

Fire does not alter vegetation in infertile prairie

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Abstract The paradigm in prairie ecology is that fire is one of the key factors determining vegetation composition. Fire can impact grassland ecosystems in various ways, including changing plant species composition and inducing nitrogen loss. I found that 17 years of different burning frequencies in infertile grassland had only a minor impact on the vegetation composition and diversity. The only major impact from increasing the frequency of fires was a decrease of *Poa pratensis* abundance. However, other plant species did not respond to the change in *Poa* abundance. This result contrasts with previous studies in savannas and more productive grasslands, where the balance between trees, grasses, and the elimination of the litter layer can result in large vegetation changes. However, in this system primary productivity was low, litter did not accumulate and no major vegetation shifts occurred. Thus, the long-term vegetation impacts of burning in an infertile, low-productivity prairie were minimal.

Keywords Fire · Net primary productivity · Nitrogen · Old field · Prairie · Vegetation composition

Introduction

Fire can significantly impact the vegetation structure and ecosystem functioning in prairies (Knapp et al.

1998). In addition to eliminating woody species, fire can directly impact herbaceous vegetation by eliminating fire-intolerant species and altering competitive interactions among species (Tester 1996; Peterson and Reich 2001). Due to the elimination of aboveground litter, fire also has indirect effects, such as increased soil temperature and increased available mineral nitrogen (Knapp et al. 1998). All of these factors impact competition among species and ultimately the structure of the plant community. In the long term, fire has the potential to decrease ecosystem nitrogen pools through volatilization of the nitrogen present in aboveground tissues (Ojima et al. 1994). However, most studies are unable to detect the long-term impacts on ecosystem fertility because of the large soil nitrogen pool, topographic soil heterogeneity, and the duration of most fire experiments (Wan et al. 2001). In addition, most studies examining ecosystem impacts of fire in grasslands are conducted in fertile systems.

Here, I report the impact of 17 years of burning at four different frequencies on vegetation structure in an abandoned agricultural field in south-central Minnesota (Knops and Tilman 2000). This field was previously cultivated and had lost approximately 80% of the soil organic matter in the top 10 cm (Knops and Tilman 2000). Light limitation is minimal because of a low-standing plant biomass and limited litter accumulation. Fertilization and shading studies within the same field have shown that nitrogen is the main factor that determines the outcome of plant competition and nitrogen limits net primary productivity (Tilman 1984, 1987, 1990). Abandoned fields in mid-central Minnesota show an early successional dominance by weedy annual plants, which are replaced by cool season C₃ grasses that have a dispersal advantage. Later in succession,

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C_3 grasses are replaced by C_4 grasses, warm season perennial grasses that have a strong advantage in competing for soil nitrogen (Inouye et al. 1987; Tilman and Wedin 1991; Foster and Tilman 2000).

I hypothesized that higher fire frequency leads to an increased dominance by C_4 grasses (Hartnett et al. 1996; Collins et al. 1998), because burning is done in the spring, which negatively impacts C_3 grasses and many forbs, which green up earlier. In contrast, C_4 grasses stay dormant much longer and might competitively benefit from a lower dominance of C_3 grasses and forbs active earlier in the spring. The second hypothesis is that fire increases the dominance of legumes because fire can lead to increased nitrogen volatilization and increased nitrogen limitation (Ojima et al. 1994), which may benefit nitrogen-fixing legumes.

Methods

This study was conducted in an old field at Cedar Creek Natural History Area that was abandoned in 1957 (Field B, Tilman 1987). Cedar Creek Natural History Area is located 45 km north of Minneapolis, Minnesota, USA (45°24'N, 93°12'W), and has a typical mid-continental climate with hot, humid summers and cold winters. The soil within this field consists of fine sand (Grigal et al. 1974), and nitrogen is the primary mineral nutrient limiting plant productivity within this field (Tilman 1984, 1987).

Burning was applied in four different treatments, with six replicates for each treatment. Plots of 8×8 m were randomly placed on a three-by-eight grid, with a 2-m buffer between them for a total of 24 plots. Burning was applied in either March or April, depending on snow melt. The four treatments applied were annual burning, burning every other year, burning every 4 years, and an intended control with no burning. Plots were established in 1983, and burning started in 1984. In 1995, a prescribed fire escaped and burned the entire experiment. In total, the fire frequency was 17 out of 17 years for the annually burned plots, 9 out of 17 for the 2-year burn interval, 5 out of 17 for the 4-year interval, and 1 out of 17 for the control plots (Fig. 1).

