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Response of the shortgrass steppe plant community to fire

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A B S T R A C T

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.

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/m^2 in productive tallgrass prairie sites in eastern Kansas (Briggs and Knapp, 1995) to less than 100 g/m^2 in shortgrass steppe of northeastern 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 C_4 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.) Sweezey. 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.