Plant Soil (2009) 323:235–247
DOI 10.1007/s11104-009-9931-2

REGULAR ARTICLE

Annual fire and mowing alter biomass, depth distribution, and C and N content of roots and soil in tallgrass prairie

Duane J. Kitchen · John M. Blair · Mac A. Callaham Jr.

Received: 11 July 2008 / Accepted: 9 February 2009 / Published online: 24 February 2009

Abstract Management practices, such as fire and mowing, can affect the distribution and quality of roots and soil C and N in grasslands. We examined long-term (13 years) effects of annual fire and mowing on fine (<2 mm) roots and soil C and N content in a native tallgrass prairie at Konza Prairie Biological Station in northeastern Kansas, USA. Using 90 cm deep soil cores, we determined that fire and mowing independently and interactively influenced the quantity and depth distribution of fine root biomass, root C and N concentration, and soil C and N content. Annual burning increased total fine root biomass by 48% and total C storage in roots by 47% compared to unburned unmowed plots, and resulted in a deeper distribution of roots. There was a significant interaction of fire and mowing, whereby mowing reduced root biomass and root C storage by ~30% in annually burned plots, but did not affect total root biomass in unburned plots. Mowing also resulted in shallower distribution of roots regardless of fire treatment. Root N concentration was reduced by 15–25% in plots that were burned, mowed, or both. Mowing effects on soil C and N were restricted to surface soils (0–10 cm), where mowing reduced soil C concentrations by ~20% and N concentrations by 17% regardless of burning treatment. In contrast, burning alone did not significantly influence soil C and N concentrations. In general, root biomass, root C and N mass, and soil C and N concentrations declined with depth, and most responses to burning and mowing exhibited significant interactions with depth. Different long-term fire and mowing regimes can significantly alter belowground root biomass and C and N dynamics in grasslands, and in particular at depths in the profile that are not typically sampled.

Keywords Fire · Grassland · Mowing · Root biomass depth distribution · Soil C and N · Tallgrass prairie

Introduction

Fire and aboveground biomass removal, by grazers or by mechanical means, affect ecological structure and processes in grasslands worldwide (Bond and Keeley 2005; Frank et al. 1998; Knapp et al. 1998b; Milchunas and Lauenroth 1993; Risser et al. 1981). In North American tallgrass prairies, fire is widely

Responsible Editor: Wim van der Putten.

D. J. Kitchen (✉)
Department of Biology, Rockford College,
5050 East State Street,
Rockford, IL 61108-2311, USA
e-mail: dkitchen@rockford.edu

J. M. Blair
Division of Biology, Kansas State University,
Manhattan, KS 66506, USA

M. A. Callaham Jr.
Southern Research Station, USDA Forest Service,
Athens, GA 30602, USA

used to control plant species composition, limit the cover of woody vegetation, and increase production of desirable forage grasses (Briggs et al. 2002; Towne and Kemp 2003). Historically, these grasslands supported large herds of ungulate grazers (i.e., bison) that removed aboveground biomass. However, mowing for hay production or to manipulate plant composition is an alternative management practice (Snaydon 1987; Tix and Charvat 2005; Van Dyke et al. 2004), which may increase in importance as grasslands are used for biofuel feedstock (Field et al. 2008). Although many studies have addressed the aboveground consequences of fire and grazing or mowing in tallgrass prairie (Collins et al. 1998; Knapp et al. 1998b), much less is known about their effects belowground.

Tallgrass prairie plant productivity and community composition are significantly altered by fire and aboveground biomass removal (Collins et al. 1998; Gibson et al. 1993; Hartnett et al. 1996; Towne and Kemp 2003). The most significant effects of fire are the removal of accumulated surface plant litter (Knapp and Seastedt 1986), which creates a more favorable light and energy environment for plant growth. Thus, fire generally stimulates aboveground plant productivity in deep soils with adequate soil water availability (Briggs and Knapp 1995), and repeated frequent fire increases the dominance of perennial C_4 grasses while reducing abundance and productivity of C_3 grasses, forbs and woody plants (Collins et al. 1998). With infrequent burning, the relative abundance of C_3 grasses, forbs and woody plants increases (Knapp et al. 1998b). Mowing and removal of aboveground biomass can also increase aboveground plant productivity in tallgrass prairie (Turner et al. 1993), and can reduce the cover of forbs and woody plants in prairie that is not burned (Gibson et al. 1993).

