

Plant Community and Soil Microbial Carbon and Nitrogen Responses to Fire and Clipping in a Southern Mixed Grassland

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Abstract

Disturbances, such as fire and grazing, play important roles in determining grassland plant community composition and soil microbial dynamics, as well as regulating the flows of carbon (C) and nitrogen (N) between the two groups of organisms. In a mixed grassland of the southern Great Plains, we tested the hypotheses that spring-season fire would increase the absolute biomass and relative proportion of C₄ grasses in the plant community, and decrease soil microbial biomass N, thereby increasing microbial C:N ratios. We also tested the hypothesis that clipping (to simulate grazing) would reduce effects of fire, with a greater reduction of fire effect corresponding to an increased frequency of clipping. Contrary to our hypothesis, C₄ grasses showed no significant treatment responses. Treatment effects were limited to C₃ grasses, and clipping was more important than fire in terms of effects on plant community composition. However, because of its greater capacity to reduce aboveground litter, fire had the greater impact on soil microbial C. Contrary to the hypothesized outcome, no significant effects of disturbance on soil microbial N were observed. This suggests that control of N cycling in this ecosystem is primarily microbial in nature, though dependent on inputs of plant C via litter. Interactions between fire and clipping were observed in litter mass, highlighting the importance of litter inputs for plant–soil nutrient feedbacks.

Resumen

Perturbaciones, tales como el fuego y el pastoreo, juegan roles importantes en determinar la composición en las comunidades de pastizales y en las dinámicas microbianas del suelo, así como en la regulación del flujo de C y N entre los dos grupos de organismos. En unos pastizales mixtos de las Grandes Planicies del Sur, nosotros probamos la hipótesis de que los fuegos de primavera aumentarían la biomasa absoluta y la proporción relativa de hierbas C₄ en las comunidades de plantas, y disminuiría el N en la biomasa microbiana del suelo, de ese modo se incrementaría las razones microbianas de C:N. Nosotros también pusimos a prueba la hipótesis de que el corte (para estimular el pastoreo) podría reducir los efectos del fuego, con una reducción mayor del efecto del fuego correspondería a un aumento en la frecuencia de recorte. Contrario a nuestra hipótesis, las gramas C₄ mostraron respuestas no significativas al tratamiento. Los efectos del tratamiento se limitaron a los gramas C₃, donde el corte fue más importante que el fuego en términos de efectos de la composición en comunidad vegetal. Sin embargo, debido a su mayor capacidad para reducir la hojarasca superficial, el fuego tiene el mayor impacto en el C microbiano del suelo. Contrario a la hipótesis propuesta, no se observaron efectos de perturbación significativa en el N microbiano del suelo. Esto sugiere que el control del ciclo de N en este ecosistema es principalmente microbiano en naturaleza, aunque depende de la entrada de C a través de la hojarasca. Las interacciones entre el fuego y el corte fueron observadas en la masa de hojarasca, resaltando la importancia de la entrada de hojarasca para la retroalimentación de nutrientes entre la planta y el suelo.

Key Words: biomass, C₃, C₄, cover, disturbance

INTRODUCTION

Disturbance is an important determinant of production, community composition, and plant–soil flows of carbon (C) and nitrogen (N) in grassland ecosystems (McGill et al. 1986; Howe 1994). Varied effects of fire and grazing or clipping on plant and soil microbial biomass (SMB) and nutrient content

have been reported. In many cases the range of responses appears to be due to site-specific differences in climate, plant community composition, and seasonality of both plant production and disturbance. Mesic mixed grasslands may have the highest potential for interactive effects of fire and grazing to be expressed in these responses (Seastedt et al. 1994; Hobbs 1996).

The bulk of extant literature on effects of fire and grazing on grassland dynamics consists of single-factor experiments addressing one or the other of these disturbance types individually (Coppedge et al. 1998; Engle and Bidwell 2001). Complex interactions between fire and herbivory influence vegetation responses at individual (Vinton and Hartnett 1992), community (Collins 1987; Hobbs et al. 1991; Collins et al. 1998), and landscape (Hobbs 1996; Coppedge et al. 1998; de Mazancourt et al. 1998, 1999; Biondini et al. 1999; Knapp et

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al. 1999; Archibald et al. 2005) scales. All of these responses may in turn impact soil microbes (Woodmansee and Wallach 1981; Schuman et al. 2002; Patra et al. 2005). In seminal experiments on community-level responses to fire and herbivory in tallgrass prairie (Hobbs et al. 1991), mowing in unburned treatments increased the likelihood that the mown area would be grazed, though no similar pattern was observed in burned treatments. Meanwhile, fire temperature and energy release, as well as N losses, were greater from ungrazed than grazed treatments (Ewing and Engle 1988; Hobbs et al. 1991).