Treatment	1983	1984	1985	1986	1987	1988	1989	1990	1991	1992	1993	1994	1995	1996	1997	1998	1999	2000	
Annual Burn		black		black		black		black		black		black		black		black		black	
Two year burn		black			black			black			black			black			black		
Four year burn		black				black				black				black				black	
Never													black						

Fig. 1 Burning regime of the four different treatments; a control, never burned, an annual, a 2-year, and a 4-year burn. Burning is indicated by *black*. Note that an accidental wildfire burned

Vegetation was sampled at the peak of standing biomass in mid-July of 1983, 1987, 1991, and 2000 by clipping a 3×10-cm strip at ground level in a different area within each plot. Each year, one strip was clipped, except in 2000 when two strips were clipped and the average of the two strips per plot was used in the analyses. All clipped samples were sorted to individual plant species and litter. All plant samples were dried to constant mass at 60°C. Species richness (e.g., the total number of species) and the Shannon–Wiener diversity index were calculated from the clipped data (Magurran 1988). Vascular plants were divided into five functional groups: C_3 and C_4 grasses, which differ in their photosynthetic pathway; legumes, nitrogen fixing broadleaves; forbs, non-nitrogen fixing broadleaves and sedges. *Equisetum laevigatum* was included in the sedge category. There was only one sample of less than 2 g of *Rubus* sp., a woody plant recorded, and this was included in the forb category.

Biomass sampling, however, does not measure any non-vascular plant change within each treatment, such as the area covered by bare soil, lichens, and mosses. In 2000, cover was estimated to measure the burning impacts on non-vascular plant changes. Cover was estimated in two 1×0.5-m areas within each plot with the total summing to 100%.

All statistical analysis was done with SPSS 14.0. The temporal effects of burning frequency were analyzed with a repeated measurement ANOVA, and factors were compared when significant with a LSD posthoc comparison. The impact of fire frequency treatments on cover was analyzed with one-way ANOVA and, when significant, a LSD post hoc comparison.

Results

For simplification, reference will be made to the intended fire treatments. However, note that an escaped prescribed fire burned all plots in 1995. The aboveground standing litter biomass and litter data from this and other work in this ecosystem suggest that a drastic increase in fire intensity due to the accumulation of litter, as has been observed in more productive

all plots in 1995, resulting in burning of 1/17 years for the control, 17/17 years for the annual, 9/17 years for the 2-year, and 5/17 years for the 4-year burn treatments

tallgrass prairie (Gibson 1988; Blair 1997), was not likely in this accidental burn. Litter biomass in the control plots is at most 50% more than in the treatments that had not burned for 2–3 years (Fig. 2). Vascular plant cover in 2000 was not significantly different (Table 1). Burning mainly changed the allocation between the litter and bare soil category; with more

litter, the less frequently fire occurs [summing the bare soil and litter category (Table 1) showed no burning effect ($P>0.3$)]. Haddad et al. (2001) observed a similar range and oscillation of litter between years within old fields at Cedar Creek. In the unburned control plots of a long-term nitrogen fertilization experiment, approximately 100–200 m distant, the amount of standing litter

