

# Season of fire manipulates bud bank dynamics in northern mixed-grass prairie

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**Abstract** In perennial grassland dominated systems, belowground bud banks regulate plant community dynamics. Plant community responses to disturbance are largely driven by the ability to generate future aboveground growth originating from belowground axillary buds. This study examined bud bank dynamics for *Bouteloua gracilis*, *Hesperostipa comata*, and *Pascopyrum smithii* following fire in northwestern mixed-grass prairie in eastern Montana, USA. Belowground axillary buds were counted and classified for three growing seasons to determine immediate and short-term effects of summer, fall, and spring prescribed burns on patterns of bud bank activity, dormancy, and mortality. Prescribed burns did not

result in immediate mortality of *B. gracilis*, *H. comata*, or *P. smithii* buds. Surprisingly, spring prescribed burns immediately increased the number of active *B. gracilis* buds. Summer fire, however, reduced *B. gracilis* active bud numbers. Fall burns immediately activated *P. smithii* buds, whereas fire did not influence any immediate bud dynamics for *H. comata*. Reduced bud numbers of *H. comata* may limit the ability to respond to fire. Season of fire directly manipulated bud activity, dormancy, and mortality for these species throughout the growing and dormant seasons following fire. Using season of fire to manipulate bud bank dynamics illustrates potential to improve post-fire management strategies based on known bud development trajectories and bud dynamics following fire.

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## Introduction

The below ground population of axillary buds is a crucial driver of aboveground growth and persistence of grassland plant communities. More than 99 % of new tiller growth originates from belowground vegetative bud banks and less than 1 % from seed in some grasslands (Benson and Hartnett 2006). Although allocation of reproductive effort varies among ecosystems (Hartnett et al. 2006), dependence

on bud banks may be expected for perennial grasslands world-wide, unless plants are very short-lived. Since bud banks are the source for future tiller growth, the size of a species' bud bank plays a decisive role in species and plant community response following disturbances, such as fire, grazing, and drought (Benson et al. 2004; Dalglish and Hartnett 2009; Carter et al. 2012).

Almost all plant species produce and maintain vegetative buds belowground, aboveground, or both (Klimešová and Klimeš 2007). But, the size of the bud bank can vary both within and among species, and plant communities (Lehtila 2000). Tiller recruitment can be meristem limited, when there are not enough buds to completely replace the aboveground tiller population, constraining primary production (Dalglish and Hartnett 2006). Although vegetative production is the primary source of new growth, bud densities can become limited or depleted if aboveground disturbances become too frequent, or occur during susceptible growth periods (Benson et al. 2004; Dalglish and Hartnett 2009). These bud limitations may have consequences for aboveground growth if the timing of disturbance, such as fire and grazing, interferes with critical phenological growth patterns of buds further inhibiting the production or maintenance of belowground buds (Carter et al. 2012; Ott and Hartnett 2012). Potential bud limitations or stored reserves regulate aboveground responses to fire and species-specific levels of adaptations to fire (Olson and Richards 1998; Rogers and Hartnett 2001; Dalglish and Hartnett 2006; Klimešová and Klimeš 2007). Given the role fire has played in shaping grasslands, perennial native grasses that evolved with frequent fire would be expected to be very efficient at maintaining bud reserves and subsequent tiller recruitment. Bud strategies of tiller recruitment and patterns of dormancy and viability of perennial native grasses involve different seasonal contributions of the bud bank. These seasonal fluxes include bud population growth rates, periods of bud sensitivity and dormancy, and potential responses to pulses of high resource availability or prolonged periods of stress (Towne and Owensby 1984).

Manipulating bud bank densities of native perennial grasses with fire may further reveal differences between bud bank dynamics of a C<sub>3</sub> and C<sub>4</sub> grass. In tallgrass prairie, C<sub>4</sub> species *Andropogon gerardii* maintained a larger dormant bud bank with longer-

living buds compared to *Dichanthelium oligosanthes*, a C<sub>3</sub> species, that relied heavily on annual replacement with new buds and very little on dormant, reserve buds (Ott and Hartnett 2012). The bud phenologies of these two species differ dramatically from one another, with C<sub>4</sub> species allowing buds to over-winter and recruit new spring tillers from pre-existing buds, and C<sub>3</sub> species producing new active buds for the beginning of the growing season. These findings in tallgrass prairie illustrate differences in bud bank age structure, phenology, and dynamics (Ott and Hartnett 2012). Therefore, differences in bud strategy may afford some species an inherent buffering potential against timing of disturbance.

Seasonal timing of fire may reinforce bud transitions dictated by differing photosynthetic pathways. Bud transitions and tiller recruitment are inherently linked to a species' aboveground growth phenology based on photosynthetic pathways (Ott and Hartnett 2012). Therefore, aboveground production shifts due to seasonal prescribed burns may reflect possible timing differences in belowground recruitment from the bud bank (Steuter 1987; Ott and Hartnett 2012). Greater than 70 % of wildfires in the western United States occur during summer, whereas most prescribed fires are conducted during spring and fall (Higgins 1984; Westerling et al. 2003; Vermeire et al. 2011). Using different seasons of fire may accelerate bud bank transitions for increased tiller recruitment from certain species, illustrating the mechanism responsible for aboveground production shifts. Furthermore, using bud banks as a quantifiable response to different seasons of fire may reveal the belowground mechanisms underlying potential plant community shifts with variously timed disturbances.