Fire in tallgrass prairie ecosystems has a well-documented stimulatory effect on annual net primary productivity (ANPP; Towne and Owensby 1984; Seastedt et al. 1991; Briggs and Knapp 1995). This increase is primarily because of enhanced growth of C₄ perennial grasses as a result of both increased light availability and the advantage conferred by C₄ grasses' higher N use efficiency following fire-induced volatilization losses of N from the soil surface litter layer (Hulbert 1988; Seastedt and Ramundo 1990; Ojima et al. 1994; Blair 1997). In southern Great Plains grasslands, fire in late winter and early spring is a common management tool, with minimal or even short-term (2–3 yr) stimulatory effects on C₄ grass production (Engle and Bidwell 2001; Ansley et al. 2006; Ansley and Castellano 2007). These shifts toward greater abundance of C₄ grass species entail a corresponding shift in the C:N stoichiometry of plant litter inputs, with uncertain but potentially significant implications for soil microbial communities (Knops et al. 2002).

In mixed-grass prairie, fire's stimulatory effects on ANPP and C₄ grass production, as well as their interactions with clipping, have been studied (Hubbard 2003). However, little is known about the concomitant effects of these factors on soil microbes. This study examines effects of fire and simulated herbivory (clipping) on plant functional composition, plant production, and SMB in a mixed-grass prairie of the southern Great Plains. This region is climatically intermediate between tallgrass prairie and shortgrass steppe sites where the relative influences of climate and disturbance on plant–soil dynamics have been more thoroughly assessed (Burke et al. 1998). We hypothesized that a late winter or early spring fire would increase the absolute biomass and relative proportion of C₄ grasses in the plant community relative to control and clipped treatments. This shift in aboveground biomass and community composition, combined with losses of volatilized N, would lead to lower SMB (via reduced inputs of aboveground plant biomass) and higher microbial biomass C:N ratios (via proportionally greater losses of N to volatilization). Clipping was hypothesized to moderate these impacts by reducing fuel loads and fire intensity, as evidenced by microbial biomass levels and C:N ratios intermediate between those of fire and control treatments.

METHODS

Study Site

Research was conducted on a 1-ha grazing enclosure on the W.T. Waggoner Ranch in Wilbarger County, Texas (lat 33°51'N, long 99°26'W, elevation 381 m). Mean annual precipitation for the site is 665 mm, bimodally distributed

with peaks in May (18% of annual total) and September (12% of annual total). Mean annual temperature is 16.1°C, with monthly average extremes ranging from 36°C in July to –2.5°C in January. Soils are classified as fine, mixed, thermic Typic Paleustolls of the Tillman series.

Dominant cool-season (C₃) grasses include Texas wintergrass (*Nasella leucotricha* [Trin & Rupr] Pohl), a native perennial bunchgrass, and Japanese brome (*Bromus japonicus* Thunb. ex Murr.), an exotic annual grass. Dominant warm-season (C₄) grasses include the perennial bunchgrass sideoats grama (*Bouteloua curtipendula* [Michx.] Torr.) and the stoloniferous, sod-forming buffalograss (*Buchloë dactyloides* [Nutt.] Engelm.). The study site was root-plowed to control honey mesquite (*Prosopis glandulosa* Torr.) and seeded with sideoats grama in 1974. It has not been burned since that time. The site was grazed by cattle at a moderate stocking rate (1 cow · 12 ha⁻¹) from the late 1800s to 1988, when livestock were removed.

Experimental Design

Vegetation and soil microbial dynamics were evaluated on experimental plots in a 2 × 3 factorial design (fire × clipping). Treatments were randomly assigned to 30 36-m² plots ($n = 5$ replicates/treatment combination). The following treatments were implemented annually beginning in 1999: 1) control (no fire, no clipping), 2) continuous clipping, 3) spring clipping, 4) spring fire, 5) spring fire plus spring clipping, and 6) spring fire plus continuous clipping. Plots in the spring-clipping treatment were mown to 5 cm height once per year in late April, and those in the continuous clipping treatment were mown monthly (except during drought). Clipped plant material was transported offsite. Plots in the fire treatment were subjected to prescribed fires in February or March 1999, 2000, 2001, and 2002, and are referred to for the remainder of the paper as 'spring' fires. Fires were ignited by first establishing a 1.5-m-wide preburned buffer around each plot, then burning each plot by igniting the upwind edge with a drip torch and allowing the wind to carry the fire as a head fire across each plot. Fire intensity for all fires in all years was classified as low to moderate, with flame heights not exceeding 1.5 m. Rainfall was measured at the site.

