

Phenology of perennial, native grass, belowground axillary buds in the northern mixed-grass prairie¹

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PREMISE OF THE STUDY: Vegetative reproduction from belowground bud banks is the primary driver of grassland systems. Despite the importance of bud banks, the timing of recruitment and the crucial link between formation and maintenance is unknown.

METHODS: We assessed patterns of belowground bud development, dormancy, and mortality associated with three perennial native grasses in the northern Great Plains. Temperature and soil moisture were measured below the soil surface to determine relationships with belowground bud development.

KEY RESULTS: Blue grama (*Bouteloua gracilis*) generated more buds over winter that remained dormant; whereas, C₃ species needle-and-thread (*Hesperostipa comata*) and western wheatgrass (*Pascopyrum smithii*), maintained limited dormant buds throughout winter. Soil temperature was a good predictor for C₄ species bud production; whereas, soil moisture was a reliable predictor for C₃ buds. Distinct differences existed between C₄ species blue grama and C₃ species needle-and-thread, whereas C₃ species western wheatgrass (*Pascopyrum smithii*) was intermediate, indicating there is likely a species-specific continuum between the C₃ and C₄ extremes rather than a stark difference.

CONCLUSIONS: The ability to predict belowground bud development is a novel insight to native perennial grasses. Native grass species' strategies and adaptability regarding belowground bud bank size and bud phenology are important factors optimizing tiller recruitment given the variable growing conditions. Patterns of bud dormancy and development will provide insight to the underlying mechanisms by which management practices and fluctuations in precipitation amount and growing season length can alter mixed-grass prairie plant community dynamics.

KEY WORDS bud bank; population; dormancy; grassland; meristem; soil moisture; soil temperature; tiller; vegetative reproduction

Vegetative reproduction in perennial grasslands relies on tiller recruitment from belowground bud banks. More than 99% of new tiller formation in the North American tallgrass prairie originates from vegetative reproduction (Benson and Hartnett, 2006). However, belowground stages of bud development are unknown for

most dominant native grasses, especially in mixed-grass prairies. Identifying phenological patterns of bud bank development could facilitate interpretation and prediction of plant community change in conjunction with disturbance or alterations in environment.

Patterns of belowground bud development, dormancy, and mortality are important because new buds, longevity of maintained buds, and overall bud dynamics determine the size of the bud bank during the growing and dormant seasons (Ott and Hartnett, 2011). The size and demography of the bud bank are considered ecological drivers in response to typical grassland disturbance processes, such as fire and grazing (Dalglish and Hartnett, 2006; Russell et al., 2013). In addition, a reserve population of dormant buds may buffer population dynamics in the face of unpredictable environmental change, such as drought or prolonged growing seasons (Ott and Hartnett, 2011). By recruiting tillers from a bud bank, perennial grasses are able to respond rapidly to their environment and are highly resilient following grazing, drought, fire, or other stresses.

Grass species containing extensive belowground bud banks may be able to opportunistically capitalize on periods of abundant resource

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availability, such as increased nitrogen following fire or early spring precipitation (Dalglish and Hartnett, 2006; Russell and Vermeire, 2015). However, some species may be meristem limited, with sparse bud banks that restrict responses to increased available resources (Dalglish and Hartnett, 2006). Species that are meristem limited may not have sufficient buds in the bud bank during the growing season to completely replace the aboveground tiller population (Watson, 1984; Geber, 1990; Aarssen, 1995; Dalglish and Hartnett, 2006).

Bud abundance or meristem limitations are not known for dominant species of mixed-grass prairie. Furthermore, quantifying bud bank dynamics in a semiarid environment may provide insight to the mechanisms responsible for certain population ecology strategies. For example, plant growth form is largely determined by patterns of bud placement and outgrowth (Hendrickson and Briske, 1997). An improved baseline understanding of dominant native perennial bud banks may elucidate mechanisms altering population processes, especially overall plant community dynamics as a function of disturbance. More detailed characterizations of bud banks are needed to determine the crucial link between formation and maintenance of the belowground meristems and ecosystem-level processes that reveal how species develop throughout an annual growth cycle. Identifying ranges of soil temperature and soil moisture required to activate buds and grow tillers can enhance the ability of management strategies to achieve a desired outcome (e.g., maximized bud activity and development). Therefore, the objectives of this study were to (1) assess bud bank dynamics in two C_3 species, needle-and-thread (*Hesperostipa comata* (Trin. & Rupr.) Barkworth) and western wheatgrass (*Pascopyrum smithii* (Rydb.) A. Löve), and a C_4 species blue grama (*Bouteloua gracilis* (Willd. ex Kunth) Lag. ex Griffiths) of mixed-grass prairie; and (2) determine the relationship between bud development to soil moisture and soil temperature. Based on previous research, which found interspecific differences in bud banks and the patterns of bud development and demography between *Andropogon gerardii* (Vitman) and *Dichanthelium oligosanthes* (Schult.) Gould in tallgrass prairie (Ott and Hartnett, 2012), we hypothesized *B. gracilis* would maintain more dormant buds than *H. comata* or *P. smithii*, and that both *H. comata* and *P. smithii* would display a more consistent pattern of bud activity throughout the year. We also hypothesized that bud abundance is positively related to soil moisture and that new bud growth of *H. comata* and *P. smithii* occurs at a cooler temperature range than that for *B. gracilis*.

