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Fire, Defoliation, and Competing Species Alter *Aristida purpurea* Biomass, Tiller, and Axillary Bud Production

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Abstract

Aristida purpurea (purple threeawn) is a competitive native perennial grass with monoculturistic tendencies and poor palatability. We examined effects of fire, defoliation, and interspecific/intraspecific planting for 1) threeawn responses in the presence of threeawn, *Bouteloua gracilis*, or *Pascopyrum smithii*, and 2) *B. gracilis* and *P. smithii* response with threeawn. Biomass, aboveground production, tillers, and axillary buds were analyzed following two fire and four clipping treatments applied to three species–pair combinations in a completely randomized factorial design with nine replications. Fire killed 36% of threeawn. Fire reduced surviving threeawn biomass 61% and reduced production 27%. Threeawn production was greatest when neither plant was clipped and least when competing species were moderately clipped, or when both plants were severely clipped. Tiller counts of burned threeawn were similar among clipping treatments, and less than non-clipped or moderately clipped plants not burned. Fire decreased threeawn axillary buds on average by 25%. Moderately clipped plants had greater production than those from other clipping treatments across species. Average threeawn percentage of pot biomass was greater with *B. gracilis* (46 ± 3% SE) than *P. smithii* (38 ± 3% SE). Fire reduced threeawn from 60 ± 3% to 23 ± 3% of pot biomass, indicating good potential for rapid reductions in threeawn dominance and restoration of plant diversity with fire.

Key Words: *Bouteloua*, *Pascopyrum*, prescribed burning, productivity, purple threeawn, simulated grazing

INTRODUCTION

Purple threeawn (*Aristida purpurea* Nutt. and varieties) is a native C_4 grass capable of invading semiarid and arid rangelands that have experienced intensive disturbance (Klipple and Costello 1960; Evans and Tisdale 1972). The ability of *A. purpurea* to outcompete other native grass species for water and essential nutrients may produce plant communities trending toward *A. purpurea* monoculture (Evans and Tisdale 1972; Hyder and Bement 1972; Fowler 1990). When *A. purpurea* is the most prominent member of the plant community, the ability of other native grass species to establish and proliferate is impaired and *A. purpurea* may remain the dominant species for 60+ yr (Costello 1944; Evans and Tisdale 1972; Horn and Redente 1998). Threeawn-dominated plant communities are a serious management concern for both livestock and wildlife because of low palatability and poor forage quality relative to many other native grass species (Meyer and Brown 1985).

Greenhouse and field trials have revealed numerous characteristics that enhance the competitive ability of *A. purpurea*. Threeawn plants produce a substantial amount of seed that enter the ground quickly and have a high probability of germination (Evans and Tisdale 1972; Fowler 1986). Post-germination, *A. purpurea* plants begin producing a robust root system, quickly gaining access to soil water and nutrient pools (Evans and Tisdale 1972; Wedin and Tilman 1993; Busso et al. 2001; Perkins and Owens 2003). Furthermore, *A. purpurea* is rarely grazed (Heitschmidt et al. 1990). In the event *A. purpurea* is defoliated, individuals respond by increasing root mass (Briske et al. 1996). This strategy increases the area the plant can access for soil water and nutrients. Threeawn shoots have a high shoot C:N ratio (Vinton and Burke 1995; Horn 1996), which is believed to indicate effective belowground competition with greater ability to absorb soil nutrients, particularly nitrogen (Tilman 1982; Tilman and Wedin 1991). Understanding the competitive response and effect of *A. purpurea* is the first step toward identifying management tools that can be used to reduce threeawn.

Fire and grazing are naturally occurring processes with which grasslands throughout the world evolved (Axelrod 1985). From a management perspective, prescribed fire and grazing can be utilized to maintain productive plant communities (Fuhlendorf and Engle 2004; Vermeire et al. 2008; Vermeire et al. 2011). *A. purpurea* is avoided by most herbivores (Klipple and Costello 1960; Heitschmidt et al. 1990), but may be negatively impacted by fire (Trlica and Schuster 1969; Steuter and Wright 1983; Parmenter 2008). *A. purpurea* has buds near the soil surface and elevated in the crown, making it more vulnerable to fire (Trlica and Schuster 1969) than species with greater proportions of their buds