Fewer studies have addressed the impacts of fire and aboveground biomass removal on ecological processes belowground, even though greater than two thirds of the plant biomass in tallgrass prairie is belowground in the form of roots and rhizomes (Risser et al. 1981) and the majority of ecosystem C and N is stored in the soil (Blair et al. 1998). Burning can increase root productivity and biomass in tallgrass prairie (Johnson and Matchett 2001; Kucera and Dahlman 1968; Seastedt and Ramundo 1990). Moreover, frequent burning also lowers soil N availability (Blair 1997), and increases the C:N ratio of roots and soil organic matter (Fynn et al. 2003; Ojima et al. 1994). In contrast, aboveground biomass removal by mowing has been reported to reduce root biomass (Todd et al. 1992) and decrease root tissue N concentrations, presumably due to loss of N with aboveground biomass removal (Turner et al. 1993). However, Benning and Seastedt (1997) found greater total root mass after 4 years of mowing in unburned prairie compared to unmowed plots, and increased root biomass in response to mowing (Dickinson and Polwart 1982) has been reported for some European grasslands.

While fire and mowing can independently influence ecological processes in grasslands, there may be important interactive or contingent effects, as seen for fire and grazing (Archibald et al. 2005; Hobbs et al. 1991). Therefore, the objectives of this study were to determine the independent and interactive effects of (a) long-term annual spring burning and (b) mowing on (1) belowground plant biomass (root biomass, depth distribution, and tissue C and N concentration) and (2) bulk soil C and N concentration in native tallgrass prairie. Based on prior studies of plant and soil responses to fire and aboveground biomass removal, our hypotheses were that: (1) Annual burning alone would increase total root biomass (mirroring increases in aboveground productivity) and increase the proportion of roots at lower soil depths, but decrease root tissue N concentration due to increased N limitation. We expected burning to increase C storage in belowground plant biomass, with little change in belowground plant N storage (i.e., greater total plant biomass, but with lower N concentrations). (2) Repeated mowing would reduce root biomass and result in a shallower depth distribution of roots. Because removal of biomass also removes nutrients (e.g., N), we predicted that mowing would decrease root tissue N concentration, resulting in a decrease in both C and N storage in root biomass. (3) There would be significant interactions between annual burning and mowing, such that the negative effects of mowing on root biomass would counteract the positive effects of fire, and the combined losses of N due to burning and mowing would reduce root tissue N concentration more than either fire or mowing alone. (4) Changes in surface litter inputs and root biomass and tissue chemistry would be reflected in altered soil C and N pools. We expected fire alone to decrease soil C content near the surface due to reduced surface litter inputs, but to potentially increase C storage deeper in the soil profile (e.g., below ~20 cm) due to greater root inputs. We expected mowing to reduce soil C and N content due to reduced root inputs, while the combination of burning and mowing was predicted to result in the greatest reductions in soil C and N.

Materials and methods

Site description

Research was conducted at the Konza Prairie Biological Station (KPBS), a 3,487 ha tallgrass prairie and Long-Term Ecological Research site in the Flint Hills of northeastern Kansas, USA (39°05′N, 96°35′W). Mean monthly temperature ranges from −2.7°C to 26.6°C, and mean annual precipitation is 835 mm, with the majority occurring in the growing season. Native vegetation is primarily tallgrass prairie dominated by perennial, C_4 grasses including big bluestem (*Andropogon gerardii*), little bluestem (*Schizachyrium scoparium*), Indiangrass (*Sorghastrum nutans*), and switchgrass (*Panicum virgatum*), with a variety of less common C_3 forbs, grasses and sedges Further details regarding soils, vegetation, and climate of KPBS are available in Knapp et al. (1998a).