MATERIALS AND METHODS

Site description—Research was conducted in semiarid, mixed-grass prairie near Miles City, Montana, USA (lat 46°24'N, long 105°56'W) from March 2012 through July 2013. Average annual precipitation for the area is 343 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. The frost-free growing season ranges from 125–150 d (Western Regional Climate Center, 2013).

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). Vegetation is dominated by perennial, native C_3 species including, needle-and-thread

(*Hesperostipa comata*), western wheatgrass (*Pascopyrum smithii*), and threadleaf sedge (*Carex filifolia* Nutt.), and C_4 species including blue grama (*Bouteloua gracilis*), and to a lesser extent, buffalograss (*Bouteloua dactyloides* (Nutt.) J. T. Columbus). Annual grasses include six-week fescue (*Vulpia octoflora* (Walter) Rydb.), field brome (*Bromus arvensis* L.), and cheatgrass (*Bromus tectorum* L.). The primary shrub species on the site is Wyoming big sagebrush (*Artemisia tridentata* Nutt. sp. *Wyomingensis* Beetle & Young) and half-shrub fringed sage (*A. frigida* Wild.). Forbs included the biennial forb, yellow salsify (*Tragopogon dubius* Scop.), and annual forbs 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.

Field sampling and laboratory methods—Tiller counts and bud assessments were conducted weekly during the growing season and twice per month during early spring and early autumn. Tiller counts and phenological stages were tracked for two growing seasons on 36 permanently marked plants for each target species of *B. gracilis* (C_4 species), *P. smithii* (C_3 rhizomatous species), and *H. comata* (C_3 caespitose species).

Tillers were classified as vegetative or reproductive based on the current aboveground growth. Because of the rhizomatous growth form of *B. gracilis* (typically found in mixed-grass prairie) and *P. smithii*, definitions of an individual were outlined prior to the start of the study and implemented throughout as follows. Tiller counts performed on *B. gracilis* plants were considered and counted as part of an individual when gaps between tillers did not exceed 3 cm (Russell et al., 2015). Because of the rhizomatous habit of *P. smithii* and the difficulty in distinguishing individual plants, tiller measurements were made by counting all tillers within a 0.25 m² quadrat and, for the sake of simplicity, were referenced as tillers per plant (Russell et al., 2015). Individual *H. comata* plants were readily distinguished because of their bunchgrass growth form (Russell et al., 2015).

Belowground bud assessments were made from tillers that were in similar phenological stages as target plants for each species. Tillers were destructively sampled, so different plants were sampled at each harvest interval from neighboring permanently marked plants that were in a similar phenological stage. Plant phenology (the series of phases in aboveground plant development throughout the year) was classified by developmental stage: vegetative (only vegetative growth evident), boot (culm stalk evident but inflorescence not visible), seed (from visible inflorescence through seed dispersal), and senescence (seeds dispersed and vegetative growth declining relative to leaf mortality) (White et al., 1991). Aboveground phenology was recorded because it can readily be assessed and was assumed to be related to bud bank phenology. Plants visibly damaged by herbivores, insects, or pathogens were excluded from further measurements.

Buds were counted and classified using a dissecting microscope and determined to be living or dead (Russell et al., 2013). Amount of active living buds, dormant buds, and dead buds were confirmed using tetrazolium and Evans blue staining procedures as described by Busso et al., (1989), Hendrickson and Briske (1997), and Russell et al. (2013). Axillary buds were stained with a 2,3,5-triphenyl tetrazolium chloride (TTC) solution to determine viability. Tillers were submerged in TTC solution at room temperature for 24 h in a completely dark environment following initial classification. Buds were

considered living/active when stained a bright pink. If dormant buds were present on a tiller, that tiller was submerged into 0.25% Evans blue solution for 20 min at room temperature following TTC staining to verify dormancy or death. Buds that did not stain with either TTC or Evan’s blue and maintained their white pigment were considered dormant (Busso et al., 1989). Dead buds were readily distinguished from dormant buds by staining a deep blue (Gaff and Okong’o-ogola, 1971).

Soil moisture was measured at each tiller harvest and phenological classification during the growing seasons of 2012 and 2013. Soil moisture was determined with a Field Scout TDR 100 soil moisture meter with 7.5-cm probes inserted vertically at the base of each target plant (Spectrum Technologies, Aurora, Illinois). Soil temperatures (in degrees centigrade) were determined from hourly measurements each day during the 2012 and 2013 growing seasons using WatchDog B-series button loggers (Spectrum Technologies, Aurora, Illinois) and daily mean temperatures were used in analyses. Each temperature button logger was inserted adjacent to the crown of each target plant at approximately 0–1 cm below the soil surface.

Statistical analysis—Tiller count data were analyzed for all species using ANOVA (MIXED procedure of SAS; Littell et al., 2006). The model included year and species as fixed effects with vegetative and reproductive tillers as response variables. Bud assessments were analyzed using ANOVA (MIXED procedure of SAS, Littell et al., 2006) with tiller harvest date as a repeated measure. ‘Plant’ was the experimental unit and statistical significance was set at $P < 0.05$. The independent factor was tiller harvest date, and response variables were active buds, dormant buds, and dead buds. In separate analyses, soil moisture and soil temperature were tested as predictor variables for *B. gracilis*, *H. comata*, and *P. smithii* bud development with logistic regression (LOGISTIC procedure of SAS; Littell et al., 2006). Plant was the experimental unit and statistical significance was set at $P < 0.05$.