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deeper in the soil, such as western wheatgrass (*Pascopyrum smithii* Rydb.), and blue grama (*Bouteloua gracilis* Willd. ex Kunth). One of the primary characteristics that allows *A. purpurea* to escape grazing pressure is the accumulation of dead material in the crown of plants (Heitschmidt et al. 1990). Fire would also reduce dead material, allowing grazers access to the regrowth of *A. purpurea*. Additionally, regrowth of *A. purpurea* after fire should have more complete nutritional quality relative to *A. purpurea* which has not been burned (Tracy and McNaughton 1997). *A. purpurea*'s susceptibility to fire damage (Steuter and Wright 1983; Parmenter 2008), improved palatability of surviving plants, and the neutral or positive response of dominant competing species in the northern Great Plains (Vermeire et al. 2011) indicate fire and grazing may be appropriate management tools for threeawn-dominated plant communities.

The purpose of this study was to develop a more complete understanding of *A. purpurea* response to fire and defoliation in the presence of other native grasses and observe the response of other native grasses to fire and defoliation in the presence of *A. purpurea*. More specifically, we hypothesize that 1) fire reduces *A. purpurea* biomass production, tiller number, and axillary buds; 2) increasing clipping severity reduces *A. purpurea* biomass production, tiller number, and axillary buds; 3) *A. purpurea* biomass, tiller, and axillary bud production are greater in an interspecific planting than an intraspecific planting; and 4) the combination of fire and clipping reduces *A. purpurea* biomass relative to competing species.

METHODS

Seeds of *A. purpurea*, *P. smithii*, and *B. gracilis* were obtained from Native American Seed Farm (Junction, Texas), USDA-NRCS Bridger Plant Materials Center (Bridger, Montana), and USDA-NRCS Bismarck Plant Materials Center (Bismarck, North Dakota), respectively, during June 2011. Seeds were germinated at 25°C with a 12-h photoperiod at Fort Keogh Livestock and Range Research Laboratory in Miles City, MT (lat 46°22′52”, long 105°53′04”). On 1 July 2011, seedlings were assigned to one of three paired combinations (*B. gracilis*/*A. purpurea*, *P. smithii*/*A. purpurea*, or *A. purpurea*/*A. purpurea*) and transplanted into plastic pots (22 cm diameter × 22 cm height) filled with a 3:1 (volume:volume) mix of washed sand sifted through a 2-mm sieve and potting mix. Sand was sterilized with the use of an electric soil sterilizer. The potting mix (Sunshine Mix 1; Sun Gro Horticulture, Inc., Vancouver, BC) contained sphagnum peat moss, coarse perlite, starter nutrient charge with gypsum, and dolomite limestone. Pots were maintained near field capacity by watering every 2–3 d throughout the experimental period with a light shower hose setting for 4–5 s per pot, which allowed for thorough wetting without water running out the bottom of pots. Throughout summer months we utilized natural lighting and greenhouse conditions followed seminatural temperatures, with July being the hottest month ranging from 15.6 to 41.2°C. Supplemental lighting was used to extend the photoperiod by 3 h starting on 7 November 2011. Temperatures were lowest throughout December in the greenhouse and were maintained between 4.8 and 25.8°C.

A factorial arrangement of two fire and four clipping treatments were applied to each of the three species–pair combinations in a completely randomized design with nine replications. Shoots were harvested for final biomass estimates and bud sampling 187 d after being transplanted into pots. Aboveground biomass for each species at time of fire was estimated by harvesting shoots from additional species–pair combinations (16 *B. gracilis*, 14 *P. smithii*, and 57 *A. purpurea*) not subjected to treatments. Production was estimated as the sum of combusted, clipped, and final biomass. The two distinct measurements of plant mass are hereafter referred to simply as biomass (i.e., final) and production. All harvested biomass was dried at 60°C for 48 h prior to weighing.