This study examined bud production and bud bank dynamics of three native perennial grass species with contrasting photosynthetic pathways and growth forms in mixed-grass prairie. The objectives of this study were to (1) assess immediate bud mortality of the C<sub>4</sub> grass *Bouteloua gracilis*, the C<sub>3</sub> caespitose grass *Hesperostipa comata*, and the C<sub>3</sub> rhizomatous grass *Pascopyrum smithii* following summer, fall, or spring prescribed burns; (2) compare active and dormant bud abundance following summer, fall, or spring prescribed burns for each species; and (3) determine the short-term seasonal fluxes in bud dormancy, bud activity, and bud mortality following summer, fall, or spring prescribed burns.

## Materials and methods

### Site description

Research was conducted at the USDA-ARS Fort Keogh Livestock and Range Research Laboratory in eastern Montana near Miles City, USA (lat 46°24'N, long 105°56'W). This site is mixed-grass prairie located in the Palouse Dry Steppe Province of the Great Plains and has a semi-arid climate at 815 m elevation. Annual precipitation averages 339 mm, with a majority occurring from mid-April to mid-September. 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 days (Western Regional Climate Center 2013).

The research area was previously burned during the late summer of 2007 and heavily grazed in 2008, leaving approximately 300 kg ha<sup>−1</sup> of remaining herbaceous stubble (Waterman and Vermeire 2011). After 2008, the study area was excluded from livestock grazing. Topography of the site is flat with minimal slopes (0–4 %) and characterized as upland plains. 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). The vegetation is dominated by perennial, native C<sub>3</sub> species including, *H. comata*, *P. smithii*, and *Carex filifolia* and C<sub>4</sub> species *B. gracilis*, and to a lesser extent, *Bouteloua dactyloides*. Annual grasses include *Vulpia octoflora*, *Bromus arvensis*, and *Bromus tectorum*. The primary shrub species on the site is *Artemisia tridentata* ssp. *wyomingensis*. Common forbs include perennial legume, *Pedimelum argophyllum*, and biennial forb, *Tragopogon dubius*. Plant nomenclature follows the USDA PLANTS database (USDA 2013).

### Experimental design and fire measurements

Fire treatments were arranged in a completely randomized design with four fire treatments (summer, fall, spring, and no fire) and four replications applied to 16, 20 × 20-m plots. Alleyways between plots were 3-m. Fuel load at the study site was approximately 1500 kg ha<sup>−1</sup> and all fires were set using the ring-fire method (Wright and Bailey 1982). Summer fires were applied following quiescence of *H. comata* and *P.*

*smithii* plants. We applied summer fire on 7 September 2011 with ambient temperatures 20–26 °C, winds 7–10 km h<sup>−1</sup>, and relative humidity 30–36 %. Fall fires were applied 3 November 2011, after the first killing frost, with ambient temperatures 8–11 °C, winds 8–12 km h<sup>−1</sup>, and relative humidity 37–41 %. Lastly, spring fires were applied 29 March 2012 during late emergence phenological stage of C<sub>3</sub> plant species with ambient temperatures 15–18 °C, winds 13–20 km h<sup>−1</sup>, and relative humidity 39–43 %.

We utilized HOBO<sup>®</sup> 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). We randomly placed thermocouples at the base of a perennial grass (1–2 cm above the soil surface) to quantify fire behavior at the plot level. Thermocouples were also placed within a 10 × 10-m square in the center of the plot (4 thermocouples plot<sup>−1</sup>) to avoid edge effects. We programed the data loggers to record temperatures at one-second intervals. Maximum temperature was identified by finding the greatest value for each time–temperature profile. Heat duration was calculated as time (s) of heat greater than 60 °C and heat dosage was the sum of the degrees >60 °C for the duration of elevated temperatures (degree-seconds). We used these measurements to derive the mean maximum temperature, heat duration, and heat dosage at the plot level.

### Field and laboratory methods

Plant density was measured at the end of the growing seasons for 2011, 2012, and 2013 by counting individual plants rooted within a 0.25-m<sup>2</sup> quadrat centered on randomly selected target plants, with three quadrats per species in each plot. *B. gracilis* was considered an individual when gaps of 3 cm (Hendrickson et al. 2000) or greater were separating neighboring *B. gracilis* individuals. *P. smithii* plant density measurements were based on number of tillers per 0.25-m<sup>2</sup> quadrat. Individuals of *H. comata* were readily distinguished due to their bunchgrass growth form.

Tiller counts and plant density measurements were conducted simultaneously. Tillers were counted for four permanently marked plants per species and plot and classified as vegetative or reproductive. Definitions

**Table 1** Thermocouple observations at the plot level for summer and fall prescribed fires near Miles City, MT

Thermocouple measurements <sup>a</sup>	Mean $\pm$ SE	Maximum	Minimum
Summer fire			
Maximum temperature (C)	172 $\pm$ 15	216	148
Heat duration (s)	110 $\pm$ 20	147	67
Heat dosage (C s)	6287 $\pm$ 663	8193	5366
Fall fire			
Maximum temperature (C)	213 $\pm$ 30	453	135
Heat duration (s)	135 $\pm$ 16	270	43
Heat dosage (C s)	6336 $\pm$ 1443	17,601	4589
Spring fire			
Maximum temperature (C)	253 $\pm$ 24	399	117
Heat duration (s)	135 $\pm$ 16	270	43
Heat dosage (C s)	7801 $\pm$ 961	13,707	1861

$n = 16$  for summer, fall, and spring fire

<sup>a</sup> Heat duration and dosage of heat 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 second (degree-seconds)

of an individual followed the same rules outlined for plant density measurements. Tiller counts for *P. smithii* were conducted within a 0.25-m<sup>2</sup> quadrat and results for *P. smithii* tiller counts were reported as tillers per 0.25-m<sup>2</sup> quadrat instead of per individual plant.