RESULTS

Four primary phenological stages (vegetative, boot, seed, and senescence) were present for all three species in 2012. Both C_3 species had two fully emerged live leaves by 16 April 2012. The C_4 grass had only one fully emerged leaf until 28 May 2012, after which aboveground vegetative growth increased rapidly and tiller elongation began by 15 June 2012. The elongation stage for all species had a maximum of three visible nodes.

TABLE 1. Average monthly soil moisture (%) and soil temperature (°C) taken at target species during the 2012 and 2013 growing seasons in eastern Montana (±SE).

Month	2012		2013	
	SM, %	Soil temp, °C	SM, %	Soil temp, °C
March	17.9 ± 2.3	17.2 ± 3.4	23.3 ± 1.7	9.1 ± 6.3
April	10.6 ± 4.3	20.7 ± 6.2	31.6 ± 6.9	10.7 ± 3.3
May	4.5 ± 1.3	10.6 ± 2.3	29.3 ± 3.6	19.8 ± 6.9
June	2.8 ± 1.2	33.2 ± 6.2	31.0 ± 6.6	30.1 ± 7.6
July	3.6 ± 0.7	35.7 ± 6.2	41.6 ± 9.3	31.8 ± 9.1
August	4.9 ± 2.1	37.0 ± 3.2	—	—
September	26.9 ± 4.3	17.4 ± 2.1	—	—
October	32.6 ± 2.9	9.4 ± 4.6	—	—

Tillers in the 2013 growing season had three primary phenology stages for all species. Unlike 2012, all three species had three fully emerged leaves with collars by 28 May 2013. Elongation for *P. smithii* began within a week of the third leaf vegetative stage; however, both *B. gracilis* and *H. comata* remained primarily vegetative through July 2013. Unlike 2012, vegetative tillers of *B. gracilis* produced a fourth fully emerged collared leaf by 2 July 2013.

Soil moisture varied throughout the 2012 and 2013 growing seasons (Table 1). Growing conditions during 2012 were extremely dry, with drought conditions occurring most of the spring and summer (36 and 44% of average, respectively). 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). Spring 2013 brought near-average spring and summer precipitation, with the exception that May precipitation was 290% of average, enabling growth of cool- and warm-season grasses following the severe drought of 2011–2012.

Vegetative tiller production varied by species and year (ANOVA, $F_{2,30} = 53.51, P < 0.0001$; Fig. 1A). The C_3 vegetative tiller production increased during 2013 in contrast to the C_4 species—*B. gracilis*—which had greater tiller production in 2012. Reproductive tiller production varied with species and year (ANOVA, $F_{2,30} = 8.79, P < 0.0001$; Fig. 1B). *Pascopyrum smithii* produced 76% more reproductive tillers in 2012 than 2013, whereas *B. gracilis* and *H. comata* produced similar numbers of reproductive tillers in both study years ($P > 0.05$).

Active bud numbers varied by species (ANOVA, $F_{22,391} = 12.85, P < 0.0001$; Fig. 2). Active buds for *B. gracilis* decreased during July 2012, but increased during December 2012 and May 2013 (Fig. 2A). Active *H. comata* buds maintained similar numbers with minor fluctuations during June 2012 and May of 2013 (Fig. 2B). Active *P. smithii* buds exhibited intra- and interannual variation that was intermediate to *B. gracilis* and *H. comata* (Fig. 2C). At the end of July 2012, *P. smithii* active buds also decreased similar to *B. gracilis* and *H. comata*.

Dormant bud numbers varied among species during study years (ANOVA, $F_{22,391} = 7.96, P < 0.0001$; Fig.3). Dormant *B. gracilis* buds increased during July 2012, but decreased by February 2013 (Fig. 3A). *Hesperostipa comata* maintained fewer dormant buds than the other species throughout the study years with slight increases (15–20%) occurring from July 2012 to September 2012 and November 2012 to May 2013 (Fig. 3B). Dormant *P. smithii* buds began increasing during June 2012 and did not decrease until February 2013 (Fig. 3C).

Bud mortality varied among species during study years (ANOVA, $F_{22,391} = 2.02, P \leq 0.004$; Fig. 4). Dead *B. gracilis* buds increased summer through fall, with peak dead buds occurring during November 2012—a more than 6-fold increase in mortality (Fig. 4A). The number of dead *B. gracilis* buds returned to predrought levels by February 2013. Dead buds of *H. comata* were minimal, except for 5–10% increases during March and May of 2012 (Fig. 4B). Dead *P. smithii* buds were similar throughout 2012, but increased 70% at the beginning of 2013 (Fig. 4C). After June 2013, *P. smithii* bud mortality decreased to similar levels observed in 2012.

