

Response of the shortgrass steppe plant community to fire

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ABSTRACT

Fire is an important driver of ecological pattern and process in grasslands worldwide, although its role in semi-arid systems is less well known. We used published studies and new experimental research to 1) provide a synthesis of existing knowledge of fire in the semi-arid grasslands of the North American Great Plains, and 2) assess the degree of similarity in semi-arid and mesic grassland responses to fire in this region. Based on published studies, burning has neutral to negative effects on aboveground productivity in semi-arid grasslands and variable effects on plant communities. To more rigorously assess fire effects, replicated experimental plots were established in ungrazed shortgrass steppe in northern Colorado and prescribed spring fire was applied in 2006 and 2007, 2006 only, or not at all. Aboveground net primary productivity decreased or remained unchanged with burning. Plant community changes included increases in perennial forbs, decreases in annual grasses and a positive response in annual forbs to the combination of fire and a wet spring in 2007. Combined, these results indicate that post-fire changes in productivity in semi-arid grasslands are neutral to negative, in contrast to positive responses in mesic grasslands, and not strongly negative as previously assumed.

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1. Introduction

Great Plains grasslands of central North America are usually divided into three types: tallgrass prairie in the east, mixed-grass prairie in the center and north and shortgrass steppe in the west (Lauenroth et al., 1999). Changes in grassland structure and function over this gradient are driven primarily by changes in mean annual precipitation, which results in a decrease in annual aboveground net primary productivity (ANPP) from 500 g/m² in productive tallgrass prairie sites in eastern Kansas (Briggs and Knapp, 1995) to less than 100 g/m² in shortgrass steppe of north-eastern Colorado (Lauenroth and Milchunas, 1991). These grasslands share fire, grazing and climatic variability as major determinants of their structure, with fire frequency in particular (assumed historical and present-day) decreasing strongly from tallgrass prairie to shortgrass steppe as a result of the gradient in productivity and fuel (Kucera, 1981; Oesterheld et al., 1999).

Fire is thought to have played a central role, perhaps the central role (Wells, 1965, 1970), in the formation of the Great Plains

grasslands (Anderson, 2006; Axelrod, 1985; Bragg, 1995). However, fire regimes in the Great Plains and elsewhere have been significantly altered by human activities in the last two centuries (Axelrod, 1985; Hart and Hart, 1997; Samson et al., 2004). Active fire suppression and fragmentation of native grassland have decreased the frequency and extent of fires, as well as modified fire seasonality (Leach and Givnish, 1996). Moreover, human-induced alterations to grazing patterns through management of domestic livestock contrast with prior episodic herbivory by native grazers. This has further reduced fire frequency by decreasing fuel loads and the probability that a fire will spread from the point of ignition (Ford and McPherson, 1996; Stewart, 1951). Unfortunately, there are few proxies, such as fire scarred trees and charcoal in lake sediments, available to reconstruct fire histories for most of the Great Plains. As there is little history to draw from, experimental research on grassland responses to various fire regimes becomes more important for developing hypotheses and forming the basis of management decisions.

Fire in grasslands removes aboveground biomass, which, in the dormant season, means removing accumulated litter with minimal damage to living tissues of the dominant perennial grasses (Anderson, 1982). Litter removal in more productive grasslands allows more solar radiation to reach the soil surface resulting in earlier and longer growing seasons, reduces competition for light,

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and may alter nutrient availability with warmer soils (Briggs and Knapp, 1995; Knapp and Seastedt, 1986). These factors would be expected to increase productivity after fire. However, the removal of litter can also lead to decreased soil moisture (Knapp and Seastedt, 1986; Redmann, 1978; Vermeire et al., 2005), which should tend to decrease ANPP. In the tallgrass prairie, where water is relatively abundant, litter buildup leads to energy limitation and burned sites have consistently higher aboveground productivity relative to unburned sites (Briggs and Knapp, 1995; Knapp and Seastedt, 1986). Thus, the factors tending to increase productivity outweigh those that would decrease it. In the drier shortgrass steppe, the weighting of these factors may be different, altering responses, qualitatively or quantitatively, to fire.

Fire has the potential to change the species composition of grassland communities directly or indirectly by affecting species and groups of species differently (Anderson, 1982; Daubenmire, 1968). Shifts in species composition have been observed in the tallgrass prairie with the dominant perennial grasses increasing in abundance and diversity decreasing due to decreases in forbs in annually burned relative to unburned areas (Abrams and Hulbert, 1987; Collins and Gibson, 1990; Gibson and Hulbert, 1987). Changes in species composition and ANPP responses to fire in shortgrass steppe are less clear. Constraints on plant–soil relationships shift from aboveground (light) to belowground (soil water) (Burke et al., 1998), suggesting that impacts of fire on soil moisture will likely determine ANPP and compositional responses in the shortgrass steppe.

Fire has been studied extensively in the mesic tallgrass prairie, but effects of fire in the drier portion of the Great Plains are poorly understood (Ford and McPherson, 1996). Several early studies reported reduced ANPP or cover of desired grass species post-fire, leading to the widespread perception that fire is detrimental in the shortgrass steppe (Bragg, 1978; Dwyer and Pieper, 1967; Hopkins et al., 1948; Launchbaugh, 1964; Trlica and Schuster, 1969). Perhaps due to the negative perceptions of burning, the effects of fire in the shortgrass steppe and mixed-grass prairie have received only sporadic attention over the last sixty years. Notably, there is a significant knowledge gap regarding vegetation responses to different fire frequencies in the dry grasslands of the western Great Plains and the most northern portions of the shortgrass steppe in particular. Recently however, general attitudes toward fire have been shifting toward a greater recognition of fire as a potential management tool and as a natural, often essential, process in ecosystems (Allen et al., 2002; Bond et al., 2005; Brown, 2000; Kreuter et al., 2008; Wright and Bailey, 1980).

Oesterheld et al. (1999) presented a conceptual model of the relative effects of fire, grazing and climatic variability on ANPP of grasslands. Fire is predicted to have large positive relative effects in mesic grasslands such as tallgrass prairie, smaller and more variable effects in grasslands receiving intermediate precipitation (600 mm annually), and negative effects in more arid grasslands. Extrapolating their model to drier systems, Oesterheld et al. (1999) predicted severe negative impacts on productivity following fire in grasslands, such as shortgrass steppe, with mean annual precipitation between 200 and 450 mm. There is abundant evidence of positive effects of fire on productivity and cover of vegetation in mesic grasslands (Abrams et al., 1986; Knapp et al., 1998; Oesterheld et al., 1999) but this model has not been experimentally tested in drier grasslands.