Sampling and Analysis

Sampling was carried out at approximately monthly intervals from June 2000 through May 2002. During each sampling period, a 1 × 1 m subplot was randomly chosen from each of the 30 6 × 6 m treatment plots. Because sampling was destructive, no subplots were resampled. The following sampling procedures were performed on each 1 × 1 m subplot.

Ocular estimates of foliar cover were recorded on each subplot, distinguishing the following cover classes: C₃ grasses by species, C₄ grasses by species, forbs, litter, and bare ground. Because various cover classes overlapped at different levels within the canopy, cover percentages may total to more than 100 on a given subplot.

Vegetation was clipped to ground level within a square 0.125-m² quadrat centered within the subplot. Clipped vegetation was bagged by category (C₃ grass, C₄ grass, forb,

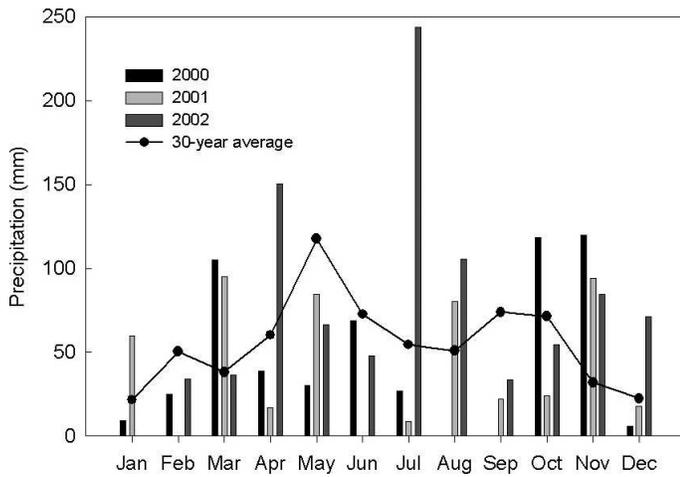


Figure 1. Monthly precipitation for 2000–2002, relative to the 30-yr average precipitation at the study site.

and litter) and dried for 5 d at 60°C. Dried vegetation was then separated into live and dead and weighed to estimate biomass.

A composite soil sample consisting of eight cores 2.5 cm in diameter and 10 cm deep was taken from each subplot. Soil samples were immediately placed on ice for transport to the laboratory and subsequently stored at 4°C until analysis. Samples were homogenized prior to laboratory analysis. A 30-g field-moist soil subsample was brought to 50% water-holding capacity and analyzed for SMB C and N using the chloroform fumigation–incubation method (Horwath and Paul 1994; Franzluebbers et al. 1999).

SMB C, SMB N, and SMB N:C were calculated as the following:

$$\text{SMB C} = C_f/K_c \text{ (Voroney and Paul 1984)}$$

$$\text{SMB N:C} = 0.56(N_f/C_f) + 0.095 \text{ (Harris et al. 1997)}$$

$$\text{SMB N} = \text{SMB C}(\text{SMB N:C}) \text{ (Harris et al. 1997)}$$

where C_f and N_f are the flushes of mineralized C and N, respectively, from fumigated soils, and $K_c = 0.43$.

Data Analysis

Data were analyzed using SAS Version 9.00 (SAS 2002). Each response variable was separately analyzed using a three-way analysis of variance factorial design with sampling date, fire, and clipping as factors. For all variables where treatment effects and treatment-by-date interactions were significant, the analysis was also carried out within each sampling date, excluding sampling date as a factor. Significant differences between treatment effects were evaluated via pairwise comparisons of least squares means.