Soil temperature was the best predictor for *B. gracilis* bud quantity; whereas, soil moisture was not a significant predictor of *B. gracilis* bud quantity (Table 2). On the other hand, soil moisture was a reliable indicator

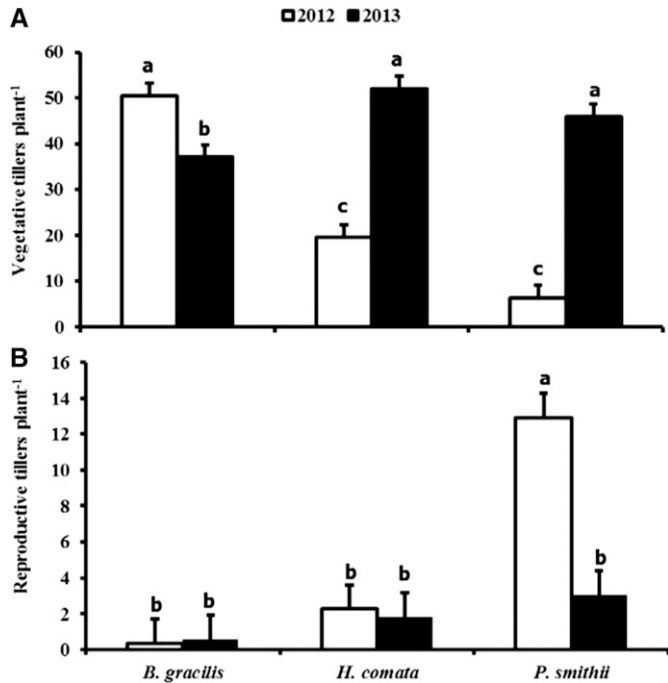


FIGURE 1 Species and year effects for (A) vegetative tillers per plant (+SEM), and (B) reproductive tillers per plant (+SEM) during 2012 and 2013 near Miles City, Montana. Tiller count data were analyzed for all species using ANOVA (MIXED procedure of SAS) and Tukey's analysis of the species and year data. Means marked with the same letter are similar within response variable ($P < 0.05$).

of bud quantity for both cool-season grasses, but soil temperature was not a significant predictor.

The probability of increased bud quantity reached 0.5 when soil moisture was 25% for *H. comata* (Fig. 5A). *Pascopyrum smithii* had a 0.5 probability of increasing buds when soil moisture was 16%, and a 0.9 probability when moisture was 25% (Fig. 5B). The probability of *B. gracilis* increasing bud quantity exceeded 0.5 when soil temperature was 6°C, and was 0.9 when soil temperature was 20°C (Fig. 5C). Probability of increased bud numbers were near 1.0 for *B. gracilis* when temperatures were 33°C.

DISCUSSION

Phenological patterns of belowground bud development, maintenance, and transitions for *B. gracilis* and *H. comata* resembled aboveground phenological patterns. *Bouteloua gracilis* maintained more dormant buds than *H. comata*, however, *H. comata* kept a more consistent pattern of bud activity throughout the year. Interestingly, *P. smithii* exhibited an intermediate bud bank. Increasing the importance of bud bank phenology strategies, northern mixed-grass prairie experiences a compressed growing season, with 90% of perennial grass growth completed by 1 July (Vermeire et al., 2009). Therefore, species' strategies and adaptability regarding belowground bud bank size and bud phenology are important factors optimizing tiller recruitment given the variable growing conditions.

Even though *P. smithii* is a C_3 grass with early aboveground growth, in this study belowground bud bank patterns aligned more with *B. gracilis* than *H. comata*. These results showcase *P. smithii*'s strategy to maintain a consistent bud supply throughout the year,

providing potential for immediate growth response to variable environmental conditions. Although meristem limitations have been demonstrated for other native, perennial species (Dalgleish and Hartnett, 2006), in our study, *P. smithii* bud banks did not show any potential to be hindered by meristem limitations.

Reproductive *P. smithii* tillers increased during drought conditions of the 2012 growing season. Spring precipitation (April–June) is considered a major driver of aboveground productivity in the northern Great Plains (Vermeire et al., 2009; Wiles et al., 2011). Our observations are similar to phenology experiments in semiarid environments (Aronson et al., 1992), in which native, perennial grasses increased reproductive tillers and transitioned earlier to reproductive development compared to matched species from Mediterranean environments (Herms and Mattson, 1992). These increases in reproductive tillers may be an effective strategy for *P. smithii* during drought because previous research shows reproductive tillers contain more mature, active buds than vegetative tillers (Ott and Hartnett, 2011) and likely function as stronger sinks under conditions of resource limitation. In semiarid environments, native, perennial grasses adapt to drought and variable precipitation by altering their bud strategies (Busso et al., 1989; Volaire, 1995; Flemmer et al., 2002). For example, drought conditions during early spring may prevent current buds from reaching a critical bud development threshold, thereby reducing overall bud production and increasing the importance of dormant bud bank strategy (McKendrick et al., 1975; van Noordwijk and De Jong, 1986; Busso et al., 1989). This was the case in our study for *B. gracilis* where dormant *B. gracilis* buds increased during July 2012 following drought conditions. In addition, limited late-spring/early-summer precipitation may have a greater effect on the maintenance of dormant buds than the growth and development of new buds.

Other studies have shown active *B. gracilis* buds transitioned into dormancy during late summer 2012, increasing the dormant bud bank going into winter (Ott and Hartnett, 2012). Increases in the size of the dormant bud bank were also observed in the C_4 species, *A. gerardii* (Dalgleish and Hartnett, 2006; Ott and Hartnett, 2012). In *A. gerardii*, bud longevity is > 2.5 yr, resulting in an accumulation of dormant buds in the bud bank (Hendrickson and Briske, 1997; Ott and Hartnett, 2012). The C_4 species appear to depend on large dormant bud banks to survive winter and recruit new tillers in the spring (Ott and Hartnett, 2012). Therefore, species like *B. gracilis* may maintain high population dominance because of their high-density dormant bud banks, enabling them to respond rapidly to a resource pulse or sustain their population during drought years (Dalgleish and Hartnett, 2006; Ott and Hartnett, 2012). In variable environments, similar to our mixed-grass prairie site, this strategy may serve C_4 grasses well because occasional droughts of short duration (less than one year) do little to hinder the recovery of large, dormant, bud bank densities (Carter et al., 2012).

