1 tillers·plant⁻¹; $P < 0.05$) during the 2012 drought. *P. smithii* vegetative tiller numbers was lowest in 2011 in burned plots with a 3-yr fire return interval for all seasons of fire relative to controls and averaged 1 reproductive tillers·plant⁻¹ more than nonburned plots during 2011 and 2012 but increased to 5 reproductive tillers·plant⁻¹ during the growing season of 2013 ($P < 0.01$). *H. comata* vegetative tillers·plant⁻¹ were greatly reduced by fire, especially 2-yr summer and 3-yr spring fire treatments (-10 and $-8, \pm 4$ tillers·plant⁻¹; $P < 0.05$). Summer fire every 3 yr was the only fire treatment that promoted a positive vegetative tillering response in *H. comata* plants compared with nonburned controls (2 ± 4 tillers·plant⁻¹; $P < 0.05$). During 2011, fall fire increased reproductive *H. comata* tillers·plant⁻¹ by 73% or more compared with other seasons of fire and nonburned plots.

Immediate Bud Response After Fire

Active *B. gracilis* buds immediately increased 54% after spring burns at 3-yr fire return intervals ($P < 0.01$; Fig. 2). In contrast, fall fire at 3- and 6-yr fire return intervals immediately reduced active buds by 95%. Summer fire at 6-yr return intervals reduced active buds by 97%. However, 2-yr summer, fall, and spring fire; 3-yr summer fire; and 6-yr spring fire maintained similar amounts of active buds before and after fire. Immediate *B. gracilis* bud mortality was similar following summer, fall, and spring fires ($0.07, 0.04, 0.1 \pm 0.07$ buds·tiller⁻¹; $P > 0.07$) and 2-, 3-, and 6-yr fire return intervals ($0.07, 0.21,$ and 0.26 ± 0.08 buds·tiller⁻¹; $P > 0.21$). Dormant *B. gracilis* buds decreased $> 50\%$ immediately after spring 3-yr burns (7 vs. 3 ± 0.5 buds·tiller⁻¹; $P < 0.01$) and increased 43% within hours after summer fire at 6-yr return intervals (4 vs. 7 ± 0.5 buds·tiller⁻¹; $P < 0.01$). Fall fire with a 3-yr return interval increased dormant buds the most by transitioning all of its buds into early winter dormancy. All other fire treatments were similar in immediate effects following fire treatments ($P > 0.05$).

Active and dormant buds of *H. comata* were similar to preburn assessments immediately after all fire treatment combinations ($P \geq 0.13$). However, *H. comata* bud mortality increased $> 80\%$ immediately

after summer and fall fire (0.6 and 0.5 vs. 0.1 ± 0.02 buds·tiller⁻¹; $P < 0.05$), with minimal mortality occurring after spring fire ($P > 0.85$).

Active buds of *P. smithii* more than doubled after summer fire every 3 yr ($P < 0.05$; Fig. 3) compared with nonburned controls. Fall fire at 3-yr intervals reduced active buds by 52%, and spring fire at 3-yr intervals reduced active buds by 47%. *P. smithii* active buds were similar to preburn assessments for all other treatment combinations ($P > 0.05$). Dormant buds of *P. smithii* were not immediately altered by season of fire, fire return interval, or their interaction ($P \geq 0.08$). Immediate bud mortality did not occur for *P. smithii* buds ($P > 0.19$).

Short-Term Bud Response (2011–2013)

Nonburned dormant bud banks of *B. gracilis* peaked during the winter, whereas active buds peaked during the growing seasons. There was a season of fire by sampling date interaction on active buds of *B. gracilis* ($P < 0.01$; Fig. 4A) due to interannual differences in precipitation. Activity of *B. gracilis* buds increased after summer burns during January 2013, whereas bud activity reached its lowest point on fall-burned plots relative to controls at the time of fire during October 2012. Dormant *B. gracilis* was driven largely by the strong overwintering bud response after summer fires at 3-yr return intervals (6.5 ± 1.1 buds·tiller⁻¹; $P < 0.05$) compared with other seasons of fire and return intervals. While a 2-yr fire return interval did not significantly deplete *B. gracilis* bud banks regardless of season, they generated fewer dormant buds as did 3-yr or 6-yr fire return intervals ($P > 0.05$). Summer-burned plots had fewer dead *B. gracilis* buds than nonburned controls during March 2012 (-0.5 ± 0.02 buds·tiller⁻¹; $P < 0.01$). Fall fire decreased dead *B. gracilis* buds during winter 2012 relative to controls (0 vs. 2.0 ± 0.1 buds·tiller⁻¹; $P < 0.05$).

