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Fire and Nitrogen Alter Axillary Bud Number and Activity in Purple Threeawn[☆,☆☆,★,★★]

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ABSTRACT

Belowground accumulation of vegetative buds provides a reservoir of meristems that can be utilized following disturbance. Perennial grass bud banks are the primary source of nearly all tiller growth, yet understanding of fire and nitrogen effects on bud banks is limited. We tested effects of fire and nitrogen addition on bud banks of purple threeawn (*Aristida purpurea* Nutt.), a perennial C_4 bunchgrass. Fire (no fire, summer fire, fall fire) and nitrogen addition (0, 46, 80 $kg \cdot ha^{-1}$) treatments were assigned in a completely randomized, fully factorial design and axillary buds were evaluated on two similar sites in southeastern Montana 1 and 2 years after fire. Permanently marked plants were assessed for live tiller production, and randomly selected tillers were sampled to determine active and dormant buds per tiller. Fire and nitrogen had opposite effects on axillary buds. Summer and fall fire reduced active buds by 42% relative to nonburned plots. Adding nitrogen at 46 or 80 $kg \cdot ha^{-1}$ increased active buds per tiller 60% compared with plots with no nitrogen addition. The number of dormant buds per tiller was similar across fire treatments and levels of nitrogen. Fire and nitrogen had interacting effects on total buds at the tiller level. Without nitrogen addition, fall and summer fire reduced total buds per tiller about 70%. Nitrogen had no effect on total buds per tiller for nonburned plants. However, total number of buds per tiller was greater with nitrogen addition following fall fire and increased with each increase in nitrogen following summer fire. Results indicate fire effectively controls purple threeawn through bud bank reduction and that nitrogen can stimulate bud production. Interacting effects of fire and nitrogen on buds reveal a potential source of inconsistency in nitrogen effects and a possible method of facilitating recovery of fire-sensitive bunchgrasses after fire.

Introduction

Vegetative reproduction is the primary driver of aboveground growth, producing as much as 99% of new tillers for perennial grasses (Benson and Hartnett, 2006). The source of the vegetative reproduction is a belowground accumulation of vegetative buds collectively called the bud bank. As a primary source of recruitment, bud banks play a large role in the ability of perennial grasses to withstand disturbance. A deeper understanding of bud bank demography is likely required to determine the mechanisms driving grass population and tillering patterns (Noble et al., 1979).

Despite the importance of vegetative reproduction in perennial grasslands, little is known about the general patterns and timing of tiller recruitment from the bud bank, especially in mixed-grass prairie. Studies on vegetative reproduction typically begin after tiller emergence without consideration of bud stages, such as production, dormancy, and outgrowth (Devitt and Stafstrom, 1995; Ott and Hartnett, 2012; Shimizu and Mori, 2001). Studies that have incorporated bud stages have focused on new tiller growth in relation to bud location and size (Hendrickson and Briske, 1997; Ott and Hartnett, 2011). Some differences in bud bank development and tiller recruitment in tallgrass species were attributed to differences in photosynthetic pathway. Big bluestem (*Andropogon gerardii* Vitman), a C_4 grass, maintained a larger dormant bud bank, consistent bud development and transitions into tillers, and possessed long-lived buds

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(5 yr or more) (Ott and Hartnett, 2012). Scribner's panicum (*Dichanthelium oligosanthes* [Schult.] Gould), a C_3 grass, maintained a smaller dormant bud bank, inconsistent bud development, and active buds year-round (Ott and Hartnett, 2012). Further understanding of bud banks of native perennial grass species will have important implications for management of populations in perennial grasslands.

Fire is an important process affecting grassland productivity, species composition, and nutrient cycling. Fire, grazing, and drought effects on plant abundance are mediated through bud banks in tallgrass prairie (Benson and Hartnett, 2006; Benson et al., 2004; Carter et al., 2012; Dalgleish and Hartnett, 2009). In fact, perennial grass bud density increased with increasing fire frequency and was greater on burned than nonburned tallgrass prairie dominated by rhizomatous species (Benson and Hartnett, 2006; Benson et al., 2004; Dalgleish and Hartnett, 2009). These results suggest greater potential for aboveground production to be limited by meristem availability on areas excluded from fire. Alternatively, bunchgrasses may be susceptible to direct bud mortality following fire, which at least temporarily limits regrowth (Busso et al., 1993; Pelaez et al., 1997; Russell et al., 2013). Indirect fire effects, such as increased soil nitrogen availability and light quality, may compensate for direct loss of buds because both have been identified as factors promoting tiller recruitment (Tomlinson and O'Connor, 2004).