Active and dormant bud dynamics for *P. smithii* were similar to both C_3 and C_4 species. Our results suggest bud banks of both C_3 species (*P. smithii* and *H. comata*) closely track intra- and inter-annual environmental changes and show more dynamic tiller recruitment than the C_4 species under variable environmental conditions. Enhancing the C_3 strategy to respond to variable conditions, *P. smithii* maintained a significant bud supply throughout the year. Previous *P. smithii* bud bank research in western South Dakota (Ott and Hartnett, 2015) showed dual investment occurred when *P. smithii* produced 60% of new tiller growth from new buds off of parent tillers, with the remaining 40% of new tiller growth occurring from rhizomes away from parent tillers (Ott and

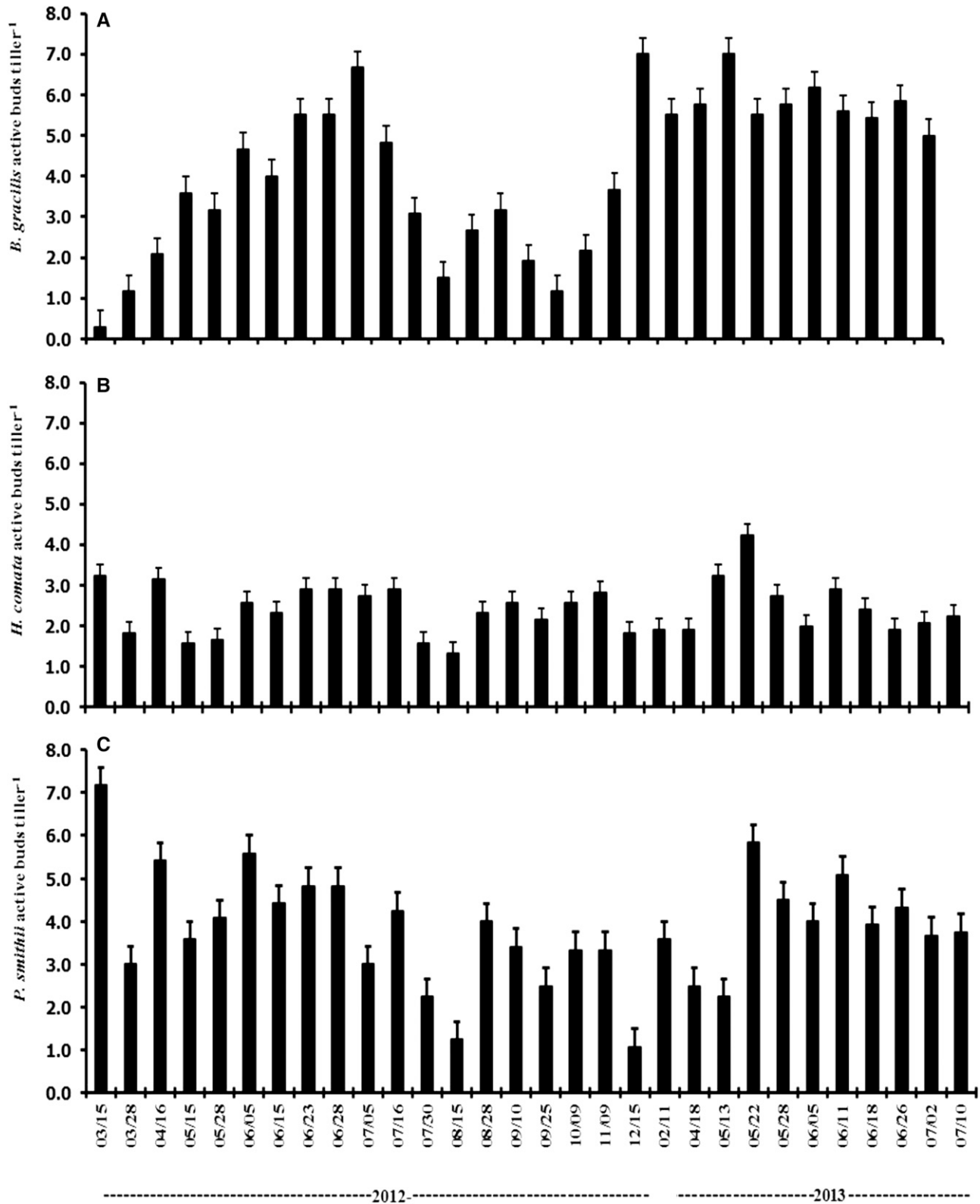


FIGURE 2 Seasonal fluctuations in active buds per tiller (\pm SEM) showing differences ($P < 0.05$) in the time frames within each species for (A) *B. gracilis*, (B) *H. comata*, and (C) *P. smithii* near Miles City, Montana.