Fire treatments consisted of 1) summer fire and 2) no fire. Fire was applied to potted plants on 27 September 2011 with the use of the fire cage method described by Vermeire and Rinella (2009) with a fuel load of $2\,000\ \mathrm{kg \cdot ha^{-1}}$ to represent typical summer fire conditions of the northern mixed-grass prairie. Fires burned with an ambient temperature of 26.7–32.2°C, 13–38% relative humidity, and 11.3 to 16.1 $\mathrm{km \cdot h^{-1}}$ winds. Six type-K thermocouples insulated with ceramic fiber and Inconel braidings (Omega Engineering, Stamford, CT) were placed 1–3 cm below the soil surface in the center of an *A. purpurea* plant crown. Thermocouples were connected to a 21X micrologger with a CR23X storage module (Campbell Scientific, Logan, UT), which was connected to a laptop computer to record time–temperature profiles at 1-s intervals during treatment. Thermocouple data were used to determine duration of temperatures greater than 60°C (duration), maximum temperature, and the sum of the products of time and temperature greater than 60°C (degree-seconds) to estimate heat dosage. At the time of fire, *A. purpurea* and *B. gracilis* had reached the seed-head stage of development, but remained green. *P. smithii* remained in the vegetative stage throughout the study.

Clipping treatments consisted of 1) no clipping of either plant, 2) no clipping of *A. purpurea* and moderate clipping of adjacent plants, 3) moderate clipping of *A. purpurea* and severe clipping of adjacent plants, and 4) severe clipping of *A. purpurea* and adjacent plants. One plant was randomly selected and marked with a pin flag to designate which received the more severe clipping treatment when both plants were *A. purpurea*. For *A. purpurea* and *P. smithii*, 10-cm and 5-cm stubble heights represent moderate and severe clipping, respectively. For *B. gracilis*, 6-cm and 3-cm stubble heights represented moderate and severe clipping, respectively. Clipping treatments were applied on 4 November 2011 with the use of hand clippers. Given grazing selection against *A. purpurea*, clipping treatments were designed to simulate expectations that utilization of *A. purpurea* would occur to a lesser degree than the competing species and only after availability of the more desired species became limited.

Concurrently with final biomass sampling, a tiller was harvested from each plant in four replications of each species–treatment combination (192 plants). The tillers were cleaned and processed in the Fort Keogh laboratory with the use of microscopic dissection procedures. Total, active, dormant, and dead buds were determined with the use of a double-staining procedure as described by Busso et al. (1989) and 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 for a 24-h period in a completely dark environment. Buds were considered active when stained a bright pink. 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 identified from dormant buds by staining a deep blue (Gaff and Okong'o-ogola 1971). Active and dormant buds were summed then multiplied by tiller counts and reported as number of live axillary buds per plant.

The maximum number of buds per tiller was based on the cumulative sum of four bud categories: 1) buds that had grown out to form tillers, rhizomes, or stolons (live or dead), 2) missing buds based on the occurrence of bud scars, 3) leaf scars, and 4) existing visible buds (Hendrickson and Briske 1997). Leaf scars located at the point of sheath attachment to the tiller base identified the position of potential buds when a bud scar could not be located. Only those axillary buds located on the basal 20 mm of the tiller (crown region) were evaluated. We recognize that some species may not possess buds in all leaf axils (Mueller and Richards 1986).

Maximum temperature, duration of heat > 60°C, and heat dosage (degree-seconds > 60°C) were each tested as predictor variables for mortality of burned *A. purpurea* with logistic regression with the use of SAS LOGISTIC (Hosmer and Lameshow 2000; Menard 2002). *A. purpurea* and competing plants had different clipping treatments and were analyzed separately in what is hereafter discussed as Experiment I (*A. purpurea*) and Experiment II (competing plant). Models for biomass, biomass production, tiller counts, and axillary buds were analyzed with the use of analysis of variance ANOVA with the MIXED procedure of SAS (Littell et al. 1996) for both experiments. Models for Experiment I and the proportion of pot biomass comprised of *A. purpurea* tested the main effects of species combination, fire, clipping treatment, and their interactions. Models for Experiment II (*A. purpurea*, *B. gracilis*, and *P. smithii* grown with *A. purpurea*) contained terms for species, fire, clipping treatment, and their interactions. Mean separations were determined with *t* tests of pairwise comparisons with the use of the PDIFF option with the LSMEANS statement following significant *F* tests on main effects or interactions, and significance for all tests was declared at $\alpha=0.05$. All results are reported as mean ± standard error of the mean (SEM).