RESULTS

In 2000, precipitation from the April-through-September growing season was below normal in every month. In 2001, precipitation was below normal for 5 of the 6 mo, with only August precipitation exceeding normal. Total precipitation for this 6-mo period was 38% of normal in 2000, and 50% of

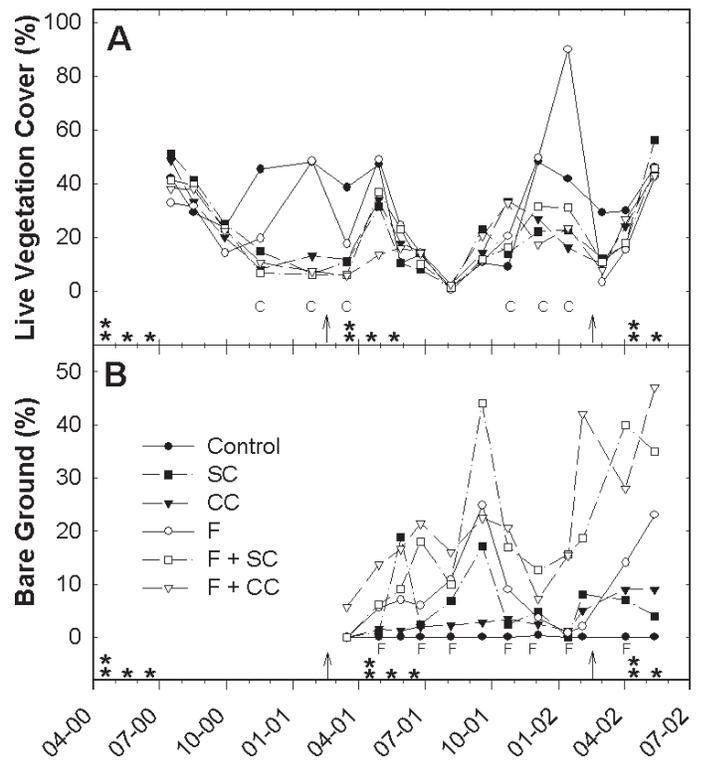


Figure 2. Percentage of cover of **A**, live vegetation and **B**, bare ground, June 2000–May 2002. Values are means of five replicates. Within individual sampling dates, significant ($P \leq 0.05$) treatment effects are indicated by C, clipping, and F, fire, along the x-axis. On the x-axis, arrows indicate dates of spring fire; double asterisks, spring clipping treatments; and all asterisks, continuous clipping treatments. Control treatment indicates no fire, no clipping; SC, spring clipping; CC, continuous clipping; F, fire only; F+SC, fire and spring clipping; and F+CC, fire and continuous clipping.

normal in 2001. Precipitation remained below normal in every month of the study period except April (Fig. 1).

Sampling date was a significant factor for all response variables (Figs. 1–4). Three-way interactions (sampling date \times fire \times clipping) were not significant for any response except C_3 annual grass cover and forb biomass.

Overall, total cover of live vegetation was reduced by clipping, with reductions occurring during late winter and early spring. Fire had no significant effect on total cover of live vegetation (Table 1). During the winter months of 2001 and 2002, cover was greater in unclipped treatments, regardless of fire treatment (Fig. 2A). Overall, both fire and clipping significantly increased the area of bare ground, with the difference increasing over time throughout the study. Significant differences in bare ground between clipping treatments occurred only in burned plots, giving rise to a significant interaction between fire and clipping for that response variable (Fig. 2B; Table 1).

Overall, continuous clipping significantly increased the cover of C_3 perennial grasses, with the differences occurring in September–December 2001 and February and May 2002 (Fig. 3A; Table 1). Both spring clipping and continuous clipping reduced the cover of C_3 annual grasses, with a significant clip-by-date interaction (Fig. 3B; Table 1). Overall,