Fall and spring burns affected *H. comata* bud activity similarly throughout the study years ($P \geq 0.18$). However, summer burns increased *H. comata* bud activity relative to controls from July 2012 to January 2013 more so than fall or spring fire treatments ($P < 0.01$; Fig. 4B). Active *H. comata* buds decreased sharply for all seasons of fire during the initiation of the 2013 growing season ($P > 0.12$) relative to controls. Dormant buds of *H. comata* responded differently to fire treatments, especially during the 2012 drought and throughout winter periods. During the peak of drought, summer- and fall-burned plots at 3- and 6-yr intervals decreased *H. comata* dormant buds compared with spring burns at all intervals and nonburned plots (-2.0 vs. -0.5 ± 0.6 buds·tiller⁻¹; $P < 0.01$). Dormant *H. comata* buds consistently increased following 2-yr and 6-yr fire return intervals throughout the study ($P < 0.01$). Fewer dead *H. comata* buds were observed during winter 2012 on fall and spring burns than controls (-0.5 and -0.5 ± 0.01 buds·tiller⁻¹; $P < 0.01$). In January 2013, reductions in dead *H. comata* were even greater

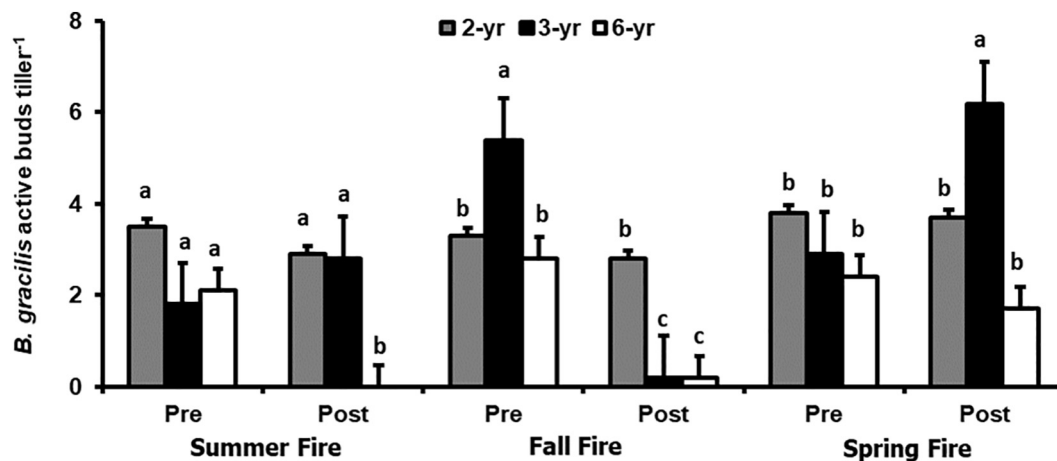


Figure 2. Active buds·tiller⁻¹ of *Bouteloua gracilis* immediately before and after seasonal fires with 2-yr, 3-yr, and 6-yr fire return intervals near Miles City, Montana (+ Standard Error of the Mean (SEM)). Means are the difference between fire treatments. Means marked with the same letter within season of fire treatment are similar ($P < 0.01$).