Experimental design

We sampled fire and mowing treatments established in 1986 as part of the "Belowground Plot Experiment" (Todd 1996). Soils were fine, mixed mesic Typic Argiustolls. Vegetation at the start of the experiment was relatively uniform and representative of ungrazed native tallgrass prairie burned at 2–3 year intervals (Collins 1987). Treatments consisted of subplots (12.5×12.5 m) with combinations of annual dormant season burning in April or long-term fire exclusion (burned vs. unburned), and annual mowing and raking to remove aboveground biomass (mowed vs. unmowed). Each whole plot was randomly assigned a fire treatment (burned vs. unburned, n=4), and split with each half randomly assigned a mowing treatment (mowed vs. unmowed, n=4). Subplots assigned to the mowing treatment were mowed to a height of 10 cm and raked (all clippings and litter completely removed) once annually in mid-growing season (late June/early July). Thus, treatment combinations sampled in our study included burning and mowing in a full factorial design. At the time of this study, plant communities had diverged under different treatments. Annually burned plots were dominated by perennial C_4 grasses (primarily *A. gerardii* and *S. nutans*), with grasses comprising more than 95% of total aboveground biomass, while in unburned plots forbs (such as *Solidago canadensis*) comprised ~44% of total aboveground biomass (Collins et al. 1998). Mowing reduced the cover of forbs and maintained dominance of the C_4 grasses in both burned and unburned treatments (Gibson et al. 1993).

Sampling procedures

Roots and soils were sampled in December 1998 (13 years after initiation of the treatments) by collecting three 4-cm diameter cores from each subplot to a depth of 90 cm or to bedrock using a hydraulic corer (Giddings Machine Company, Fort Collins, CO). Intact cores were divided into 10 cm increments, and stored in polyethylene bags at ~2°C until processing. Soil was passed through a 4 mm sieve to separate large root segments from soil. A subsample of approximately 25 *g* of soil was then passed through a 1 mm sieve and picked intensively to obtain a root-free sample for total bulk soil C and N analyses. All large root fragments and remaining soil were then washed over a 250 µm sieve to collect root biomass. Rhizomes were separated from fine (<2 mm) roots, and soil and roots were dried to constant weight at 60°C. Root samples were weighed, and roots from the 20–90 cm depths were combined into 20–40 cm, 40–60 cm, and 60–90 cm increments. Ground root and soil samples were analyzed for C and N concentration using a Carlo-Erba model NA-1500 C/N autoanalyzer (Carlo-Erba, Milan, Italy), following soil acidification to remove carbonates (Harris et al. 2001). Mean root C and N concentrations for the entire soil profile were calculated on a weighted basis by multiplying mean root tissue C and N concentration for each depth increment by the root biomass in each depth increment.

Statistical analyses

Values for the three cores per plot were averaged before analysis for a total of n=4 samples per treatment combination. The PROC MIXED procedure of SAS (version 8.0, SAS Institute 1999) was used to analyze the data. For analysis of data pooled across the entire profile, we used a split plot design, with burning as the whole plot effect and mowing as a subplot effect. For data that was analyzed with soil depth as a factor, we used a split-split plot design with burning as the main plot effect, mowing as the first split (subplot) effect, and soil depth as an additional split (sub-subplot) effect. Comparisons of means were done by least significant difference using the LSMEANS statement and PDIFF option. Where appropriate, significant interactions between treatments by depth were identified using the SLICE option in the MIXED procedure of SAS. Because of small sample sizes and the inherent variability of plant roots and soils, the significance level was set at $\alpha=0.10$ for some statistical comparisons, otherwise $\alpha=0.05$.

Results

Root biomass

The effects of burning and mowing on total root biomass over the entire 0–90 cm profile (Fig. 1) were contingent upon one another, as indicated by a significant burn x mowing interaction term ($P=0.0874$). Annual burning increased total root biomass by 48% compared to unburned plots, but only in the absence of mowing. In contrast, mowing significantly reduced total root biomass by about 32%, but only in burned plots. Mowing had no net effect on total root biomass in unburned plots. Thus, annual burning by itself had a positive effect on total root biomass, while the effect of mowing varied as a function of fire treatment (Fig. 1).