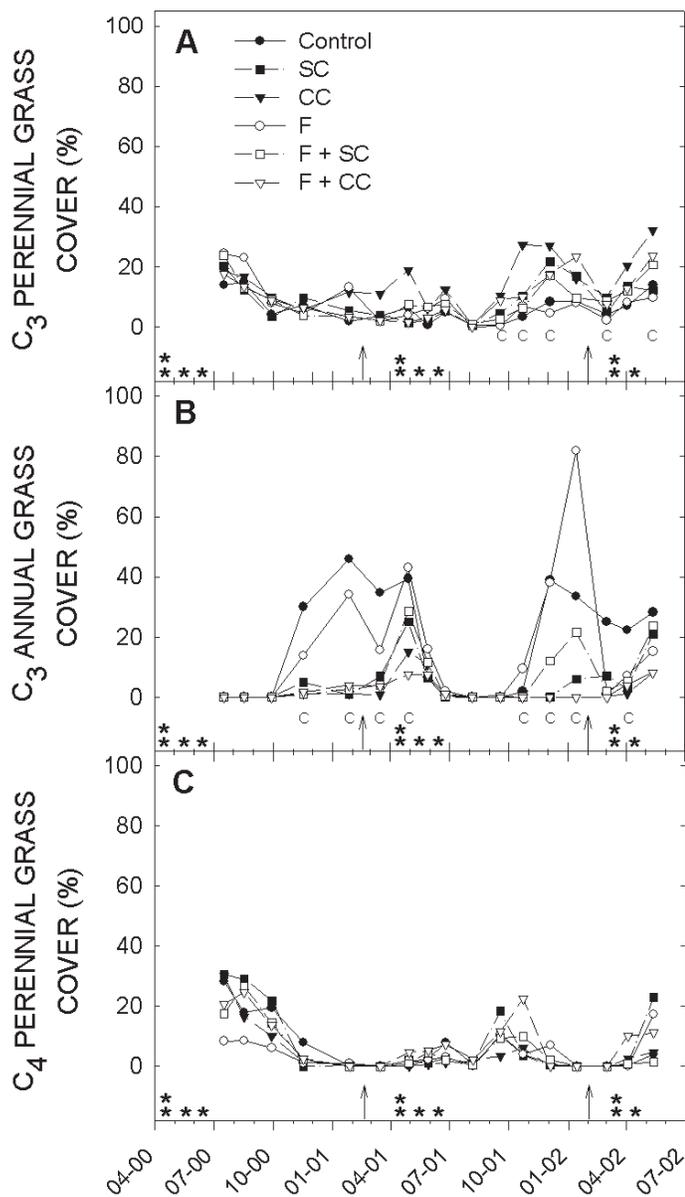


Figure 3. Percentage of live cover of **A**, C_3 perennial grasses, **B**, C_3 annual grasses, and **C**, C_4 perennial grasses, June 2000–May 2002. Values are means of five replicates. Significant ($P \leq 0.05$) treatment effects within individual sampling dates are indicated by C, clipping, along the x-axis. On the x-axis, arrows indicate dates of spring fire; double asterisks, spring clipping treatments; and all asterisks, continuous clipping treatments.

fire did not affect the cover of either C_3 grass functional type. Neither fire nor clipping affected the cover of C_4 grasses (Fig. 3C; Table 2).

Neither fire nor clipping had any effect on any plant biomass response (Table 3). All components of plant biomass declined substantially over the period of June–August 2001.

Both fire and clipping reduced litter mass overall, with a significant interaction due to the fact that the decrease under fire and clipping in combination was greater than that under either disturbance in isolation (Fig. 4; Tables 3 and 4).

SMB C and N displayed similar seasonal fluctuations, peaking once per year from late summer to late fall. Soil

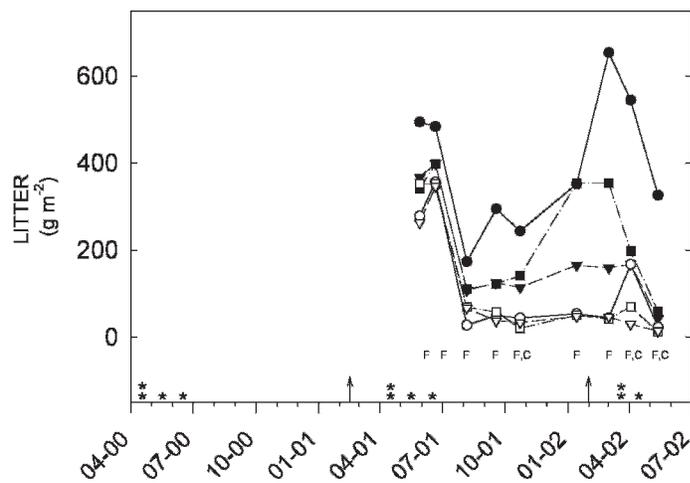


Figure 4. Litter mass, May 2001–May 2002. Values are means of five replicates. Significant ($P \leq 0.05$) treatment effects within individual sampling dates are indicated by F, fire and C, clipping, along the x-axis. On the x-axis, arrows indicate dates of spring fire; double asterisks, spring clipping treatments; and all asterisks, continuous clipping treatments.

microbial C:N ratios showed less amplitude in seasonal change, and appear to have had a separate and higher peak in early spring and early summer, while otherwise paralleling the pattern seen in SMB C and N. Overall, fire reduced SMB C, whereas clipping had no effect. Fire and sampling date interacted significantly in the microbial C response, with fire effects appearing within 3 to 6 mo following fire, in July and September 2000 and August 2001 (Table 5). Neither fire nor clipping significantly affected SMB N or soil microbial C:N ratios (Tables 5 and 6).