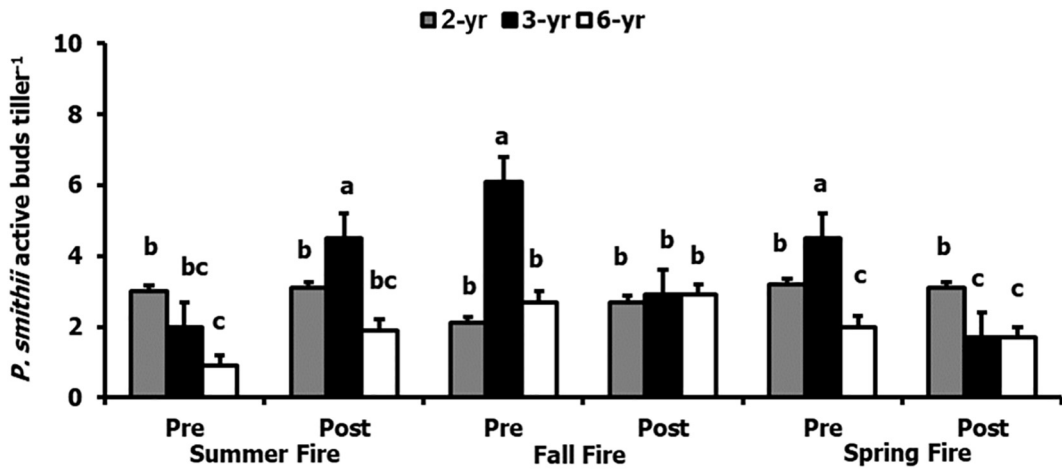


Figure 3. Active buds-tiller⁻¹ of *Pascopyrum smithii* immediately after summer, spring, and fall fires paired with 2-yr, 3-yr, and 6-yr fire return intervals near Miles City, Montana (+ SEM). Each season of fire was analyzed separately, and means are the differences between fire treatments. Means marked with the same letter within season of fire treatment are similar ($P < 0.05$).