We used published literature and new experimental results to test specific predictions regarding grassland responses to fire across precipitation gradients. Experimental work was conducted in the northern portion of the shortgrass steppe in Colorado, and was designed to compare different frequencies of dormant season (spring) prescribed burns over a two-year period with unburned

controls. We hypothesized that (1) ANPP would be lower after fire and more frequent fire would result in greater reductions, (2) there would be no substantial changes in overall plant community composition in response to fire, and (3) annual species would be more responsive to fire than perennials. The first hypothesis is derived from the model presented by Oesterheld et al. (1999). As the shortgrass steppe is dominated by a small number of long-lived perennial grass species and is relatively species poor, major changes in the community after two years were not expected. However, fire, as a disturbance with the potential to change the competitive environment, might provide an opportunity for annual species to increase in abundance (D'Antonio, 2000; Keeley, 2006; Keeley et al., 2003).

2. Methods

2.1. Site description

This research was conducted at the Shortgrass Steppe Long-Term Ecological Research site located on the USDA Agricultural Research Service Central Plains Experimental Range, about 20 km northeast of Nunn, Colorado, USA (40° 49' N, 104° 46' W). The climate is semi-arid with mean annual precipitation of 321 mm, greater than 80% of which occurs in the growing season of April through September (Lauenroth and Sala, 1992). Precipitation varies markedly from year to year (Lauenroth and Milchunas, 1991). In 2006, the growing season precipitation was 197 mm, 28% below the mean of 272 mm. The 2007 growing season precipitation was 249 mm, only 9% below the long-term mean. In the years directly preceding the study, precipitation was greater than average in 2005 and average to very low in 2002–2004. Mean monthly temperatures range from –4 °C in January to 22 °C in July (Lauenroth and Burke, 2008). Soils are primarily Aridic Argiustolls and Ustic Haplargids. Vegetation is dominated by the C₄ bunch grass *Bouteloua gracilis* (Willd. ex Kunth) Lag. ex Griffiths and other perennial graminoids including *Buchloe dactyloides* (Nutt.) Englm., *Carex duriuscula* C.A. Mey, *Sporobolus cryptandrus* (Torr.) A. Gray and *Elymus elymoides* (Raf.) Swezey. Other common species include the perennial forb *Sphaeralcea coccinea* (Nutt.) Rydb. and the succulent *Opuntia polyacantha* Haw.

2.2. Experimental design

Treatment plots were located in a level, undisturbed area from which cattle were excluded five years prior to and throughout the study. Plots (20 × 20 m) were arranged in four blocks and within each block the three treatments (annual spring burn, triennial spring burn and unburned control) were randomly assigned, yielding four replicates per treatment in a randomized complete block design. The spring fire treatment was chosen for this study to permit direct comparison with results from the tallgrass prairie in which spring fire is commonly employed for management and experimental purposes (Knapp et al., 1998). To facilitate sampling, each plot was divided in half: one half for ANPP, soil and other destructive sampling, the other for plant cover and non-destructive sampling. All sampling occurred at least 1 m from the edge of the plots.

Both annual and triennial burn plots were burned on May 8, 2006, using drip torches to ignite the fires. Fire lines were re-set as necessary to ensure that >95% of the plot burned. Annual burn plots were burned a second time on April 9, 2007. As this study compares the first two years of these treatments, they will be referred to as 'burned' and 'unburned' for 2006 and 'burned 2×', 'burned 1×' and 'unburned' for 2007.

2.3. Abiotic responses

Volumetric water content of the soil was measured at two locations within each plot using ECH₂O EC-20 probes (Decagon Devices Inc.) inserted at random locations along one side of the plots, 1.5 m from the edge. These probes provided measurements of soil moisture integrated over the upper 20 cm of soil. Soil moisture measurements were made manually every three to eleven days from the day of the burn until mid-September. All plots were measured on the same days. Soil temperature was measured in two locations within each plot. At each location sensors were placed at depths of 5–10 cm and 15–20 cm. Temperature was recorded every 30 min over the course of the growing season with HOBO data loggers (Onset Computer Corporation). Daily minimum, maximum and mean temperatures were derived from these data and were used as dependent variables in the statistical analyses.

2.4. Vegetation responses

Plant species composition was sampled in late July each year. Canopy cover was visually estimated to the nearest percent in five randomly located 2 × 2 m quadrats in each treatment plot. Estimations were made separately in each of the four 1 × 1 m subplots of each quadrat. Subplot cover estimates were averaged at the quadrat level. Relative cover (cover of species *i*/total cover) was used in all analyses. Species richness, evenness and the Shannon diversity index were calculated for each quadrat (Magurran, 1988).

Aboveground biomass for ANPP estimates was collected during the first two weeks in August (peak biomass) each year (Knapp et al., 2007; Lauenroth and Sala, 1992). Ten 0.25 m² quadrats were randomly located in each treatment plot. All aboveground biomass except cacti and previous years' growth of sub-shrubs were collected. Current year's growth was sorted into functional groups by growth form (grass, forb, sub-shrub) and life history (annual, perennial). Litter, both standing dead and detached plant material was collected in half of the quadrats. All materials were dried at 60 °C for a minimum of 48 h and weighed.

Density of flowering tillers was determined in five randomly located 0.25 m² quadrats in each treatment plot. Counts were made in mid-September to early October, between peak flowering and senescence. Analyses focused on *B. gracilis* alone and all perennial grass species combined because there were not enough flowering tillers of other species for individual statistical comparisons.

2.5. Statistical analysis

All statistical analyses were performed using PROC MIXED in SAS version 9.1 (SAS, 2002). Data were square root or log transformed, if necessary, to achieve homogeneity of variance. Bonferroni adjustments were used to correct *P*-values where multiple comparisons were made. Analysis of variance (ANOVA) was used to test for treatment differences and treatment by functional group interactions, where applicable, in ANPP, cover, diversity measures, litter mass and flowering tiller density. Treatment and functional groups were treated as fixed factors and block as a random factor. Repeated measures ANOVAs were used to test for differences between treatments and over time for soil moisture and soil temperature. Treatment, day of year and depth (soil temperature only) were fixed factors. Block and plot were random factors. Individual probes were considered subjects in the repeated measures analysis. One outlier was removed prior to analyses for litter mass and non-significant (*P* > 0.05) interactions of fixed factors were removed from all analyses. To investigate the possible relationship between ANPP and litter mass an analysis of

covariance (ANCOVA) was performed with litter mass and year as explanatory variables.