DISCUSSION

These results show that the effects of fire and clipping on vegetation vary across plant functional types, both in relation to the nature and timing of disturbance, and in relation to other factors such as precipitation. Those factors are also important in the translation of aboveground plant community responses into effects on soil microbes. Of particular importance in that translation are the relative magnitudes of plant contributions, via surface litter inputs, to soil microbial C and N.

Cover and biomass of C_4 grasses were both low relative to years with average growing-season precipitation (Hubbard 2003). The significance of sampling date as a factor in all response variables highlights the strong seasonal variation in plant production and soil microbial dynamics in this ecosystem.

Bare Ground and Herbaceous Cover Responses

Both fire and clipping increased the area of bare ground, and were additive in that clipping-related increases in bare ground were much greater in the presence of fire. Fire probably contributed more than clipping to the increase in bare ground via the removal of virtually all surface litter, with clipping's smaller role attributable to the reduction in the quantity of current-season standing biomass entering

Table 1. Analysis of variance results (*P*) for the effects of fire and clipping on different cover variables, once sampling date effects are considered.

Response	Fire	Clipping	Fire × clipping	Fire × date	Clipping × date
Live vegetation	0.4337	0.0007	0.9189	0.0100	< 0.0001
Bare ground	< 0.0001	0.0001	0.0379	< 0.0001	0.2338
C ₃ perennial grasses	0.3910	0.0042	0.0595	0.1917	0.0002
C ₃ annual grasses	0.9981	< 0.0001	0.6757	0.0011	< 0.0001
C ₄ perennial grasses	0.7583	0.5084	0.0794	0.0348	0.4539

subsequent seasons' litter pool. The interpretation of litter removal as the primary mode of fire effects on bare ground is further supported by the finding that fire did not significantly affect the cover of any individual plant functional type.

Treatment-related reductions in total herbaceous cover were due to clipping alone, mainly because of reductions in cover of C₃ annuals in the late winter and early spring (Towne and Owensby 1984; Collins 1987; Howe 1994, 1995, 2000; Engle and Bidwell 2001). That spring and continuous clipping reduced the cover of C₃ annual grasses, whereas fire did not, suggests that the timing as well as the mode of biomass removal is important to the system response. In late winter, when fire treatments were applied, C₃ annual grasses were still in a state of vegetative growth. However, when clipping began in April, seeds had already begun to form. Thus, the observed reduction in C₃ annual grass cover in response to clipping may be primarily due to a large reduction in the subsequent season's seed bank. In addition, more of the biomass is removed by clipping than by fire. It is also possible that reductions of the litter layer rendered conditions less favorable for germination of *B. japonicus* seeds (Whisenant 1990), though the lack of significant fire effects on C₃ annual cover suggests that this is a minor mechanism. The increase of C₃

perennial grass cover in response to continuous clipping raises the possibility that they are competitively excluded by C₃ annuals if left unclipped (Whisenant et al. 1984), but the methods employed in this study permitted no direct assessment of that hypothesis. However, because C₃ perennial grasses increased significantly under continuous but not spring clipping, repeated clipping may have reduced C₃ annual grasses below some threshold level at which competitive interactions cease.

The lack of any significant response of C₄ grasses to fire or clipping contrasts with the literature from tallgrass prairie research (Towne and Owensby 1984; Collins 1987; Howe 1994, 1995, 2000; Engle and Bidwell 2001), as well as previous work at the study site (Hubbard 2003). C₄ grass production during the study period may have been limited by below-normal growing season precipitation, and/or reduced resources and space due to earlier growth of C₃ grasses.

