FIRE AND NITROGEN EFFECTS ON A PURPLE THREEAWN-DOMINATED PLANT COMMUNITY IN THE NORTHERN GREAT PLAINS

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Fire and nitrogen effects on a purple threeawn-dominated plant

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MASTER OF SCIENCE

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ABSTRACT

Purple threeawn (*Aristida purpurea* Nutt. varieties) is a native grass capable of rapidly increasing on rangelands, forming near monocultures, creating a stable state. Rangelands throughout the Great Plains and Intermountain West have experienced increases in purple threeawn abundance, leading to reductions in overall forage quality and community diversity. Our objectives were to: 1) examine prescribed fire and nitrogen as tools to shift species composition in a purple threeawn invaded community, 2) reveal vegetation management strategies appropriate for reducing purple threeawn abundance 3) quantify fire effects on purple threeawn plant characteristics and 4) determine the relationship between purple threeawn survival and fire behavior. Fire reduced purple threeawn abundance one-growing season post-fire, with sustained reductions two-growing seasons post-fire. Nitrogen had no effect on purple threeawn abundance. Heat duration and dosage were good predictors of purple threeawn mortality. Summer prescribed fire appears to be the best management tool to reduce purple threeawn abundance.

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DEDICATION

I dedicate this thesis to my family and friends. You have supported me in everything I have ever done and each of you has had a profound impact on my life.

PREFACE

Chapters 2 and 3 of this thesis were written as manuscripts that will be submitted to peer-reviewed journals. Chapter 2, "Fire and nitrogen effects on purple threeawn abundance in northern mixed-grass prairie," will be submitted to *Rangeland Ecology and Management*. Chapter 3, "Fire effects on purple threeawn basal area, tiller production, and survival," will be submitted to *Fire Ecology*. Each chapter follows the style and guidelines of the respective journal in which it was intended to be submitted.

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CHAPTER 1. PURPLE THREEAWN: AN OPPORTUNISTIC NATIVE GRASS

Introduction

The North American grassland biome evolved under variable climatic conditions, recurrent fire, and extensive grazing by large free-roaming ungulates (Axelrod 1985). The interaction of these three factors facilitated the development of heterogeneous ecosystems such as tallgrass prairie, mixed-grass prairie, and shortgrass steppe (Fuhlendorf and Engle 2001). With the advent of European settlement, grassland heterogeneity declined through the loss of wild ungulates, farming practices, the introduction of non-native species, less frequent use of fire, and the confinement of domestic livestock (Samson et al. 2004). As grassland became more homogenous the prevalence of individual species or functional groups within plant communities shifted. Perennial threeawn (*Aristida purpurea* Nutt. varieties) is an example of a species which has thrived under the disturbance regime of post-European settlement (Costello 1944; Evans and Tisdale 1972).

The *Aristida* genus is comprised of nearly 300 species found in warm and temperate grassland ecosystems throughout the world (Allred 1984). Many *Aristida* species are native to North America, where 60 species have been identified, and 40 of those species occur in the United States (Hitchcock and Chase 1951). The majority of the species that inhabit the western rangelands of the U.S. belong to the *Aristida purpurea* complex (Costello 1944; Evans and Tisdale 1972; Heitschmidt et al. 1990), which is currently described as one species (*Aristida purpurea* Nutt.) with seven varieties (Allred 1984). *Aristida purpurea* (Nutt.) and *Aristida purpurea* var. *longiseta* (Steud. and Vasey) represent the primary perennial threeawn varieties occurring in the northern Great Plains (Larson and Whitman 1942).

Aristida purpurea (purple threeawn) is a C_4 perennial bunchgrass which typically occupies dry hillsides, ecological sites with coarse-textured soils, and recently disturbed areas (Evans and Tisdale 1972; Fowler 1984; Judd 1974; Smeins et al. 1976). Purple threeawn has evolved traits that enable it to thrive under sub-optimal conditions. This grass is a prolific seed producer (Evans and Tisdale 1972) and the primary mode by which purple threeawn colonizes an area is through the establishment of seedlings. Attached to each seed are three sharp awns that facilitate dispersal of purple threeawn seeds across the landscape (Fowler 1986). In addition, purple threeawn seeds develop a sharp callus which promotes rapid self-burial and germination. Following germination, purple threeawn allocates a substantial amount of energy to root production (Evans and Tisdale 1972; Van Auken and Brown 1998), which is a significant competitive advantage in semi-arid grasslands (Burke et al. 1998). By investing in root production rather than shoot production, purple threeawn seedlings gain access to soil water and nutrients found deeper in the soil and are less susceptible to drought stress (Fowler 1986; Perkins and Owens 2003). Purple threeawn's seed morphology and root physiology work in concert to produce a long-lived, highly fecund plant.

Numerous authors have reported the effects of grazing on purple threeawn with highly variable results (Heitschmidt et al. 1989; Kinuncan and Smeins 1992; Taylor et al. 1997; Hart and Ashby 1998; Gillen et al. 2000). The lack of congruity among results suggests herbivory has no direct effects on purple threeawn. This hypothesis is supported by the fact that purple threeawn is well-equipped to avoid herbivory. The presence of sharp awns, accumulation of dead material within the plant, and relatively high silica content of shoots deter herbivores from utilizing purple threeawn (Heitschmidt et al. 1990). Furthermore, when purple threeawn is defoliated the plant responds by allocating energy to root production (Briske et al. 1996). This strategy provides a competitive advantage to purple threeawn, because the majority of rangeland grasses allocate energy to shoot re-growth following defoliation (Briske et al. 1996). The low palatability of purple threeawn plants and its tendency to increase root mass following defoliation produces a competitive rangeland grass with the ability to escape grazing pressure.

Purple threeawn is an important component of semi-arid grassland communities (Judd 1974; Hyder et al. 1975). However, threeawn typically comprises less than 10% of relative community composition. Although purple threeawn is part of the native plant community, this grass has the potential to become invasive under certain conditions. Many authors have described rangelands where purple threeawn has expanded beyond its historical abundance and become the dominant component of a plant community (Costello 1944; Tomanek 1955; Hyder and Everson 1968; Evans and Tisdale 1972; Horn and Redente 1998). The catalyst for these expansions appears to be intensive ecological disturbance, such as plowing, prolonged over-grazing, exclusion of grazing, and fire suppression (Costello 1944; Evans and Tisdale 1972; Smeins et al. 1976; Milchunas et al. 1989).

A common goal of land managers is to maintain diverse, native plant communities capable of providing wildlife habitat and adequate forage for profitable livestock production. When purple threeawn becomes the primary constituent of a plant community, this goal becomes difficult to achieve. Furthermore, purple threeawn-dominated plant communities indicate ecological processes have been altered, and an alternative stable state has been reached (Hyder and Bement 1972; Coffin et al. 1996). Therefore, the development of land management strategies aimed at reducing purple threeawn abundance and increasing native plant diversity would benefit land managers with threeawn-dominated plant communities.

Nitrogen addition has been tested as a means of reducing purple threeawn abundance, but has yielded mixed results. Purple threeawn cover decreased when ammonium nitrate was applied to a purple threeawn-dominated plant community in central Colorado (Hyder and Bement 1972). However, purple threeawn cover remained stable and biomass increased when liquid urea was applied to an old field dominated by perennial threeawn in the same area (Horn and Redente 1998). The inconsistent response of purple threeawn to nitrogen additions suggests further research is needed to develop a more complete understanding of the relationship between nitrogen and purple threeawn. From a plant community perspective, nitrogen appears to contribute to the advancement of ecological succession in purple threeawn dominated plant communities (Horn and Redente 1998). Although nitrogen additions may not produce reductions in purple threeawn abundance, other species within the community may take advantage of the increase in available nitrogen. As ecological succession progresses, the plant community will become more diverse as different species begin to expand, resulting in a gradual displacement of purple threeawn.

Prescribed fire has been used in several ecosystems to improve livestock grazing and shift plant community composition (Wright and Bailey 1982; Howe 1995). Previous research suggests prescribed fire will reduce purple threeawn basal area, cover, and biomass production for 1-5 years (Trlica and Schuster 1969; Steuter and Wright 1983; Parmenter 2008; Killgore et al. 2009). The susceptibility of purple threeawn to fire is likely a product of its hemicryptophyte growth form (Raunkinauer 1934; Wright 1971; Ewing and Engle 1988) and elevated growing points (Wright and Bailey 1982; Engle et al. 1998). Although fire seems to be detrimental to purple threeawn, few studies have attempted to determine the relationship between fire behavior (e.g., heat dosage, heat duration) and purple threeawn response. Furthermore, fire has the potential to be a highly effective restoration tool in the northern Great Plains, because the dominant species within the region respond positively or neutrally to fire (Vermeire et al. 2011).

My objective was to assess the effects of prescribed fire and nitrogen amendments on purple threeawn-dominated plant communities of the northern Great Plains. I conducted two experiments. Experiment 1 focused on purple threeawn and plant community response to different seasons of fire and nitrogen amendments. Experiment 2 was designed to reveal fire effects on individual purple threeawn plants and to identify fire behavior variables that can predict purple threeawn mortality. Both experiments generated data that will be important for future fire and purple threeawn research.

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CHAPTER 2. FIRE AND NITROGEN EFFECTS ON PURPLE THREEAWN ABUNDANCE IN THE NORTHERN MIXED-GRASS PRAIRIE[1]

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[1] This chapter is co-authored by Dustin Strong, Lance Vermeire, and Amy Ganguli. Dustin Strong (graduate student) was the primary author responsible for collecting data, statistical analysis, interpreting statistical outputs, and comprising the information presented in this chapter.

Abstract

Purple threeawn (*Aristida purpurea* Nutt. varieties) is a native grass capable of increasing on rangelands, forming near monocultures, and creating a stable state. Productive rangelands throughout the Great Plains and Intermountain West have experienced increases in purple threeawn abundance, reducing overall forage quality. Our objectives were to 1) reveal the effects of prescribed fire and nitrogen amendments on purple threeawn abundance and 2) assess non-target plant response post-treatment. Season of fire (no fire, summer fire, fall fire) and different levels of nitrogen (0, 46, 80 kg N $\cdot$ ha^{-1}) were factorially arranged in a completely randomized design in southeastern Montana in different years at two similar sites. We evaluated fire and nitrogen effects on purple threeawn basal cover, relative composition, and current-year biomass one growing season post-fire at two sites, and two growing seasons post-fire at one site. Spring weather post-fire was very different between years, impacting community response. Initial purple threeawn biomass at both sites was 1214 ± 46 kg $\cdot$ ha^{-1}. When post-fire growing conditions were wet, current-year biomass of purple threeawn was reduced 90 and 73% with summer and fall fire, respectively. Under dry post-fire growing conditions, purple threeawn current-year biomass was reduced 73 and 58% with summer and fall fire, respectively. Nitrogen additions had no effect on purple threeawn current-year biomass at either site. C_3 perennial grass current-year biomass doubled with nitrogen additions and was not impacted by fire during a wet spring. Nitrogen additions and fire had no effect on C_3 perennial grass current-year biomass following a dry spring. Two years post-fire purple threeawn basal cover and current-year biomass had not recovered and C_3 perennial grass current-year biomass was similar in all plots. Nitrogen had no effect on purple threeawn abundance. Prescribed fire during the summer appears to be a highly effective tool for reducing purple threeawn abundance. Keywords: *Aristida*, grassland, nitrogen amendments, prescribed burning, restoration, vegetation management

Introduction

Purple threeawn-dominated plant communities occur throughout the Great Basin and Great Plains. In most instances, purple threeawn (*Aristida purpurea* (Nutt.)) varieties are the primary species forming these near monocultures on rangelands. The catalyst for purple threeawn expansion appears to be intensive ecological disturbances such as plowing, prolonged overgrazing, exclusion of grazing, and fire suppression (Costello 1944; Evans and Tisdale 1972; Smeins et al. 1976; Milchunas et al. 1989). Management strategies aimed at reducing purple threeawn dominance are the first steps in rehabilitating plant communities where purple threeawn has expanded beyond its historical prevalence.