RESULTS

Experiment I. *Aristida purpurea* Response

Mortality was 36% (52/144) for *A. purpurea* plants exposed to fire and resulted in substantial reductions of biomass for this species. None of the 144 nonburned *A. purpurea* plants died. Mortality increased with duration of heat ($P < 0.01$) and heat dosage ($P < 0.01$; Fig. 1). However, maximum temperature was not a good predictor of *A. purpurea* mortality ($P > 0.24$). Duration of heat was the best predictor of plant mortality, with the *C*-statistic (0.71) indicating the model correctly assigned greater probability of mortality for 71% of all pairs where one plant lived and one died. The Hosmer–Lameshow test also indicated the model fit the data well ($P > 0.17$). *A. purpurea* individuals had a 50% probability of survival when temperatures were greater than 60°C for 5 min. Heat dosage closely followed duration of heat as a reliable predictor of plant mortality, with a *C*-statistic of 0.64 and a good fit for the model ($P > 0.10$). Unless otherwise stated, all other results were based on surviving plants only.

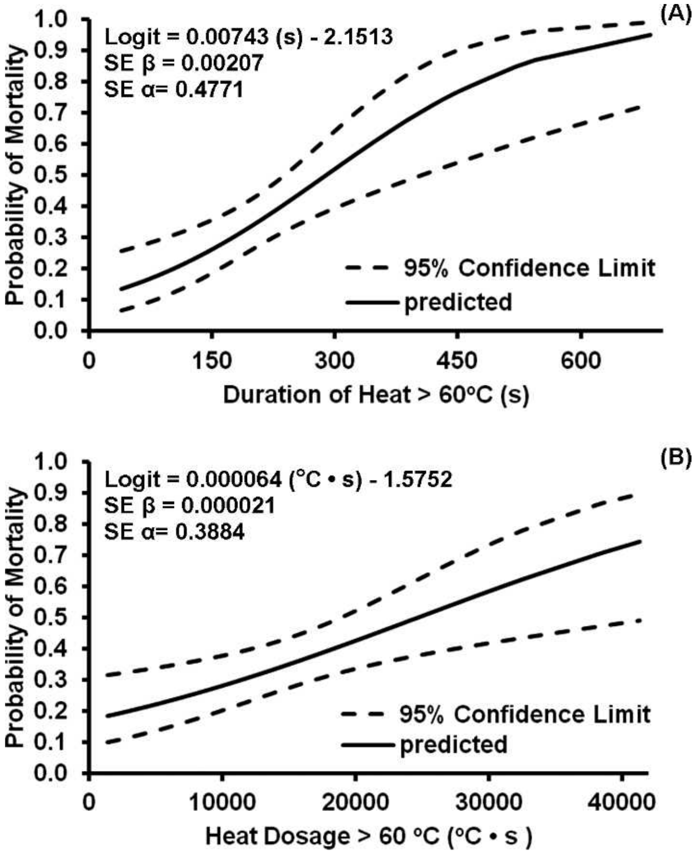

Figure 1. Predicted mortality and 95% confidence intervals for an *Aristida purpurea* individual based on **A**, duration of heat greater than 60°C at the soil surface; and **B**, heat dosage measured as degree-seconds greater than 60°C. Probability of mortality $=(e^{\alpha+\beta x})\cdot(1+e^{\alpha+\beta x})^{-1}$.

Fire and clipping interacted in their effects on *A. purpurea* biomass at the end of the experiment ($P < 0.01$; Table 1). As expected, nonburned plants that were moderately or severely clipped had less biomass than nonclipped plants. Surprisingly, biomass was less for nonburned plants when their neighbor was clipped than when neither plant was clipped. Biomass did not differ among clipping treatments for burned plants. Burned plants, across clipping treatments, had less *A. purpurea* biomass than nonburned plants that were not clipped.

Fire effects on production varied by species combination ($P < 0.04$). *A. purpurea* grown with *B. gracilis* produced 22% less biomass when burned and 21% less than non-burned *A. purpurea* grown with *A. purpurea* (Fig. 2). Fire did not reduce production of *A. purpurea* when planted with *P. smithii* or *A. purpurea* (Fig. 2). Production was greatest when neither plant was clipped and least when the competing species was

Table 1. Fire and clipping effects on mean (SEM) tiller number and biomass of *Aristida purpurea* (Experiment I) and competing species (Experiment II).