Hartnett, 2015). Our results support those of Ott and Hartnett (2015) in that *P. smithii* optimizes both growth strategies. Additionally, our results show that *B. gracilis* and *H. comata* operate on

opposing ends of the bud bank spectrum, while *P. smithii* is intermediate showing similarities to both C_3 and C_4 strategies. The bud bank dynamics and differences found in this study may be

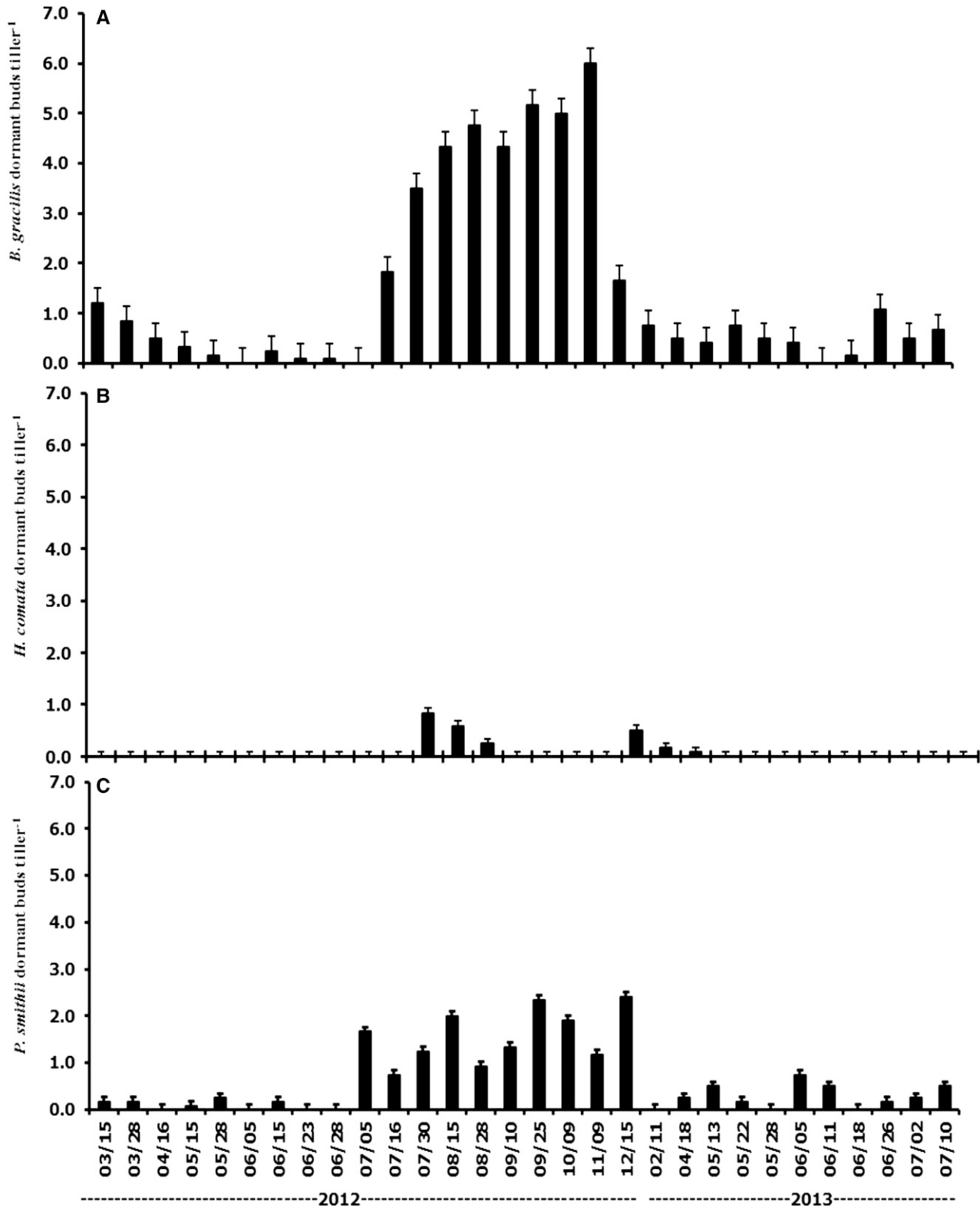


FIGURE 3 Seasonal effects on dormant buds per tiller (\pm SEM) showing differences ($P < 0.05$; $P < 0.01$) in the time frames within each species for (A) *B. gracilis*, (B) *H. comata*, and (C) *P. smithii* for two growing seasons including one winter dormancy period near Miles City, Montana.

explained in part by mode of photosynthesis, based on a pattern that can be surmised from previous studies (Ott and Hartnett, 2012). Photosynthetic pathway (C_3 vs. C_4) primarily determines

optimal growing temperature range, active growth periods, dormant periods, phenology, and geographic distribution (McIntyre, 1970). Because C_3 and C_4 species differ in aboveground phenological