The seed morphology and root physiology of purple threeawn produce a long-lived, highly fecund plant with the ability to inhabit extreme environments (Judd 1974; Fowler 1984). Purple threeawn reproduces primarily by seed and has a sharp callus and three awns which allow for rapid burial and wind dispersal, respectively. Following germination, purple threeawn initiates root growth relatively early and generally produces a robust root system (Evans and Tisdale 1972). This large root structure offers purple threeawn a significant advantage in semi-arid grasslands enabling it to take advantage of soil water and nutrients deeper in the soil (Burke et al. 1998).

Purple threeawn is an important component of native plant communities on semi-arid rangelands. Purple threeawn will typically contribute 5-10% to the relative composition of a plant community (Hyder et al. 1975; Smeins et al. 1976). The ability of purple threeawn to readily colonize bare ground and inhabit hillsides increases soil stability by reducing wind and water erosion on these sensitive areas. However, the same characteristics that enable purple threeawn to occupy demanding environments enable purple threeawn to dominate more productive plant communities. A purple threeawn-dominated plant community presents a significant problem to livestock producers, because purple threeawn is generally avoided by livestock (Heitschmidt et al. 1990; Anderson and

Briske 1995). Furthermore, when livestock do utilize purple threeawn, its poor overall forage quality (Meyer and Brown 1985) often reduces livestock performance. From an ecological perspective, a purple threeawn-dominated plant community will remain in a stable state for 60+ years (Tomanek 1955; Horn and Redente 1998). The identification of management strategies that reduce purple threeawn abundance and stimulate the transition out of a purple threeawn-dominated state are needed to improve overall palatability of these plant communities and diversify plant community composition.

Nitrogen amendments have been reported to reduce purple threeawn cover and growing season biomass in eastern Colorado (Hyder and Bement 1972), however, the mechanism was not clear. Furthermore, a similar experiment was conducted 30 years later in the same area and there was no change in purple threeawn cover or growing season biomass of purple threeawn with nitrogen additions (Horn and Redente 1998). Additional research on purple threeawn and nitrogen is needed to develop a more complete understanding of the relationship between these factors.

Aristida species, in general, appear to be sensitive to fire (Trlica and Schuster 1969; Parmenter 2008), yet little information is available directly comparing purple threeawn response to different seasons of fire. Spring fire reduced perennial threeawn current-year biomass for two growing-seasons post-fire in the southern mixed-grass prairie (Steuter and Wright 1983), but spring fire in the northern Great Plains may negatively impact the dominant C_3 (cool-season) perennial grasses (White and Currie 1983). Additionally, the dominant C_3 perennial grasses in the northern Great Plains appear to be resilient to fire and tend to respond positively to summer and fall burning (Engle and Bultsma 1984; Steuter 1987; Vermeire et al. 2011). Therefore, summer and fall fire may reduce purple threeawn abundance and have a minimal impact on the dominant C_3 perennial grasses. The objectives of this study were to 1) evaluate the efficacy of nitrogen amendments and prescribed fire during different seasons as tools to reduce purple threeawn (target plant) abundance and 2) assess non-target plant response following fire and nitrogen treatments.

Materials and methods

Study area

We conducted this research in semi-arid mixed-grass prairie near Terry, Montana, USA from July 2010 to July 2012. Average annual precipitation for the area is 295 mm, with the majority occurring April through September. Average temperature is 6.6°C, with extremes of 43.8°C in the summer and -42.8°C in the winter. The frost-free growing season typically ranges from 105 to 135 days (Western Regional Climate Center, Reno, NV).

The research area is located within approximately 30 000 ha of abandoned cropland seeded to crested wheatgrass from 1936-1942 (McWilliams and Van Cleave 1960). We selected two similar sites in order to test the effects of fire and nitrogen on purple threeawn. Site 1 (46°41′N 105°18′W) was treated in 2010-2011 and Site 2 (46°43′N 105°18′W) was treated in 2011-2012. Both sites are sandy ecological sites characterized by flat, upland plains situated over the Degrand soil series (a fine-loamy over sandy or sandy-skeletal, mixed, superactive, frigid Aridic Argiustolls; USDA, NRCS, Web Soil Survey, 2010). Site 1 had been moderately to heavily grazed from April 1 to July 15 and from September 1 to November 14 for a minimum of 40 years, with the majority of utilization occurring in the spring. Site 2 had been moderately to heavily grazed from May 1 to July 14 and from October 15 to November 22 for a minimum of 40 years, with the majority of utilization occurring in the spring. During the summer of 2009 we fenced each site to exclude cattle.

Vegetation at the study sites was dominated by the perennial C_4 (warm-season) bunchgrass purple threeawn (*Aristida purpurea* Nutt.) and the perennial C_3 bunchgrass crested wheatgrass (*Agropyron cristatum* (L.) Gaertn). Other C_4 perennial grasses present 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 grasses included needle-and-thread (*Hesperostipa comata* (Trin. & Rupr.) Barkworth), Sandberg bluegrass (*Poa secunda* J. Presl), and intermediate wheatgrass (*Thinopyrum intermedium* (Host) Barkworth & D.R. Dewey). Annual grasses were sixweeks fescue (*Vulpia octoflora* (Walt.) Rydb.), field brome (*Bromus arvensis* L.), and cheatgrass (*B. tectorum* L.). The sub-shrub green sage (*Artemisia campestris* L.) was present in addition to hairy goldenaster (*Chrysopsis villosa* (Pursh.) Nutt.), the perennial legume, silverleaf Indian breadroot (*Pediomelum argophyllum* (Pursh.) J. Grimes), and the biennial forb, yellow salsify (*Tragopogon dubius* Scop.). Annual forbs included field cottonrose (*Logfia arvensis* (L.) Holub), woolly plantain (*Plantago patagonica* Jacq.), and rough false pennyroyal (*Hedeoma hispida* Pursh.). Plant nomenclature follows the USDA PLANTS database (USDA, NRCS 2010)

Experimental design and treatment application

We combined fire and nitrogen amendments in a fully factorial 3 × 3 arrangement by randomly assigning three fire treatments (no fire, summer fire, fall fire) and three levels of nitrogen (0, 46, 80 $kg \cdot ha^{-1}$) with three replications to 27, 20 × 20 m plots at each site. Fuel load at each site was approximately 2000 $kg \cdot ha^{-1}$ and all fires were set using the ring-fire method (Wright and Bailey 1982). Summer fires were applied when purple threeawn seeds began dropping and fall fires were applied following the first killing frost. High fuel connectivity ensured complete fire coverage of all burned plots. We applied summer fire to Site 1 on 12 August 2010 with ambient temperatures 28-32°C, winds 8-11 $km \cdot h^{-1}$, and relative humidity 36-42%. Fall fires were applied at Site 1 on 18 October 2010 with ambient temperatures 17-18°C, winds 8-13 $km \cdot h^{-1}$, and relative humidity 35-37%. Nitrogen amendments were applied in the spring and coordinated around predicted precipitation. We broadcasted nitrogen amendments (granular urea) to individual plots at

Site 1 on 26 April 2011, with ambient temperatures of 10-13°C. Precipitation fell as rain the evening of April 26. We applied summer fire at Site 2 on 7 September 2011 with ambient temperatures 29-31°C, winds 5-13 km · h^{-1}, relative humidity 15-20%. Fall fires were applied at Site 2 on 31 October 31 2011 with ambient temperatures 16-20°C, winds 13-30 km · h^{-1}, and relative humidity 28-34%. We applied nitrogen amendments to individual plots at Site 2 on April 5 2012 with ambient temperature 10-13°C. The first post-application precipitation fell as rain on 26 April 2012.

Vegetation measurements

To asses vegetation response to our treatments we measured standing crop, annual herbaceous yield, basal cover, bare ground, litter, and relative composition. All vegetation sampling occurred at peak biomass (mid-July). We read four random 5 m transects at 20-cm intervals using the point-intercept transect method to quantify basal cover, bare ground, litter, and relative composition. Standing crop was estimated by clipping all vegetation to ground level in five, randomly placed 0.25 m^2 quadrats within each plot. Vegetation was sorted by purple threeawn and the functional groups, C_3 perennial grass, C_4 perennial grass, annual grass, and forb. Annual herbaceous yield (current-year biomass) was estimated by sorting current-year growth from collected standing crop for all functional groups. Standing crop was the sum of current-year biomass and residual biomass from previous years' growth. Harvested vegetation was dried at 60°C for 48-hours and weighed to the nearest 0.01 g.

Statistical analysis

We analyzed data from Site 1 and Site 2 using generalized least squares (MIXED procedure of SAS, Littell et al. 2006) to quantify plant community response one growing season post-fire. Our model included treatment year, fire, nitrogen, and all interactions as fixed effects. Year effects were a product of spring weather and will be discussed as such.

We used basal cover, bare ground, litter, relative composition, standing crop, current-year biomass, and current-year biomass by functional group as response variables and our experimental unit was plot. We collected data from Site 1, one and two growing seasons post-fire. We analyzed these data using generalized least squares (MIXED procedure of SAS, Littell et al. 2006) with year as a repeated measure. The model included year, fire, nitrogen, and all interactions as fixed effects. Our response variables were consistent across models. We set statistical significance at $P < 0.05$ for both sets of models.

Results

Growing conditions at Site 1 (2011) and Site 2 (2012) were very different one year post-fire (Fig. 2.1). Spring 2011 (April-June) provided a record amount of precipitation (251% of average; Fig.1) and Spring 2012 was drier than average (25% below average; Fig. 2. 1). Regionally, 2012 was the second driest spring on record (Western Regional Climate Center, Reno, NV). Precipitation in the northern Great Plains has the greatest effect on current-year biomass during April-June (Heitschmidt and Vermeire 2005).

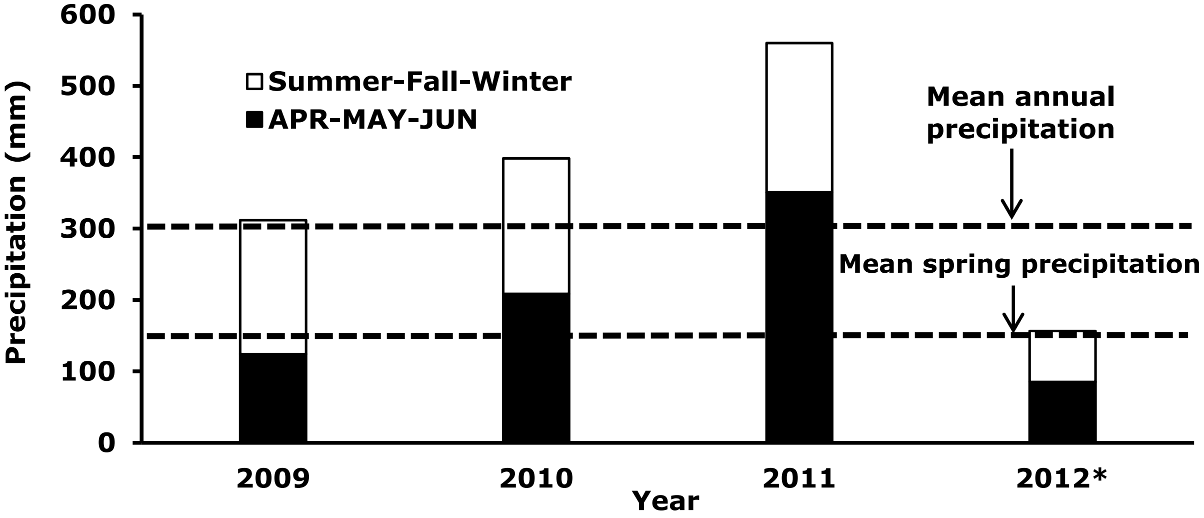

Figure 2.1. Mean annual precipitation for Terry, MT from 2008-2012 (*2012 total is through August).