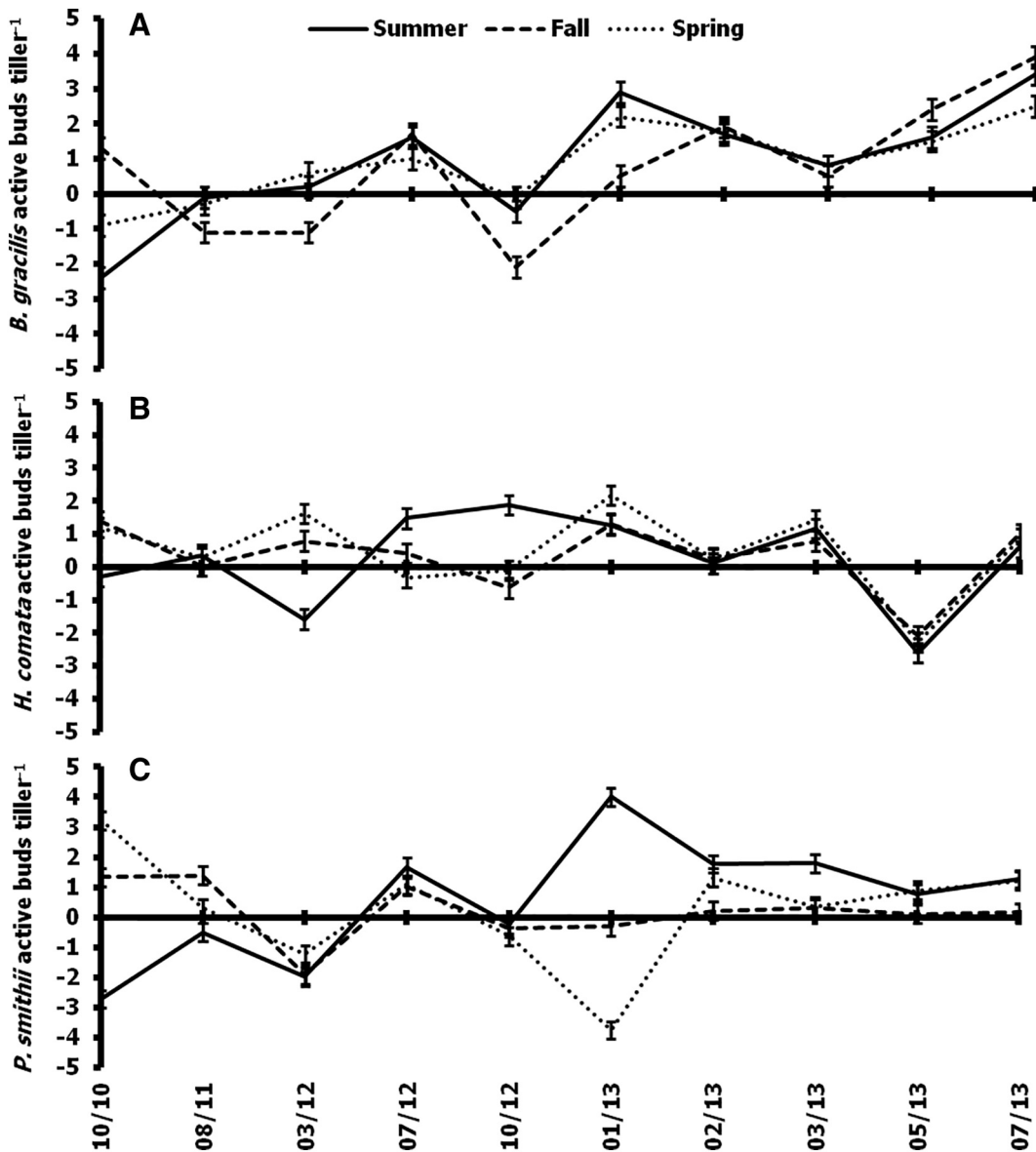


Figure 4. Short-term seasonal fluctuations of *Bouteloua gracilis*, *Hesperostipa comata*, and *Pascopyrum smithii* active buds following season of fire treatments relative to nonburned controls near Miles City, Montana (\pm SEM; $P < 0.01$). Means are the differences between fire treatments and controls with no fire.

for fall and spring burns compared with summer burned and nonburned plots (-1.5 and -1.2 vs. 0.3 ± 0.01 buds·tiller $^{-1}$; $P < 0.01$).

Season of fire and time of tiller harvest had interacting effects on bud activity for *P. smithii* ($P < 0.01$; Fig. 4C). Summer fire increased the 2013 overwintering *P. smithii* bud bank with maintained activity throughout the start of the 2013 growing season compared with fall and spring fire ($P < 0.01$) and control plots. Dormant *P. smithii* buds fluctuated tremendously throughout 2012 and 2013 (data not shown). Dormant *P. smithii* buds decreased by $\geq 70\%$ in July 2012 and January 2013 on summer-burned plots compared with fall- and spring-burned plots (-2.0 vs. 0.5 , 1.5 ± 0.1 buds·tiller $^{-1}$ for summer, fall, and spring, respectively; $P < 0.01$). However, summer-burned dormant buds increased 63% or more during October 2012 compared with fall and spring burns and increased again by 35% in February 2013 relative to controls. Short-term response of *P. smithii* dormant buds also varied

by fire return interval ($P < 0.01$). Dormant *P. smithii* buds differed among 2-yr (0.23 ± 0.10 buds·tiller $^{-1}$), 3-yr (-0.20 ± 0.10 buds·tiller $^{-1}$), and 6-yr (0.34 ± 0.10 buds·tiller $^{-1}$) fire return intervals relative to controls. Dead *B. gracilis* buds increased on 6-yr fire return interval plots (0.13 ± 0.07 buds·tiller $^{-1}$) relative to controls but were similar on 2-yr (0.0 ± 0.07 buds·tiller $^{-1}$) and 3-yr (0.0 ± 0.07 buds·tiller $^{-1}$) fire return interval plots relative to controls. Dead buds of *P. smithii* only varied by sampling date ($P < 0.01$). Dead *P. smithii* buds peaked during July 2012 and 2013 (0.59 and 0.45 ± 0.11 buds·tiller $^{-1}$, respectively) relative to controls.

Fire return interval and sampling date interacted in their effects on active buds·tiller $^{-1}$ for *B. gracilis* ($P < 0.01$; Fig. 5A), *H. comata* ($P < 0.01$; Fig. 5B), and *P. smithii* ($P < 0.01$; Fig. 5C). Active buds·tiller $^{-1}$ were similar for *B. gracilis* and *H. comata* following all fire return intervals until October 2012. During winter 2012, there were more active