Tillers were harvested from two individuals of each grass species for immediate and seasonal bud assessments. Tillers were harvested from two randomly determined individuals 12–24 h before prescribed burn treatments. Within 12–24 h after prescribed burn treatments, tillers were harvested from two randomly chosen individuals (pre- and post-burn individuals were different) to determine immediate bud mortality or activation. More specifically, tillers used for immediate bud assessments were harvested on 7 and 8 September 2011 (summer burns), 3 and 4 November 2011 (fall burns), and 29 March 2012 (spring burns). In order to address seasonal fluctuations for each species' bud bank, two individuals for each species were sampled on each plot throughout 2 years (30 July 2011, 15 March 2012, 21 July 2012, 4 November 2012, 25 January 2013, 24 February 2012, 27 March 2013, 5 May 2013, and 21 July 2013).

Buds were counted using a dissecting microscope. Bud activity (i.e., active buds, dormant buds, and dead buds) was confirmed using Tetrazolium and Evans Blue staining procedures (Busso et al. 1989; Hendrickson and Briske 1997). Tillers were submerged in Tetrazolium solution at room temperature for 24 h

following initial classification. Active buds stained pink and dormant and dead buds retained a white or yellowish color. If non-stained buds were present on a tiller, that the tiller was submerged into Evan's Blue solution at room temperature following the tetrazolium staining for 20 min. Upon completion of Evan's Blue staining, dormant buds maintained white pigment, whereas, dead buds stained dark blue.

#### Statistical analysis

Data were analyzed by species using analysis of variance (MIXED procedure of SAS, Littell et al. 2006) in order to quantify bud bank response immediately before and after summer, fall, and spring prescribed burns compared to non-burned plots. The model included burn treatment (fire, no fire) and season of prescribed burning (summer, fall, spring) and their interactions as fixed effects with plots as a random effect. Active, dormant, and dead buds were used as response variables, and the experimental unit was plot.

Data were collected prior to fire treatments and throughout one and two post-fire growing seasons to determine bud dynamics and plant community response. These data were analyzed using analysis of variance (MIXED procedure of SAS, Littell et al. 2006) with tiller harvest date as a repeated measure. The model included tiller harvest date and season of

fire and their interactions as fixed effects for bud bank dynamics.

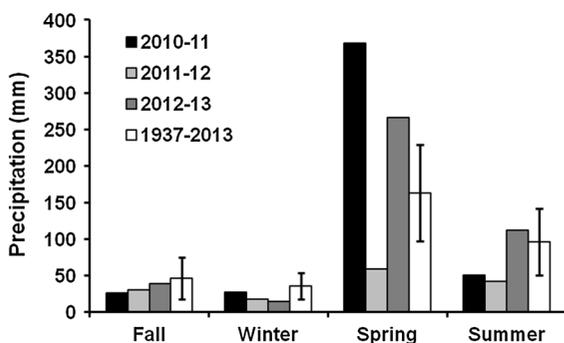
For aboveground dynamics, the model included year, fire, and their interactions as fixed effects. Response variables consisted of plant density, vegetative tillers, and flowering tillers. Pre-treatment data taken from 2011 were utilized as a covariate. If pre-treatment measurements were not significant ( $P > 0.05$ ), they were eliminated from the model. We set statistical significance at  $\alpha = 0.05$  for all models.

## Results

Growing conditions prior to the start of treatments in 2011 (April–June) were extremely wet, with record (226 % of average) spring precipitation (Fig. 1). The following winter, spring, and summer were 40 % below average precipitation (Fig. 1). Spring 2012 was the second driest on record and drought conditions persisted throughout eastern MT and the northern Great Plains (Western Regional Climate Center, Reno, NV Western Regional Climate Center 2013). Spring of 2013 (two growing seasons following fire) was 63 % greater than average, and summer precipitation was 17 % greater than average, enabling growth of cool- and warm-season grasses following severe drought of 2011–2012.

### *Bouteloua gracilis* dynamics

Plant density was similar across fire treatments ( $P = 0.15$ ; Table 2) and between 2012 and 2013 (33



**Fig. 1** Fall (Oct–Dec), winter (Jan–Mar), spring (Apr–Jun), and summer (Jul–Sep) precipitation for each study water year (Oct–Sep) and 76-year mean ( $\pm$ SD) seasonal precipitation near Miles City, MT

**Table 2** Plant density by species and fire treatment averaged across one and 2 years after fire near Miles City, MT

Fire treatment	<i>B. gracilis</i> Plants m <sup>-2</sup>	<i>H. comata</i>	<i>P. smithii</i>
Non-burned	22	20	45
Summer fire	25	14	58
Fall fire	35	15	54
Spring fire	45	14	42
SEM	8	3	8

vs  $31 \pm 5$  plants m<sup>-2</sup>;  $P = 0.77$ ). Vegetative tillers nearly doubled the second post-fire growing season ( $50$  vs  $25 \pm 4$  tiller plant<sup>-1</sup>;  $P < 0.01$ ), but were similar across fire treatments ( $P = 0.73$ ) compared to non-burned plots. Reproductive tillers varied by the interacting effects of year and season of fire ( $P < 0.01$ ). Reproductive tillers during 2012 were similar regardless of the season of fire treatment ( $< 1 \pm 1$  tiller plant<sup>-1</sup>); however, during 2013 reproductive tillers increased following summer, fall, and spring burns ( $17$ ,  $20$ ,  $16 \pm 1$  tiller plant<sup>-1</sup>, respectively) compared to non-burned plots ( $7 \pm 1$  tiller plant<sup>-1</sup>).