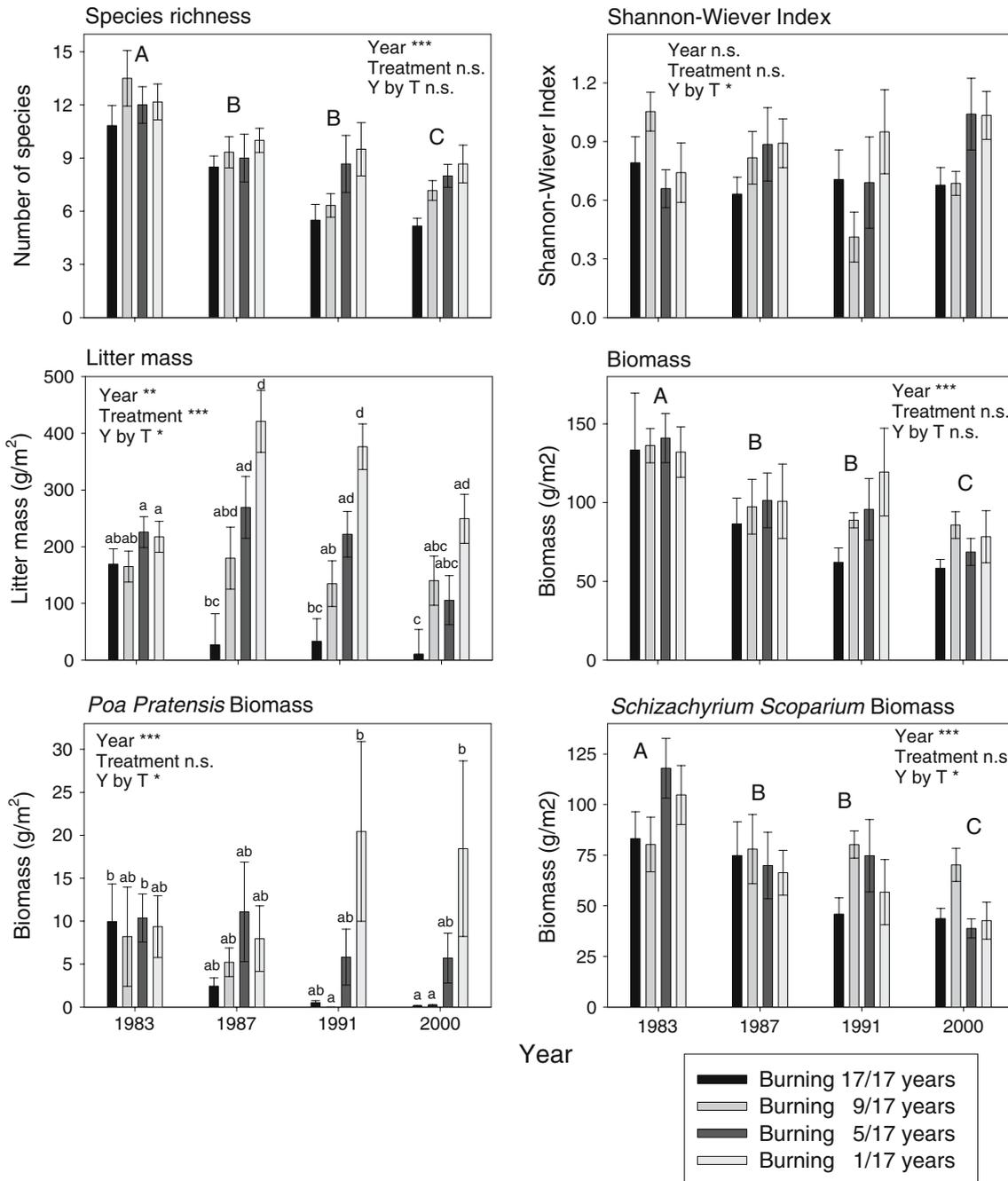


Fig. 2 Temporal vegetation changes under the four different burn frequencies; 17/17 years, 9/17 years, 5/17 years, and 1/17 years burning treatments. Given are the means \pm 1 SE. Data were analyzed with a repeated measurement ANOVA of year ($df_{3,60}$), treatment ($df_{3,20}$), and year by treatment (Y by T , $df_{9,60}$)

interaction. ^{NS} $P>0.05$; * $P<0.05$; ** $P<0.01$; *** $P<0.001$. Significant differences among years are indicated by capital letters ($P<0.05$ of a LSD comparison), if there was no significant LSD difference among any of the year by treatment interactions. Lower case letters denote $P<0.05$ of each individual measurement

Table 1 Mean cover (± 1 SE) by burning treatment measured in 2000

Category	17/17 years	9/17 years	5/17 years	1/17 years	F value
Bare soil	34.8 \pm 5.9 a	15.8 \pm 3.8 b	19.5 \pm 3.6 b	6.3 \pm 2.1 c	8.3***
Litter	3.5 \pm 2.3 a	10.0 \pm 0.6 ab	12.4 \pm 1.3 b	22.3 \pm 5.4 c	6.8**
Lichens	0 \pm 0 a	3.3 \pm 1.0 b	1.5 \pm 0.7 ab	2.3 \pm 1.0 b	3.1*
Mosses	19.7 \pm 5.4	16.0 \pm 4.9	13.1 \pm 2.1	10.3 \pm 4.8	0.8 ^{NS}
Vascular plants	42.0 \pm 2.1	55.0 \pm 4.2	58.7 \pm 8.7	53.5 \pm 2.5	2.0 ^{NS}

F values are from a one-way ANOVA, $n=6$ for each treatment. Different letters denote $P<0.05$ in a Tukey post-hoc comparison

^{NS} $P>0.05$; * $P<0.05$; ** $P<0.01$; *** $P<0.001$

in 1995 was 183 g/m² (SE 36, $n=5$) (Tilman 1987; Wedin and Tilman 1996).