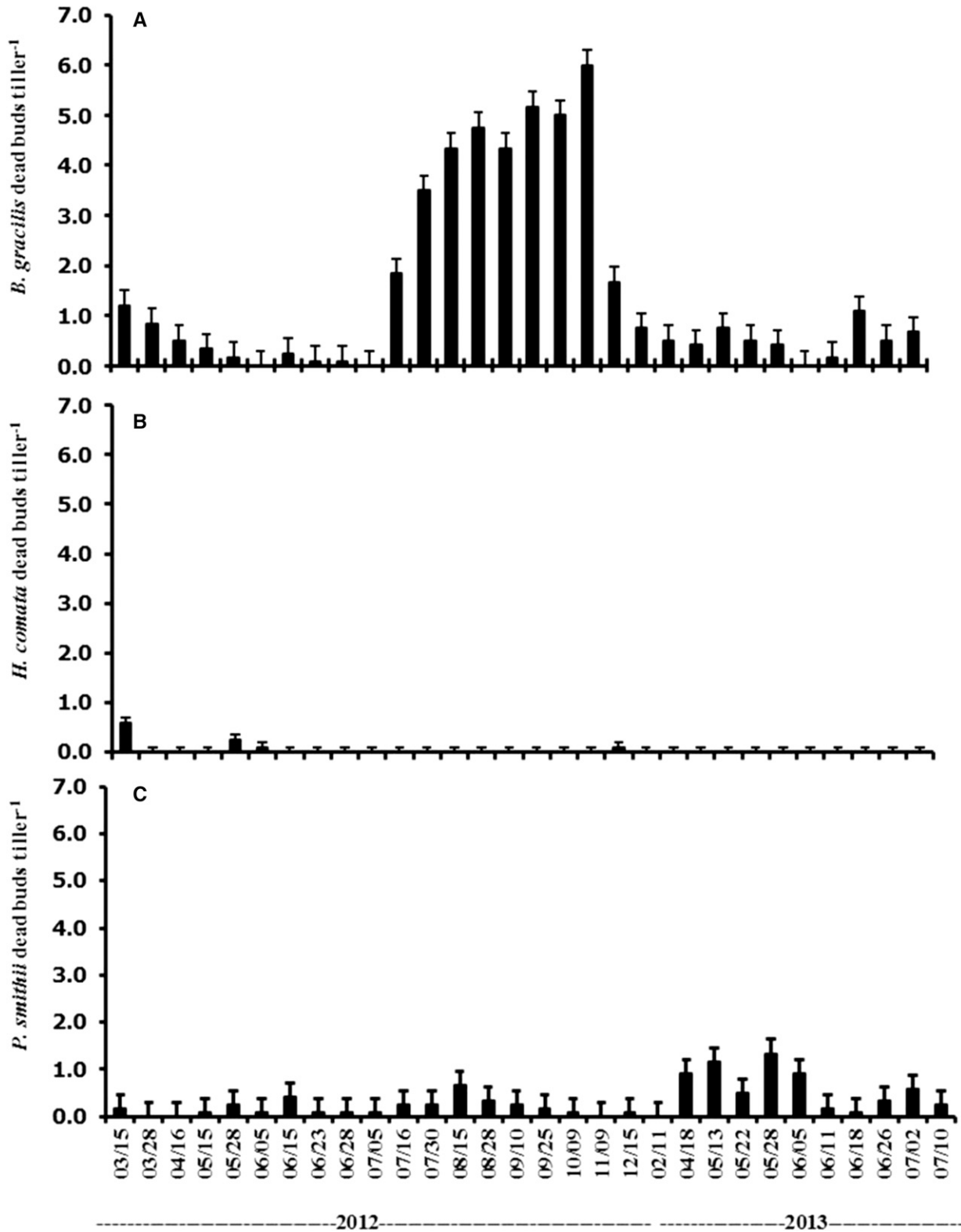


FIGURE 4 Dormant buds per tiller (\pm SEM) showing differences ($P < 0.05$; $P < 0.01$) in the time frames within each species for (A) *B. gracilis*, (B) *H. comata*, and (C) *P. smithii* for two growing seasons including one winter dormancy period near Miles City, Montana.

patterns, belowground bud development and transitions between activity and dormancy may be expected as well (Ott and Hartnett, 2012).

Differences between belowground bud bank strategies of C_3 and C_4 grasses showed C_4 species (*A. gerardii*) maintained a larger dormant bud bank, more consistent bud development and transition to tillers,

TABLE 2. Predictive ability of variables used in logistic regression model to test for bud quantity in eastern Montana.

Predictor variable	Model information		
	C-statistic ^a	H-L test ^b	$P > \chi^2$
<i>B. gracilis</i>			
Soil moisture (%)	0.65	0.15	0.83
Soil temperature (°C)	0.89	0.26	0.03
<i>H. comata</i>			
Soil moisture (%)	0.86	0.41	0.04
Soil temperature (°C)	0.57	0.63	0.69
<i>P. smithii</i>			
Soil moisture (%)	0.93	0.40	0.03
Soil temperature (°C)	0.70	0.06	0.36

^aC-statistic is the predictive ability of the model.

^bHosmer-Lemeshow goodness of fit test (higher value = better fit).

and buds lived for multiple years compared to a C_3 species (Ott and Hartnett, 2012). This C_4 bud strategy aligns with our results for *B. gracilis*, showing an extensive reserve of dormant buds compared to C_3

year. As a result of unique species-specific bud bank dynamics, an inherent ability to buffer against timing of disturbance may exist, providing an opportunity for management of mixed-grass prairies.

Aboveground growth patterns often

vary by photosynthetic pathway, yet species-specific variation leads to substantial overlap in phenology. Therefore, similar relationships may be expected with bud phenology. Further examination of additional species is needed. However, our observations that *P. smithii* used both C_4 and C_3 strategies support the proposition that species-specific bud phenology varies along a gradient between the previously described C_4 and C_3 patterns.