3. Results

3.1. Literature synthesis

Using web-based bibliographic search techniques, we identified 27 studies published between 1948 and 2006 describing vegetation responses to fire in the drier portion of the Great Plains (mean annual precipitation ≤ 600 mm) (Supplementary Table 1). These studies covered an area from Canada to Texas and from the Rocky Mountains to central Kansas (Fig. 1). The majority were conducted in mixed-grass prairie (15, 56%) with fewer in the shortgrass steppe (5, 19%) and the Nebraska Sandhills prairie (4, 15%). Three grassland studies (11%) from central New Mexico in the transition into Chihuahuan desert were included where precipitation regimes were similar to those of the Great Plains sites. These studies varied substantially in the attributes of the fires studied, including the seasonality, frequency and origin (natural vs. prescribed).

In general, responses of vegetation to fire varied considerably, but there were no apparent trends with respect to season of fire, grazing history, mean or actual precipitation (Fig. 2; Scheintaub,

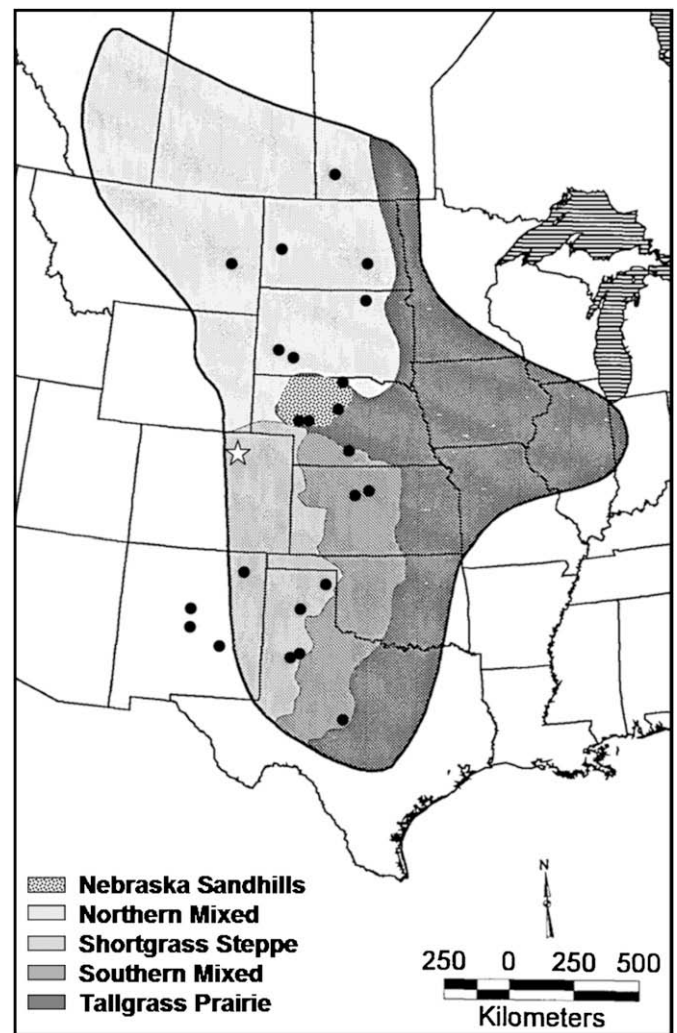


Fig. 1. Map of the North American Great Plains region with locations of previously published studies (dots) and this study (star). See text for details. Adapted from Lauenroth et al. (1999).

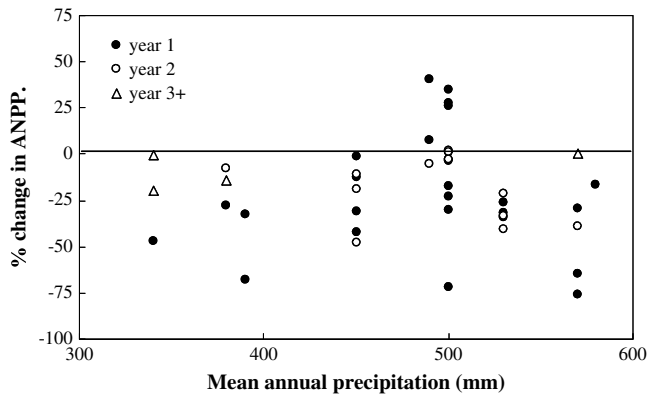


Fig. 2. Percent change in aboveground net primary productivity ((burned – unburned)/unburned) in one, two, or three or more years after fire as a function of mean annual precipitation. Data from Brockway et al. (2002), Dix (1960), Dwyer and Pieper (1967), Engle and Bultsma (1984), Gartner et al. (1978), Hopkins et al. (1948), Launchbaugh (1964), Morrison et al. (1986), Owensby and Launchbaugh (1977), Pfeiffer and Steuter (1994), Shay et al. (2001), Steuter (1987), Trlica and Schuster (1969).

2008). Total ANPP was reported to decrease in the first year after burning in 55% of the cases. ANPP increased 15% of the time and did not differ significantly in the remaining cases. Responses of forbs, grasses and species recorded individually varied from large reductions to substantial increases (Supplementary Table 1; Scheintaub, 2008). Based on these studies, fire effects on total ANPP in the region appear to be relatively consistent in direction (neutral to negative), but variable in magnitude. The variability was not easily attributed to any particular site or fire characteristic. Studies conducted in shortgrass steppe followed the regional pattern.

Our literature findings suggest that the effects of fire on plant community composition, cover, diversity and tiller density followed patterns similar to the effects on ANPP. For example, species diversity increased (Kirsch and Kruse, 1972), decreased (Biondini et al., 1989; Wolfe, 1972) or was unaffected (Brockway et al., 2002; Morrison et al., 1986; Shay et al., 2001) by fire. Soil moisture, temperature and nitrogen were measured in a few studies to provide some mechanistic explanations for vegetation responses (Schacht and Stubbendieck, 1985; Shay et al., 2001; Trlica and Schuster, 1969; White and Currie, 1983; White et al., 2006). Unfortunately, data are too limited concerning soil responses to fire for robust statements to be made about how soil temperature, moisture or nutrients relate to vegetation responses. Several authors noted that climatic and geographic variability had effects at least as great as fire and some interactions between climate or site

and fire were reported (Biondini et al., 1989; Dix, 1960; Engle and Bultsma, 1984; White and Loftin, 2000; Whisenant and Uresk, 1989; White et al., 2006).