First year response (wet vs. dry spring)

Standing crop and current-year biomass. Pre-treatment standing crop was similar between Site 1 and Site 2, despite the extra year of rest from grazing for Site 2. Summer and fall fire reduced standing crop by 46% (1549 versus 2873 ± 71 kg · ha^{-1}; $P < 0.01$) and 39% (1740 versus 2873 ± 71 kg · ha^{-1}), respectively, with no difference between seasons of fire. Spring weather and nitrogen interacted in their effects on standing crop ($P < 0.01$; Fig. 2.2), with nitrogen causing the greatest increase in standing crop when applied during a wet spring.

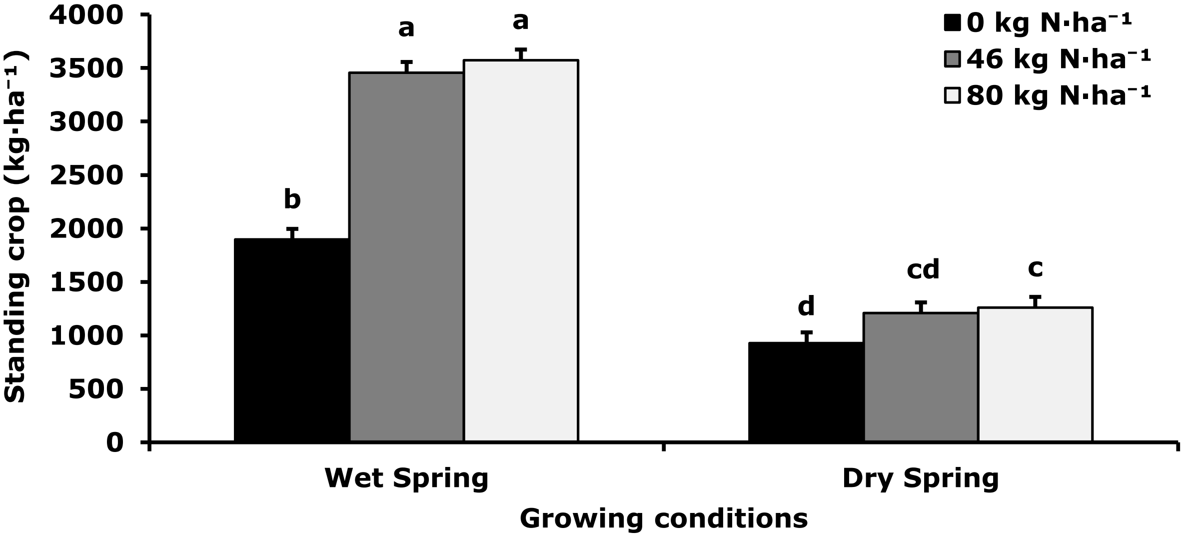

Figure 2.2. Nitrogen effects on standing crop (+ SEM) under different spring growing conditions. Means marked with the same letter are similar (P < 0.05).

Summer and fall fire negatively impacted current-year biomass following a wet spring, with summer fire having a greater effect than fall fire ($P < 0.01$; Fig. 2.3A). Fire had no effect on current-year biomass following a dry spring. Nitrogen amendments increased current-year biomass when applied during a wet and dry spring, with no difference between 46 and 80 kg N · ha^{-1} within spring weather ($P < 0.01$; Fig. 2.3B).

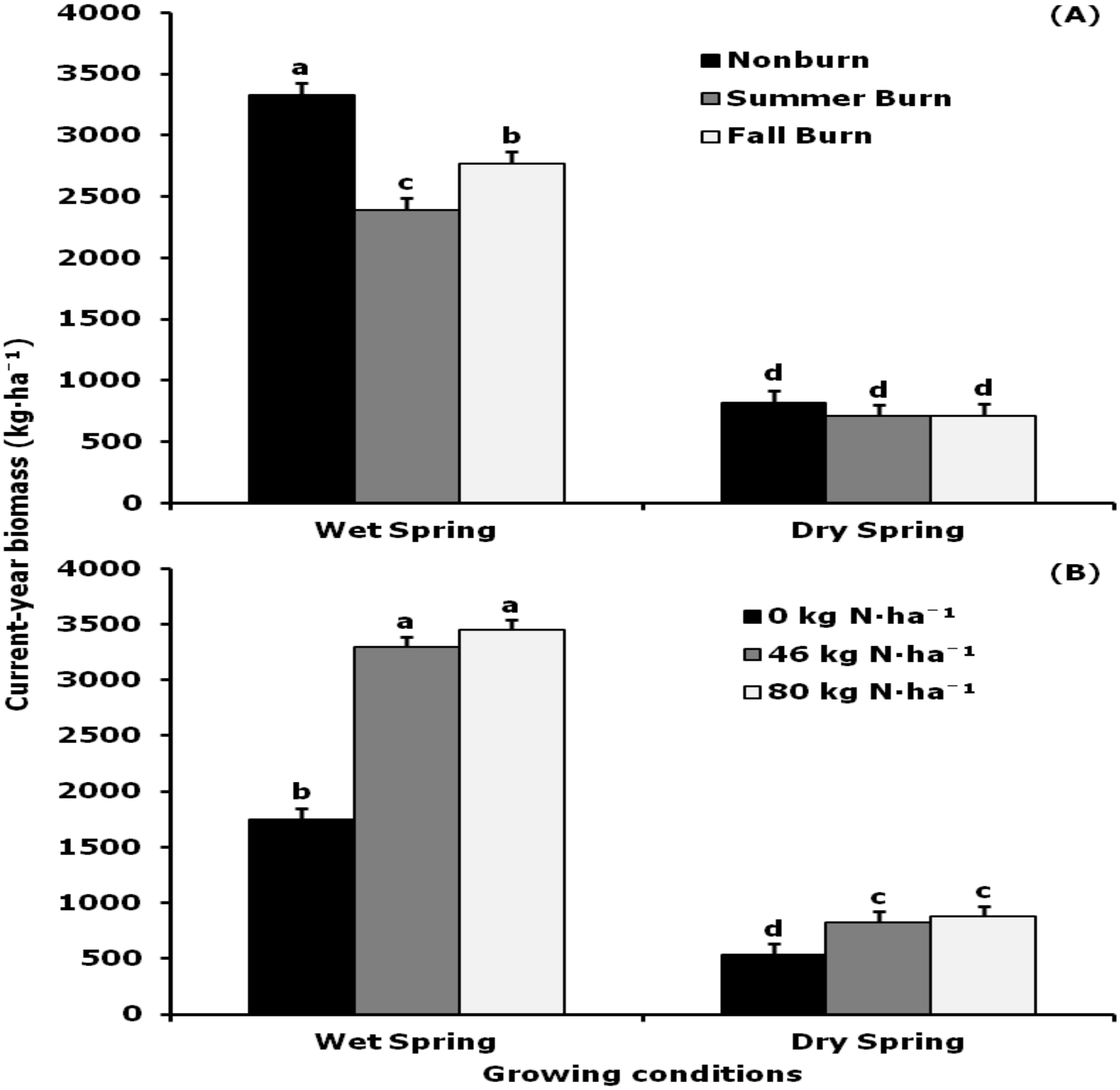

Figure 2.3. Current-year biomass (+ SEM) (A) one growing season post-fire under different spring growing conditions and (B) and the growing season of nitrogen application (+ SEM) under different spring growing conditions. Means marked with the same letter within treatment are similar (P < 0.05).

Purple threeawn current-year biomass was reduced by fire ($P < 0.01$; Fig. 2.4). Summer fire had a greater effect on purple threeawn than fall fire following a wet spring, but season fire effects were similar following a dry spring. Summer fire yielded a 90% reduction in current-year biomass following a wet spring and a 73% reduction following a dry spring. Fall fire reduced purple threeawn current-year biomass 65% following a wet spring and 58% following a dry spring. Nitrogen amendments had no effect on purple threeawn current-year biomass (345 ± 30 kg · ha^{-1}).

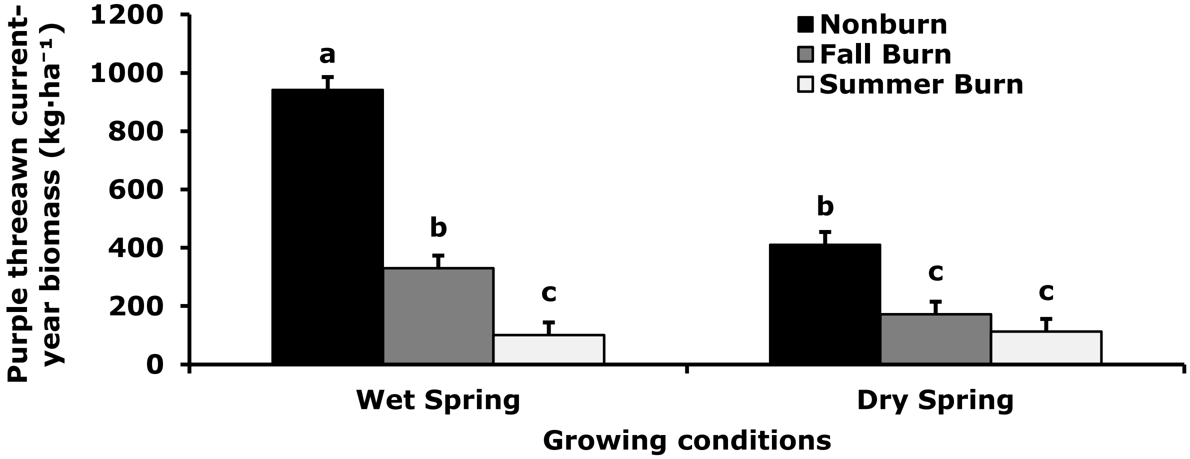

Figure 2.4. Purple threeawn current-year biomass (+ SEM) one growing season post-fire under different spring growing conditions. Means marked with the same letter are similar (P < 0.05).

Current-year biomass of C_3 perennial grass was similar between burned and nonburned plots regardless of spring weather (1262 ± 75 kg · ha^{-1}, $P > 0.09$). Nitrogen amendments more than doubled current-year biomass of C_3 perennial grass during a wet spring, but had no effect during a dry spring ($P < 0.01$; Fig. 2.5).

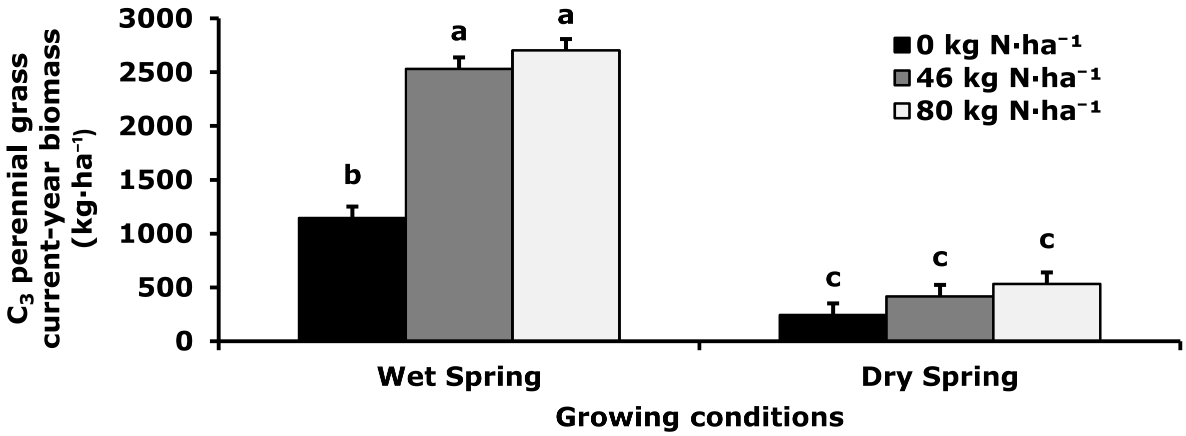

Figure 2.5. Nitrogen effects on C_3 perennial grass current-year biomass (+ SEM) under different spring growing conditions. Means marked with the same letter are similar (P < 0.05).