Data partially supported our hypothesis that soil moisture and soil temperature are positively related to bud quantities in that only soil temperature was a good predictor for the C_4 species and only soil moisture was a good predictor for the C_3 species. Above- and belowground growth are known to depend on soil moisture and temperature (Cable, 1975; Kaspar and Bland, 1992; Ott and Hartnett, 2012). The temperature range—for which the probability of *B. gracilis* increasing bud numbers was 0.5–0.9—closely matches the relationships between soil temperature and belowground biomass production for *B. gracilis* (Morrow and Power, 1979). In addition to soil moisture and soil temperature, endogenous growth cues may have contributed to increases in bud numbers. Endogenous growth cues include hormonal control over bud development that involve

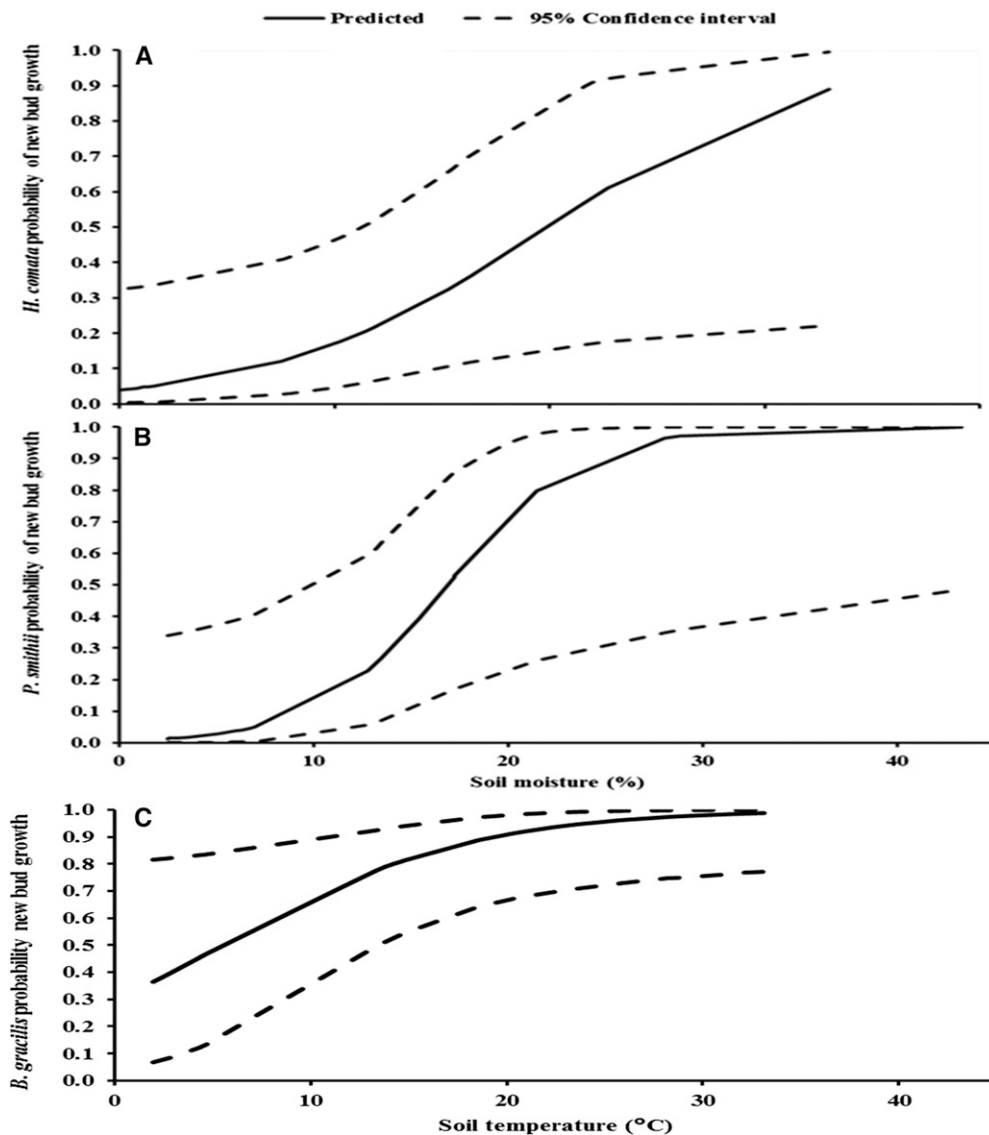


FIGURE 5 Predicted bud quantity and 95% confidence interval for and (A) *H. comata* and (B) *P. smithii* as a function of soil moisture, and (C) *B. gracilis* bud development as a function of soil temperature (°C) near Miles City, MT.

complex interactions among auxin, cytokinin, strigolactone, and bud development stages to determine bud activity, dormancy, and tiller emergence (Dun et al., 2006; Waldie et al., 2010).

Understanding the patterns and factors influencing bud development dynamics is important for developing a mechanistic and predictive understanding of grassland response to disturbances such as fire, grazing, and drought. The ability to predict belowground bud development could enhance the utilization of management tools to manipulate tiller recruitment from the bud bank. For example, seasonal timing of fire affected the number of dormant, active, or total live *B. gracilis* buds within 24 h (Russell et al., 2015). Descriptions of bud bank phenology can provide insight to the timing and action of disturbances and its potential effects on tiller population dynamics. Linking aboveground phenology with belowground bud phenology illustrates potential mechanisms regulating bud development and maintenance, which may ultimately determine plant community dynamics.

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