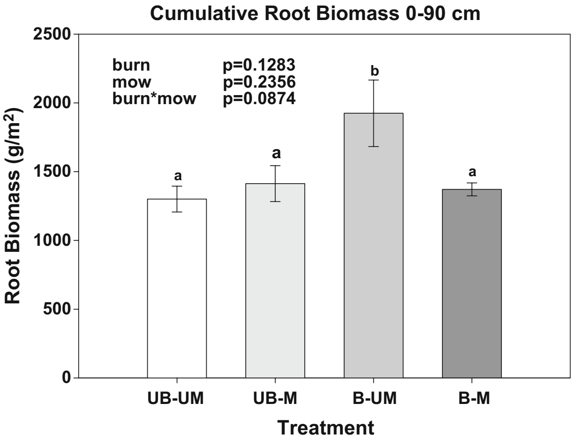


Fig. 1 Effect of long-term annual burning and mowing on total root biomass (mean±1 SE) across the entire 90-cm sampled profile in plots that were unburned unmowed (UB-UM), unburned and mowed annually (UB-M), annually burned unmowed (B-UM), or both annually burned and mowed (B-M). Results of a two-way ANOVA of the effects of burning and mowing are presented, and letters above bars indicate significant differences among treatment combinations at $\alpha=0.10$

A more detailed analysis of root biomass using depth increment as an additional effect revealed significant effects of depth, and significant interactions of burning and mowing treatments with depth. Table 1 summarizes the results of three-way analyses of the effects of burning, mowing, and depth increment on root biomass, root C and N concentration and standing stocks, and tissue C:N ratio. For root biomass, there was a significant main effect of burning, and a significant two-way interaction between burning and mowing, reflecting the positive effect of burning on root biomass, but only in the absence of mowing. As expected, there was a highly significant reduction in root mass with depth, as well as a significant two way-interaction between burning and depth and a three-way interaction among burning, mowing and depth. In order to address these interactions, we performed separate analyses of the effects of burning and mowing by depth increment (Fig. 2). Mean root biomass at each depth increment was greatest in the burned only treatment, and analysis by depth indicated that the increase with annual burning was significant in both the shallowest (0–10 cm) and deepest (60–90 cm) increments (Fig. 2). The effects of mowing on root biomass varied as a function of fire treatment, as reflected by a significant burning x mowing interaction, and with depth as reflected by a three-way burning x mowing x depth interaction (Table 1). Mowing tended to reduce root biomass throughout the profile in annually burned plots, with significant reductions at 0–10 cm, 10–20 cm and 60–90 cm depth increments (Fig. 2). In contrast, mowing significantly increased root biomass in the upper 10 cm of unburned plots, while having little impact on lower depth increments (Fig. 2).

The differential effects of fire and mowing on root biomass as a function of depth resulted in significant shifts in the proportional depth distribution of roots (data not shown). In general, annual burning in-

Table 1 Results of mixed model 3-way ANOVAs of the effects of annual burning, mowing, and sampling depth on root biomass, root tissue C and N concentrations (%), and total root standing stocks of C and N (g/m^2) after 13 years of treatment applications in the Belowground Plot Experiment at Konza Prairie Biological Station, Kansas, USA

Effect	df	Root biomass (g/m^2)		Root C (%)		Root C (g C/m^2)		Root N (%)		Root N (g N/m^2)		Root C:N	
		F	*P*-value	*F*	*P*-value	*F*	*P-value*	*F*	*P-value*	*F*	*P-value*	*F*	*P-value*
Burn (B)	1	9.79	0.0119	0.00	0.9820	7.84	0.0221	14.20	0.0005	2.40	0.1495	18.12	0.0013
Depth (D)	4	117.7	<0.0001	13.14	<0.0001	107.23	<0.0001	21.06	<0.0001	160.63	<0.0001	14.95	<0.0001
B x D	4	3.05	0.0555	1.20	0.3376	1.44	0.2750	1.30	0.2845	0.39	0.8092	1.46	0.2379
Mow (M)	1	2.68	0.1346	1.54	0.2611	2.35	0.1591	9.98	0.0029	3.63	0.0965	4.67	0.0535
B × M	1	5.62	0.0420	7.65	0.0324	5.52	0.0432	9.79	0.0032	2.11	0.1878	12.51	0.0047
M × D	4	1.79	0.1652	3.54	0.0214	2.04	0.1239	0.80	0.5290	0.52	0.7227	0.43	0.7862
B × M × D	4	4.72	0.0064	3.75	0.0171	3.03	0.0394	2.10	0.0973	0.87	0.4943	1.75	0.1653

df degrees of freedom, total *df* based on *Satterthwaite's* method

creased the proportion of total root biomass occurring deeper in the soil profile, whereas mowing tended to shift root biomass distribution to shallower depths. For example, annual burning without mowing significantly increased the proportion of total fine root biomass in the 60–90 cm increment (12%) compared to all other treatments (mean=6%). In contrast, mowing significantly increased the proportion of total fine root mass in the top 10 cm (mean=60%), compared to unmowed treatments (mean=51%).