Herbaceous Biomass Responses

The lack of treatment effects on C₃ grass biomass suggests that the clipping-induced decreases in C₃ annual cover, and accompanying increases in C₃ perennial cover, may amount to compensation in terms of biomass. Taken together, these response patterns also account for the lack of treatment effects on total standing crop and total live standing crop. In unburned tallgrass prairie, neither clipping nor grazing produced any net change in individual plant biomass of *Andropogon gerardii* or *Panicum virgatum* (because of compensation via increased relative growth rate). However, in burned areas, the response to clipping and grazing was increased in *A. gerardii* (resulting in increased biomass), but absent from *P. virgatum* (Vinton and Hartnett 1992). A simulation model (de Mazancourt et al. 1998), applied to an African savanna grassland (de Mazancourt et al. 1999), found that grazing optimization (i.e., compensatory growth) occurred only when herbivory reduced ecosystem

Table 2. Percentage of cover (± 1 SE) of total live vegetation, bare ground, C₃ perennial grasses, C₃ annual grasses, and C₄ perennial grasses, June 2000–May 2002.¹

	No clipping	Spring clipping	Continuous clipping
Total live vegetation	a	b	b
No fire	30.4 \pm 2.1	21.6 \pm 2.1	22.0 \pm 2.1
Spring fire	28.6 \pm 2.1	21.2 \pm 2.1	20.0 \pm 2.1
Bare ground			
No fire	0.0 \pm 1.7 c	4.8 \pm 1.7 bc	3.3 \pm 1.7 c
Spring fire	8.9 \pm 1.7 b	18.8 \pm 1.7 a	21.3 \pm 1.7 a
C ₃ perennial grasses	b	b	a
No fire	6.2 \pm 1.5	8.8 \pm 1.5	15.0 \pm 1.5
Fire	8.0 \pm 1.5	9.1 \pm 1.5	9.8 \pm 1.5
C ₃ annual grasses	a	b	b
No fire	18.1 \pm 2.0	4.8 \pm 2.0	2.3 \pm 2.0
Spring fire	16.3 \pm 2.0	6.6 \pm 2.0	4.9 \pm 2.0
C ₄ perennial grasses			
No fire	6.1 \pm 1.3	8.0 \pm 1.3	4.7 \pm 1.3
Spring fire	4.3 \pm 1.3	5.4 \pm 1.3	8.0 \pm 1.3

¹Different lowercase letters indicate significantly different means (*P* < 0.05). Letters follow values if a significant fire × clipping interaction is present. Otherwise, letters follow treatment labels and indicate differences between the relevant rows and/or columns.

Table 3. Analysis of variance results (*P*) for the effects of fire and clipping on different biomass variables, once sampling date effects are considered.

Response	Fire	Clipping	Fire × clipping	Fire × date	Clipping × date
C ₃ grasses	0.0784	0.1179	0.4428	0.0647	0.8470
C ₄ grasses	0.6798	0.3610	0.5459	0.0143	0.3147
Forbs	0.4584	0.6093	0.2582	0.4163	0.9810
Total standing crop	0.1961	0.9778	0.4995	0.0474	0.2110
Live standing crop	0.3253	0.0777	0.9085	0.0015	0.1291
Litter	< 0.0001	0.0523	0.1092	0.0016	0.2419

Table 4. Mean biomass ($\text{g} \cdot \text{m}^{-2}$, ± 1 SE) of C_3 grasses, C_4 grasses, forbs, total standing crop, live standing crop, and litter.¹

	No clipping	Spring clipping	Continuous clipping
C_3 grass biomass			
No fire	67.1 \pm 8.7	86.6 \pm 8.7	90.5 \pm 8.7
Spring fire	87.9 \pm 8.7	104.0 \pm 8.7	90.7 \pm 8.7
C_4 grass biomass			
No fire	38.8 \pm 14.4	46.0 \pm 14.4	44.7 \pm 14.4
Spring fire	21.8 \pm 14.4	35.0 \pm 14.4	58.0 \pm 14.4
Forb biomass			
No fire	78.5 \pm 6.7	83.2 \pm 6.7	85.4 \pm 6.7
Fire	90.8 \pm 6.7	92.1 \pm 6.7	76.6 \pm 6.7
Total standing crop			
No fire	449.8 \pm 25.7	471.8 \pm 25.7	441.2 \pm 25.7
Spring fire	435.9 \pm 25.7	408.4 \pm 25.7	430.1 \pm 25.7
Live standing crop			
No fire	184.3 \pm 14.9	215.8 \pm 14.9	220.5 \pm 14.9
Spring fire	200.6 \pm 14.9	231.1 \pm 14.9	225.3 \pm 14.9
Litter	a	ab	b
No fire a	396.2 \pm 49.7	261.7 \pm 28.4	182.9 \pm 19.3
Spring fire b	116.1 \pm 19.8	113.9 \pm 19.9	98.2 \pm 18.6

¹Different lowercase letters within treatment headings indicate significantly different means ($P < 0.05$).

losses of N relative to the amount that would have left the system had the biomass been burned rather than consumed by herbivores. Although no direct measurements of insect numbers were made in our study, anecdotal observations suggest that high abundance of and intense herbivory by grasshoppers may be the most likely explanation for the parallel decline in all plant biomass components across all treatments between June and August 2001, as reported in other studies (Callaham et al. 2000).