Cover changes

Seventeen years of different fire frequency had no effect on the vascular plant cover (Table 1). Fire had the largest impact on bare soil and litter cover, with bare soil increasing significantly and litter decreasing with increased fire frequency (Table 1). Fire also had a significant negative effect on lichen cover, but had no effect on moss cover (Table 1). However, these patterns were not linearly associated with fire frequency, and the largest differences were seen in the annual burn as compared to the other burning treatments.

Temporal vascular plant changes

Standing live biomass declined by 47% from 135 g/m² in 1983 to 72 g/m² in 2000, independent of burning treatments (Fig. 2). This decline was largely driven by a decline in the biomass of the dominant C₄ grass *Schizachyrium scoparium* from 96 g to 48 g/m². The plot level species richness also declined by 40%, but there were no significant changes in the Shannon–Wiener diversity index, indicating that this decline was caused by the loss of rarer, less dominant plant species. However, the total number of species recorded in all plots did not change much among the years and varied from 39 species in 1983 to 38 in 1987 to 39 in 1991, and to 37 species in 2000. In total, 58 different plants species have been recorded over the 17 years of sampling. Thus, the species richness decline was at a local plot level, not at the larger field level.

Species and functional group changes

Schizachyrium was the dominant plant species accounting for 69–76% of the total aboveground biomass at each sampling date (Fig. 2). The second most abundant species was *Poa pratensis* (C₃ grass), then *R. acetosella* (forb), *Andropogon gerardii* (C₄ grass),

Panicum oligosanthes (C₃ grass), and *Agrostis scabra* (C₃ grass). *Schizachyrium* was the only species present in all plots at all sampling dates, and only *Poa*, *Rumex*, *Agrostis*, and *Panicum* were present in more than half of the measured plots. This makes analyzing individual species' response to fire and the interaction of time with fire problematic. Except for *Schizachyrium*, *Poa*, and *Lespedeza capitata*, no other species showed a significant treatment or treatment by year effect.

C₄ grasses are the dominant plant functional group and *Schizachyrium* the dominant grass species within the C₄ grasses (Fig. 3). Fire frequency had no impact on the C₄ grass abundance, and the variability among plots and treatments was as high in 1983, the year before the burning started, as in 2000 (Fig. 3). Significant changes were detected over time with fire in the other four functional groups. The most consistent change was a decrease of C₃ abundance with increasing fire frequency (Fig. 3), which was driven by *Poa* (Fig. 2). This is the most abundant C₃ grass, contributing 80% of the biomass in the control burned treatment, which only burned once. The remaining C₃ biomass is made up of five species, of which *Agrostis scabra* and *P. oligosanthes* comprise the largest part, but neither showed a significant effect. *Poa* was also the most abundant introduced plant species and caused the increase in the introduced species category with increasing fire frequency (Fig. 3).

Corresponding with the decrease of C₃ abundance with increasing fire frequency, there was a significant increase in legume and sedge abundance. The legume abundance was driven by an increase in *L. capitata*; however, even in 2000 *Lespedeza* was only present in three out of the six annually burned plots. The sedge category was made up of *Cyperus filiculmis* and unidentified *Carex* and *Cyperus* plants that did not flower and were only identifiable to the genus level. Most of the sedge species at the study site were clonal, and sedge abundance also varied strongly among plots.

Sixty percent of the plant diversity within this experiment is made up of forbs, but only *R. acetosella*, which was present in 86% of the sampled plots, was