Root C and N

Weighted mean root C concentrations (0–90 cm) averaged 38% across all treatments and were not significantly affected by burning or mowing. Analysis with depth as a factor revealed that root C concentrations were generally lowest in the deepest samples ($P<0.0001$), but still no significant main effects of burning or mowing (Table 1). As a result, the total mass (standing stock) of C in roots was a function of treatment level responses of root biomass, and was greatest in plots that were burned only (721 *g* C/m^2) compared to unburned plots (491 *g* C/m^2) or plots that were burned and mowed (508 *g* C/m^2) (Table 2). Mowing reduced the standing stock of root C by 30%, but only in plots that were annually burned (Table 2), reflecting effects of mowing on root biomass.

Burning and mowing, alone or in combination, reduced root tissue N concentrations averaged over the entire (0–90 cm) profile (Table 2). A significant two-way interaction between burning and mowing occurred, whereby mowing reduced root N concentration in unburned plots, but not in burned plots (Table 2). In the analysis including depth as an effect, root N concentration was generally greatest at 0–10 cm, and was markedly reduced in lower depth increments (Fig. 3a). There were also significant main effects of burning and mowing (both reduced root tissue %N), and root N concentration in the surface 10 cm was ~35% greater in unburned, unmowed plots than in burned or mowed treatments (Fig. 3a). A significant burn x mowing interaction occurred (Table 1), whereby mowing consistently reduced root N concentrations across all depths in unburned plots but not in burned plots (Fig. 3a). In both the 20–40 cm and 40–60 cm increments, root N was significantly lower in the combined burning and mowing treatment relative to the unburned, unmowed

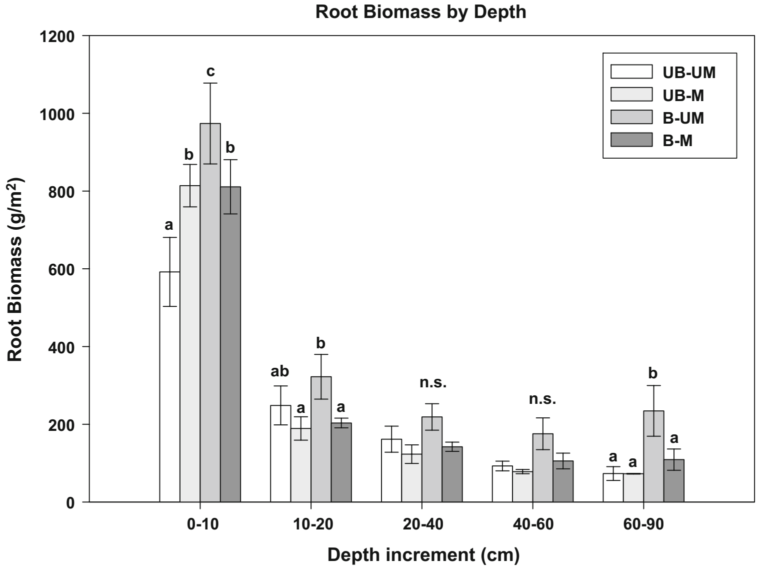


Fig. 2 Effect of long-term annual burning and mowing on total root biomass (mean±1 SE) in each of five soil depth increments (note that although root mass in the 10–20 cm and 20–40 cm increments is similar, the 20–40 cm increment is twice the volume). Letters indicate significant differences among treatment combinations at α=0.10. See Fig. 1 for description of treatment combination codes

control, while burned only and mowed only treatments had intermediate values (Fig. 3a).

Comparison of the magnitude of treatment effects on root biomass and root N concentrations indicated that the mass of N stored in roots (standing stock N) was influenced more by differences in root biomass than root N concentration (Figs. 3a, b). Across the entire 90-cm profile, there was no effect of burning on total root N mass in spite of reduced N concentrations in burned plots (Table 2). Mowing significantly reduced total root N mass, but only in plots that were burned (Table 2). Root N standing stocks varied significantly with depth (Fig. 3b). At each depth increment, there was a trend (α=0.10) for greater root N mass in the burned only treatment at 0–10 cm, 10–20 cm, and 60–90 cm increments, despite the negative effects of burning on root N concentration.