Measurement	Clipping[1]	No fire	Fire
Experiment I			
Biomass (g · plant^{-1})	NN	4.46 (0.23) a[2]	0.88 (0.28) cd[3]
	NM	2.94 (0.23) b	0.75 (0.30) d
	MS	1.53 (0.23) c	0.81 (0.30) cd
	SS	1.00 (0.23) cd	0.51 (0.31) d
Tillers (*n*)	NN	28 (1.6) a	15 (1.6) d
	NM	24 (1.6) ab	17 (1.6) cd
	MS	23 (1.6) ab	18 (1.6) cd
	SS	21 (1.6) bc	17 (1.6) cd
Experiment II			
Biomass (g · plant^{-1})	NN	3.44 (0.16) a	1.18 (0.17) c
	MN	2.00 (0.16) b	1.21 (0.18) c
	SM	0.93 (0.16) cd	0.73 (0.20) cd
	SS	0.96 (0.16) cd	0.63 (0.18) d

[1] NN=no clipping of either plant, NM=no clipping of *A. purpurea* and moderate clipping of adjacent species, MS=moderate clipping of *A. purpurea* and severe clipping of adjacent species, SS=severe clipping of *A. purpurea* and adjacent species.

[2] Means within measurement with a common letter do not differ ($P > 0.05$).

[3] Exclusion of killed plants from biomass data reduced *n* for burned fire × clipping means from 27 to 18, 16, 16, and 15 for NN, NM, MS, and SS, respectively.

moderately clipped, or when both plants were severely clipped ($P < 0.04$; Table 2).

Fire and clipping interacted in their effects on *A. purpurea* tiller numbers ($P < 0.05$; Table 1). Severe clipping reduced tiller numbers for nonburned plants compared to when neither plant was clipped. Tiller counts of burned plants did not differ among clipping treatments, all of which had fewer tillers than nonburned plants that were not clipped or moderately clipped. Severe clipping yielded similar *A. purpurea* tiller counts regardless of fire. Fire decreased the number of live axillary buds per plant by 25% ($P < 0.01$). *A. purpurea* produced 75 ± 5 axillary buds without fire and 56 ± 5 axillary buds with fire. Species combinations alone did not affect *A. purpurea* biomass ($P > 0.68$), axillary buds ($P > 0.17$), or tiller numbers ($P > 0.14$).

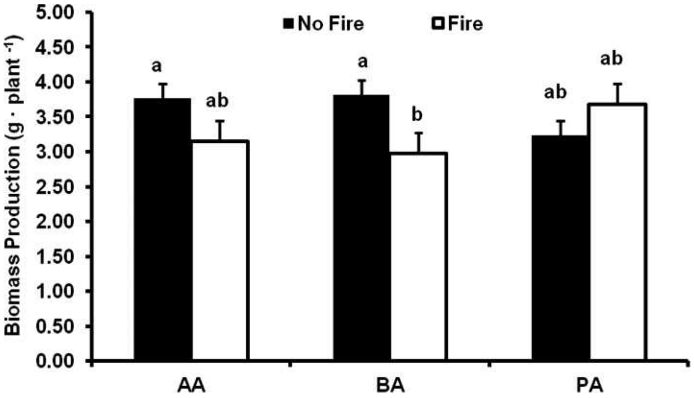

Figure 2. Mean *Aristida purpurea* biomass production and SEM bars in response to fire and species combination. A=*A. purpurea*, B=*Bouteloua gracilis*, and P=*Pascopyrum smithii*. Exclusion of killed plants from production data reduced *n* for burned fire × species combination means from 36 to 27, 19, and 19 for AA, BA, and PA, respectively. Means with a common letter do not differ ($P > 0.05$).

Experiment II. Competing Plant Responses

Fire effects on biomass varied by species ($P < 0.01$; Table 3). Fire reduced biomass of *B. gracilis* by 60% and *A. purpurea* by 61%. Biomass was similar between burned and nonburned *P. smithii*. Clipping effects on biomass varied by fire treatment ($P < 0.01$) and by species ($P < 0.03$). Without fire, moderately clipped plants with nonclipped neighbors had less biomass than those with neither plant clipped and more biomass than severely clipped plants (Table 1). However, when plants were burned, biomass was reduced only when both plants were severely clipped relative to moderately and nonclipped plants. Severe clipping reduced *A. purpurea* biomass compared to moderate or no clipping and any clipping reduced *B. gracilis* biomass (Fig. 3). Biomass of *P. smithii* decreased with increasing clipping intensity.