Nitrogen is typically the most limiting nutrient for plant productivity (Knapp et al., 1998; Owensby et al., 1970; Seasstedt and Knapp, 1993) and is believed to be influential for activation of grass buds, bud outgrowth, and tiller initiation from bud banks (Tomlinson and O'Connor, 2004). Previous studies have examined nitrogen effects on grass tiller demography (Briske and Butler, 1989; Derner and Briske, 1999), but few have examined nitrogen effects directly on the bud bank. Directly measuring buds per tiller, Dalgleish et al. (2008) noted nitrogen addition caused a statistically nonsignificant increase in bud production that translated into and explained most of an increase in population growth rate for the C_4 species, prairie dropseed (*Sporobolus heterolepis* [A. Gray]). On the basis of bud outgrowth and tiller emergence from bud banks, Williamson et al. (2012) reported inconsistent effects of nitrogen among three C_4 grasses and suggested C_3 and C_4 grasses may respond to different cues. More detailed characterization of bud banks is necessary in order to better comprehend species responses and thresholds following stimuli, such as fire or nitrogen.

We selected purple threeawn (*Aristida purpurea* Nutt.) to evaluate fire and nitrogen effects on bud banks. Purple threeawn is a native C_4 bunchgrass that is typically a minor component of the vegetation and considered midsuccessional but capable of dominating semiarid rangelands more than 60 yr following repeated or intensive disturbance (Costello, 1944; Evans and Tisdale, 1972; Horn and Redente, 1998; Hyder and Everson, 1968; Larson and Whitman, 1942; Smeins et al., 1976). The presence of sharp awns, accumulation of dead material within the plant, and high silica content of shoots also deter animals from grazing purple threeawn (Dufek et al., 2014; Heitschmidt et al., 1990). Therefore, it is often considered a weed species and improved understanding of bud bank response to fire and nitrogen should aid in development of threeawn management strategies.

The purpose of this study was to quantify purple threeawn axillary bud production response to fire and nitrogen treatments. Recent research indicates purple threeawn is susceptible to direct fire-induced mortality and that fire reduces threeawn cover, biomass, and tiller abundance of surviving plants (Russell et al., 2013; Strong et al., 2013a, 2013b). Further, fire reduced tillers and buds per plant by similar percentages under greenhouse conditions (Russell et al., 2013). Therefore, we predicted buds per tiller to be similar following summer fire, fall fire, or no fire and for buds per plant to be reduced by fire because of reduced tiller numbers (hypothesis 1). Reported effects of nitrogen on bud production have been limited and inconsistent (Dalgleish et al., 2008; Klimesova et al., 2009; Williamson et al., 2012) with no such data for purple threeawn. Nitrogen addition has reduced threeawn abundance (Hyder and Bement, 1972) but has more often been reported to have no effect on cover, biomass, or tiller abundance (Horn and Redente, 1998; Strong et al., 2013a, 2013b). With the premise that aboveground measures of plant abundance are reflections of the bud bank (Benson and Hartnett, 2006), we hypothesized that nitrogen addition would not alter the number of buds per tiller or buds per plant (hypothesis 2).

Materials and Methods

Study Site

Research was conducted in semiarid mixed-grass prairie in eastern Montana, near Terry. The site is within a 30 000-ha area that was broadly farmed and then abandoned and seeded to crested wheatgrass between 1936 and 1942 (McWilliams and Van Cleave, 1960). Average annual precipitation is 295 mm, with most occurring as rain from April through September. Temperature ranges from 43.8°C in summer to -42.8°C in winter and averages 6.6°C. The frost-free growing season is 105 to 135 days. Two sites, approximately 4.2 km apart, were evaluated. Both study sites are level upland plains on sandy ecological sites dominated by the Degrand soil series, a fine-loam over sandy or sandy-skeletal, mixed, superactive, frigid Aridic Argiustolls. The Degrand soil series is a deep, well-drained soil. Both sites had been moderately to heavily grazed (0.12 animal unit months$\cdot$ha^{-1}) for at least 40 yr, with most utilization during spring. Site 1 (lat 46°41′28″N, long 105°18′16″W) had been grazed from 1 April to 15 July and from 1 September to 14 November, and Site 2 (lat 46°43′51″N, long 105°18′16″W) was grazed from 1 May to 14 July and from 15 October to 22 November in recent decades. Livestock grazing was excluded from study sites in early summer 2009 and throughout the study.