Current-year biomass of C_4 perennial grass was similar following a wet and dry spring (42 ± 9 kg · ha^{-1}; $P > 0.19$). Current-year biomass of C_4 perennial grass was similar in burned and non-burned plots (41 ± 11 kg · ha^{-1}, $P > 0.49$) but increased in plots receiving 46 (59 versus 17 ± 11 kg · ha^{-1}, $P < 0.03$) and 80 kg N · ha^{-1} (48 versus 17 ± 11 kg · ha^{-1}). Forb current-year biomass more than doubled in non-burned plots receiving 46 (516 ± 55 kg · ha^{-1}, $P < 0.03$) and 80 kg N · ha^{-1} (411 ± kg · ha^{-1}) compared to the control (196 ± 55 kg · ha^{-1}) following a wet spring. All other treatment combinations yielded values similar to the control (196 ± 55 kg · ha^{-1}). Following a dry spring, forb current-year biomass was similar in all plots (106 ± 55 kg · ha^{-1}). Annual grass current-year biomass was similar across nitrogen treatments regardless of spring weather (9 ± 3 kg · ha^{-1}; $P > 0.29$). Following a wet spring, summer and fall fire reduced annual grass current-year biomass 56% (16 versus 36 ± 4 kg · ha^{-1}) and 94% (2 versus 36 ± 4 kg · ha^{-1}; $P < 0.01$), respectively. Following a dry spring, annual grass current-year biomass was similar across treatments (0 ± 4 kg · ha^{-1}).

Ground cover. Purple threeawn basal cover (Table 2.1) was greater in all plots following a dry spring than a wet spring ($P < 0.01$). Regardless of spring weather, summer and fall fire reduced purple threeawn basal cover 94 and 85%, respectively. Purple threeawn basal cover was similar for 0, 46, and 80 kg N · ha^{-1} ($P > 0.69$). Needle-and-thread basal cover (Table 2.1) was affected by spring weather ($P < 0.01$) and fire ($P < 0.01$). Nitrogen amendments had no effect on needle-and-thread basal cover ($P > 0.49$). Bare ground (Table 2.1) was greater following a dry spring ($P < 0.01$) than a wet spring. Summer fire resulted in the greatest increases of bare ground, followed by fall fire. Plots receiving 46 kg N · ha^{-1} had less bare ground than plots receiving 0 kg N · ha^{-1}, but bare ground in plots treated with 80 kg N · ha^{-1} was intermediate and similar to plots receiving 46 and 0 kg N · ha^{-1} ($P < 0.03$).

Table 2.1. Ground cover response to spring growing conditions, fire, and nitrogen amendments by effect and component[1].

	Basal cover %		
Effect	**Purple threeawn**	**Needle-and-thread**	**Bare ground (%)**
Wet Spring	11.3 b	0.7 b	46.6 b
Dry Spring	15.2 a	1.8 a	66.4 a
No burn	32.5 a	2.1 a	32.4 c
Fall burn	5.3 b	0.7 b	65.6 b
Summer burn	2.0 b	0.9 b	71.6 a
0 kg $N\cdot ha^{-1}$	13.8 a	1.1 a	60.3 a
46 kg $N\cdot ha^{-1}$	13.6 a	1.1 a	53.8 b
80 kg $N\cdot ha^{-1}$	12.4 a	1.6 a	55.4 ab

[1] Means with the same letters within an effect and component are similar (*P* < 0.05).

Fire and spring weather interacted in their effects on crested wheatgrass basal cover(*P* < 0.01; Fig. 2.6). Crested wheatgrass basal cover tripled with summer fire and more than doubled with fall fire following a wet spring. Following a dry spring, crested wheatgrass basal cover in burned plots was similar to nonburned plots. Crested wheatgrass basal cover was greater in plots receiving 46 and 80 kg $N \cdot ha^{-1}$ (3.6 and 3.2 ± 0.4%, *P* < 0.01) than plots receiving 0 kg $N \cdot ha^{-1}$ (1.7 ± 0.4%).

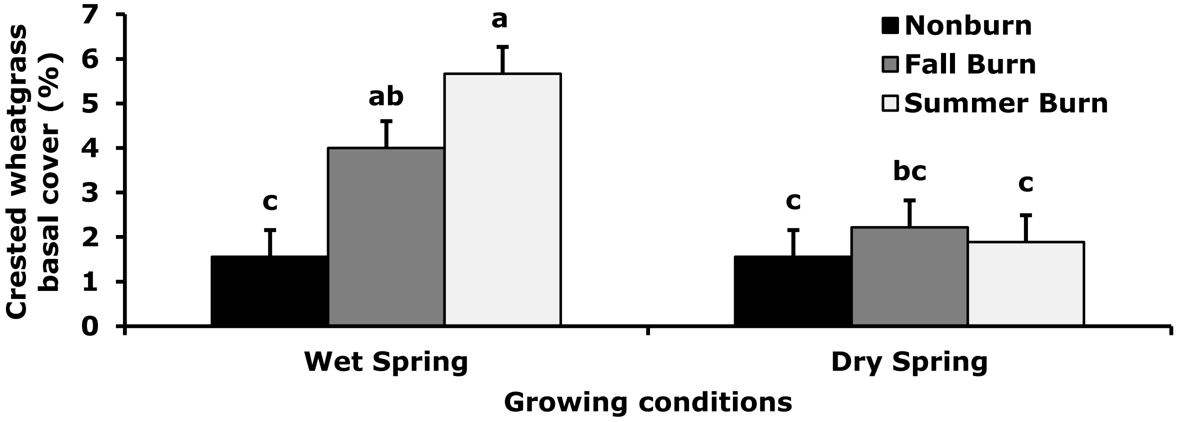

Figure 2.6. Crested wheatgrass basal cover (+ SEM) one growing season post -fire under different spring growing conditions. Means marked with the same letter are similar (P < 0.05).

Litter was greater following a wet spring than a dry spring (35.6 versus 7.8 ± 1.3%, $P < 0.01$). Fire and nitrogen interacted in their effects on litter, with litter increasing in nonburned plots receiving nitrogen amendments ($P < 0.01$; Fig. 2.7). However, nitrogen did not affect litter cover for summer or fall burned plots.

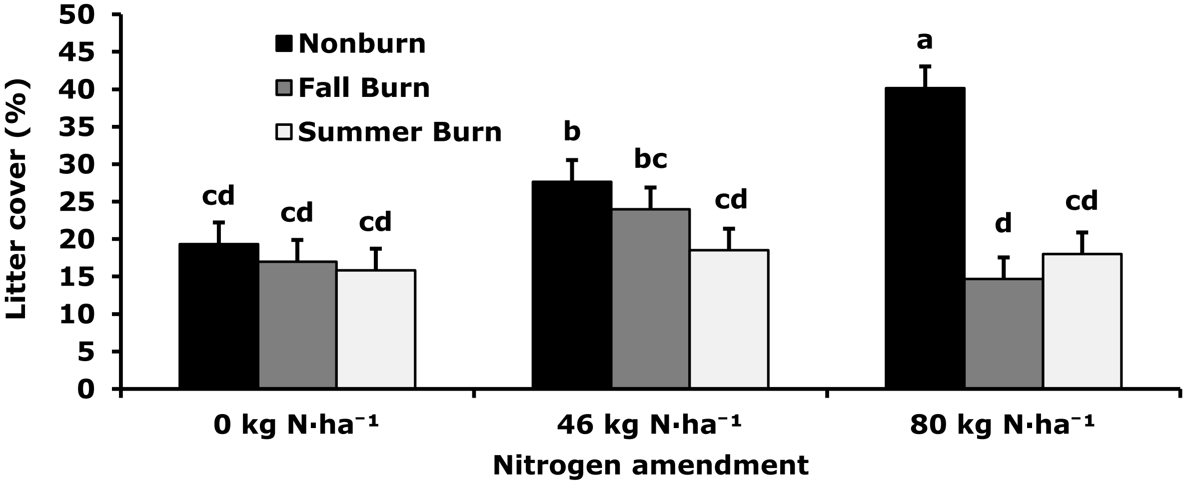

Figure 2.7. Fire × nitrogen effect on litter (+ SEM). Means marked with the same letter are similar (P < 0.05).

Relative composition. Summer fire reduced purple threeawn composition by 50% following a dry spring and 63% following a wet spring ($P < 0.01$; Fig. 2.8). Fall burned plots were similar to nonburned plots during a wet year, but purple threeawn comprised a smaller percentage of relative composition during a dry year. Purple threeawn composition was similar in plots receiving 46 and 80 kg $N \cdot ha^{-1}$ (40.9 and 37.3 ± 2.1%) and less than plots receiving no nitrogen (50.7 ± 2.1%, $P < 0.01$). Summer fire doubled crested wheatgrass composition following a wet spring and more than tripled it following a dry spring ($P < 0.01$; Fig. 2.8). Following a wet spring, crested wheatgrass composition on fall burned plots was similar to that of nonburned plots. Following a dry spring, crested wheatgrass composition more than doubled in fall burned plots. Nitrogen amendments of 46 and 80 kg $N \cdot ha^{-1}$ were similar to each other (42.4 and 43.0 ± 2.1%) and greater than 0 kg $N \cdot ha^{-1}$ (30.6 ± 2.1%, $P < 0.01$).

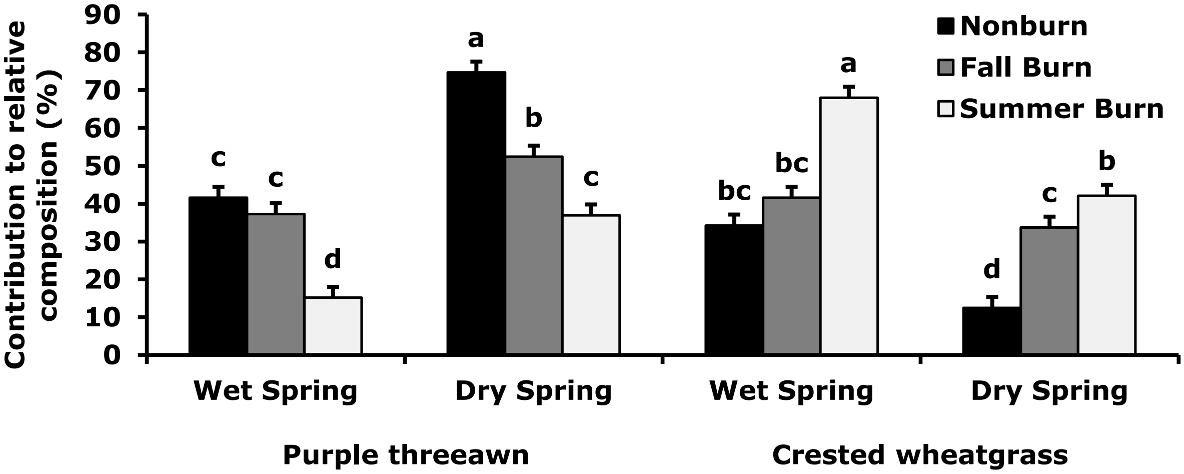

Figure 2.8. Contribution of purple threeawn and crested wheatgrass to relative composition (+ SEM) one growing season post-fire under different spring growing conditions. Means marked with the same letter within species are similar (P < 0.05).

Spring weather and nitrogen interacted in their effects on needle-and-thread composition ($P < 0.03$). Following a wet spring, needle-and-thread composition was similar across nitrogen treatments (8.8 ± 2.8%). Following a dry spring, needle-and-thread composition more than doubled with 80 kg N · ha^{-1} (16.4 ± 2.8%) compared to plots receiving 0 kg N · ha^{-1} (6.9 ± 2.8%) and 46 kg N · ha^{-1} produced an intermediate value (8.3 ± 2.8%). Needle-and-thread in burned plots was similar to nonburned plots (9.7 ± 2.0%, $P > 0.49$).