Fire effects on biomass production varied by species ($P < 0.01$; Table 3). Fire reduced biomass production of *P. smithii* by 31% and *A. purpurea* by 27%, whereas *B. gracilis* production was similar between burned and nonburned plants. *A. purpurea* was most productive among nonburned plants, but with fire, production was similar to that of *B. gracilis*.

Table 2. Effects of clipping intensity on mean biomass production, axillary buds, and tillers for *Aristida purpurea* (Experiment I) and competing species (Experiment II).

	Clipping treatment[1]					
Measurement	NN	NM	MS	SS	SEM	*P* value
Experiment I						
Production (g · plant^{-1})	3.88 a[3]	3.06 b	3.51 ab	3.29 b	0.22	0.04
Axillary buds[2] (*n*)	75	68	64	54	6.7	0.18
Experiment II						
Production, (g · plant^{-1})	3.18 b	3.78 a	3.13 b	3.26 b	0.17	0.02
Axillary buds (*n*)	75	80	82	67	9.1	0.66
Tillers (*n*)	23	21	20	20	1.3	0.39

[1] NN=no clipping of either plant, NM=no clipping of *A. purpurea* and moderate clipping of adjacent species, MS=moderate clipping of *A. purpurea* and severe clipping of adjacent species, SS=severe clipping of *A. purpurea* and adjacent species.

[2] Axillary buds include dormant and active bud estimates.

[3] Means within measurement with a common letter do not differ ($P > 0.05$).

Table 3. Fire effects on mean (SEM) biomass and production for competing species (Experiment II).

Measurement	Species	No fire	Fire
Biomass, (g · plant^{-1})	*Aristida purpurea*	2.56 (0.14) a[1]	1.01 (0.16) c
	Bouteloua gracillis	1.38 (0.14) bc	0.55 (0.15) d
	Pascopyrumsmithii	1.55 (0.14) b	1.26 (0.16) bc
Production (g · plant^{-1})	*A. purpurea*	4.59 (0.18) a	3.35 (0.21) b
	B. gracillis	3.24 (0.18) b	3.38 (0.20) b
	P. smithii	3.23 (0.18) b	2.23 (0.21) c

[1] Means within measurement with a common letter do not differ ($P > 0.05$).

Moderately clipped plants had greater production than those from other clipping treatments across species (Table 2).

Tiller counts increased ($P < 0.01$) from *P. smithii* to *A. purpurea*, then *B gracilis* (10, 22, and 31 ± 1 tiller · plant^{-1}) and axillary buds were nearly twice as abundant ($P < 0.01$) for *B. gracilis* (112 buds) as they were for *P. smithii* (53 buds) or *A. purpurea* (63 ± 8 buds). Fire reduced tillers across species from 23 to 18 ± 1 tiller · plant^{-1} ($P < 0.01$). There were no clipping treatment effects on tiller number ($P > 0.38$). Dormant and active axillary bud counts were similar across fire ($P > 0.16$) and clipping ($P > 0.66$) treatments.

Proportional *A. purpurea* Biomass

Excluding killed plants, the percentage of pot biomass comprised of *A. purpurea* was greater ($P < 0.01$) when grown with *B. gracilis* (57 ± 3%) than with *P. smithii* (45 ± 3%). Fire reduced *A. purpurea* from 60 ± 2% to 41 ± 4% of the pot biomass ($P < 0.01$). Percentage of pot biomass was similar across clipping treatments ($P > 0.28$).

Including plants that were killed, *A. purpurea* comprised a greater ($P < 0.05$) percentage of the pot biomass when grown with *B. gracilis* (46 ± 3%) than with *P. smithii* (38 ± 3%). Fire reduced *A. purpurea* from 60± 3% to 23 ± 3% of the pot biomass ($P < 0.01$). The inclusion of killed plants indicated a clipping effect ($P < 0.04$). No treatments differed from nonclipped plants with nonclipped neighbors (41 ± 4%). However, severe clipping of both plants reduced the percentage of pot biomass attributed to *A. purpurea* (32 ± 4%) compared to nonclipped plants with moderately clipped neighbors (46 ± 4%) and moderately clipped plants with severely clipped neighbors (48 ± 4%).