Vegetation at the two study sites was dominated by purple threeawn and the perennial, introduced C_3 bunchgrass, crested wheatgrass (*Agropyron cristatum* [L.] Gaertn). Before treatment, these two species comprised 80–90% of the vegetation composition by weight (Strong et al., 2013b). Other C_4 perennial grasses included sand dropseed (*Sporobolus cryptandrus* [Torr.] A. Gray), blue grama (*Bouteloua gracilis* [Willd. *ex* Kunth] Lag. *ex* Griffiths), buffalograss (*B. dactyloides* [Nutt.] Engelm.), and tumblegrass (*Schedonnardus paniculatus* [Nutt.] Trel.). Other C_3 perennial graminoids included needle-and-thread (*Hesperostipa comata* [Trin. & Rupr.] Barkworth), western wheatgrass (*Pascopyrum smithii* [Rydb.] A. Löve), and Sandberg bluegrass (*Poa secunda* Presl). Cool-season annual graminoids were six weeks fescue (*Vulpia octoflora* [Walt.] Rydb.), Japanese brome (*Bromus arvensis* L.), and cheatgrass (*B. tectorum* L.). The subshrub, green sage (*Artemisia campestris* L.) was present, in addition to the perennial legume silverleaf Indian breadroot (*Pediomelum argophyllum* [Pursh.] J. Grimes) and the perennial forb yellow salsify (*Tragopogon dubius* Scop.). Annual forbs included field cottonrose (*Logfia arvensis* (L.) Holub) and rough false pennyroyal (*Hedeoma hispida* Pursh.).

Field Treatments and Sampling

Site 1 was assessed 2 years (2012) after initial fire treatments and Site 2 was assessed 1 year (2012) and 2 years (2013) after fire treatment. Fire and nitrogen amendments were combined in a fully factorial 3 × 3 arrangement with three replications by randomly assigning three fire treatments (no fire, summer fire, fall fire) and three levels of nitrogen (0, 46, 80 kg·ha^{-1}) to 27 plots (20 × 20 m) at each site. Fires were set using the ring-fire method (Wright and Bailey, 1982) and fuel loads were 2046 ± 294 kg·ha^{-1}. Summer fires were applied when purple threeawn seeds began dispersing and fall fires were applied after the first killing frost (< -2°C). We applied summer fire to Site 1 on 12 August 2010 (28–32°C, winds at 8–11 km h^{-1}, and 36–42% relative humidity) and Site 2 on 7 September 2011 (29–31°C, 5–13 km h^{-1} winds, and 15–20% relative humidity). Fall fires were applied at Site 1 on 18 October 2010 (17–18°C, 8–13 km h^{-1} winds, and 35–37% relative humidity) and at Site 2 on 31 October 2011 (16–20°C, winds at 13–30 km·h^{-1}, and 28–34% relative humidity).

Nitrogen amendments were applied in the spring and timed to coincide with cool temperatures and predicted precipitation to reduce nitrogen volatilization. Nitrogen was broadcasted as granular urea to individual plots. Site 1 was fertilized on 26 April 2011, with ambient temperatures of 10–13°C and rain later that evening. Site 2 was fertilized on 5 April 2012 with ambient temperature 10–13°C. The first precipitation after fertilization fell as rain on 26 April 2012.

Spring (Apr-Jun) precipitation explains most of the variation in productivity for the northern Great Plains (Heitschmidt and Vermeire, 2005; Vermeire et al., 2008, 2009) and varied radically throughout the 3 years of study. Spring precipitation was 227% (317 mm), 79% (110 mm), and 148% (207 mm) of the long-term mean (140 mm) during 2011, 2012 and 2013, respectively.