Bud mortality did not occur immediately following fire in any season ( $P = 0.41$ ; Table 3). Short-term changes in bud mortality due to season were minimal throughout the two post-fire growing seasons ( $P = 0.15$ ) and, overall, the number of dead buds was very low. Dead buds were most abundant during late winter ( $P < 0.01$ ). Dead buds typically peaked during the winter following all prescribed burn treatments. The number of dead buds following fire was statistically different throughout the next two years; however, dead buds tiller<sup>-1</sup> never exceeded 0.25 and often were less than 0.01 buds tiller<sup>-1</sup>. Surprisingly, bud mortality was similar between dry and wet years. Active bud development was nearly 3.5-fold greater immediately following spring burns compared to fall and summer fires, resulting in fewer dormant buds following spring fires ( $P < 0.01$ ). In contrast to spring burns, summer fire immediately decreased active buds 36 % ( $P < 0.01$ ). Consequently, dormant buds increased immediately following summer fire ( $P < 0.01$ ). Fall fire did not affect active or dormant buds ( $P > 0.05$ ).

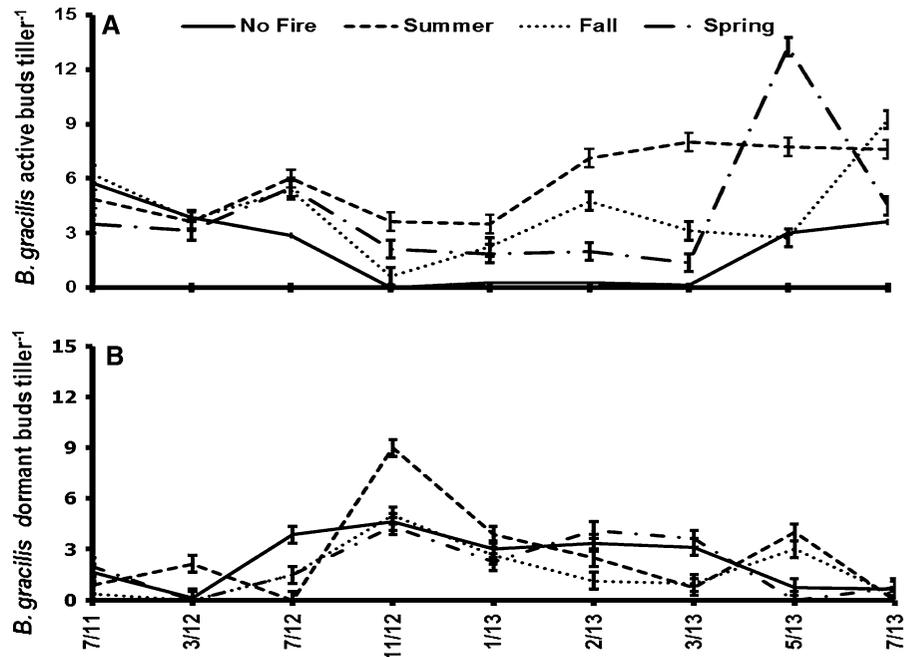
Season of fire affected active bud bank dynamics differently during the two growing seasons following fire ( $P < 0.01$ ; Fig. 2). Summer burns resulted in more

**Table 3** Immediate (<24 h) summer, fall, and spring fire effects on active, dormant, and dead axillary bud means belonging to *B. gracilis*, *H. comata*, and *P. smithii* tillers near Miles City, MT

Measurement	Summer		Fall		Spring		SEM	P value
	No fire	Fire	No fire	Fire	No fire	Fire		
<i>B. gracilis</i>								
Active	3.9a	2.5b	4.9	4.3	2.4b	8.3a	0.7	<0.01
Dormant	0.3b	1.1a	0.3	0.3	1.5a	0.3b	0.3	0.01
Dead	0.0	0.0	0.0	0.3	0.0	0.0	0.1	0.41
<i>H. comata</i>								
Active	1.4	1.0	1.1	1.4	4.3	3.9	0.3	0.43
Dormant	0.0	0.4	0.4	0.8	0.0	0.0	0.2	0.55
Dead	0.1	0.4	0.1	0.3	0.4	0.3	0.2	0.56
<i>P. smithii</i>								
Active	3.4	2.9	3.6b	5.8a	3.9	3.8	0.5	0.05
Dormant	0.0	0.3	0.3	0.3	0.0	0.1	0.1	0.57
Dead	0.0	0.4	0.3	0.1	0.3	0.3	0.2	0.43

Means within bud classification and season of fire are similar when followed by a common letter ( $P > 0.05$ )

**Fig. 2** Bud dynamics of *B. gracilis* from July 2011 to July 2013 following no fire, summer, fall, and spring prescribed fire near Miles City, MT on *B. gracilis* **a** active buds tiller<sup>-1</sup> ( $P < 0.01$ ) ( $\pm$ SEM) and **b** dormant buds tiller<sup>-1</sup> ( $P < 0.01$ ) ( $\pm$ SEM)

