Rangeland Ecol Manage 66:267–273 | May 2013 | DOI: 10.2111/REM-D-11-00226.1

Different Fire Frequency Impacts Over 27 Years on Vegetation Succession in an Infertile Old-Field Grassland

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Abstract

We examined the effect of fire on vegetation composition with the use of an experiment with four different fire frequencies (annual, 2-yr interval, 4-yr interval, and an intended control with no burning) over a 27-yr period in an infertile, old-field grassland at the Cedar Creek Ecosystem Science Reserve, located in Minnesota, United States. We measured the plant species' aboveground biomass in permanent plots in 1983, 1987, 1991, 2000, and 2010. None of these fire frequencies, even after 27 yr, had a large impact on the vegetation composition. The plant functional groups' responses to fire frequency were consistent with their respective dominant species. The most abundant C_4 grass, little bluestem (*Schizachyrium scoparium* Michx.), did not change in biomass with fire frequency over time. The biomass of the introduced, invasive grass, Kentucky bluegrass (*Poa pratensis* L.) decreased significantly with increasing fire frequency, but this decrease did not result in change to the rate and trajectory of vegetation change. Bush clover (*Lespedeza capitata* Michx.), the only legume in the community, strongly increased with more frequent fire, but only after 20 yr. Species richness and litter mass decreased significantly with increasing fire frequency. These small fire-induced vegetation changes contrast with large fire-induced vegetation changes in fertile grasslands. Management strategies using fire in infertile grasslands can lower *Poa* abundance; however, increased fire also decreased overall plant diversity.

Key Words: C_3 and C_4 grasses, fire frequency, grassland, legumes, *Lespedeza capitata*, old field, *Poa pratensis*, *Schizachyrium scoparium*, species richness, succession

INTRODUCTION

Fire is one of the most important ecological factors affecting vegetation communities by eliminating woody species (Briggs et al. 2002; Towne and Kemp 2003) and herbaceous fire-intolerant species as well as altering competitive interactions among species. Therefore, fire has long been used to manage grasslands to minimize undesirable plants and increase livestock production (Uys et al. 2004; Pyke et al. 2010).

Most studies examine ecosystem impacts of fire in fertile and mixed tree-grass vegetation systems with high productivity. These studies of more productive ecosystems often show that fire can induce large vegetation shifts and diversity changes (Towne and Kemp 2003; Grace et al. 2007; Pyke et al. 2010). However, vegetation responses to fire in grassland and savanna ecosystems are highly variable and depend on location and ecosystem type. In the North American tallgrass prairie, high-frequency prescribed fires can suppress shrubs and trees and facilitate the establishment and growth of C_4 grasses and forbs in fertile and mixed tree-grass vegetation systems (Collins and Steinauer 1998; Reich et al. 2001; Reed et al. 2005; Peterson and Reich 2008). In Texas, USA, repeated fires in any season reduce C_3 grass cover and increase C_4 grass cover (Ansley et al. 2010). In southern Africa, grasslands have a diverse array of forbs but far fewer grass species, suggesting that forb species tolerate a wider range of season and frequency of fires than the dominant grasses (Uys et al. 2004). In Australia, the effects of frequently applied dormant-season (i.e., winter or early spring) fires shift grassland communities toward C_4 grass dominance at the expense of C_3 grasses and woody plants (Morgan and Lunt 1999; Prober et al. 2007). In the presence of spring fire, C_4 grass species outcompete most forbs and C_3 grass competitors (Howe 1995), because C_4 grass species green up much later in the growing season (Hartnett et al. 1996; Collins and Steinauer 1998). In addition, C_4 grasses also have a higher nitrogen and water-use efficiency than C_3 grasses (Reichman 1987).

In contrast to studies of more productive ecosystems, our 2000 study of 17 yr of different burning frequencies in an infertile grassland in North America revealed only small changes in the vegetation composition and diversity. The 2000 study showed no significant changes in aboveground productivity or in the abundance of the dominant C_4 plant species (Knops 2006). Some studies have indicated that fire may change the rate and trajectory of vegetation change by decreasing the abundance of the exotic invader C_3 grass, Kentucky bluegrass, which has been increasing in abundance in recent decades (Murphy and Grant 2005; Travnicek et al. 2005; Ansley et al. 2010). This increase could negatively impact ecosystem function, lower plant diversity, and alter seasonal forage distribution (Hendrickson and Lund 2010).

Funding for this research was provided by Cedar Creek LTER NSF funding and Natural Science Foundation of China (31100306).

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Manuscript received 16 December 2011; manuscript accepted 5 January 2013.

Therefore, *Poa* has been identified as a problematic exotic, introduced grass species in US grasslands (Hendrickson and Lund 2010). In a different study at the same site used in the present study, 21 unburned old fields that differed in abandonment age also showed an increase in *Poa* over time, and the dominant species had a strong influence on the diversity (Miles and Knops, 2009a). Over time, plots dominated by little bluestem had faster rates of compositional change than plots dominated by Kentucky bluegrass (Miles and Knops, 2009b). In our 2000 study, little bluestem dominated the plant biomass across all fire treatments. Kentucky bluegrass was the second most abundant species, increasing over time in the 4-yr–interval fire treatments (Knops 2006).