Laboratory Methods

Two tillers were harvested from two live purple threeawn plants in each replication of fire-nitrogen treatment combination during the seed-shattering stage, then cleaned, and processed in the Fort Keogh Livestock and Range Research Laboratory near Miles City, Montana, USA (lat 46°24′N, long 105°56′W) using microscopic dissection procedures. Tillers from Site 1 were harvested on 6 September 2012, and those on Site 2 were harvested 25 August 2012 and 15August 2013. Active, dormant, and dead buds per tiller were quantified using a double-staining procedure (Busso et al., 1989; Hendrickson and Briske, 1997). Axillary buds were stained with a 2, 3, 5-triphenyl tetrazolium chloride (TTC) solution to determine viability. Tillers were submerged in TTC solution in a completely dark environment for a 24-hour period at room temperature. Buds that stained bright pink at the conclusion of the 24-hour staining period were considered active. If dormant buds were present, the tiller was submerged into 0.25% Evan's 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). Only axillary buds located on the basal 20 mm of the tiller (crown region) were evaluated. Ten plants were randomly selected and permanently marked with flagging in each plot on Site 2 in conjunction with another study assessing fire effects on plant mortality (Strong et al., 2013a). Mean live tiller counts from marked plants were calculated for each plot and multiplied by total and active buds per tiller to determine buds per surviving plant.

Statistical Analysis

The study was initially designed to examine fire and nitrogen effects on buds across sites and by time since fire and nitrogen treatment. However, major differences in spring precipitation among years confounded effects of year, site, and time since treatment. Therefore, each unique combination of year, site, and time since treatment was labeled with an identifier that was used as a random variable. Bud-per-tiller data were tested to assess fire and nitrogen addition effects with models for analysis of variance using the MIXED procedure of SAS (Littell et al., 2006). Model assumptions for normality were tested using Shapiro-Wilk tests with the UNIVARIATE procedure of SAS, and the normality hypothesis was not rejected for any of the data. Models for active, dormant, and total (active and dormant) buds per tiller included the effects of fire treatment, nitrogen addition, and their interactions. Analysis of dead buds was initially planned but excluded because only two dead buds were detected across all samples of live tillers. Total and active buds per plant were analyzed with models for analysis of covariance, using pretreatment tillers per plant as a covariate and the effects of fire treatment, nitrogen addition, and their interactions for Site 2 one year after fire treatments. Plot was the experimental unit for all models. Mean separations were determined with tests of pairwise comparisons using the PDIFF option with the LSMEANS statement following significant F tests on main effects or interactions. Statistical significance was declared at $P < 0.05$ for all tests.

Results

Fire and nitrogen interacted in their effects on total axillary buds per tiller ($P < 0.0001$; Fig. 1). Without nitrogen addition, fall and summer fire reduced total buds per tiller about 70%. Nitrogen addition did not affect total buds per tiller for plots with no fire. However, number of buds per tiller was greater with nitrogen addition following fall fire and increased with each increase in nitrogen following summer fire. Addition of 80 kg N·ha^{-1} following fall or summer fire yielded total bud counts per tiller that were only 17% less than those with no fire and no nitrogen addition.

There was a similar tendency for fire and nitrogen to have interacting effects on active axillary buds per tiller ($P = 0.0778$) that reflected differences observed for total buds per tiller. However, active buds per tiller response simplified to main effects of fire ($P < 0.0001$) and nitrogen ($P = 0.0002$). Fall and summer fire similarly reduced active buds by 42% relative to plots with no fire (Fig. 2A). Adding nitrogen at either 46 or 80 kg·ha^{-1} increased active buds per tiller 60% compared with plots with no nitrogen addition (Fig. 2B). The number of dormant buds per tiller was similar across fire treatments ($P = 0.1815$; Fig. 2A) and levels of nitrogen ($P = 0.2087$; Fig. 2B).

Scaling up, fall and summer fire reduced total buds per plant 61 to 75% ($P < 0.0001$) and active buds per plant 66–72% ($P < 0.0001$; Fig. 3A). Number of dormant buds per plant was similar across fire

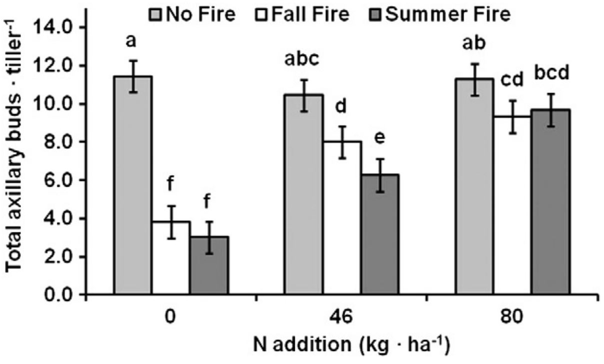

Fig. 1. Interacting effects of fire and nitrogen addition on total (active and dormant) axillary buds tiller^{-1} for purple threeawn and standard errors of the comparison. Means with a common letter are similar ($P > 0.05$).