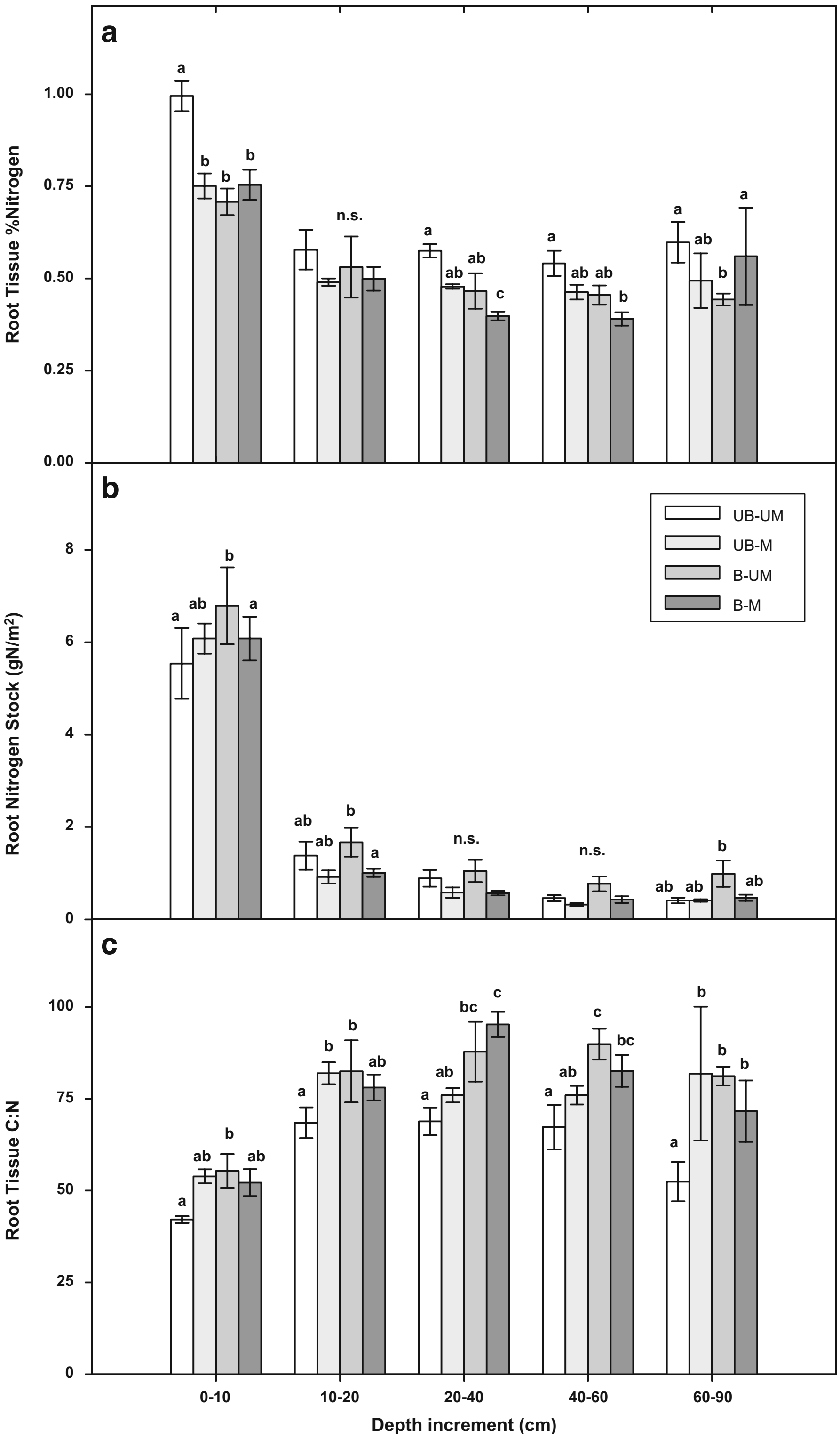
The quality of root tissue (as indicated by C:N) was affected by both burning and mowing, and varied with depth. Mean root tissue C:N across the entire 0–90 cm profile was lowest (highest quality) in the unburned unmowed plots, and was significantly increased by burning or mowing, either alone or in combination (Table 2). Analysis including depth indicated significant main effects of burning, mowing and depth, as well as a significant burn x mowing interaction (Table 1). In all depth increments, root C:N was generally lowest in the unburned unmowed treatment, and increased in response to burning, mowing or both treatments combined (Fig. 3c), though