Our literature search identified three key gaps in the types of fire studies conducted in the semi-arid grasslands of the Great Plains. First, there is little known concerning effects of multiple fires and different fire frequencies on these grassland plant communities. Only seven (26%) studies investigated the effects of multiple fires. Shay et al. (2001) and Biondini et al. (1989) investigated the effects of three burns, but both studies compared annual burning with unburned controls. Knowledge of the effects of different fire frequencies, especially viewed over longer intervals, can be an important foundation for using prescribed fire in management. Second, there has been relatively little long-term monitoring of vegetation responses to fire. Long-term, multiple fire studies are needed to disentangle fire and climate effects on vegetation responses, especially in these semi-arid grasslands which have inherently high variability in precipitation (Knapp and Smith, 2001). The majority of studies (19, 70%) reported observations of the second growing season following one or more fires, but few (6, 22%) reported results after more than three growing seasons. Finally, there is geographical gap with the northern portion of the shortgrass steppe and the northwestern part of the mixed-grass prairie, having received little attention in regards to fire response (Fig. 1).

3.2. Fire experiment – abiotic responses

Soil moisture differed over the course of the growing season each year (2006: $F_{27,600} = 193.14$, $P < 0.0001$; 2007: $F_{19,431} = 137.38$, $P < 0.0001$) in response to precipitation events, but did not differ between fire treatments in either year (2006: $F_{1,10} = 0.38$, $P = 0.553$; 2007: $F_{2,9} = 1.78$, $P = 0.222$).

Soil temperatures converged among treatments within a few weeks after the fires in both years, so we focused on temperature data from only the first three to four weeks following the fires. Other studies have previously determined soil temperature differences between burned and unburned sites tend to be greatest directly after fire (Blair, 1997; Bremer and Ham, 1999; Shay et al., 2001; Vermeire et al., 2005). In 2006, the minimum, maximum and mean soil temperatures at both depths (5–10 and 15–20 cm) did not differ between burned and unburned plots in the first three weeks after the fire ($P > 0.15$). In 2007, treatment differences were small ($< 1^\circ\text{C}$) and observed in only the first week following the fire (data not shown).

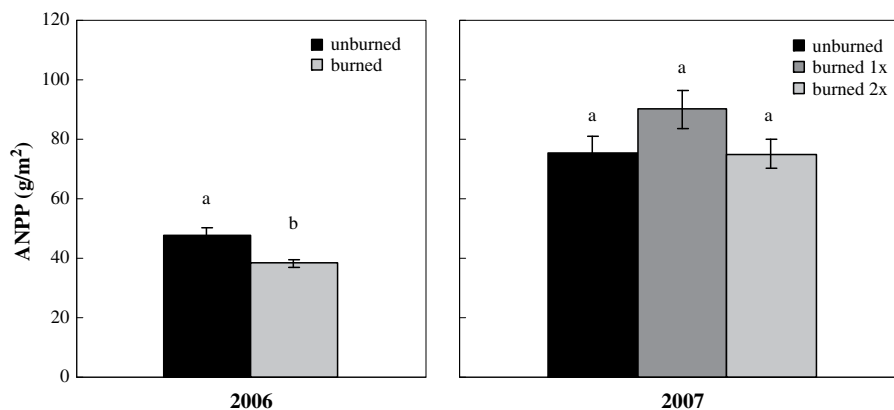


Fig. 3. Total aboveground net primary productivity (mean \pm SE) in different fire treatments in 2006 and 2007 in the shortgrass steppe of northern Colorado. In the 2007 panel, burned 1 \times and 2 \times indicate plots were burned once in 2006 (1 \times) or plots were burned in both 2006 and 2007 (2 \times). Different letters above bars indicate significant ($P < 0.05$) differences among fire treatments. per: perennial, ann: annual.

3.3. Fire experiment – vegetation responses

Total ANPP was 20% lower in burned than unburned plots in 2006 ($F_{1,3} = 12.88, P = 0.037$), but there were no significant differences between treatments in 2007 ($F_{2,6} = 1.62, P = 0.274$) (Fig. 3). In 2006, perennial grass productivity was 27% lower and annual grass 74% lower in burned plots, while perennial forb productivity was 26% higher (Fig. 4). Annual grass productivity was 88% lower in burned 2× plots relative to unburned plots in 2007. Perennial forb productivity appeared to increase from unburned to burned 2× plots, but this trend was not significant in 2007 ($P = 0.195$) (Fig. 4).

There was a 60% reduction in litter mass in burned plots in 2006 ($F_{1,3} = 80.71, P = 0.003$) and marginally significant differences between treatments in 2007 ($F_{2,6} = 4.44, P = 0.066$). By the end of the second growing season litter mass did not differ between burned 1× and unburned plots, but was lower in burned 2× plots. There was a positive relationship between litter mass and ANPP (2006: $\ln(\text{ANPP}) = 3.480 + 0.0038 \times \text{litter mass}$, 2007: $\ln(\text{ANPP}) = 4.242 + 0.0140 \times \text{litter mass}$, $r^2 = 0.726, P < 0.005$) suggesting a facilitative, or at least neutral, effect of litter on ANPP (Fig. 5).

Total plant cover did not differ between treatments in either year (2006: $F_{1,3} = 5.27, P = 0.105$; 2007: $F_{2,6} = 0.83, P = 0.481$). However, relative cover of plant functional groups differed between treatments in both years (2006: $F_{4,272} = 4.14, P = 0.003$; 2007: $F_{8,264} = 3.06, P = 0.003$). In 2006, annual grasses had lower relative cover on burned plots. In 2007, annual forbs had greater relative cover in burned 2× plots (Fig. 6). Total species richness, richness of individual plant functional groups, species evenness and the Shannon diversity index did not differ between treatments in either year ($P > 0.05$). Neither the total density of flowering tillers