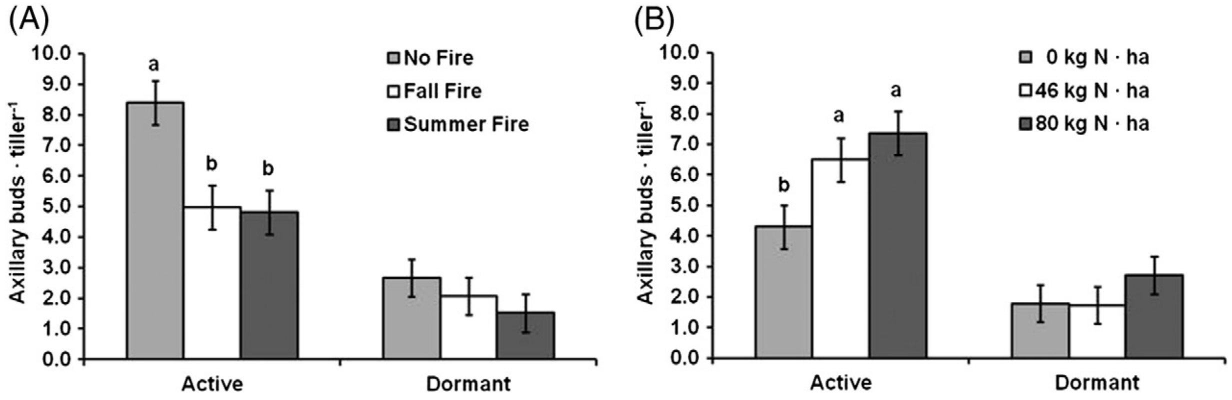

Fig. 2. Fire treatment **(A)** and nitrogen treatment **(B)** effects on active and dormant axillary buds tiller^{-1} of purple threeawn and standard errors of the comparison. Means within a panel and bud class followed by the same letter are similar ($P > 0.05$).

treatments ($P = 0.2404$) and comprised less than 25% of the total. Addition of 80 kg N·ha^{-1} increased total buds per plant 70% ($P = 0.0084$) relative to no nitrogen addition and 46 kg N·ha^{-1} had no detectable effect (Fig. 3B). Addition of 80 kg N·ha^{-1} increased active buds per plant 84% ($P = 0.0458$). Although adding 46 kg N·ha^{-1} increased buds per tiller, the number of active buds per plant after adding 46 kg N·ha^{-1} was intermediate and did not differ from that of 0 or 80 kg N·ha^{-1} treatments. Number of dormant buds per plant was similar among nitrogen treatments ($P = 0.8682$) and less than 18% of the total buds per plant were dormant.

Discussion

We hypothesized that 1) buds per tiller would be similar following summer fire, fall fire, or no fire and for buds per plant to be reduced by fire because of reduced tiller numbers and 2) nitrogen addition would not alter the number of buds per tiller or buds per plant. Fire and nitrogen each altered number of buds at both, the tiller and plant level, and had interacting effects on total buds per tiller. Support was limited for the hypothesis that fire reduces buds per plant solely through a reduction in tiller numbers. The greater relative reduction in buds per plant than for buds per tiller indicated fire reduced live tillers per surviving plant, as well as buds per tiller. Summer and fall fire caused similar reductions in total and active buds per plant. However, fire also reduced the number of active buds per tiller, indicating that burned plants having fewer buds per plant than nonburned plants was not due entirely to a reduction in tiller number. Contrary to our second hypothesis, buds were responsive to nitrogen, with total buds per plant increasing after addition of 80 kg N·ha^{-1} and active buds per tiller increasing with both levels of nitrogen addition. Fire and nitrogen effects on axillary buds proved to be more complex than originally hypothesized in that the two interacted when total buds were assessed on a per-tiller basis. Although fire clearly reduced total buds per tiller when no nitrogen or 46 kg N·ha^{-1} was added, adding 80 kg N·ha^{-1} mitigated fire effects. Additionally, nitrogen stimulated total bud production per tiller when plants had burned but had no effect on plants that had not burned.