Table 2 Summary of mean root responses to fire and mowing treatments over the entire 0–90 cm profile, based on two-way ANOVA of burning and mowing effects

Response variable	Treatments				
	UB-UM	UB-M	B-UM	B-M	α
Root C mass (g C/m2)	491a (45)	548ab (50.4)	721b (99.1)	508a (22.7)	0.05
Root N concentration (%)	0.79a (0.05)	0.66b (0.03)	0.60b (0.02)	0.63b (0.02)	0.05
Root N mass (g N/m2)	9.63ab (0.9)	9.00ab (0.6)	11.3a (1.0)	8.56b (0.4)	0.05
Root tissue C:N	54.1a (1.5)	62.3b (2.4)	69.5c (3.2)	65.1bc (1.81)	0.05

Root N content and root C:N values are weighted averages (value for each depth increment multiplied by the proportion of total root biomass in that increment). Standard errors are given in parentheses. For each variable, means with a common letter are not significantly different at the level indicated in the final column. See Fig. 1 for description of treatment combination codes

Fig. 3 Effect of long-term annual burning and mowing on **a** root tissue N concentration **b** total root N storage and **c** root tissue C:N (mean±1 SE) in five soil depth increments. Letters indicate significant differences among treatment combinations at α=0.05. See Fig. 1 for description of treatment combination codes

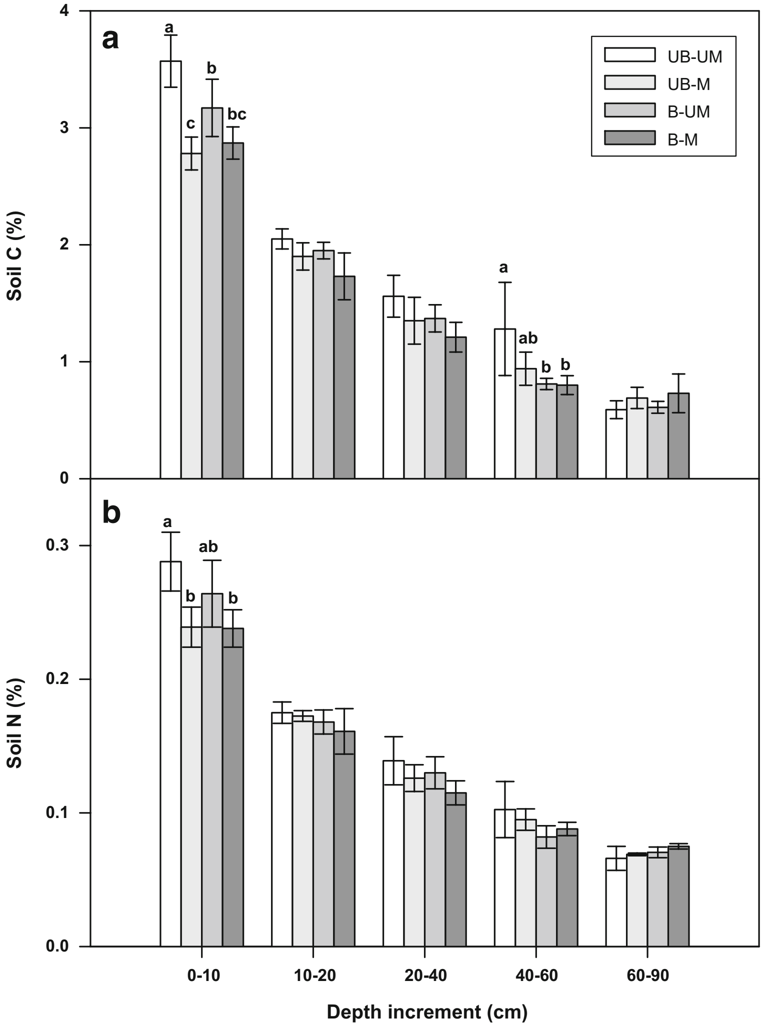


the significance of differences among treatments varied with depth.