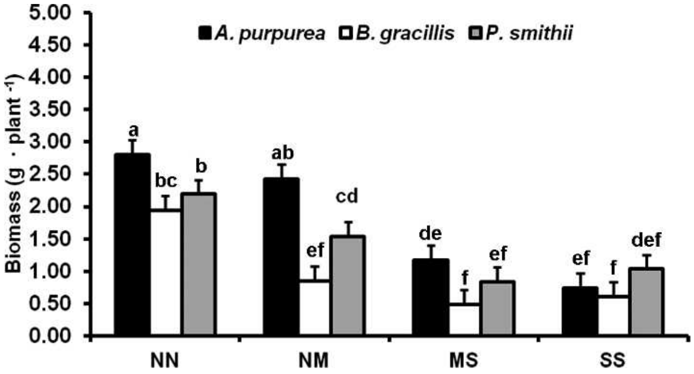

Figure 3. Mean biomass and SEM bars by species grown with *Aristida purpurea* and clipping treatment. Clipping treatments consisted of NN=no clipping of either plant, NM=no clipping of *A. purpurea* and moderate clipping of adjacent species (NM), MS=moderate clipping of *A. purpurea* and severe clipping of adjacent species (MS), SS=severe clipping of *A. purpurea* and adjacent species, respectively. Means with a common letter do not differ ($P > 0.05$).

DISCUSSION

We observed considerable mortality of *A. purpurea* when exposed to fire, and heat duration and dosage were excellent predictors of this response. Data support hypothesized reductions in *A. purpurea* biomass production and axillary buds due to fire. However, our data demonstrate that fire alone did not directly reduce *A. purpurea* tiller production for surviving plants. As hypothesized, severe clipping reduced *A. purpurea* production and tiller number relative to no clipping at all, but no clipping of *A. purpurea* and moderate clipping of its neighbor caused a similar reduction in productivity. Results do not support anticipated increases in biomass, tiller production, and axillary bud production of *A. purpurea* in interspecific compared to intraspecific plantings. The only case in which species combination affected production, tiller number, or axillary buds was that fire reduced production of *A. purpurea* when grown with *B. gracilis*. Our data partially support the hypothesis that the combination of fire and clipping decreases *A. purpurea* biomass relative to *B. gracilis* and *P. smithii* biomass composition in that there was a strong fire effect, but clipping effects were only observed when including plants killed by fire.

Effects of fire on *A. purpurea* production align with previous work on perennial threeawns throughout the High Plains of Texas (Trlica and Schuster 1969; Steuter and Wright 1983) and the short-grass steppe in the Chihuahuan Desert (Parmenter 2008). Postfire reduction of *A. purpurea* plant size in the Chihuahuan Desert demonstrated more than 4 yr were required to recover prefire basal cover fully (Parmenter 2008). However, postfire drought was speculated to have contributed to the slow recovery of *A. purpurea*. Nevertheless, fire and drought may provide opportunities for species, such as *B. gracilis* or *P. smithii*, that evolved under this type of regime in semiarid environments to thrive in a previously *A. purpurea*–dominated site.

In addition to reductions in *A. purpurea* production, axillary bud and tiller numbers were also reduced by fire. Inhibiting vegetative reproduction of *A. purpurea* could be a crucial management factor because of bunchgrasses' capacity for rapid biomass recovery, which primarily occurs by abundant tillering from preformed axillary buds (Fidelis et al. 2012). Caespitose grasses, such as *A. purpurea*, also possess the ability to increase root mass, accumulate nutrients underneath the crown, and rapidly expend released nutrients to increase tillering (Briske et al. 1996; Derner et al. 1997). Therefore, limiting the reproductive potential of the *A. purpurea* bud bank by decreasing axillary bud production reduces an individual's ability to recover rapidly within a growing season. Furthermore, decreasing the amount of axillary buds reduces the potential for new *A. purpurea* tillers to form from pre-existing tillers, providing a greater opportunity for more fire-resilient species, such as *B. gracilis* or *P. smithii*, to become established.