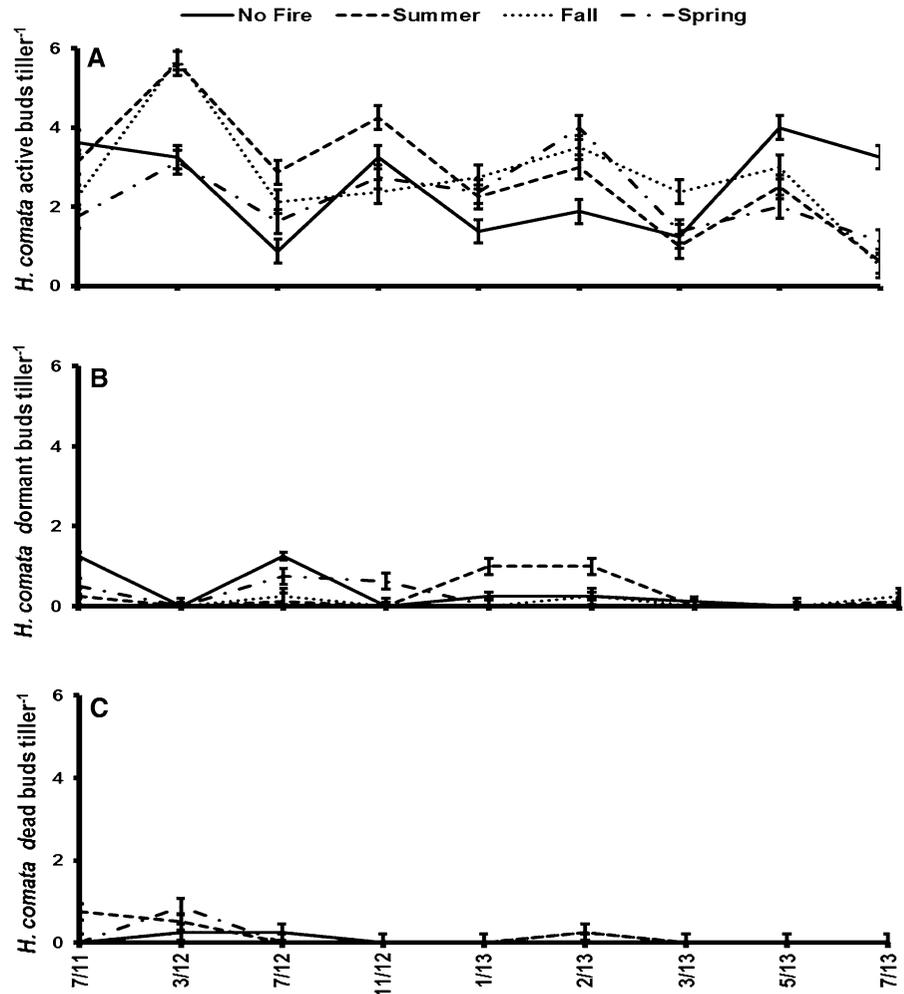


active buds than fall or spring-burned plots throughout winter ( $P < 0.01$ ). Fall burns tripled new active buds by the end of the second post-fire growing season compared to non-burned plots ( $P < 0.01$ ). Spring burns increased active buds at the beginning of the second post-fire growing season compared to non-burned plots and by then all buds were active ( $P < 0.01$ ). Summer, fall, and spring burning increased active buds compared to non-burned plots

during the drought of the first post-fire growing season (6.0, 5.4 and 5.5 vs  $2.3 \pm 0.6$  buds tiller<sup>-1</sup>;  $P < 0.01$ ).

Dormant buds decreased the first growing season following summer, fall, and spring burns compared to non-burned plots ( $P < 0.01$ ; Fig. 2). Summer burned plots increased dormant buds entering the first winter after fire, whereas fall and spring burns were similar to non-burned plots ( $P < 0.01$ ). At the initiation of the second post-fire growing season, dormant buds

**Fig. 3** Short-term bud dynamics of *H. comata* from July 2011 to July 2013 following no fire, summer, fall, and spring prescribed fire near Miles City, MT, on *H. comata* **a** active buds tiller<sup>-1</sup> ( $P < 0.01$ ) ( $\pm$ SEM), **b** dormant buds tiller<sup>-1</sup> ( $P < 0.05$ ) ( $\pm$ SEM) and **c** dead buds tiller<sup>-1</sup> ( $P < 0.05$ ) ( $\pm$ SEM)



increased with summer and fall burns ( $P < 0.01$ ). Dormant buds transitioned into active buds during May of the second growing season after spring fire and two months later after summer fire. The number of dead buds was similar among fire treatments ( $P = 0.15$ ). There was always  $<1$  dead bud tiller<sup>-1</sup>, but the number of dead buds was greatest during late winter ( $P = 0.01$ ).