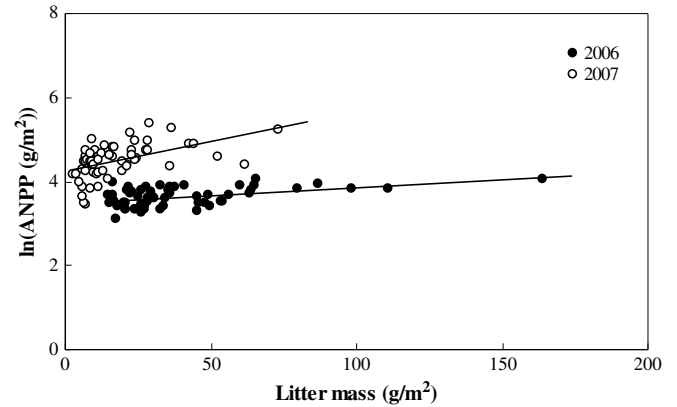


Fig. 5. Relationship between aboveground net primary productivity (ANPP) and litter mass for two years at the Shortgrass Steppe Long-Term Ecological Research site. 2006: $\ln(\text{ANPP}) = 3.480 + 0.0038 \times \text{litter mass}$, 2007: $\ln(\text{ANPP}) = 4.242 + 0.0140 \times \text{litter mass}$, $r^2 = 0.726, P < 0.005$.

nor the density of flowering tillers of the dominant *B. gracilis* differed between treatments in either year ($P > 0.30$). Means and variances for all biotic responses are included in Supplementary Table 2.

4. Discussion

Compiled and synthesized, the literature provided only partial support for the predictions of Oesterheld et al. (1999) that fire would have a severe negative effect on the aboveground productivity of semi-arid grasslands. The effects of fire on ANPP are perhaps better described as neutral to negative in grasslands receiving less than 600 mm mean annual precipitation. These effects did not become more strongly negative as precipitation decreased, as predicted by Oesterheld et al. (1999). Based on the first two years of experimental fires, the shortgrass steppe in northern Colorado appears to respond modestly following one or two consecutive spring fires. Total ANPP decreased in 2006, but not in 2007, which is consistent with the variable responses reported by other studies (Brockway et al., 2002; Dix, 1960; Dwyer and Pieper, 1967; Engle and Bultsma, 1984; Launchbaugh, 1964; Shay et al., 2001; Trlica and Schuster, 1969). Perennial forb ANPP appeared to increase slightly with fire. Cover of annual plants, though small relative to the cover of perennials, was the most responsive to both weather and fire. Annual forbs responded positively to the combination of fire and the wet spring weather in 2007. This response may have been mediated by the reduction in

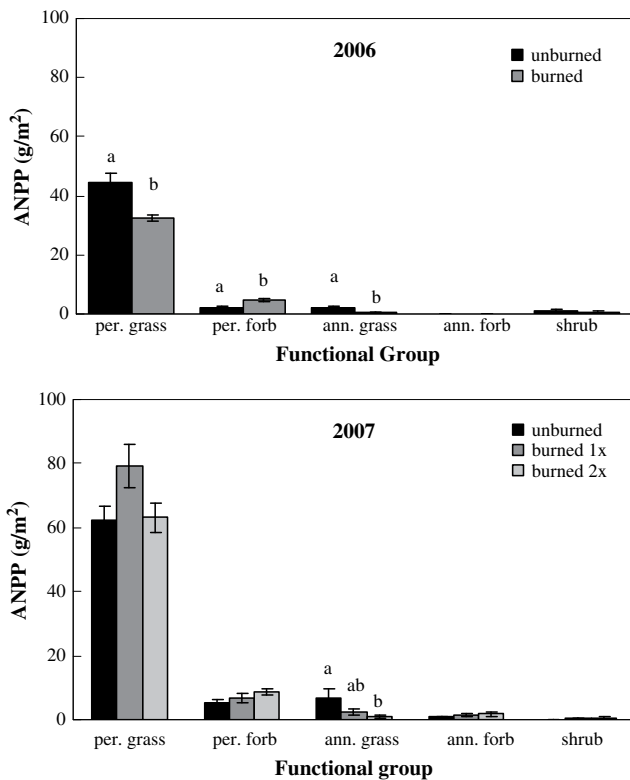


Fig. 4. Aboveground net primary productivity (mean ± SE) by functional group in different fire treatments divided by functional group for 2006 and 2007. Different letters above bars indicate significant differences among fire treatments. In the 2007 panel, burned 1× and 2× indicate that plots were burned once in 2006 (1×) or plots were burned in both 2006 and 2007 (2×). per: perennial, ann: annual.

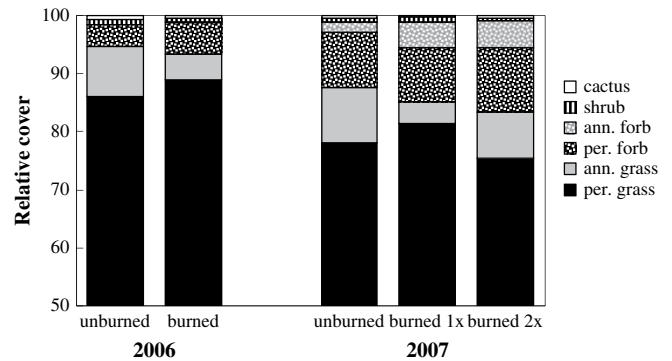


Fig. 6. Relative cover by functional group in different fire treatments for 2006 and 2007 in the shortgrass steppe of northern Colorado. In the 2007 panel, burned 1× and 2× indicate that plots were burned once in 2006 (1×) or plots were burned in both 2006 and 2007 (2×). See text for statistical results. per: perennial, ann: annual.

litter in the burned 2× plots. Annual grasses decreased in both years. The already low diversity of the shortgrass steppe did not appear to be affected by fire, at least in the short term.

Two factors, climatic context and timing of the fire, may account for the decrease in productivity in burned plots in 2006, but not in 2007. First, the prescribed fire date was later in 2006 than in 2007 and the C₃, and to a lesser extent C₄, grasses were already physiologically active at the time of the 2006 fire. By consuming some live tissue, the fire may have negatively impacted plants more in 2006 than in 2007. Second, the early summer following the 2006 spring burns was very dry and may have led to greater post-fire water stress, a phenomenon noted even in mesic tallgrass prairie (Knapp, 1984, 1985). The prescribed burns in 2007 were earlier and conducted in the context of a wet spring and early summer.

The results from these two years support the importance of the season of fires in the shortgrass steppe. The dormant season fire in 2007 had minimal impact on productivity, while fire at the beginning of the growing season in 2006 had negative, though relatively small, effects on the system. The system recovered quickly from the effects of the 2006 fire, even in plots that were burned again in 2007. Similarly, Ford and Johnson (2006) found growing season fire to have a greater effect on perennial grass cover in shortgrass steppe than fires in the dormant season.