Spring weather and fire interacted in their effects on forb composition ($P < 0.01$) and annual grass composition ($P < 0.01$). Following a wet spring, summer (5.8 ± 1.0%) and fall fire (3.5 ± 1.0%) similarly reduced forb composition compared to nonburned plots (8.9 ± 1.0%). Following a dry spring, forb composition was similar in summer burned (3.8 ± 1.0%), fall burned (3.1 ± 1.0%), and nonburned plots (2.7 ± 1.0%). Forb composition was similar in plots receiving 0, 46, and 80 kg N · ha^{-1} (4.6 ± 0.7%, $P > 0.29$). Summer and fall fire reduced annual grass composition (1.4 ± 0.5%) and (0.2 ± 0.5%) compared to nonburned plots (4.2 ± 0.5%), following a wet spring. Following a dry spring, annual grasses were almost nonexistent in burned (0.0 ± 0.5%) and nonburned plots (0.1 ±

0.5%). Annual grass composition was similar in plots receiving 0, 46, and 80 kg N · ha^{-1} (1.0 ± 0.4%, $P > 0.29$).

Second year response (site 1)

Standing crop, current-year biomass, functional group current-year biomass, and ground cover had similar trends one and two years post-fire. Therefore, we are only reporting purple threeawn and crested wheatgrass basal cover and relative composition, as well as purple threeawn and C_3 perennial grass current-year biomass.

Change in current-year biomass of purple threeawn was characterized by a year × fire interaction ($P < 0.01$; Fig. 2.9). Summer and fall fire reduced purple threeawn current-year biomass 90 and 65% in Year 1, with differences between seasons of fire. In Year 2, plots treated with fall fire had similar values to nonburned plots as well as fall burned plots one year post-fire. Conversely, plots treated with summer fire had less purple threeawn biomass than nonburned and fall burned plots and similar values to summer burned plots one year post-fire.

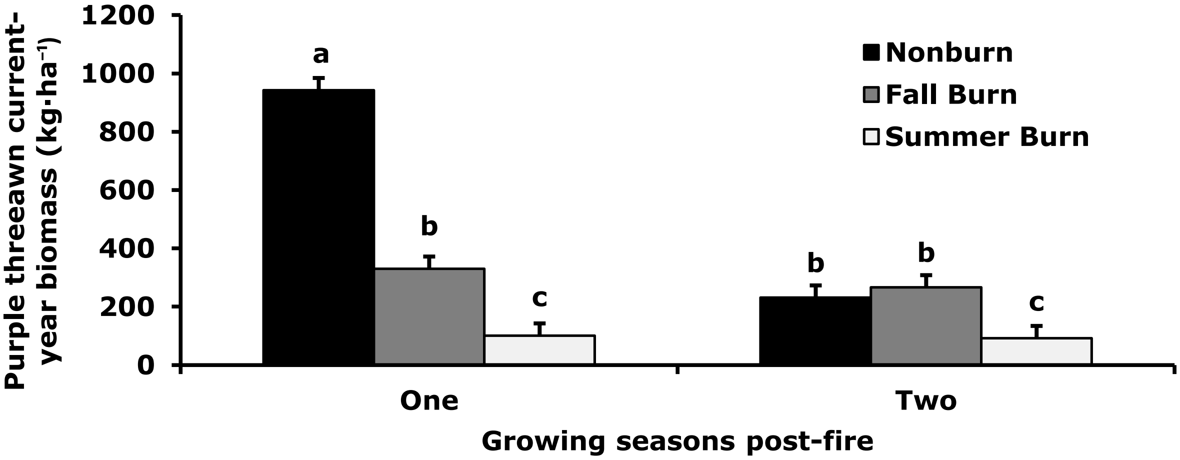

Figure 2.9. Purple threeawn current-year biomass (+ SEM) one (2011) and two (2012) growing seasons post-fire. Means marked with the same letter are similar ($P < 0.05$).

Year and nitrogen interacted in their effects on purple threeawn current-year biomass (*P* < 0.01; Fig. 2.10A). Purple threeawn current-year biomass was similar in plots receiving no nitrogen between years, and 0 kg N · ha^{-1} was similar to 46 and 80 kg N · ha^{-1} in Year 1. In Year 2, purple threeawn current-year biomass in plots treated with 46 and 80 kg N · ha^{-1} were similar to each other, but less than plots receiving 0 kg N · ha^{-1} nitrogen. Current-year biomass of C_3 perennial grass was similar between nonburned and burned plots (1306 ± 77 kg · ha^{-1}).

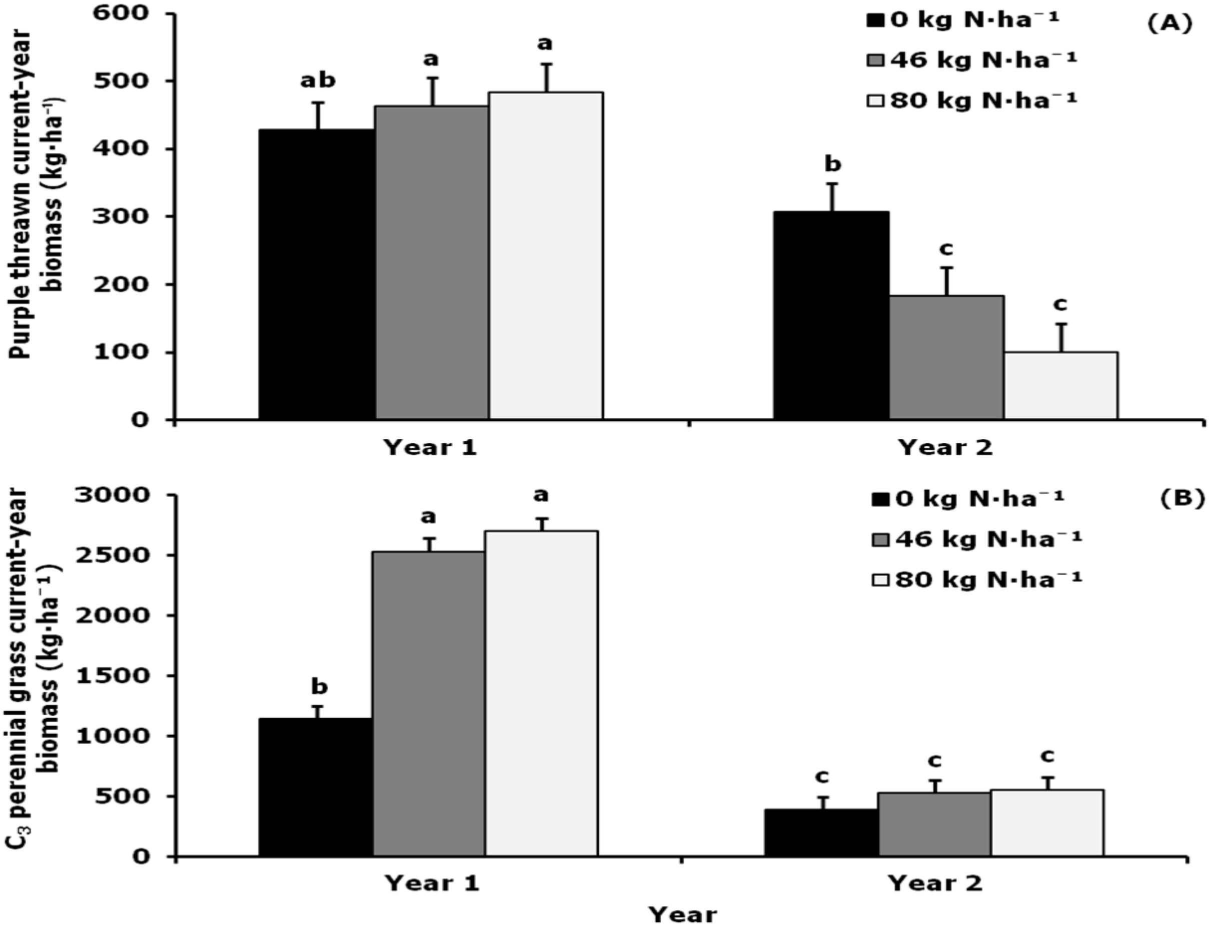

Figure 2.10. Nitrogen effects on (A) purple threeawn and (B) current-year biomass of C_3 perennial grass the growing season of nitrogen application (2011) and one growing season post-nitrogen application (2012). Means (+ SEM) marked with the same letter are similar within species (P < 0.05).

Year and nitrogen interacted in their effects on C_3 perennial grass current-year biomass (*P* < 0.01; Fig. 2.10B). In Year 1, nitrogen amendments more than doubled current-year biomass, with no difference between nitrogen amendments. In Year 2, plots that received nitrogen amendments produced similar amounts of biomass as plots that did not receive nitrogen amendments.

Basal cover. Purple threeawn basal cover (Table 2.2) was greater in Year 2 than Year 1 ($P < 0.01$). Fire negatively impacted purple threeawn basal cover, with summer fire having a greater impact than fall fire ($P < 0.01$). Summer and fall fire reduced purple threeawn basal cover 95 and 76% one year post-fire, with sustained reductions two years post-fire. Nitrogen amendments did not alter purple threeawn basal cover ($P > 0.39$). Crested wheatgrass basal cover (Table 2.2) was greater Year 2 than Year 1 ($P < 0.01$). Fire increased crested wheatgrass basal cover, with a greater increase after summer than fall fire ($P < 0.01$). Plots receiving 46 and 80 kg N · ha^{-1} produced similar crested wheatgrass basal cover which was greater than plots receiving 0 kg N · ha^{-1} ($P < 0.01$). Needle-and-thread basal cover (Table 2.2) was less in Year 1 than Year 2 ($P < 0.03$), but similar within fire ($P > 0.19$) and nitrogen ($P > 0.69$) treatments.

Table 2.2. Basal cover (%) response to years' post-fire, fire, and nitrogen amendments by effect and species[1].

Effect	Purple threeawn	Crested wheatgrass	Needle-and-thread
Year 1	11.3 b	3.7 b	0.7 b
Year 2	17.9 a	8.4 a	2.2 a
No burn	33.8 a	3.9 c	1.6 a
Fall burn	8.2 b	6.1 b	1.7 a
Summer burn	1.8 c	8.3 a	1.2 a
0 kg N·ha^{-1}	16.6 a	4.1 b	1.8 a
46 kg N·ha^{-1}	14.4 a	7.2 a	1.4 a
80 kg N·ha^{-1}	12.7 a	7.0 a	1.2 a

[1] Means marked with the same letter within an effect and species are similar ($P < 0.05$).

Relative composition. Purple threeawn composition (Table 2.3) was greater in Year 2 than Year 1 ($P < 0.04$). Summer and fall fire reduced purple threeawn composition

64 and 15%, respectively. Purple threeawn composition was less for plots receiving 46 and 80 kg N · ha^{-1} ($P < 0.01$) than plots not receiving nitrogen amendments. Needle-and-thread composition (Table 2.3) was similar across years ($P > 0.79$), seasons of fire ($P > 0.49$), and nitrogen amendments ($P > 0.19$).

Table 2.3. Response of purple threeawn and needle-and-thread composition to years' post-fire, fire, and nitrogen amendments by effect and species[1].

	Relative composition (%)	
Effect	**Purple threeawn**	**Needle-and-thread**
Year 1	31.3 b	8.8 a
Year 2	36.6 a	7.8 a
No burn	46.1 a	5.9 a
Fall burn	39.0 b	9.8 a
Summer burn	16.8 c	9.2 a
0 kg N·ha^{-1}	41.5 a	11.6 a
46 kg N·ha^{-1}	31.0 b	8.3 a
80 kg N·ha^{-1}	29.0 b	5.0 a

[1] Means marked with the same letter within effect and species are similar ($P < 0.05$)

Crested wheatgrass composition was similar in Year 1 and Year 2 (50.0 ± 1.6%, $P > 0.08$). Fire and nitrogen interacted in their effects on crested wheatgrass composition ($P < 0.01$; Fig. 2.11). In general, crested wheatgrass composition was greater for all treatment combinations than the control. Summer burned plots with 46 and 80 kg N · ha^{-1} had more crested wheatgrass than all other treatments and were similar to each other. Crested wheatgrass composition in plots receiving summer fire and 0 kg N · ha^{-1} was less than summer burned plots receiving 46 and 80 kg N · ha^{-1}, fall burned plots with no nitrogen added, nonburned plots receiving 46 kg N · ha^{-1}, and nonburned plots receiving 0 kg N · ha^{-1}.