Studies have often reported that legumes positively respond to increased fire frequency (Ritchie and Tilman 1995) because legume species are positively responding to fire-induced nitrogen losses (Knops et al. 2000) or fire-induced increased cation availability (Ritchie and Tilman 1995). In addition, legumes may be more fire tolerant than nonlegumes (Towne and Knapp 1996). However, legumes are also strongly limited in dispersal because they often have relatively large seeds, susceptible to intense herbivory (Knops et al. 2000). Legumes were absent in this experiment for the first 10 yr. However, in the 2000 study we found bush clover, a common prairie legume (Lau et al. 2008) present at very low biomass after 17 yr. If legumes have a competitive advantage in frequently burned grasslands, we would expect a rapid increase in abundance after initial establishment.

For this current study, we examined vegetation changes in a 1983-established experiment with late spring burns applied at four frequencies, namely, annual, 2-yr interval, 4-yr interval, and control (an intended fire exclusion). Vegetation differed in *Poa* abundance for more than 20 yr (Knops 2006). This study examines changes in the treatment plots over the whole period, including during the last 10 yr (2000–2010). We formulated the following hypotheses: 1) Higher fire-frequency favors increased C_4 grass dominance and lowers C_3 grass dominance because spring burning increases the competitive advantage of warm-season C_4 grasses over the cool-season C_3 grasses and forbs that green up earlier in the spring (Hartnett et al. 1996; Collins and Steinauer 1998); 2) higher fire frequency will yield a rapid increase in legume abundance after initial establishment in the frequent burn treatments (Towne and Knapp 1996) because fire can provide a competitive advantage for legumes through increasing cation availability (Ritchie and Tilman 1995); 3) *Poa*'s fire-induced abundance differences among treatments (Schacht and Stubbendieck 1985; Willson and Stubbendieck 1997) will cause changes in species richness and species composition; 4) burning will increase aboveground plant biomass compared with fire suppression (control) because soils in the burned areas will warm up faster in the spring, increasing the length of the growing season (Gartner et al. 1986) and litter removal increases light availability (Amatangelo et al. 2008).

MATERIALS AND METHODS

Study Area

This study was set up in an old field, abandoned in 1957 at the Cedar Creek Ecosystem Science Reserve in south-central Minnesota, United States (lat 45°24′N, long 93°12′W). Previous cultivation led to the loss of approximately 80% of the soil organic matter in the top 100 mm at this experimental site (Knops and Tilman 2000) and nitrogen is the primary mineral nutrient limiting plant productivity (Tilman 1984, 1987). This tallgrass prairie region has a typical midcontinental climate with hot, humid summers, and cold winters. July, the warmest month, averages 28.5°C (range 13.9–39.5); January, the coldest month, averages –5.6°C (range –27 to 12.8). Snow covers the ground for 4–5 mo each year. Average rainfall from 1983 to 2000 was 796 mm and fluctuated from 579 mm to 1 163 mm, but there was no discernible trend over this time period.

Chronosequence studies of abandoned agricultural fields showed that vegetation composition shifted from annual forbs to C_3 grasses then to C_4 grasses (Inouye et al. 1987). Little bluestem, Kentucky bluegrass, scribner's panicum (*Panicum oligosanthes* Schult.), bush clover, rigid goldenrod (*Solidago rigida* L.), gray goldenrod (*Solidago nemoralis* Aiton.), sheep sorrel (*Rumex acetosella* L.), and Pennsylvania sedge (*Carex pensylvanica* Lam.) are common herbaceous species (Tilman 1987).

Experiment Design

Plots were established in 1983 and burning started in 1984. Twenty-four plots were randomly placed in a three-by-eight grid with each treatment having six 8×8 m replicates and 2-m buffers (see Knops 2006 for more details). The four treatments were annual burning, burning every other year (2-yr interval), burning every 4 yr (4-yr interval), and an intended control with no burning (control). Burning by using a strip head fire technique was done each spring in March or April depending on snow melt, with typical air temperatures of 15–25°C, relative humidity of 25–45% and winds $< 20 \text{ km} \cdot \text{h}^{-1}$ (Reich et al. 2001). Fires generally burned at low intensities, with mean flame lengths < 1 m (Knops, personal observation). Burning was applied in later spring, either March or April, because C_4 grasses stay dormant much longer and might competitively benefit from a lower dominance of C_3 grasses and forbs, which are active earlier in the spring (Hartnett et al. 1996; Collins and Steinauer 1998). In 1995, a prescribed fire escaped and burned the entire experiment. In total, the effective fire frequency was thus 27 out of 27 yr for the annually burned plots, 15 out of 27 for the 2-yr burn interval, 8 out of 27 for the 4-yr interval, and 1 out of 27 for the control plots.

Sampling Methods

Vegetation was sampled at the peak of standing biomass in mid-July of 1983, 1987, 1991, 2000, and 2010 by clipping a 0.1×3 m long strip at ground level in a different area within each plot. All clipped samples were sorted to individual plant species and litter. All plant samples were dried to constant mass at 60°C. Vascular plants were divided into five functional groups: 1) cool-season C_3 grasses; 2) warm-season C_4 grasses; 3) herbaceous legumes—comprised solely of the species bush clover; 4) herbaceous forbs; and 5) sedges. No woody species were recorded. Species richness (the total number of species per 3 000 cm^2) and the Shannon diversity index were calculated from species composition data (based on proportional biomass,