Overall, the shortgrass steppe exhibits very different responses to fire than the mesic tallgrass prairie. While total ANPP tends to increase with repeated burning in tallgrass prairie (Briggs and Knapp, 1995), it appears to change little or decrease in the drier grasslands of the Great Plains. Annual burning in tallgrass prairie results in increases in dominant grasses at the expense of forbs (Collins and Gibson, 1990). In contrast, forb production and cover appear to increase when the shortgrass steppe is burned. Diversity in tallgrass prairie tends to be highest in infrequently burned plots, with fewer species in unburned or annually burned areas (Collins and Gibson, 1990). Fire did not affect the diversity of the shortgrass steppe, although two years is almost certainly not long enough to observe changes in these communities of mostly long-lived perennials. Other studies of fire in mixed-grass prairie and shortgrass steppe have demonstrated that diversity was not influenced by fire (Brockway et al., 2002; Morrison et al., 1986; Shay et al., 2001). It is clear that community and ecosystem responses to fire in more arid grasslands cannot be generalized from the well-studied tallgrass prairie. Negative perceptions of fire effects and a dearth of experimental work have limited our understanding of fire in the shortgrass steppe. While changes in productivity are not the largely positive ones seen in mesic grasslands, they are not necessarily the strongly negative ones often cited (Hopkins et al., 1948; Oesterheld et al., 1999; Wright and Bailey, 1980). A string of years with above-average precipitation may also give the system a more mesic character and shift the response in a more positive direction.

The role of litter in determining ANPP responses to fire in grasslands also differed between tallgrass prairie and shortgrass steppe. Positive post-fire ANPP responses of tallgrass prairie are driven by the removal of the accumulated litter by fire (Hulbert, 1988; Knapp and Seastedt, 1986). Litter removal increases soil temperature and light at the soil surface, increasing growing season length and leading to increased productivity in frequently burned prairie (Hulbert, 1988; Knapp and Seastedt, 1986). The more arid and less productive shortgrass steppe has minimal litter accumulation (Burke et al., 1998) and might be expected to be unresponsive to fire-induced litter reductions. However, a relationship between ANPP and litter mass was found, although it was the opposite of that in tallgrass prairie. This suggests that litter may facilitate, or at least not inhibit, primary production in shortgrass steppe, perhaps due to enhanced water relations (e.g. less evaporative loss). Further investigation would be needed to determine the mechanisms

involved in the relationship between litter and ANPP in shortgrass steppe.

4.1. Management implications

Fire is increasingly being used as a management tool in the shortgrass steppe with little supporting experimental research on the response of the ecosystem to this manipulation, including interactions with climate and grazing (Ford and McPherson, 1996). For example, the interactions between different frequencies of fire and different grazing intensities in shortgrass steppe are not currently known. The USDA Forest Service National Grasslands in the shortgrass steppe, Pawnee (northern Colorado), Comanche (southern Colorado) and Kiowa (northern New Mexico), have conducted prescribed fires in early spring with the general goal of reintroducing a natural ecosystem process. Specific goals include reducing undesired plant species and providing habitat for Mountain Plover (*Charadrius montanus*), a grassland bird. The Mountain Plover is a species of conservation concern in shortgrass steppe and has been observed to be attracted to burned areas (Knopf and Wunder, 2006; Svingen and Giesen, 1999). The birds generally nest in disturbed areas with short, sparse vegetation, though the appropriate observational and experimental work has not been done to determine whether prescribed spring fire actually increases Mountain Plover population viability (Dinsmore, 2003). Moreover, possible positive effects of spring burning on Mountain Plovers need to be balanced with other ecosystem changes due to fire, particularly those that result from a long-term change in fire regime. In general, though, shortgrass steppe appears to be quite resilient with respect to fire.

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Appendix. Supplementary data

Supplementary data associated with this article can be found in the online version, at doi:10.1016/j.jaridenv.2009.05.011.

References

- Abrams, M.D., Hulbert, L.C., 1987. Effect of topographic position and fire on species composition in tallgrass prairie in northeast Kansas. *American Midland Naturalist* 117, 442–445.
- Abrams, M.D., Knapp, A.K., Hulbert, L.C., 1986. A 10-year record of aboveground biomass in a Kansas tallgrass prairie – effects of fire and topographic position. *American Journal of Botany* 73, 1509–1515.
- Allen, C.D., Savage, M., Falk, D.A., Suckling, K.F., Swetnam, T.W., Schulke, T., Stacey, P.B., Morgan, P., Hoffman, M., Klingel, J.T., 2002. Ecological restoration of Southwestern ponderosa pine ecosystems: a broad perspective. *Ecological Applications* 12, 1418–1433.