These results are the first to directly show bud bank reductions of an opportunistic native grass due to prescribed burning at both tiller and plant levels. Fire reduced threeawn buds per plant to a much greater extent than observed by Russell et al. (2013) under well-watered greenhouse conditions. Aboveground threeawn biomass was reduced 90% and 73% with summer and fall fire in wet postfire growing conditions and 73% and 58% under dry postfire growing conditions (Strong et al., 2013b). After accounting for the fact that we measured only surviving plants, our bud results are comparable with reduced aboveground measures of threeawn abundance observed by Strong et al. (2013b), which incorporated effects of plant mortality. This suggests reductions in aboveground productivity were most likely the result of a depleted bud bank and, consequently, decreased tillering. Furthermore, sustained bud bank reductions with summer and fall fire should limit future tillering.

Reductions of buds following fire were likely direct heat effects due to threeawn's bunchgrass growth form and elevated meristematic crown positions. Bunchgrasses are especially sensitive to fire

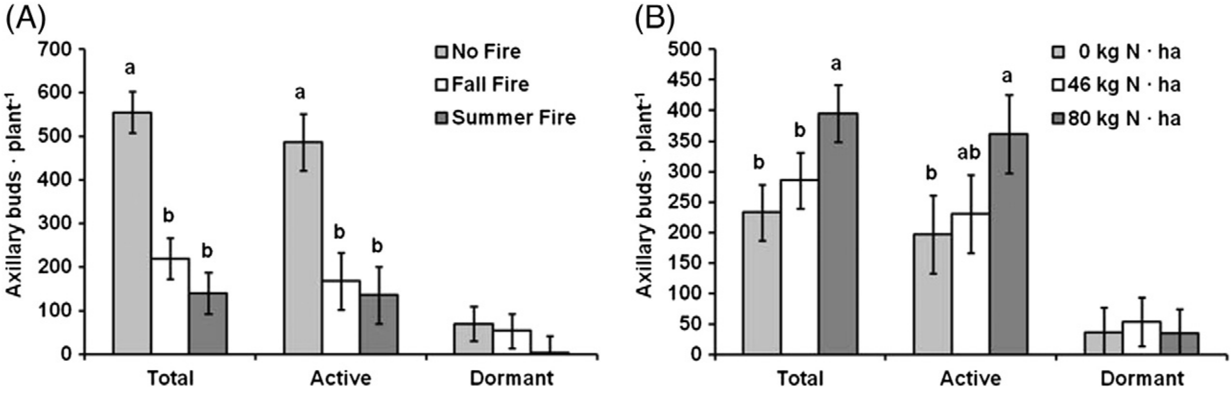

Fig. 3. Total, active and dormant axillary buds per plant by fire treatment **(A)** and nitrogen addition treatment **(B)** and standard errors of the comparison. Means within a panel and bud class followed by the same letter are similar ($P > 0.05$).

when plant material accumulates within the crown of the plant because the additional fuel can increase heat dosage (Wright, 1971). The susceptibility of bunchgrass buds has been observed directly, with more dead buds and fewer live buds soon after fire (Busso et al., 1993; Pelaez et al., 1997; Russell et al., 2013). Similar vulnerability has been observed indirectly, for threeawn in particular, through reduced cover and biomass and increasing plant mortality with increasing fuel load (Russell et al., 2013; Strong et al., 2013a, 2013b). In contrast, bud density has regularly been reported to increase with fire in tallgrass prairie dominated by rhizomatous species (Benson and Hartnett, 2006; Benson et al., 2004; Dalgleish and Hartnett, 2009). Photosynthetic pathway may affect bud phenology and help explain differential responses among species to timing of fire or other disturbances. For example, Ott and Hartnett (2012) suggested C_3 grasses are likely more vulnerable to spring fire than C_4 grasses because overwintering C_3 tillers are active, whereas many C_4 buds are still dormant during the spring fire season. However, growth habit is likely a better indicator of bud bank response to fire because bunchgrasses tend to have more elevated crowns and greater exposure of buds to heat damage.