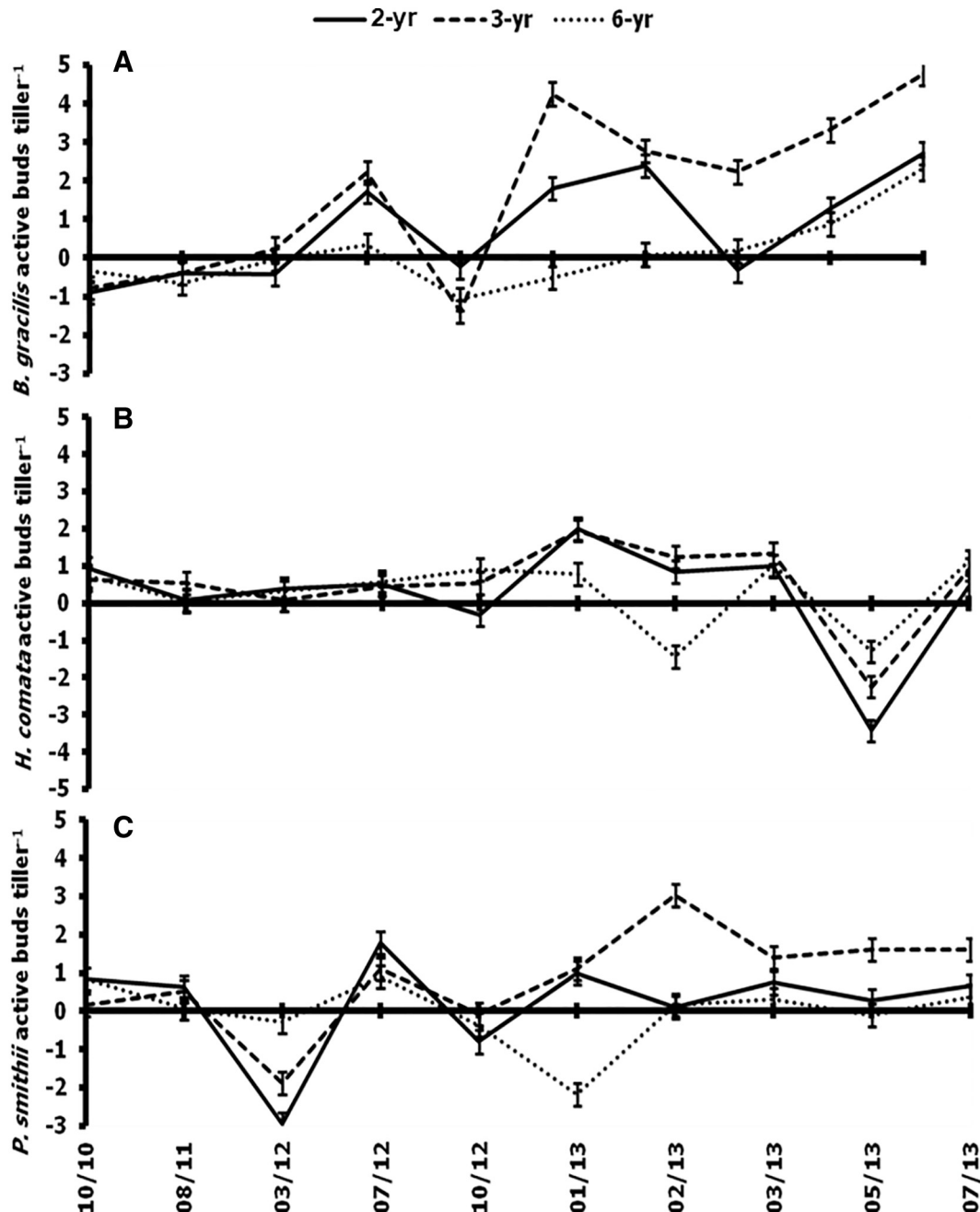


Figure 5. Short-term seasonal fluctuations of *Bouteloua gracilis*, *Hesperostipa comata*, and *Paspopyrum smithii* active buds·tiller $^{-1}$ after 2-, 3-, and 6-yr fire return intervals near Miles City, Montana (\pm SEM; $P < 0.01$). Means are the differences between fire treatments and controls with no fire.

buds·tiller⁻¹ for plots burned on a 2-yr and 3-yr return intervals than controls for *B. gracilis* and *H. comata* until March 2013. At the beginning of the 2013 growing season (May 2013), active buds·tiller⁻¹ for *B. gracilis* increased with 3-yr fire return intervals but for *H. comata* decreased active buds relative to controls for all fire return intervals. Three-yr fire return intervals maintained at least 50% more active *B. gracilis* buds·tiller⁻¹ than 2-yr and 6-yr fire return intervals relative to controls after March 2013. Active *P. smithii* buds·tiller⁻¹ increased for 3-yr return intervals during winter 2013 and remained more abundant through the end of the study. Plots burned at 6-yr return intervals decreased bud activity during winter and maintained limited bud activity compared with 3-yr return intervals, but activity was similar to those following 2-yr burns relative to controls.