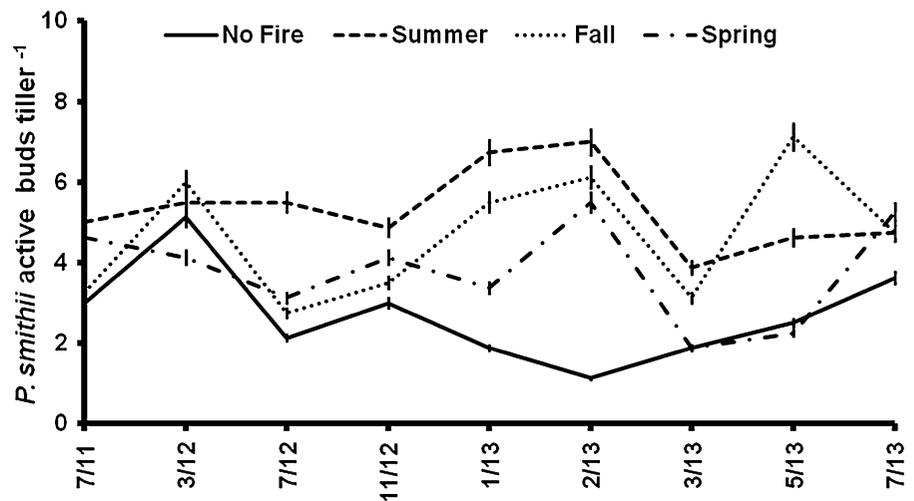
#### *Hesperostipa comata* dynamics

Plant density was similar among fire treatments ( $P = 0.50$ ; Table 2). In addition, density estimates did not differ between the subsequent two post-fire growing seasons (16 and  $15 \pm 2$  plants m<sup>-2</sup>;  $P = 0.83$ ). Both vegetative and reproductive tiller numbers were similar among fire treatments, but each

differed between post-fire study years ( $P < 0.01$ ). Vegetative tillers increased from 15 to  $33 \pm 3$  tillers plant<sup>-1</sup> and reproductive tillers increased from 0.2 to  $5 \pm 1$  tillers plant<sup>-1</sup> between 2012 and 2013 ( $P < 0.05$ ). Fire had little effect on vegetative or reproductive tillers, regardless of the season in which it occurred ( $P = 0.46$  and 0.60, respectively).

*Hesperostipa comata* bud activity was not immediately impacted by fire ( $P = 0.43$  and 0.55; respectively; Table 3). Fire also had no immediate effect on bud mortality regardless of season ( $P = 0.56$ ). Despite the lack of immediate fire effects, season of fire played a key role in active bud dynamics throughout two growing seasons after fire (Fig. 3a). At the end of the first growing season, summer burns increased active buds compared to fall and spring burns and non-burned plots ( $P < 0.01$ ). At the end of the second

**Fig. 4** Active buds tiller<sup>-1</sup> ( $P < 0.01$ ) for *P. smithii* from July 2011 to July 2013 following no fire, summer, fall, and spring prescribed fire active buds tiller<sup>-1</sup> near Miles City, MT ( $\pm$ SEM)



winter (February 2013), active buds were more abundant following fall and spring burns compared to summer burns and non-burned plots ( $P < 0.01$ ). Active buds were reduced entering the second post-fire growing season by summer and spring burns ( $P < 0.01$ ). These fire effects continued throughout the second growing season for summer, fall and spring burns, with 81, 85 and 65 % reductions, respectively.

Dormant buds were minimal, but varied between winter and growing seasons depending on the season of fire ( $P < 0.05$ ; Fig. 3b). Dormant buds were not present on *H. comata* tillers during winter of the first year following all seasons of fire. The following July, dormant buds increased for spring burns and non-burned plots. During the winter of the second year, dormant buds increased following summer burns compared to all other seasons of fire, including non-burned plots ( $P < 0.05$ ; Fig. 3b). However, similar dormant bud densities were maintained among all treatments ( $P = 0.18$ ) at the start of the second growing season. Mortality of buds occurred only during the beginning of the first growing season following spring burns ( $P < 0.05$ ; Fig. 3c). Spring burns increased dead buds compared to fall burns and non-burned plots during March 2012. No bud mortality was observed at the conclusion of the first and second growing seasons ( $P = 0.12$ ).

#### *Pascopyrum smithii* dynamics

Plant density was similar among fire treatments ( $P = 0.53$ ; Table 2) and did not differ between one

and two post-fire growing seasons ( $58$  and  $42 \pm 6$  plants  $m^{-2}$ ;  $P = 0.07$ ). Summer and fall fire increased vegetative tillers ( $15 \pm 2$  tillers  $0.25 m^{-2}$  for each;  $P = 0.04$ ) relative to non-burned plots ( $9 \pm 2$  tillers  $0.25 m^{-2}$ ). Tiller counts following spring fire were intermediate and similar to all fire treatments ( $12 \pm 2$  tillers  $0.25 m^{-2}$ ). Year and season of fire had interacting effects on reproductive tillers ( $P = 0.03$ ). Reproductive tillers abundance was  $<1$  tiller  $0.25 m^{-2}$  and similar among all seasons of fire treatment during the first post-fire growing season. However, during the second post-fire growing-season reproductive tillers increased following summer and fall fires ( $8$  and  $7 \pm 1$  tillers  $0.25 m^{-2}$ ) compared to spring-burned and non-burned plots ( $2$  and  $1 \pm 1$  tillers  $0.25 m^{-2}$ ).

Summer, fall, and spring fire had no immediate effect on dormant or dead buds for *P. smithii* ( $P = 0.57$  and  $0.43$ , respectively; Table 3). However, development of active buds increased 61 % immediately following fall fire ( $P < 0.05$ ). Development of active buds primarily occurred during the second year following fire ( $P < 0.01$ ; Fig. 4). Active, overwintering buds increased following summer and fall fire compared to spring burns and non-burned plots ( $P < 0.01$ ). Increased activity of buds continued through the winter for summer, fall, and spring burns compared to non-burned plots ( $P < 0.01$ ). By the beginning of the second post-fire growing season, only fall and summer fires increased bud activity ( $P < 0.01$ ), and active bud counts became similar across all fire treatments by the middle of the second growing season ( $P = 0.25$ ).