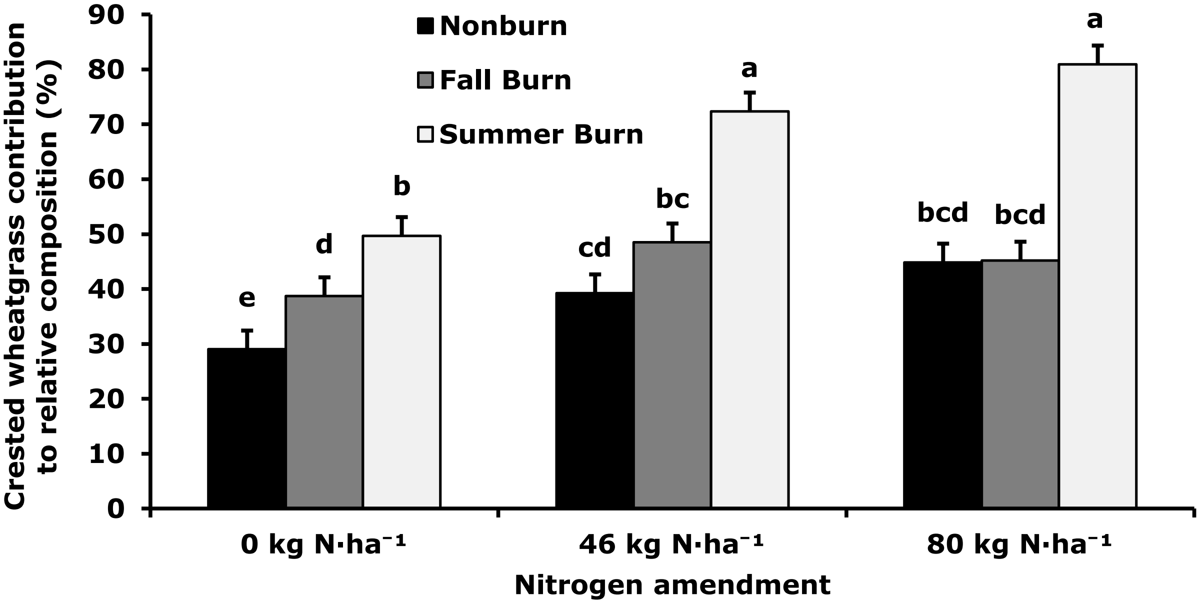

Figure 2.11. Fire × nitrogen effect on crested wheatgrass composition (+ SEM). Means marked with same letter are similar ($P < 0.05$).

Discussion

Purple threeawn response

Prescribed fire reduced purple threeawn abundance one growing season post-fire. Additionally, purple threeawn showed no signs of recovery two years post-fire. Our observed decreases in current-year biomass of purple threeawn are similar to observations from the southern mixed prairie (Steuter and Wright 1983). In addition to reductions in current-year biomass, our results show fire reduced purple threeawn basal cover, similar to experiments in shortgrass prairie and desert grassland (Trlica and Schuster 1969; Parmenter 2008; Killgore et al. 2009). Purple threeawn's sensitivity to fire stems from its hemicryptophyte (bunchgrass) growth form (Raunkiaer 1934) and its elevation of meristems into the crown of the plant as the growing season progresses (Ewing and Engle 1988). Bunchgrasses are generally more susceptible to fire damage because litter accumulates in the crown of these species over time, increasing the fuel load associated with individual plants. Higher fuel loads result in greater heating duration and heat dosage associated with individual plants, increasing the probability of fire damage occurring (Wright 1971; Engle et al. 1998).

Summer fire produced greater or similar reductions in purple threeawn abundance compared to fall fire. Purple threeawn is a C_4 grass and was likely active when we applied summer fires, but dormant when fall fires were applied. Summer fire may be more desirable in ecosystems where plant communities evolved with recurrent summer fire (e.g. northern Great Plains) because species in these systems tend to be fire resilient (Wright and Bailey 1982) and will respond positively or remain stable with growing season fire (Bates et al. 2009; Vermeire et al. 2011). Our results are strengthened by a consistent response one year post-fire following very different post-fire growing conditions. The lack of recovery by purple threeawn in Year 2 at Site 1 suggests prescribed fire will negatively impact purple threeawn for at least two-growing seasons post-fire in the northern Great Plains. Our results could be a product of the dry spring growing conditions in Year 2, however, purple threeawn appears to be relatively resistant to drought (Fowler 1984) and may increase in abundance during dry years. Additionally, purple threeawn has a high root:shoot ratio (Perkins and Owens 2003) and low quality litter (Horn and Redente 1998), two characteristics important for resource allocation in semi-arid grasslands (Burke et al. 1998). Furthermore, the prevalence of purple threeawn on coarse-textured soils indicates purple threeawn prefers dry conditions.

Nitrogen had no direct effect on purple threeawn abundance. Our results are contrary to the initial report from eastern Colorado where purple threeawn yield and cover decreased with nitrogen additions (Hyder and Bement 1972), but similar to a second report from the same area where cover remained stable and yield increased or remained stable with nitrogen additions (Horn and Redente 1998). The negative impact of nitrogen on purple threeawn from the initial report appears to be a product of fortuitous events (Hyder et al. 1975). Research plots were treated with nitrogen in the fall and received above-average temperatures and rainfall the following spring. The nitrogen amendments in conjunction with the above average temperatures are believed to have caused purple threeawn to mobilize carbohydrates and begin growth. When spring temperatures returned to normal, mortality occurred in purple threeawn (Hyder et al. 1975).

Although nitrogen did not reduce purple threeawn abundance the growing season of nitrogen application, we observed a decrease in current-year biomass of purple threeawn in nitrogen treated plots in Year 2 at Site 1. The record amount of rainfall received the spring we applied nitrogen amendments to Site 1, produced a robust stand of C_3 perennial grass (crested wheatgrass). The increased production of C_3 perennial grass increased litter cover in nitrogen amended plots, possibly preventing the establishment of purple threeawn seedlings (Fowler 1986) and impeding growth of established purple threeawn plants. Our results and the results of others suggest purple threeawn does not respond negatively to nitrogen amendments, but can be harmed when nitrogen amendments are combined with unique weather conditions.

C_3 perennial grass response

Nitrogen amendments increased C_3 perennial grass (crested wheatgrass) abundance and had the greatest effect when applied during a wet spring. The sensitivity of crested wheatgrass to nitrogen additions is documented in other studies (Black 1968; McGinnies 1968; Power and Alessi 1970) and was expected. Previous literature on rangeland fertilization in the northern Great Plains examined plant community response to nitrogen amendments and showed current-year production could be increased six times normal production with sustained effects for two to three years (Rogler and Lorenz 1957; Cosper et al. 1967; Power 1974). However, those experiments used nitrogen amendments as high as 1000 kg N $\cdot$ ha^{-1} applied in successive years. Our study illustrates the influence of spring precipitation on nitrogen utilization and the yearly variation of weather conditions in the northern Great Plains. Furthermore, nutrient additions to rangelands are not recommended because they are rarely cost-effective (Rauzi 1978), decrease community diversity (DiTommaso and Aarssen 1989), increase the probability of invasion by weed species, and alter nutrient cycling over time (Wedin 1996).

Fire had no effect or a positive effect on C_3 perennial grass abundance, with similar trends from Year 1 to Year 2, indicating crested wheatgrass benefited from the removal of purple threeawn. Our results align with previous studies in northern mixed prairie that reported fire effects on C_3 perennial grass production (Steuter 1987; Engle and Bultsma 1984; Vermeire et al. 2011). One discrepancy between our study and previous work is we conducted our study on old agricultural fields seeded to crested wheatgrass, whereas previous results were from experiments on native prairie. Crested wheatgrass' positive response to fire has been documented in other studies (Lodge 1960; Ralph and Busby 1979) and is indicative of the common fire history between the Eurasian steppe and North American grasslands.

Crested wheatgrass is the most widely planted introduced grass on western rangelands and can be a management concern due to its ability to inhibit the establishment of native plants and lower overall soil quality (Dormaar et al. 1995; Klein et al. 1988; Lesica and DeLuca 1996). The increases in crested wheatgrass following the removal of purple threeawn, coupled with the land use history of our site, indicates purple threeawn invaded a plant community dominated by crested wheatgrass and was displacing the nonnative grass. The results of our study indicate that purple threeawn could be tested for its ability to displace crested wheatgrass.

Management implications

Earlier research suggested purple threeawn could be reduced with nitrogen amendments, and results were interpreted as nitrogen having a direct effect on purple threeawn. However, our results indicate nitrogen amendments had no impact on purple threeawn abundance under typical growing conditions. Additionally, the tendency of nutrient additions to negatively impact overall ecosystem structure and function counterbalance any positive effects on individual species. Prescribed fire, when applied during the summer, appears to be a highly effective rangeland management tool for reducing purple threeawn abundance. Our results show crested wheatgrass increases following the removal of purple threeawn from the plant community. A reduction in purple threeawn and increase in crested wheatgrass would be desirable from a livestock management standpoint, increasing overall palatability of the plant community. Furthermore, fire removes litter accumulation in the crown of purple threeawn plants mitigating one of purple threeawn's herbivory avoidance mechanisms, and increasing the amount of forage available. The high impact of summer fire on purple threeawn abundance and sustained reductions for at least two growing seasons post-fire, indicates summer prescribed fire may be the most appropriate management tool for rehabilitating purple threeawn-dominated plant communities.

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CHAPTER 3. FIRE EFFECTS ON PURPLE THREEAWN BASAL AREA, TILLER PRODUCTION, AND SURVIVAL[1]

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[1] This chapter is co-authored by Dustin Strong, Amy Ganguli, and Lance Vermeire. Dustin Strong (graduate student) was the primary author responsible for collecting data, statistical analysis, interpreting statistical outputs, comprising the information presented in this chapter.

Abstract

Fire is an important ecological process in grassland ecosystems. Fire behavior associated with wild and prescribed fires is variable, but plays an important role in how a plant responds to fire. Purple threeawn (*Aristida purpurea* Nutt. varieties) is a grass native to North America with poor forage quality and the ability to form near monocultures. Additionally, *Aristida*-dominated communities have been observed world-wide. Therefore, the identification of tools to reduce purple threeawn abundance is desirable. We assessed the effects of summer and fall prescribed fire on purple threeawn plant basal area, tiller production, and plant survival one growing season post-fire in the northern Great Plains. Thermocouples and portable data loggers were used measure the maximum temperature, heat duration, and heat dosage individual purple threeawn plants experienced. Fire reduced purple threeawn basal area 53-64% ($P \leq 0.001$) and tiller production 57% ($P \leq 0.001$). Heat dosage (C-statistic=0.69) and heat duration (C-statistic = 0.65) were good predictors of purple threeawn mortality. Results indicate purple threeawn is a fire sensitive species. The ability to predict purple threeawn mortality could enhance the efficacy of prescribed fire as tool to rehabilitate purple threeawn-dominated plant communities. Keywords: *Aristida*, fire behavior, mortality, summer fire, vegetation management, thermocouples

Introduction

Fire is an important ecological process in grasslands and is characterized by high variability in its wild and prescribed forms. The variability associated with every fire is largely determined by season of fire, fuel characteristics, and weather (Wright and Bailey 1982). The responses of grassland plant communities to fire during different seasons, under variable fuel characteristics, and weather conditions are well-documented (Dix 1960, Cable 1967, Steuter and Wright 1983, Engle and Bultsma 1984). Although season of fire, fuel characteristics and weather are the primary drivers of fire variability, there are opportunities to augment that information by quantifying attributes of fire behavior (e.g., heat duration, heat dosage, rate-of-spread) using thermocouples or other devices. Measuring fire behavior could improve our understanding of the mechanisms driving individual plant and community response to fire (McDaniel *et al.* 1997, Vermeire and Rinella 2009).