Discussion

Season of fire and fire return interval effects varied by species and sampling date. Short-term effects of fire treatments were maintained for at least two growing seasons after fire treatments. Belowground bud bank response illustrated the potential for *B. gracilis* and *P. smithii* bud banks to mediate aboveground fire effects by having well-protected vegetative buds and by altering the pattern and timing of tiller recruitment during growing and dormant seasons. These belowground responses illustrate mechanisms that native perennial grasses use to maintain belowground meristems and aboveground processes. The following discussion is structured similarly to the integration of the findings in the results (Aboveground Response, Immediate Bud Response Following Fire, and Short-Term Bud Response (2011–2013)). Discussing both aboveground and belowground relationships relative to bud banks is important in understanding the unique processes and patterns of active and dormant buds at a population-level focus to enlighten community-level dynamics. On the basis of both aboveground and belowground assessments in this study, we have learned that each species' bud bank is unique and dynamic, undergoing continuous inputs and outputs closely tied to aboveground management, particularly the season and return interval of fire.

Aboveground Response

Interannual variation in spring precipitation and time since fire were primary drivers in aboveground responses for this study. Aboveground plant density and reproductive tillers of *B. gracilis* exhibited signs of recovery in 2013 after drought effects of 2012. Similar results have been observed regarding *Bouteloua curtipendula* (Michx.) Torr., a C₄ bunchgrass, after summer fire with consecutive droughts (Castellano and Ansley, 2007). Species with large bud banks mediate drought effects (Carter et al., 2012). In our study, *B. gracilis* maintained a large belowground bud bank despite the drought, and this later contributed to aboveground growth in 2013 when more favorable growing conditions occurred.

Summer 2-yr fire reduced *H. comata* plant density and vegetative tillers relative to controls, which was somewhat expected because *H. comata* is considered a fire-sensitive species. *H. comata* buds may be sensitive to heat damage due to the species bunchgrass growth form. Plant litter can accumulate in bunchgrass crowns, prolonging heat exposure (Wright, 1971; Engle et al., 1998). *H. comata* is also more likely than *B. gracilis* and *P. smithii* to become meristem limited because it only contains 2–3 buds·tiller⁻¹ (Russell et al., 2015). Summer fires may have exacerbated all these conditions because summer fire results in more complete fuel combustion (Ansley et al., 2006). In this study, summer fires burned with more intensity than fall- or spring-burned plots, based on thermocouple results of increased maximum temperature, heat duration, and heat dosage compared with fall and spring burned plots (see Table 1).

P. smithii increased plant density and vegetative tillers during the drought with 2- and 3-yr fire return intervals relative to controls. Our

results on *P. smithii* buds showed high plasticity in the timing of tiller recruitment and overwintering bud bank, with active buds transitioning to tiller in either the spring or fall, which may also be attributed to *P. smithii*'s unique response to fire (Engle and Bultsma, 1984; Vermeire et al., 2011). In addition, flexible tiller recruitment timing of *P. smithii* has been shown to facilitate both conservative and foraging growth strategies due to environmental variability and changing resource availability (Ott and Hartnett, 2015b). Increased production of *P. smithii* during the first growing season after fire has been observed in other studies (White and Currie, 1983; Whisenant and Uresk, 1990; Vermeire et al., 2011). Even without fire, plant density of *P. smithii* decreased during 2012, yet tillers per plant increased during 2012, further highlighting a potential tradeoff between tillers recruited close to the parent plant or far away from the parent plant along the rhizome. Buds borne at the base of tillers typically contribute to local persistence by producing phalanx tillers, while buds on rhizomes are prepared to respond to injury and enable tiller dispersal away from the parent plant (guerilla tillers) (Ott and Hartnett, 2015b).