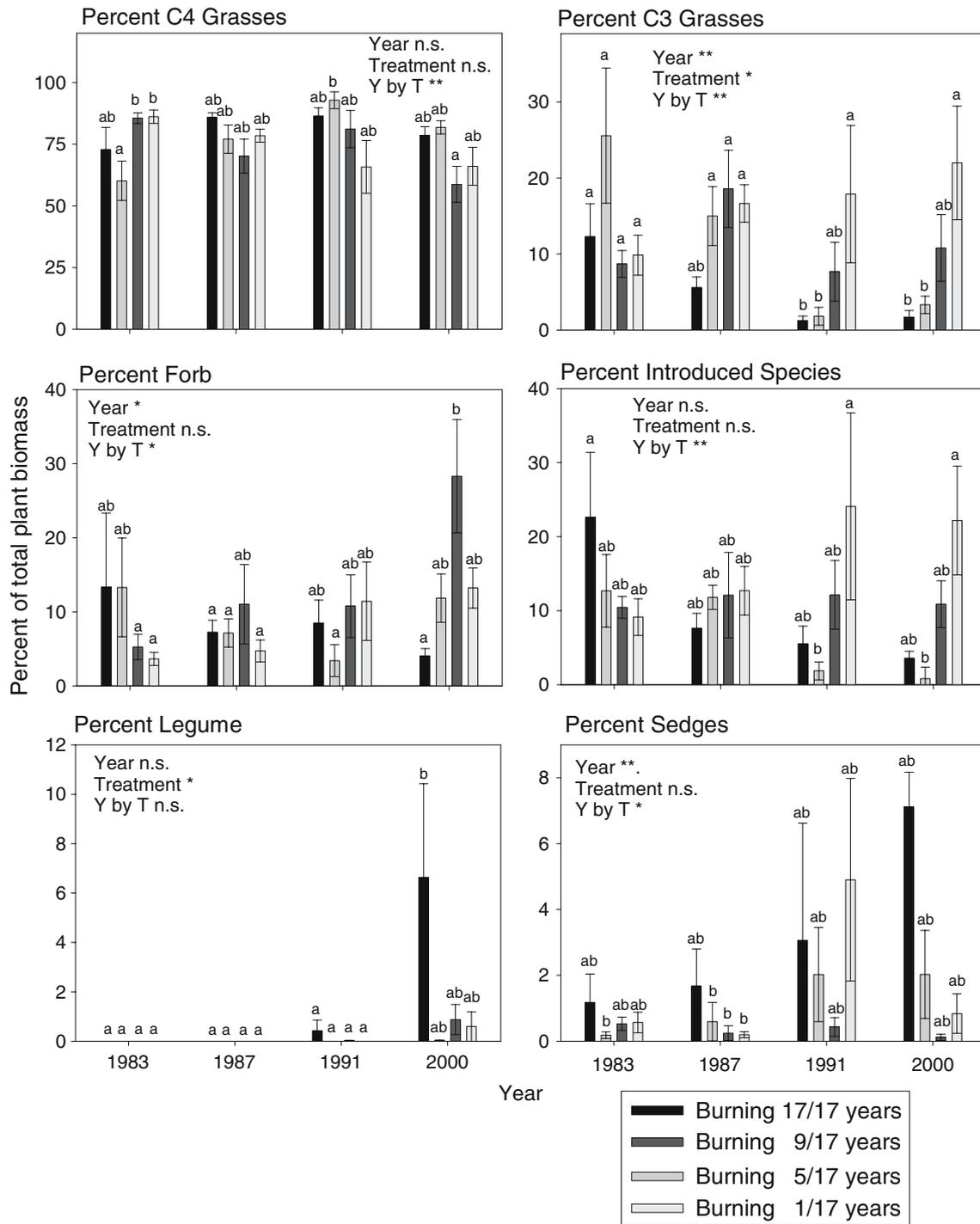


Fig. 3 Temporal vegetation changes of the percent plant functional abundance of the biomass under the four different burn frequencies; 17/17 years, 9/17 years, 5/17 years, and 1/17 years burning treatments. Given are the means ±1 SE. Data were

analyzed with a repeated measurement ANOVA of year ($df_{3,60}$), treatment ($df_{3,20}$), and year by treatment (Y by T, $df_{9,60}$) interaction. ^{NS} $P > 0.05$; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$. Lower case letters denote $P < 0.05$

frequent enough to analyze and showed no significant pattern. *Achillea millefolium* occurred in 27% of the plots, and all other forbs were observed in less than 10% of the plots. The striking increase in percent of forb abundance in the 4-year burn treatment in 2000

(Fig. 3) was caused by the abundance of *Solidago nemoralis*, *Liatrix aspera*, *Artemisia campestris*, *Fragaria virginiana*, and *A. millefolium*; however, none of these individual plant species showed a significant pattern.