Prescribed fire is a tool grassland managers can use to alter community structure, improve forage availability, and reduce the dominance of unwanted plants (Pyke *et al.* 2010). Grasses in the *Aristida* genus have demonstrated the ability to become the dominant member of a plant community, a phenomenon documented in North America, Africa, and Australia (Horn and Redente 1998, Paton and Rickert 1989, Kepe 2005). In North America, purple threeawn (*Aristida purpurea* Nutt. varieties) is a native perennial grass with poor overall forage quality and the ability to form near monocultures and dominate for 60+ years (Costello 1944, Horn and Redente 1998). Nitrogen has been tested as a tool to reduce purple threeawn abundance with mixed results (Hyder and Bement 1972, Horn and Redente 1998). Fire appears to be a highly effective tool for reducing purple threeawn abundance (Chapter 2), yet the mechanism driving purple threeawn's negative response to fire is unclear. In general, bunchgrasses, or tussock forming grasses like purple threeawn, tend to be fire sensitive due to heavier fuel loads associated with individual plants and elevated growing points (Wright and Bailey 1982).

Fire damage to plant tissue is believed to occur when temperatures are sustained above 60 °C for an extended period of time (Stinson and Wright 1969, Wright and Bailey 1982) and is directly related to fuel load (Bebawi and Campbell 2002*a*, *b*). Thermocouples enable collection of fire temperature data we can use to calculate heat duration (seconds above 60°C) and total heat dosage (sum of the degrees>60 °C for each second) at the plant or community level. These measurements coupled with season of fire, fuel characteristics, and weather enable more complete descriptions of fire events, as well as the responses of plant communities. By taking detailed fire measurements, we increase the repeatability of a particular fire, enhancing our ability to use fire to achieve a desired outcome (e.g., purple threeawn reduction). The identification of a range where heat duration and/or heat dosage have the greatest impact on purple threeawn could improve the efficacy of prescribed fire as a management tool for purple threeawn-dominated plant communities. The objectives of our study were to 1) assess the effect of fire on purple threeawn tiller production and basal area and 2) determine the relationship between purple threeawn survival and maximum temperature, heat duration and heat dosage.

Methods

Study area

We conducted this research in semi-arid mixed-grass prairie on Bureau of Land Management property near Terry, Montana, USA from July 2011 to July 2012. Average annual precipitation for the area is 295 mm, with the majority occurring April through September. Mean annual temperature is 6.6 °C, with extremes of 44 °C during the summer and -43 °C during the winter. The frost-free growing season typically ranges from 105 to 135 days (Western Regional Climate Center, Reno, NV).

Our study site was located within approximately 30 000 ha of abandoned cropland seeded to crested wheatgrass from 1936-1942. The area was characterized by flat, upland plains situated on a sandy ecological site over the Degrand soil series (a fine-loamy over sandy or sandy-skeletal, mixed, superactive, frigid Aridic Argiustolls) (USDA, NRCS Web Soil Survey, 2010). Our study site was located within a Bureau of Land Management grazing allotment that had been moderately to heavily grazed for at least 40 years. In 2009 we constructed a 3.2 ha exclosure was constructed to prevent cattle from grazing the research plots.

Vegetation at our study site was dominated by the perennial C_4 (warm-season) bunchgrass purple threeawn (*Aristida purpurea* (Nutt.)) and the perennial C_3 (cool-season) bunchgrass crested wheatgrass (*Agropyron cristatum* (L.) Gaertn). Other C_4 perennial grasses present 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 grasses included needle-and-thread (*Hesperostipa comata* (Trin. & Rupr.) Barkworth), Sandberg bluegrass (*Poa secunda* J. Presl), and prairie Junegrass (*Koeleria macrantha* (Ledeb.) J.A. Schultes). Annual grasses were sixweeks fescue (*Vulpia octoflora* (Walt.) Rydb.), field brome (*Bromus arvensis* L.), and cheatgrass (*B. tectorum* L.). The sub-shrub green sage (*Artemisia campestris* L.) was present, in addition to, hairy goldenaster (*Chrysopsis villosa* (Pursh) Nutt.), the perennial legume, silverleaf Indian breadroot (*Pediomelum argophyllum* (Pursh.) J. Grimes) and the biennial forb, yellow salsify (*Tragopogon dubius* Scop.). Annual forbs included field cottonrose (*Logfia arvensis* (L.) Holub), woolly plantain (*Plantago patagonica* Jacq.), and rough false pennyroyal (*Hedeoma hispida* Pursh.). Plant nomenclature follows the USDA PLANTS database (USDA, NRCS 2010).

Experimental design and treatment application

This study was nested within a larger project where we tested fire and nitrogen effects on purple threeawn abundance by randomly assigning three levels of fire (no fire, summer fire, fall fire) and three levels of nitrogen (0, 46, 80 $kg \cdot ha^{-1}$) with three replications to 27 20 × 20 m plots (Chapter 2). Our focus for this study was fire effects on purple threeawn and 18 of our experimental plots received fire and nitrogen amendments. We randomly selected 10 purple threeawn plants in each plot and measured them prior to treatment application and one growing season post-fire. To discourage edge effects, plants selected were located at least 5 m from the edge of the plot.

We applied summer and fall fires on 7 September 2011 and 31 October 2011, respectively. All fires were set using the ring-fire method (Wright and Bailey 1982) and average fuel load for each plot was 2000 kg · ha^{-1}. Summer fires were applied when purple threeawn seeds began dropping and fall fires were applied following the first killing frost. Summer fires were applied with ambient temperature 29-31 °C, relative humidity 15-20 %, winds of 5-13 km · h^{-1}, and fine fuel moistures of 16-27 %. Fall fires were applied with ambient temperature 16-20 °C, relative humidity 28-34 %, winds of 13-30 km · h^{-1}, and fine fuel moistures of 8-11 %. Good fuel continuity allowed for 100 % coverage of all plots, across season of fire.

Thermocouple measurements

We used HOBO® U12 J, K, S, T Thermocouple Data Loggers (Onset Computer Corporation, Bourne, MA) with K-type Thermocouples (Omega Engineering, Inc., Stanford, CT) to create time-temperature profiles at the plot level and for individual plants. We placed thermocouples in each plot within the crown of a target plant (10 thermocouples · plot^{-1}) and programmed the data loggers to record temperatures at one-second intervals. Maximum temperature was identified by finding the greatest value for each time-temperature profile. Heat duration was calculated as time (seconds) of heat greater than 60 °C and heat dosage was the sum of the degrees > 60 °C for each second (degree-seconds). We used these measurements to derive the mean maximum temperature, heat duration, and dosage experienced at the plot level (Table 3.1) as well as the plant level. Although we had 10 thermocouples in each plot, improper thermocouple installation prevented us from collecting data on all plants assigned a thermocouple (i.e. thermocouple tips that were not located in the crowns of purple threeawn plants). Those plants were not included in our plant level analysis, resulting in the differences in sample size for summer (n = 55) and fall fires (n = 73).

Table 3.1. Thermocouple observations at the plot level for summer and fall prescribed fires.

Thermocouple measurements	Summer fire		
	Mean±SE	Maximum	Minimum
Maximum temperature (C)	225±10	283	189
Heat duration (s)	221±14	314	163
Heat dosage (C·s)	10284±834	15017	6929
	Fall fire		
Maximum temperature (C)	223±16	292	155
Heat duration (s)	127±3	146	118
Heat dosage (C·s)	7505±681	11771	4691

n=9 for summer and fall fire.

Vegetation measurements

We quantified plant response to treatments by measuring basal area, vegetative, reproductive, and total tiller production in July of each year. Basal area for individual plants was determined by using a string and ruler to measure the circumference of each target plant. We conducted tiller counts on each plant to determine total tiller production and used number of vegetative tillers to derive the percentage of total tiller production comprised of vegetative tillers.

Statistical analysis

We analyzed plot level plant data using generalized least squares (MIXED procedure of SAS; Littell *et al.* 2006). The model included season of fire and nitrogen as fixed effects. Response variables were plant basal area, vegetative, reproductive, total tillers, and percentage of total tillers in the vegetative state. All plants were used to determine treatment effects on basal area, however, only plants that survived were used to determine treatment effects on tiller production and percentage of total tillers in the vegetative state. Plot was the experimental unit and we set statistical significance at $P < 0.05$. In a second analysis, we tested maximum temperature, heat duration, and heat dosage as predictor variables for purple threeawn mortality with logistic regression (LOGISTIC procedure of

SAS; Littell *et al.* 2006). Plant was the experimental unit and we set statistical significance at $P < 0.05$.

Results

Plant basal area and tiller production

Nitrogen did not have a significant effect on any of our response variables (P = 0.100). Summer and fall fire reduced ($P \leq 0.001$) purple threeawn plant basal area to 18 and 14 cm^2 compared to 39 ± 2 cm^2 for nonburned plants, with no difference between seasons of fire. Similarly, summer and fall fire reduced ($P \leq 0.001$) vegetative tiller production to 16 and 17 tillers · plant^{-1}, respectively, compared to 38 ± 2 tillers · plant^{-1} for nonburned plants, with no difference between seasons of fire. Reproductive tiller production was least for summer burned plants (5 tillers · plant^{-1}), intermediate for nonburned plants (10 tillers · plant^{-1}), and greatest for fall burned plants (13 ± 1 tiller · plant^{-1}, $P \leq 0.001$). Fire reduced total tiller production and summer fires had a greater effect than fall fires ($P \leq 0.001$; Fig. 3.1A). The percentage of total tillers that were vegetative was similar between nonburned and summer burned plants. However, fall fire reduced the percentage of total tillers that were vegetative because of increased reproductive tiller production ($P \leq 0.001$; Fig. 3.1B).

Plant survival

Fire behavior measurements from individual plants illustrate differences between summer and fall fires (Table 3.2). Average heat dosage and duration was greater during summer fires than fall fires. Fuel load and connectivity was similar between plots, however fuel moisture was greater for summer fires than fall fires. Additionally, weather conditions varied between seasons with fall fires having stronger winds, lower fine fuel moisture, ambient temperature, and greater relative humidity than summer fires.