Immediate Bud Response After Fire

Season of fire and fire return interval treatments immediately affected bud activity of *B. gracilis* and *P. smithii*. Similar season of fire results have shown immediate increased numbers and activity of *B. gracilis* and *P. smithii* (Russell et al., 2015). Immediate fire effects on bud activity align with the bud transitions between dormant and active (Devitt and Stafstrom, 1995; Cline, 1997; Beveridge, 2006) where buds enter different developmental stages that have varying degrees of sensitivity or responses to hormone signals (Stafstrom and Sussex, 1992; Shimizu and Mori, 2001; Morris et al., 2005). Bud activity is regulated by hormones that allow previously dormant buds to transition into active buds following environmental cues or development program signals (Shimizu and Mori, 2001; Reece et al., 2007). Buds represent a large investment and are carefully modulated in response to environmental factors, such as light quality, soil moisture, nitrogen and carbon availability, and growth and development of other plant parts (Vesk and Westoby, 2004; Dun et al., 2006). If environmental conditions are not favorable, buds enter into temporary dormancy until growing conditions have improved or vice versa (Shimizu and Mori, 2001).

This reversible developmental transition from dormancy to growth occurs rapidly (Stafstrom and Sussex, 1992; Devitt and Stafstrom, 1995; Shimizu and Mori, 1998). Dormant axillary buds on Alaska pea (*Pisum sativum* L.) seedlings showed visible growth within 8 h after defoliation (Devitt and Stafstrom, 1995). Three days later, active buds became dormant again, illustrating that pea axillary buds can be stimulated to undergo more than one complete growth-dormancy cycle during the course of a few days (Devitt and Stafstrom, 1995). Other studies on *Zea* L. and *Brassica* L. have found ribosomal protein genes increase or decrease during multiple growth-dormancy cycles in order to control bud development (Larkin et al., 1989; Bonham-Smith et al., 1992; Stafstrom and Sussex, 1992).

In agreement with the hypotheses, bud mortality of *B. gracilis* and *P. smithii* did not differ between prefire and immediate postfire assessments. However, *H. comata* bud mortality increased immediately after summer and fall fire. Summer and fall fire thermocouple measurements were consistently greater than those of spring fire. Increased bud mortality, decreased plant density, and decreased vegetative tillers of *H. comata* after summer fire further support the premise that *H. comata* is a summer fire-sensitive species and is meristem limited (Distel and Bóo, 1996). Even though our study showed immediate *H. comata* bud mortality, Russell et al. (2015) did not show the same effects after spring, summer, or fall fire, but by the end of the study, *H. comata* contained 73% fewer buds on burned plots compared with control plots citing meristem limitations. Due to these meristematic limitations, *H. comata* may follow cyclic periods of abundance both

aboveground and belowground through decreased tillering and recruitment from the bud bank based on recent aboveground management.

Short-Term Bud Response (2011–2013)

Short-term dynamics of bud banks varied tremendously according to their fire history. Previous research has emphasized increased bud density of *C*₄ species during the winter (Ott and Hartnett, 2012). In addition, this study's results indicate summer and spring fire can also increase overwintering active buds relative to controls. Warm-season grasses maintain a larger overwintering bud bank, with long-living buds (> 1 yr) resulting in mixed-aged bud banks capable of tillering (Ott and Hartnett, 2012; Ott and Hartnett, 2015a). Summer and fall fire likely accelerated *C*₄ bud overwintering, allowing maximum bud development and storage to prepare for the upcoming growing season (Russell et al., 2017). Although *P. smithii* is a *C*₃ grass, belowground bud development and transitions between growth and dormancy closely resemble those of *C*₄ species following fire events (Russell et al., 2017). Summer fire increased active *P. smithii* buds throughout the 2013 winter and into the 2013 growing season.

In previous studies, the degree of metabolic activity and outgrowth of axillary buds has been similar on perennial grass plants coming from sites with different grazing intensities and history (Hendrickson and Briske, 1997; Flemmer et al., 2002; Russell et al., 2013). Following all seasons of fire and fire return intervals, *H. comata* consistently decreased active buds during May 2013 relative to controls. All *H. comata* active buds synchronized bud transitions for tiller emergence in the upcoming 2013 growing season. Buds that overwintered provided more mature buds to start transitioning early in the growing season and to complete reproduction and new bud production before experiencing competition from other species. Similar responses were observed with other *C*₃ species in tallgrass prairie (Ott and Hartnett, 2012). Two-yr and 3-yr interval burns increased overwintering active *H. comata* buds, illustrating the potential to manipulate overwintering strategies.