Maintenance of dormant buds differed among fire treatments ( $P < 0.05$ ) and over time ( $P < 0.01$ ). Generally, dormant buds were reduced by summer, fall, and spring fires ( $0.7$ ,  $0.5$ , and  $0.9 \pm 0.2$  buds tiller<sup>-1</sup>) compared to non-burned plots ( $1.5 \pm 0.2$  buds tiller<sup>-1</sup>). Dormant buds were most abundant during July and November of the first growing season and February 2013 ( $1.5$ ,  $1.6$  and  $1.5 \pm 0.3$  buds tiller<sup>-1</sup>) and fewest during March 2012 ( $0.2 \pm 0.3$  buds tiller<sup>-1</sup>), with no consistent seasonal pattern for maxima and minima ( $P < 0.01$ ). Mortality of buds was relatively minor during the first post-fire growing season (March  $0.5$ , July  $0.1$ , November  $0.4 \pm 0.1$  buds tiller<sup>-1</sup>;  $P < 0.01$ ). However, bud mortality increased ( $P < 0.01$ ) during initiation of the second growing season (March  $1.2$  and May  $1.1 \pm 0.1$  buds tiller<sup>-1</sup>) with no observed fire effects ( $P = 0.74$ ).

## Discussion

To determine the role of native perennial grass bud banks in mixed-grass prairie response to fire we assessed immediate bud mortality of *B. gracilis*, *H. comata*, and *P. smithii* following summer, fall, and spring prescribed burns. Prescribed burns did not result in immediate mortality of *B. gracilis*, *H. comata*, or *P. smithii* buds. As expected, results supported the overall premise that bud bank dynamics differ among these species. Active and dormant bud abundance following seasonal prescribed burns differed for each species and short-term seasonal fluxes in bud dormancy, bud activity, and bud mortality varied according to the season of burning.

### Aboveground dynamics

Plant density was similar for the three species among all seasons of fire, including non-burned plants, and for 2 years following fire. Similar densities among summer, fall, and spring fire and non-burned controls combined with variable spring precipitation suggest that these native perennial grasses are well adapted to fire and spring drought (Russell et al. 2013). These responses are indicative of their evolutionary history and plant adaptations (Engle and Bultsma 1984; Umbanhowar 1996; Pausas and Schwilk 2012).

*Bouteloua gracilis* and *H. comata* tiller numbers decreased the first post-fire growing season, regardless

of season of burning. Drought effects likely stunted vegetative and reproductive tiller emergence, especially for *C<sub>3</sub>* species, since spring precipitation was 44 % below the long-term (1937–2012) average during the first post-fire growing season. Spring precipitation is better than annual or growing season precipitation for predicting peak standing crop in eastern Montana (Vermeire et al. 2008; 2009; Wiles et al. 2011). Reductions in tillers during the first year following fire treatments are similar to responses in tallgrass prairie, where tillers were reduced by drought, but increased the following year because of bud bank recovery (Carter et al. 2012). By the second post-fire growing season both total and reproductive tillers more than doubled. Similar second year response following fire has been observed in northern mixed-grass prairie, where perennial grasses made a substantial recovery the second year following fire during drought conditions (Engle and Bultsma 1984; Vermeire et al. 2011).

### Immediate season of fire effects on bud bank dynamics

Neither summer, fall, nor spring fire affected bud mortality for any species immediately after fire. Survival of species during a fire event usually depends on available vegetative buds to generate new growth (Dalglish and Hartnett 2009). Belowground buds are well protected from direct effects of fire due to the buffering capacity of soil and soil moisture (Alexander 1982; Bradstock and Auld 1995). In contrast, aboveground vegetation is susceptible to fire and 1 min at a temperature of only 60 °C is, in most cases, sufficient to coagulate proteins and cause lethal damage to aboveground plant tissue (Precht et al. 1973). Both *B. gracilis* and *P. smithii* axillary bud resistance to fire stem from their geophyte growth form (Raunkiaer 1934). This type of growth form maintains underground storage organs, which helps the plant survive adverse environmental conditions such as drought or fire (Raunkiaer 1934).

Due to its bunchgrass growth form, *H. comata* may be more sensitive to fire due to the elevation of meristems into the crown of the plant as the growing season progresses (Ewing and Engle 1988). Bunchgrasses are generally more susceptible to fire damage because litter accumulates in the crown of these species over time, potentially increasing the fuel load and resulting in greater heat duration and heat dosage

(Wright 1971; Wright and Bailey 1982; Engle et al. 1998). Bud mortality in bunchgrasses has been reported to be greater in the middle of the plant compared to the outer edges where litter accumulation is less (Morgan and Lunt 1999). Fire reduced axillary buds  $\text{plant}^{-1}$  25–70 % for *Aristida purpurea*, a bunchgrass that is common throughout the Great Plains, but generally a minor component (Russell et al. 2013; Russell and Vermeire 2015). In contrast to previously observed fire responses of bunchgrasses, immediate bud mortality did not occur in this study for *H. comata*. This may be due to the dense bunch-form of *H. comata*, which may have extinguished the fire or decreased heat duration due to lack of oxygen at the crown. Some plants, like *H. comata*, protect vegetative buds through the sheath of the tiller, where top removal of fine fuels has minimal effects on well-protected axillary buds that are just above the soil surface (Morgan and Lunt 1999). When a fire occurs in grasslands, it generally sweeps across the top of vegetation with minimal heat transfer to the base (Wright 1971). Due to *H. comata*'s coarse stems and dense plant crown, the base of the plant may have been compacted adequately enough to prevent direct heat transfer to the buds (Haile 2011). Heat threshold conditions required to produce greater than 0.5 probability of mortality for *H. comata* are 56,985 °C s, 10.4 min above 60 °C, 628 °C maximum temperature, and 8500 kg ha<sup>-1</sup> fuel load (Haile 2011). The thresholds reported for *H. comata* are substantially greater than the fire intensities recorded for summer, fall, or spring fire treatments for this study.