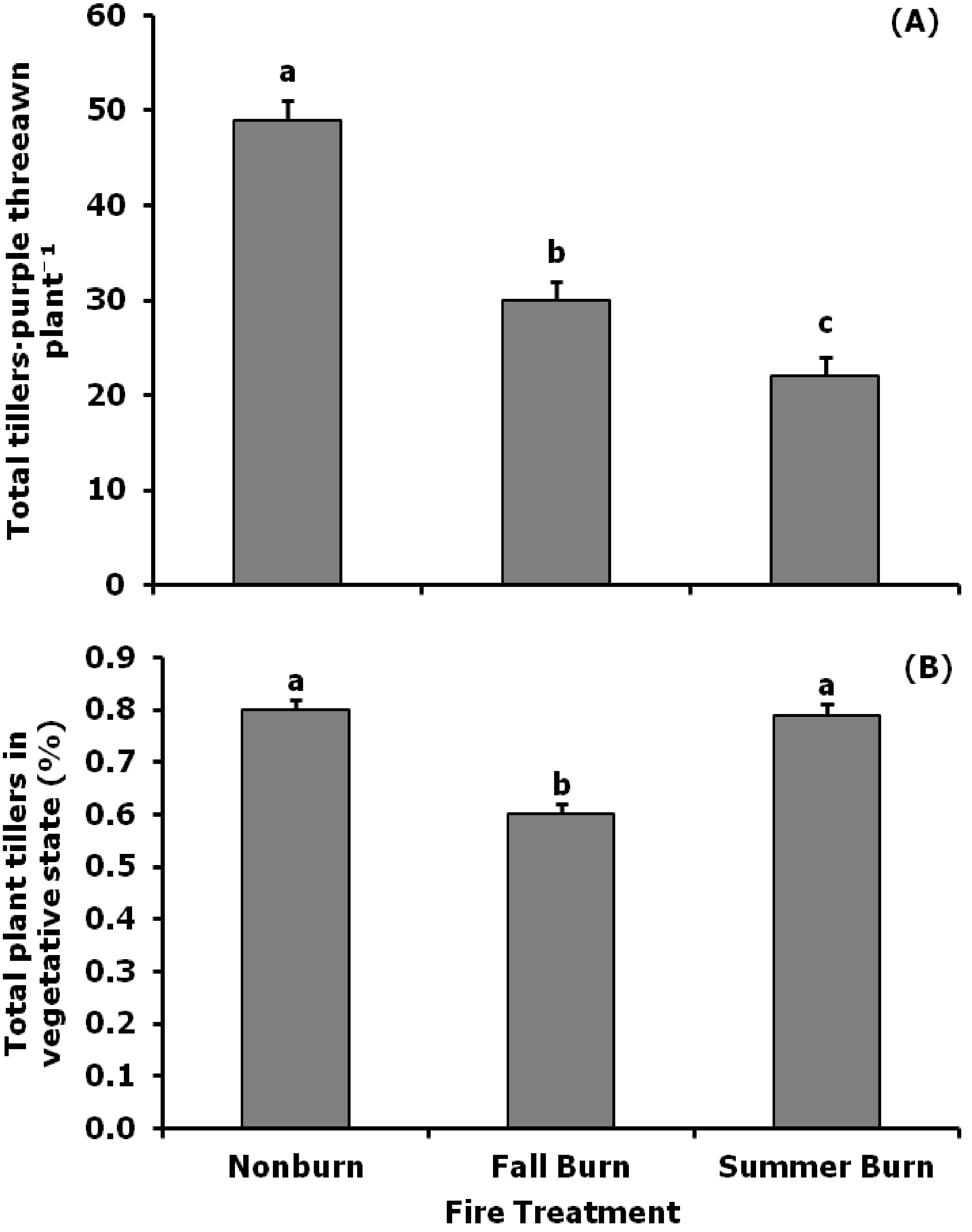

Figure 3.1. Fire effects on (A) total tiller production·purple threeawn plant^{-1} (+ SEM) and (B) percentage of total tillers in the vegetative state (+ SEM) one growing-season post-fire. Means marked with the same letter are similar ($P < 0.05$).

Table 3.2. Mean and range of thermocouple observations for individual plants[a] during summer and fall prescribed fire.

Thermocouple measurements	Summer fire		
	Mean±SE	Maximum	Minimum
Maximum temperature (C)	222±13	433	86
Heat duration (s)	232±17	894	52
Heat dosage (C·s)	10352±617	25624	1094
		Fall fire	
Maximum temperature (C)	241±11	487	85
Heat duration (s)	129±4	245	68
Heat dosage (C·s)	8205±413	18706	1771

n=55 for summer fire. n=73 for fall fire.
[a]used to build logistic regression model.

Fire resulted in 10 % mortality of purple threeawn plants (13 of 128) and mortality was directly related to heat dosage and duration. Furthermore, summer fire accounted for 75 % (10 of 13 plants) of purple threeawn mortality. Heat dosage was the best predictor of plant mortality, but heat duration was a reliable predictor as well (Table 3.3). Maximum temperature was not a significant predictor of plant mortality.

Table 3.3. Predictive ability of fire variables used in logistic regression model to test for purple threeawn mortality.

Predictor variable	Model information		
	C-statistic[a]	H-L test[b]	P>Chi^{-2}
Heat dosage (°C·s)	0.69	0.47	0.04
Heat duration (s>60°C)	0.65	0.92	0.02
Maximum temperature(°C)	0.55	≤0.01	0.54

[a]*C*-statistic is the predictive ability of the model.
[b]Hosmer-Lemeshow goodness of fit test (higher value = better fit).

When heat dosage rose above 10 000 °C · s, the probability of plant mortality exceeded 0.1 (Fig. 3.2A). With heat duration, the probability of plant mortality reached 0.1 when temperatures were sustained above 60 °C for 3 minutes (Fig. 3.2B). The 95 % confidence intervals illustrate most of our data points were located on the lower end of heat dosage and duration, limiting our ability to make precise predictions about purple threeawn mortality at the upper range of heat dosage and duration.

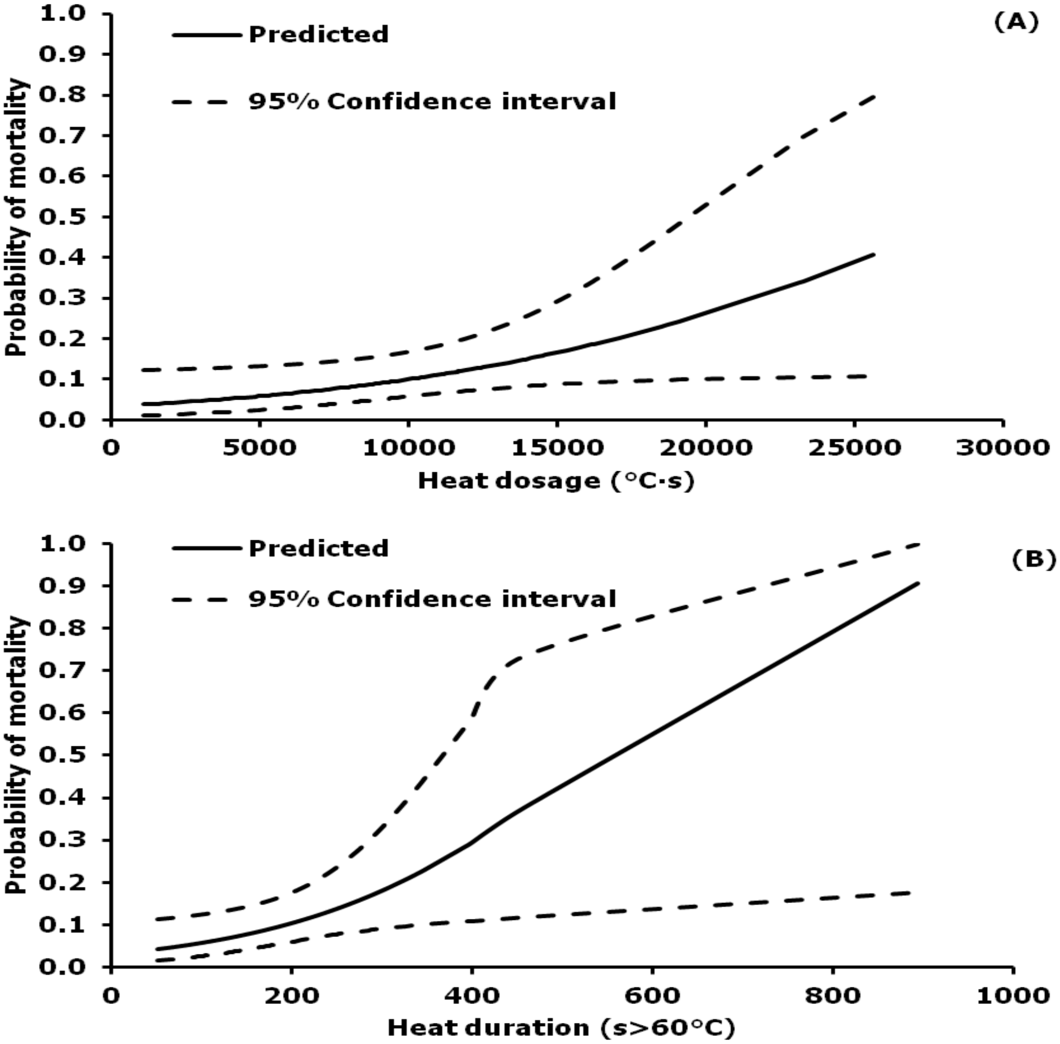

Figure 3.2. Predicted mortality and 95 % confidence interval for purple threeawn as a function of (A) heat dosage and (B) heat duration.

Discussion

Fire negatively impacted purple threeawn tiller production and basal area. Our observations are similar to experiments in New Mexico (Killgore *et al.* 2009), where fire reduced purple threeawn basal area and plants did not recover to pre-fire size for 4-5 years post-fire (Parmenter 2008). Reductions in basal area following fire are common in bunchgrasses due to the removal of litter accumulation near the center of the plant, and the high probability of plant tissue damage from the combustion of that litter (Ewing and Engle 1988). Our observed reductions in total tiller production correspond with other studies that reported reductions in current-year biomass and cover of purple threeawn following fire (Steuter and Wright 1983, Chapter 2). Our results and the findings of others suggest purple threeawn is susceptible to fire damage. Response of other *Aristida* species to fire is less clear. For example, the relative density of *Aristida ramosa* and *A. calycina* decreased with spring burning in Australia, but increased following a late-summer burn (Paton and Rickert 1989). Similarly, *A. junciformis* relative abundance was greater in nonburned plots than plots burned during the winter or spring in Africa (Fynn *et al.* 2005). Further testing is needed to draw conclusions about the fire sensitivity of *Aristida* species outside of North America.

Fall fire increased reproductive tiller production and summer fire decreased reproductive tiller production. Our fall fire observations support previous purple threeawn research in the southern mixed prairie on reproductive tiller production post-fire (Trlica and Schuster 1969). Although, vegetative reproduction is the most common form of propagation for native grasses in many grassland ecosystems (Benson *et al.* 2004), seed production appears to be important for purple threeawn propagation. Purple threeawn is a prolific seed producer, (Evans and Tisdale 1972) with highly viable seeds well-adapted to wind and animal dispersal (Fowler 1986). Therefore, our data indicate summer fire is more detrimental to purple threeawn due to the observed reductions in total and reproductive tiller production.

Our data supported the hypothesis that heat dosage and duration are the driving factors behind plant production and mortality. Furthermore, our results indicated maximum temperature does not accurately predict plant mortality and support the findings of others (Bebawi and Campbell 2002*a*; Vermeire and Roth 2011). The majority of our data points for heat dosage and duration were distributed at the lower end of their respective ranges. That type of distribution indicates other factors (e.g., fuel load, rate-of-spread) were limiting the amount of heat dosage and duration each plant was experiencing. Therefore, mortality greater than 10 % may not have been attainable under the conditions in which we burned. Additionally, summer fire produced greater heat duration and dosage and appeared to have a greater effect on purple threeawn mortality than fall fire.

Prescribed fire is one of many vegetation management tools at the disposal of grassland managers. The propensity of fire to reduce tiller production of purple threeawn, as well as other *Aristida* species, suggests fire could be used to improve community diversity in *Aristida*-dominated plant communities world-wide. In the northern Great Plains, purple threeawn is rarely utilized by cattle due to poor forage quality relative to other species in the area. Fire should increase the overall palatability of purple threeawn, which even with fire-related reductions, increases overall forage availability. Summer fire caused greater reductions in total and reproductive tillers than fall fire, potentially limiting seed production. Additionally, other native grass species of the northern Great Plains are resilient to summer fire (Vermeire *et al.* 2011), which suggests fire could be used to improve community diversity. Heat dosage and duration appear to be the primary fire behavior variables determining purple threeawn mortality. With that information, managers can implement prescribed fire to purple threeawn-dominated plant communities under conditions that will maximize heat dosage and duration, thus increasing purple threeawn mortality. Our study is one example of how measuring certain fire variables can enhance our understanding of plant response to fire. As fire research progresses, the identification of which fire variables are driving plant or community response will improve the efficacy of prescribed fire as a vegetation management tool.

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