Three-yr fire return intervals increased active buds throughout the 2013 winter and growing season for *B. gracilis* and *P. smithii* compared with 2- and 6-yr fire return intervals and controls. The response of active buds to 3-yr fire return intervals illustrates the adaptive nature of these native species to recurring fire in mixed-grass prairie. Because fire is recognized as a contributing factor in shaping plant communities, the Intermediate Disturbance Hypothesis (IDH) may be a valid model for understanding frequent fire effects on plant community composition and bud bank dynamics.

The IDH outlined by Connell (1961), Paine (1966), and Grime (1973) posits that species richness will be greatest at intermediate temporal spans after disturbance (Connell, 1978). According to IDH, the optimal amount of disturbance (neither too rare, nor too frequent) within an ecosystem enables different ecological niches to be filled due to life-history characteristics (i.e., reproductive effort, bud development, tiller emergence) and differing responses to disturbance. On the basis of contrasting life history traits of *C*₃ and *C*₄ species devoted toward bud outgrowth, intermediate fire return intervals allow both *C*₃ and *C*₄ species to maximize bud activity to maintain mixed-grass prairie dynamics and populations. This finding corresponds to previous research in tallgrass prairie and illustrates the potential of intermediate fire return intervals to maximize species richness and grass productivity (Collins and Barber, 1985; Collins, 1987, 1992).

Summer fire decreased dormant *P. smithii* buds during the 2012 drought and also during January 2013 relative to controls. On the basis of previous drought literature, dormant buds of *P. smithii* should have increased (Busso et al., 1989; Flemmer et al., 2002; Carter et al., 2012). However, dormant buds decreased in conjunction with increased vegetative tillering during the 2012 drought. Unlike the other *C*₃ species (*H. comata*), *P. smithii* is not meristem limited and buds appear to thrive following fire and during drought conditions. This contrasts with previous

studies that have reported decreased bud densities and increased bud dormancy during drought years (Gardner, 1942; McIntyre, 1976; Carter et al., 2012). However, those drought studies were not preceded by fire. Summer fire treatments may have provided a buffer against consecutive-yr drought conditions by increasing nutrient availability and signaling buds to transition out of dormancy. Results of decreased dormant buds during drought and after summer fire further emphasize the adaptive, resilient nature of *P. smithii* (Engle and Bultsma, 1984; Heitschmidt et al., 1999; Vermeire et al., 2011).

Implications

Earlier research suggested bud banks of *C*₃ species differ from *C*₄ species, and results were interpreted to mean overwintering strategies were the primary driver of these differences. However, these results indicate that bud banks of *P. smithii*, a *C*₃ species, more closely align with *C*₄ bud bank strategies after fire and drought. In addition, *B. gracilis* and *P. smithii* bud banks are resistant to fire. Prescribed fire during the spring at 3-yr return intervals immediately increased *B. gracilis* bud activity and decreased bud dormancy. Summer prescribed fire at 3-yr return intervals increased *P. smithii* bud activity within hours of burning. The immediate responses of these two dominant perennial grasses illustrate the importance of incorporating bud responses in planning prescribed fire and assessing the aftermath of prescribed fire and wildfire in mixed-grass prairies. This aspect may be extremely beneficial for rangeland managers looking to shift community composition toward a certain species or in managing postfire landscapes. Identifying the role drought has on bud banks should be evaluated with more research. Furthermore, unreported biotic interactions are unknown factors that should be considered in future research.

Because mixed-grass prairies in the northern Great Plains evolved with frequent fire (5–10 yr) (Wright and Bailey, 1982), fire most likely has served as an environmental cue for tiller recruitment from the bud bank. Three-yr fire return intervals appear to be beneficial for bud banks of two dominant native perennial species. These results suggest recurring fire acts as a stimulant for axillary buds to activate tiller initiation. A single fire alone may not be an adequate environmental cue, and frequent fire with return intervals of 3 yr may provide more positive feedback from the bud bank to initiate growth of perennial grasses. Furthermore, immediate and short-term seasonal fluctuations provide a temporal scale with which to recommend burning and at what rate responses may occur.

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