Activity of *B. gracilis* buds increased immediately following spring fires. Additionally, fall fire immediately increased active bud development of *P. smithii*. Spring and fall fire served as catalysts for both species, stimulating new bud growth, transitioning dormant buds into active buds, and initiating buds into future tillers within 24 h of burning. Immediate active bud responses were not expected, but may be possible due to the removal of litter and existing vegetation (Wright and Bailey 1982) and evolutionary response (Towne and Owensby 1984).

Immediate bud bank responses to fire may also be due to temporary transitions in buds. In many cases, newly formed axillary buds enter transition stages of temporary growth or dormancy (Devitt and Stafstrom 1995; Shimizu and Mori 2001). Buds cycle through these temporary transition stages until a developmental

or environmental cue signals buds to become fully dormant or undergo growth. The timing of spring fire most likely manipulated C<sub>4</sub> buds during temporary transition periods and acted as an environmental signal for buds to enter active growth. Similarly, the timing of fall fire manipulated developing C<sub>3</sub> buds to increase activity and growth. In contrast, summer fires decreased *B. gracilis* bud activity and increased bud dormancy. Axillary buds in temporary transitions can become developmentally arrested if an environmental cue signals heat or drought-induced quiescence. These dormant axillary buds resume development at a later time, depending on their developmental program, or in response to environmental cues (Stafstrom and Sussex 1992; Shimizu and Mori 1998). This temporary bud strategy is possible since northern mixed-grass prairie evolved under summer fire regimes where temporary dormancy of buds may be advantageous in order to cope with increased summer fire intensity and heat stress (Higgins 1984; Umbanhowar 1996).

#### Season of fire effects on short-term bud bank dynamics

*Bouteloua gracilis* bud banks were more active during drought if burned the previous year. Non-burned plants increased dormant buds compared to burned plants during summer drought. Bud bank activity of *B. gracilis* likely increased due to increased nitrogen availability following fire (Cui and Caldwell 1997; Enquist et al. 1998). Since *B. gracilis* total buds did not increase during drought conditions, it is likely that *B. gracilis* bud banks were able to recover by transitioning dormant buds into active buds, contributing to plant community persistence in challenging environments following drought and fire.

By the end of the study, *H. comata* had the smallest bud bank of all species and contained 73 % fewer buds on burned plots compared to control plots. When species do not maintain a large population of below-ground buds throughout the growing season, meristem limitations occur which limit the plants ability to respond to disturbance. Since bud production did not increase as tiller production increased, bud banks of *H. comata* were not replenished and plants became meristem limited. Depleted bud banks of *H. comata* also align with previous bud bank studies in tallgrass prairie that reported C<sub>3</sub> species maintain a smaller bud bank with short-lived buds and tiller recruitment

occurs from current year's buds only (Ott and Hartnett 2012). Therefore, in northern mixed-grass prairie, *H. comata* would be expected to closely track inter-annual environmental changes and demonstrate fluctuating bud populations and potential meristem limitations due to variable environmental conditions.

Unlike bud banks of *H. comata*, *P. smithii*, also a C<sub>3</sub> grass, maintained a large overwintering reserve of dormant and active buds following summer and fall fires. New bud growth and increased bud activity for *P. smithii* during winter dormancy following spring, and summer fires are similar to this study's C<sub>4</sub> bud bank results and C<sub>4</sub> bud response in tallgrass prairie. For C<sub>4</sub> species, young buds and older buds produced in previous years comprise the overwintering bud bank (Ott and Hartnett 2012). Similar to *P. smithii* bud bank results, overwintering bud banks of C<sub>4</sub> species in tallgrass prairie remain active in order to rapidly transition into new tillers before warmer summer temperatures occur (Ott and Hartnett 2012).

## Conclusions

Native, perennial grasses in mixed-grass prairie rely heavily on the maintenance of the bud bank to regenerate and persist in environments dominated by fire, drought, and herbivory, common characteristics of the northern Great Plains. Belowground bud banks respond positively by increasing bud activity and having minimal bud mortality following moderate fire intensity. Both *B. gracilis* and *P. smithii* responded to fire with increased bud activity throughout winter dormancy, replenishing bud bank reserves and capitalizing upon early spring resources (e.g., precipitation). This plant strategy is effective in northern mixed-grass prairie due to variation in precipitation patterns. Furthermore, summer, fall, and spring fires manipulated C<sub>3</sub> and C<sub>4</sub> grasses differently, illustrating the potential for flexible resource allocation and growth tradeoffs. Differences in species responses to season of fire can influence future patterns of reproduction and community dynamics of perennial grasses. Manipulating bud bank dynamics by season of fire illustrates potential to improve management strategies following wildfires or planning prescribed burns based on the trajectory of bud development. Incorporating knowledge of bud bank dynamics will also inevitably improve overall predictions of grassland vegetation

response to fluctuating environmental growing conditions.

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