Discussion

Overall, 17 years of different burning frequencies had only a minor impact on plant species composition, no impact on aboveground productivity, and no impact on the most abundant C_4 plant species, *S. scoparium*. Nitrogen losses due to fire are likely limited, because the dominant pools of nitrogen are in both the soil and belowground biomass. Aboveground mid-summer biomass contains less than 0.5% of the total nitrogen and even less after plant senescence before burning takes place. In addition, most of the productivity of the dominant C_4 grasses is belowground, and the low litter quality might have led to strong immobilization of nitrogen in dead plant material. This might be an explanation for the overall decline in productivity over the 17 years of this experiment. Thus, in this grassland system, where competition for light is low, C_4 grasses do not benefit from the released competition of plants, such as the C_3 grasses, and some of the forbs that are negatively impacted by fire.

An increased limitation of nitrogen over time might also make competition for soil nitrogen increasingly important in this community, resulting in a decline of plot level diversity, even though there is likely to be increasing bare soil with high light availability. Species richness in 2000 was linearly positively correlated with plot biomass ($F=30.8$, $R^2=0.3$, $P<0.01$, $n=24$), further supporting that there is no negative impact of plant biomass on diversity.

The largest impact of fire on the vascular vegetation composition was on the abundance of *P. pratensis*, which was nearly absent in annually or biannually burned plots in 2000. This is similar to the response of *Poa* to spring burning in more productive prairie (Towne and Owensby 1984; Smith and Knapp 1999). However, in contrast to a more productive prairie, the lower abundance of *Poa* in burned plots here was not associated with an increase in diversity and dominance of C_4 grasses (Towne and Owensby 1984; Smith and Knapp 1999). The increase of *Poa* was also not linearly related to fire frequency. *Poa* comprised 5% of the vascular plant cover in the 4-year burn rotation and 22% in the control plots that only burned once. Thus, an occasional fire is sufficient to strongly lower *Poa* abundance, which is the most abundant introduced species.

Supporting the hypotheses and consistent with other studies (Leach and Givnish 1996; Towne and Knapp 1996), legume cover increased with fire frequency. However, the magnitude of this change was small, occurring only in a few plots in the annually burned treatment and only after more than 10 years of burning.

It is important to note that this study was conducted in a low-productive, secondary prairie on nutrient poor, sandy soils. This contrasts with most long-term fire studies that have been conducted in more productive mesic prairies and grasslands such as Konza prairie, which have aboveground productivity three to eight times greater than the prairie in this study. These studies have shown that increased fire frequency can increase productivity in frequently burned watersheds (Briggs and Knapp 1995; Towne and Knapp 1996; Knapp et al. 1998) through the removal of accumulated litter, which strongly decreases light availability at the soil level (Knapp and Seastedt 1986; Collins et al. 1998). In less productive mixed and short-grass prairie, fire results in increased water limitation and thereby reduces ANPP (Redman 1978; Engle and Bultsma 1984; Steuter 1987). Fire effects on diversity are less well known and much more variable because they depend on the relative dominance of C_3 and C_4 species and on the season when burning takes place (Collins and Gibson 1990). However, in more productive prairie, fire can lead to a decrease in diversity due to an increase in C_4 dominance, which can be modulated by grazing (Collins et al. 1998). Thus, fire's impact on prairie productivity and species composition strongly depends on the ecosystem's productivity. These data suggest that the impacts of fire are minimal in low-productivity sites, where litter does not accumulate to levels that lower light availability.

At the same site as this study, but in a forest-grassland continuum, Reich et al. (2001) found that 32 years of different fire frequencies resulted in a shift from 90% dominance by trees to 80% dominance by grasses with increasing fire frequency, and this was accompanied by large changes in nitrogen cycling and vegetation composition. Thus, fire can also have strong impacts in infertile sites if shifts in dominance between major functional groups occur. However, Reich's study took place in a more productive unplowed savanna, which had double the aboveground herbaceous productivity in the frequently burned areas.

In conclusion, fire can have profound effects on the composition of grassland species if there is a major buildup of litter, or if fire eliminates woody tree invasion. However, as this study illustrates, if litter does not accumulate and there is no tree invasion, the impacts of 17 years of different fire treatments on vegetation composition are minor. The most abundant introduced species, *P. pratensis*, did strongly respond to fire and was only abundant with infrequent burning. However, this change in *Poa* abundance had no detectable impact on diversity or on any other plant species. Thus, fire is not always a key factor structuring prairie vegetation in infertile sites.

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