Nitrogen is a key resource for plant growth (Seasstedt and Knapp, 1993), and some evidence suggests that nitrogen is important for bud activity and tillering, although multiple mechanisms are likely involved in each (Bonser and Aarssen, 2003; Briske and Derner, 1998; Tomlinson and O'Connor, 2004). We observed that both levels of nitrogen additions increased active buds per tiller to a similar degree. Therefore nitrogen appears to have been a qualitative cue directly involved with stimulating threeawn bud development. The increase in active buds following nitrogen addition was surprising in that others have observed little or no effect of nitrogen on threeawn cover, tiller number, or biomass (Horn and Redente, 1998; Strong et al., 2013a, 2013b) and aboveground measures are expected to reflect the bud bank (Benson and Hartnett, 2006). Tilman and Wedin (1991) observed some species to allocate more resources to reproduction with increasing nitrogen availability. Although it is possible the additional buds would yield greater tiller density given more time, grass buds are thought to be short-lived (Ott and Hartnett, 2012). Additionally, nitrogen addition increased biomass of some competing species (Strong et al., 2013b), which should limit space and resources for future threeawn tillering. The comparison between our results and the aboveground responses reported by others suggests the increase in buds does not translate into more aboveground productivity in the short term. In contrast, Dalgleish et al. (2008) noted that nitrogen addition sometimes increased the probability of tiller emergence from the bud bank but did not alter the number of buds per tiller or probability of bud survival for two bunchgrasses and concluded that any increase in the bud bank was from increased tillering and activation of existing buds. Similarly, Hendrickson and Briske (1997) observed grazing-induced reduction of the bud bank through reductions in plant density and tillers per plant, but grazing had no effect on buds per tiller. In our case, only the 80-kg nitrogen treatment showed increases in total and active buds per plant. The magnitude of the increases was similar to that of active buds per tiller, indicating that the increase in buds per plant was the result of more buds per tiller rather than more tillers. The specific reason why the additional bud production did not yield more tillers could not be determined from the data we collected, but numerous environmental factors can influence tiller initiation (Anderson et al., 2001; Williamson et al., 2012). Carter et al. (2012) observed similar results in mesic restored grassland, with greater bud density 1 year after severe drought and no change in stem density, and they suspected the response was due to increased nitrogen availability.

The reduction we observed in active buds per tiller indicates that bud mortality exceeded bud production after fire, but the data do not directly indicate which factor was more important. We were unable to determine whether mortality was primarily immediate or delayed because few dead buds were observed by sampling 10 to 24 months after fire. If mortality was delayed and driven by reallocation of resources, it is possible that rather than increasing bud production, nitrogen reduced bud mortality for burned plants. Alternatively, the greater number of buds following nitrogen addition to burned plants would necessarily have arisen from increased bud production if most mortality occurred during the period between fire and subsequent spring nitrogen application. We believe most mortality occurred shortly after fire, as reported for other bunchgrasses (Busso et al., 1993; Pelaez et al., 1997). This could indicate that the number of buds per tiller was constrained by intraplant competition without fire, whereas nitrogen was a limiting factor after fire reduced tiller numbers. The increase in active buds was not accounted for simply by transition of dormant to active buds because neither fire nor nitrogen altered number of dormant buds per tiller or per plant. Therefore, nitrogen addition appears to have generated new active buds on burned plants.

Implications

Fire and nitrogen had counteractive effects on purple threeawn axillary buds. Fire reduced buds through what we believe was direct bud mortality, whereas nitrogen addition increased bud production at tiller and plant levels. Threeawn bud responses to fire correspond well with previously observed reductions in aboveground abundance and increased plant mortality, further indicating that fire is an effective method of reducing purple threeawn. However, neither reductions nor lack of change in aboveground production observed by others following nitrogen addition could be explained by the bud bank because one would expect increased production with the increased number of threeawn buds. The greater number of buds could yield increased future tiller growth if the bud bank is maintained long enough but failed to do so during the one to two growing seasons after treatment.

More broadly speaking, our results lend support to the idea that nitrogen is important for bud development and may explain how nitrogen often increases tiller density. Additionally, the interaction of fire and nitrogen indicates effects on buds were conditional in that only burned plants responded to nitrogen, possibly due to a reduction in intraplant competition. This could help explain why bud response to nitrogen has been variable. Finally, there is potential for using targeted nitrogen application to increase bud banks and hasten postfire recovery if buds of more desirable bunchgrasses that are sensitive to fire respond similarly to those of purple threeawn.

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