Because of the resistance and resiliency of *B. gracilis* and *P. smithii* to fire (Vermeire et al. 2011), we expected to elicit increased production responses of these more desirable, native perennial grass species. The observed reductions in *P. smithii* production may be a short-term response given the timing of postfire sampling. *Pascopyrum smithii* production has been shown to more than double on burned sites the second year following fire (Vermeire et al. 2011). In the same study, *P. smithii* standing crop was 47% greater for burned than nonburned sites following a summer fire with a wet spring in the northern Great Plains. Our observation of similar biomass production between burned and nonburned *B. gracilis* is consistent with previous research illustrating consistently high allocation of resources belowground throughout the growing season, short-shoot growth form, and high regrowth potential (Menke and Trlica 1981).

We expected defoliation of either *B. gracilis* or *P. smithii* to release resources available for increased growth of *A. purpurea*, as suggested by competition theory (Wardle et al. 1999). However, we observed reduced *A. purpurea* production when the more palatable neighboring species were moderately defoliated and increased production of neighboring species when they were moderately defoliated. The mechanism responsible for this result is not clear, based on the data collected. Defoliation of *A. purpurea* has been shown to shift carbon allocation from shoots to roots (Briske et al. 1996; Busso et al. 2001), and indirect results of defoliated neighboring plants (Briske and Hendrickson 1998) may have further prioritized capture of belowground space and resources. Thus, energy invested toward construction and maintenance of extensive root densities may compromise *A. purpurea*'s short-term ability to increase aboveground biomass. Alternatively, additional resource demand by the defoliated neighbor plants could have increased belowground competition.

The reduced biomass production following moderate clipping of neighboring species could be a short-term response. For example, Busso et al. (2001) reported positive correlations between root length, density, and total biomass production on nondefoliated *A. purpurea* plants. Further, Smith and Knapp (2003) reported as much as a 2-yr delay in aboveground responses due to neighbor removal in C_4-dominated grassland. In our study, 61 d may not have been sufficient time for *A. purpurea* to respond positively to neighbor defoliation, but undoubtedly allowed expression of negative effects. Further research is needed to elucidate this interaction, including the time for which these reductions can be sustained. There is evidence that slight shifts in aboveground species dominance can provide advantageous opportunities for *B. gracilis* and *P. smithii* to increase production postfire (Vermeire et al. 2011). Thus, sustainable changes in species composition could be expected, given the findings of our current work. It is also important to point out that the impacts of neighbor clipping on *A. purpurea* tiller numbers were different in the presence versus absence of fire. In the presence of fire, defoliation does not play an important role in reducing tiller counts of *A. purpurea*, and in the absence of fire, clipping reduced tiller counts.

Defoliation effects on *B. gracilis* and *P. smithii* in this study were consistent with other studies (Milchunas et al. 1990; Manley et al. 1997; Hart and Ashby 1998) and suggest these species are capable of persisting with *A. purpurea*. Production of *B. gracilis* and *P. smithii* biomass following moderate defoliation demonstrates these species' potential to resist competitive exclusion by the more competitive *A. purpurea*. Other research has reported that certain responses to disturbance may suppress the overall greater competitive ability of a dominant species, potentially displacing dominant species (Briske and Hendrickson 1998; Hendon and Briske 2002). Multiple studies have reported that diverse rangelands are resilient to the effects of postfire grazing, such as tallgrass prairie (Fuhlendorf and Engle 2004), sagebrush steppe (Bruce et al. 2007; Bates et al. 2009), and semiarid grasslands (Guevara et al. 1999; Drewa and Havstad 2001). More specifically, deferment of grazing during the first postburn growing season in shortgrass steppe has had no effect on forage production compared to sites grazed at a moderate stocking rate (Augustine et al. 2010).

MANAGEMENT IMPLICATIONS

Restoring naturally occurring processes, such as fire and grazing in the northern Great Plains, is consistent with management strategies that account for processes to which these species are adapted. Therefore, it is doubtful that employing these types of strategies will result in complete eradication of *A. purpurea*, but instead will most likely increase grazing capacity and native plant diversity. Our results demonstrate potential for prescribed burning and grazing to decrease *A. purpurea* biomass and encourage increases in abundance of other native plant species to disrupt near-monocultures of *A. purpurea*. The degree to which *A. purpurea*–dominated communities are affected by prescribed burning and grazing remains unknown. However, our results indicate that *A. purpurea* biomass reductions due to fire and postfire defoliation may be important factors in reducing *A. purpurea* abundance. Future research should focus on timing and intensity of prescribed burning in conjunction with postfire grazing strategies on rangelands in order to alter *A. purpurea*–dominated sites.

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