- Anderson, R.C., 1982. An evolutionary model summarizing the roles of fire, climate, and grazing animals in the origin and maintenance of grasslands: an endpaper. In: Estes, J.R., Tylor, R.J., Brunken, J.N. (Eds.), *Grasses and Grasslands: Systematics and Ecology*. University of Oklahoma Press, Norman, OK, pp. 297–308.
- Anderson, R.C., 2006. Evolution and origin of the central grassland of North America: climate, fire, and mammalian grazers. *Journal of the Torrey Botanical Society* 133, 626–647.
- Axelrod, D.L., 1985. Rise of the grassland biome, central North-America. *Botanical Review* 51, 163–201.
- Biondini, M.E., Steuter, A.A., Grygiel, C.E., 1989. Seasonal fire effects on the diversity patterns, spatial distribution and community structure of forbs in the northern mixed prairie, USA. *Vegetatio* 85, 21–31.
- Blair, J.M., 1997. Fire, N availability, and plant response in grasslands: a test of the transient maxima hypothesis. *Ecology* 78, 2359–2368.
- Bond, W.J., Woodward, F.I., Midgley, G.F., 2005. The global distribution of ecosystems in a world without fire. *New Phytologist* 165, 525–537.
- Bragg, T.B., 1978. Effects of burning, cattle grazing and topography on vegetation of the Choppy Sands Range site in the Nebraska Sandhills prairie. In: Hyder, D.N. (Ed.), *Proceedings of the First International Rangeland Congress*. Society for Range Management, Denver, CO, pp. 248–253.
- Bragg, T.B., 1995. The physical environment of the Great Plains grasslands. In: Joern, A., Keeler, K.H. (Eds.), *The Changing Prairie*. Oxford University Press, Oxford, pp. 49–81.
- Bremer, D.J., Ham, J.M., 1999. Effect of spring burning on the surface energy balance in a tallgrass prairie. *Agricultural and Forest Meteorology* 97, 43–54.
- Briggs, J.M., Knapp, A.K., 1995. Interannual variability in primary production in tallgrass prairie – climate, soil moisture, topographic position, and fire as determinants of aboveground biomass. *American Journal of Botany* 82, 1024–1030.
- Brockway, D.G., Gatewood, R.G., Paris, R.B., 2002. Restoring fire as an ecological process in shortgrass prairie ecosystems: initial effects of prescribed burning during the dormant and growing seasons. *Journal of Environmental Management* 65, 135–152.
- Brown, J.K., 2000. Introduction and fire regimes. Gen. Tech. Rep. RMRS-GTR-42. In: Brown, J.K., Smith, J.K. (Eds.), *Wildland Fire in Ecosystems: Effects of Fire on Flora*, vol. 2. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Ogden, UT, pp. 1–7.
- Burke, I.C., Lauenroth, W.K., Vinton, M.A., Hook, P.B., Kelly, R.H., Epstein, H.E., Aguiar, M.R., Robles, M.D., Aguilera, M.O., Murphy, K.L., Gill, R.A., 1998. Plant-soil interactions in temperate grasslands. *Biogeochemistry* 42, 121–143.
- Collins, S.L., Gibson, D.J., 1990. Effects of fire on community structure in tallgrass and mixed-grass prairie. In: Collins, S.L., Wallace, L.L. (Eds.), *Fire in North American Tallgrass Prairies*. University of Oklahoma Press, Norman, OK, pp. 81–98.
- D'Antonio, C.M., 2000. Fire, plant invasions, and global changes. In: Mooney, H.A., Hobbs, R.J. (Eds.), *Invasive Species in a Changing World*. Island Press, Covelo, CA, pp. 65–93.
- Daubenmire, R., 1968. Ecology of fire in grasslands. *Advances in Ecological Research* 5, 209–266.
- Dinsmore, S.J., 2003. Mountain Plover (*Charadrius montanus*): a Technical Conservation Assessment [Online]. U.S. Department of Agriculture, Forest Service, Rocky Mountain Region. <http://www.fs.fed.us/r2/projects/scp/assessments/mountainplover.pdf>.
- Dix, R.L., 1960. The effects of burning on the mulch structure and species composition of grasslands in western North Dakota. *Ecology* 41, 49–56.
- Dwyer, D.D., Pieper, R.D., 1967. Fire effects on blue grama-pinyon-juniper rangeland in New Mexico. *Journal of Range Management* 20, 359–362.
- Engle, D.M., Bultsma, P.M., 1984. Burning of northern mixed prairie during drought. *Journal of Range Management* 37, 398–401.
- Ford, P.L., Johnson, G.V., 2006. Effects of dormant- vs. growing-season fire in shortgrass steppe: biological soil crust and perennial grass responses. *Journal of Arid Environments* 67, 1–14.
- Ford, P.L., McPherson, G.R., 1996. Ecology of fire in shortgrass prairie of the southern Great Plains. Gen. Tech. Rep. RM-GTR-285. In: Finch, D.M. (Ed.), *Ecosystem Disturbance and Wildlife Conservation in Western Grasslands: a Symposium Proceedings*. U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station, Fort Collins, CO, pp. 20–39.
- Gartner, F.R., Butterfield, R.I., Thompson, W.W., Roath, L.R., 1978. Prescribed burning of range ecosystems in South Dakota. In: Hyder, D.N. (Ed.), *Proceedings of the First International Rangeland Congress*. Society of Range Management, Denver, CO, pp. 687–690.
- Gibson, D.J., Hulbert, L.C., 1987. Effects of fire, topography and year-to-year climatic variation on species composition in tallgrass prairie. *Vegetatio* 72, 175–185.
- Hart, R.H., Hart, J.A., 1997. Rangelands of the Great Plains before European settlement. *Rangelands* 19, 4–11.
- Hopkins, H., Albertson, F.W., Riegel, A., 1948. Some effects of burning upon a prairie in west-central Kansas. *Transactions of the Kansas Academy of Science* 51, 131–141.
- Hulbert, L.C., 1988. Causes of fire effects in tallgrass prairie. *Ecology* 69, 46–58.
- Keeley, J.E., 2006. Fire management impacts on invasive plants in the western United States. *Conservation Biology* 20, 375–384.
- Keeley, J.E., Lubin, D., Fotheringham, C.J., 2003. Fire and grazing impacts on plant diversity and alien plant invasions in the southern Sierra Nevada. *Ecological Applications* 13, 1355–1374.
- Kirsch, L.M., Kruse, A.D., 1972. Prairie fire and wildlife. In: Komarek, E.V. (Ed.), *Proceedings of the Tall Timbers Fire Ecology Conference*. Tall Timbers Research Station, Tallahassee, FL, pp. 289–303.
- Knapp, A.K., 1984. Water relations and growth of three grasses during wet and drought years in a tallgrass prairie. *Oecologia* 65, 35–43.
- Knapp, A.K., 1985. Effect of fire and drought on the ecophysiology of *Andropogon gerardii* and *Panicum virgatum* in a tallgrass prairie. *Ecology* 66, 1309–1320.