The lack of treatment effects on forbs in this study is likely because of their low biomass during the study period.

Litter and Soil Microbial C and N Responses

Both fire and clipping reduced litter mass, but fire's larger relative reduction in litter mass may explain why SMB C declined in response to fire, but not to clipping. That decline occurred 3–6 mo following fire, suggesting that the combustion of recent litter that would otherwise be decomposed by soil microbes was indeed responsible (Bruulsema and Duxbury 1996). Contrary to hypothesized results, fire did not reduce SMB N. This may be because of differing relative importance of sources of microbial C and N; microbes tightly retain and

Table 5. Analysis of variance results (P) for the effects of fire and clipping on different microbial variables, once sampling date effects are considered.

Response ¹	Fire	Clipping	Fire \times clipping	Fire \times date	Clipping \times date
Microbial C	0.0271	0.8516	0.3864	< 0.0001	0.0656
Microbial N	0.3878	0.7048	0.2754	0.2610	0.0275
Microbial C:N	0.3508	0.2692	0.0469	0.0085	0.3181

¹C indicates carbon; N, nitrogen.

Table 6. Mean (± 1 SE) microbial biomass carbon (C), nitrogen (N), and microbial C:N ratio.¹

	No clipping	Spring clipping	Continuous clipping
Microbial C ($\text{mg C} \cdot \text{kg}^{-1}$ soil)			
No fire a	1002.6 \pm 32.2	999.9 \pm 32.2	949.8 \pm 32.2
Spring fire b	923.0 \pm 31.7	905.1 \pm 32.2	939.5 \pm 31.9
Microbial N ($\text{mg NH}_4^+ \cdot \text{kg}^{-1}$ soil)			
No fire	116.9 \pm 5.3	112.6 \pm 5.3	106.0 \pm 5.2
Spring fire	108.0 \pm 5.1	103.9 \pm 5.4	112.2 \pm 5.4
Microbial C:N			
No fire	8.11 \pm 0.11	8.41 \pm 0.11	8.55 \pm 0.10
Fire	8.50 \pm 0.11	8.43 \pm 0.11	8.39 \pm 0.11

¹Different lowercase letters within treatment headings indicate significantly different means ($P < 0.05$).

dominate the cycling of N derived primarily from soil inorganic pools, but may be limited by inputs of plant C to drive those processes (Knops et al. 2002).

Fire in tallgrass prairie has been found to reduce both SMB C and SMB N (Ajwa et al. 1999). In New Zealand tussock grasslands, fire reduced soil organic C, SMB C, and SMB N up to 30 mo after burning (Ross et al. 1997). In tallgrass prairie, SMB C and SMB N declined in response to clipping generally, and to fire in dry years, with differences occurring during a period of a few months following treatments (Garcia and Rice 1994). However, other studies have found that fire increases SMB C via a long-term increase in root production (Ojima et al. 1994; Fynn et al. 2003). It is important to note that these increases, in contrast to those associated with changes in surface litter inputs, likely extend below the surface 10 cm of soil. Increased SMB C has been observed in response to clipping, presumably via stimulation of microbial growth in response to increased root exudation from defoliated plants (Hamilton and Frank 2001).

MANAGEMENT IMPLICATIONS

In contrast to earlier results at the study site, fire had no impact on cover or biomass of C_4 grasses. As such, its effectiveness in boosting C_4 grass production is likely contingent on adequate growing-season precipitation. Moreover, long-term effects of fire on belowground plant productivity may differ from the short-term patterns observed in this study. Clipping significantly affected species composition of C_3 grasses, with repeated clipping episodes reducing the abundance of C_3 annuals and increasing that of C_3 perennials. These effects were more pronounced in fire treatments, highlighting the need for land managers to consider the interactive effects of fire and other means of biomass removal in formulating vegetation management strategies.

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