- Knapp, A.K., Briggs, J.M., Blair, J.M., Turner, C.L., 1998. Patterns and controls of aboveground net primary production in tallgrass prairie. In: Knapp, A.K., Briggs, J.M., Hartnett, D.C., Collins, S.L. (Eds.), *Grassland Dynamics: Long-term Ecological Research in Tallgrass Prairie*. Oxford University Press, New York, pp. 193–221.
- Knapp, A.K., Briggs, J.M., Childers, D.L., Sala, O.E., 2007. Estimating aboveground net primary production in grassland and herbaceous dominated ecosystems. In: Fahey, T.J., Knapp, A.K. (Eds.), *Principles and Standards for Measuring Net Primary Production*. Oxford University Press, New York, pp. 27–48.
- Knapp, A.K., Seastedt, T.R., 1986. Detritus accumulation limits productivity of tall-grass prairie. *Bioscience* 36, 662–668.
- Knapp, A.K., Smith, M.D., 2001. Variation among biomes in temporal dynamics of aboveground primary production. *Science* 291, 481–484.
- Knopf, F.L., Wunder, M.B., 2006. Mountain Plover (*Charadrius montanus*). In: Poole, A. (Ed.), *The Birds of North America Online*. Cornell Laboratory of Ornithology, Ithaca. http://bna.birds.cornell.edu/BNA/account/Mountain_Plover.
- Kreuter, U.P., Woodward, J.B., Taylor, C.A., Teague, W.R., 2008. Perceptions of Texas landowners regarding fire and its uses. *Rangeland Ecology and Management* 61, 456–464.
- Kucera, C.L., 1981. Grasslands and fire. Gen. Tech. Rep. WO-26. In: Mooney, H.A., Bonnicksen, T.M., Christensen, N.L., Lotan, J.E., Reiners, W.A. (Eds.), *Proceedings of the Conference: Fire Regimes and Ecosystem Properties*. U.S. Department of Agriculture, Forest Service, Washington, DC, pp. 90–111.
- Lauenroth, W.K., Burke, I.C., 2008. *Ecology of the Shortgrass Steppe: a Long-term Perspective*. Oxford University Press, New York.
- Lauenroth, W.K., Burke, I.C., Gutmann, M.P., 1999. The structure and function of ecosystems in the central North American grassland region. *Great Plains Research* 9, 223–260.
- Lauenroth, W.K., Milchunas, D.G., 1991. Short-grass steppe. In: Coupland, R.T. (Ed.), *Natural Grasslands: Introduction and Western Hemisphere*. Elsevier, New York, pp. 183–226.
- Lauenroth, W.K., Sala, O.E., 1992. Long-term forage production of North-American shortgrass steppe. *Ecological Applications* 2, 397–403.
- Launchbaugh, J.L., 1964. Effects of early spring burning on yields of native vegetation. *Journal of Range Management* 17, 5–6.
- Leach, M.K., Givnish, T.J., 1996. Ecological determinants of species loss in remnant prairies. *Science* 273, 1555–1558.
- Magurran, A.E., 1988. *Ecological Diversity and Its Measurement*. Chapman and Hall, London.
- Morrison, L.C., DuBois, P.D., Kapustka, L.A., 1986. The vegetational response of a Nebraska Sandhills grassland to a naturally occurring fall burn. *Prairie Naturalist* 18, 179–184.
- Oesterheld, M., Loreti, J., Semmartin, M., Paruelo, J.M., 1999. Grazing, fire and climate effects on primary productivity of grasslands and savannas. In: Walker, L.R. (Ed.), *Ecosystems of Disturbed Ground*. Elsevier, New York, pp. 287–306.
- Owensby, C.E., Launchbaugh, J.L., 1977. Controlling prairie threeawn (*Aristida oligantha* Michx) in central and eastern Kansas with fall burning. *Journal of Range Management* 30, 337–339.
- Pfeiffer, K.E., Steuter, A.A., 1994. Preliminary response of sandhills prairie to fire and bison grazing. *Journal of Range Management* 47, 395–397.
- Redmann, R.E., 1978. Plant and soil-water potentials following fire in a northern mixed grassland. *Journal of Range Management* 31, 443–445.
- Samson, F.B., Knopf, F.L., Ostlie, W.R., 2004. Great Plains ecosystems: past, present, and future. *Wildlife Society Bulletin* 32, 6–15.
- SAS, 2002. SAS version 9.1. SAS Institute, Inc., Cary, NC.
- Schacht, W., Stubbendieck, J., 1985. Prescribed burning in the loess hills mixed prairie of Southern Nebraska. *Journal of Range Management* 38, 47–51.
- Scheintaub, M.R., 2008. *The Response of the Shortgrass Steppe to Fire*. Thesis. Colorado State University, Fort Collins, Colorado.
- Shay, J., Kunec, D., Dyck, B., 2001. Short-term effects of fire frequency on vegetation composition and biomass in mixed prairie in south-western Manitoba. *Plant Ecology* 155, 157–167.
- Steuter, A.A., 1987. C-3 C-4 Production shift on seasonal burns northern mixed prairie. *Journal of Range Management* 40, 27–31.
- Stewart, O.C., 1951. Burning and natural vegetation in the United States. *Geographical Review* 41, 317–320.
- Svingen, D., Giesen, K., 1999. Mountain Plover (*Charadrius montanus*) response to prescribed burns on the Comanche National Grassland. *Journal of Colorado Field Ornithology* 33, 208–212.
- Trlica, M.J., Schuster, J.L., 1969. Effects of fire on grasses of Texas high plains. *Journal of Range Management* 22, 329–334.
- Vermeire, L.T., Wester, D.B., Mitchell, R.B., Fuhlendorf, S.D., 2005. Fire and grazing effects on wind erosion, soil water content, and soil temperature. *Journal of Environmental Quality* 34, 1559–1565.
- Wells, P.V., 1965. Scarp woodlands, transported grassland soils and concept of grassland climate in Great Plains region. *Science* 148, 246–249.
- Wells, P.V., 1970. Historical factors controlling vegetation patterns and floristic distributions in the central plains region of North America. In: Dort, W.,

- Jones, J.K. (Eds.), Pleistocene and Recent Environments of the Central Great Plains. University of Kansas Press, Lawrence, KS, pp. 211–221.
- Whisenant, S.G., Uresk, D.W., 1989. Burning upland, mixed prairie in Badlands National Park. *Prairie Naturalist* 21, 221–227.
- White, C.S., Loftin, S.R., 2000. Response of 2 semiarid grasslands to cool-season prescribed fire. *Journal of Range Management* 53, 52–61.
- White, C.S., Pendleton, R.L., Pendleton, B.K., 2006. Response of two semiarid grasslands to a second fire application. *Rangeland Ecology and Management* 59, 98–106.
- White, R.S., Currie, P.O., 1983. Prescribed burning in the northern Great Plains – yield and cover responses of 3 forage species in the mixed grass prairie. *Journal of Range Management* 36, 179–183.
- Wolfe, C.W., 1972. Effects of fire on a sand hills grassland environment. In: *Proceedings of the Tall Timbers Fire Ecology Conference*. Tall Timbers Research Station, Tallahassee, FL, pp. 241–255.
- Wright, H.A., Bailey, A.W., 1980. *Fire Ecology and Prescribed Burning in the Great Plains: a Research Review*. U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station, Ogden, UT.