Soil C and N

Bulk soil C and N concentration declined exponentially with depth (Fig. 4a, b). Mean soil C concentrations ranged from 3.1% in the surface horizon to 0.7% in the 60–90 cm increment, and soil N ranged from 0.26% in the top 10 cm to 0.07% in the 60–90 cm increment. A three-way ANOVA of treatment effects and depth (data not shown) indicated a significant effect of depth ($P<0.0001$) and a significant interaction between mowing and depth on both soil C ($P=0.0162$) and N ($P=0.0029$) concentrations, but no main effects of burning or mowing. However, separate two-way ANOVAs by depth increment revealed significant effects of burning and mowing on soil C and N concentrations in the top 10 cm, as well as effects on soil C in the 40–60 cm increment (Fig. 4). In the top 10 cm, soil C concentrations were highest in the unburned unmowed plots, and were significantly reduced by burning and by mowing, either alone or in combination (Fig. 4a). The greatest reduction was from mowing alone, which resulted in a 22% reduction in mean soil C concentration (2.78% C) compared to the unburned unmowed treatment (3.57% C). Burning alone resulted in an 11% decrease (3.17% C), while burning and mowing combined (2.87% C) was not significantly different than either

Fig. 4 Effect of long-term annual burning and mowing on bulk soil **a** C and **b** N concentrations (mean±1 SE) in each of five depth increments. Letters indicate significant differences among treatment combinations at α=0.10. See Fig. 1 for description of treatment combination codes



burning or mowing alone (Fig. 4a). In the 40–60 cm increment, soil C concentration was again greatest in the unburned unmowed treatment, and was significantly reduced by burning alone or in combination with mowing (Fig. 4a). Only soil N concentrations in the upper 10 cm were affected by the treatments, with a decrease in N concentration in response to mowing, but not to burning alone (Fig. 4b).

Discussion

Root responses

Root biomass and chemistry responded to both fire and mowing, although the specific effects of fire and mowing differed and were often contingent upon one another. Annual burning alone increased root mass, increased standing stocks of C and N in root biomass, decreased root tissue quality (reduced N concentration, greater C:N ratio), and led to a proportionally deeper root distribution, relative to unburned prairie. Thirteen years of annual burning increased total root biomass by 48% (Fig. 1), with significant increases in both shallow and deeper root mass (Fig. 2). These results suggest that the well-documented increases in aboveground plant productivity in response to fire in tallgrass prairies (Briggs and Knapp 1995) are mirrored by similar responses belowground. These results are also consistent with previous comparisons of total root biomass in frequently burned and unburned tallgrass prairie (Johnson and Matchett 2001; Kucera and Dahlman 1968; Seastedt and Ramundo 1990). Such changes in root biomass and depth distribution may reflect shifts in plant community composition, with frequent burning increasing the cover of perennial C_4 grasses, known for having extensive fibrous root systems (Weaver 1954). Differences in species-level allocation to roots may also play a role, as frequently burned prairie tends to have lower availability of soil N (Blair 1997) and more frequent and severe water deficits (Briggs and Knapp 1995), which may lead to great allocation of assimilated C to root growth (Chapin 1980; Reynolds and D'Antonio 1996).

In contrast to annual burning, aboveground biomass removal by mowing generally reduced root biomass, though there were significant interactions with fire treatment. In annually burned prairie dominated by C_4 grasses, mowing reduced total root biomass (Fig. 1). Surprisingly, mowing increased root biomass in the upper 10 cm of soil in unburned prairie (Fig. 2), but had little effect at lower depth increments, resulting in no significant effect of mowing on total root biomass in unburned prairie (Fig. 1). Aboveground biomass removal by grazers or by mechanical means often reduces root productivity or biomass (Gao et al. 2008; Johnson and Matchett 2001), but has been reported to have variable effects on belowground biomass in other studies (Dickinson and Polwart 1982; McNaughton et al. 1998; Milchunas and Lauenroth 1993; van der Maarel and Titlyanova 1989).

In all treatments, root biomass was highest in the surface increments (68–78% of total root biomass was in the upper 20 cm) and declined exponentially with depth (Fig. 2). Dahlman and Kucera (1965) reported similar root biomass depth distribution in a Missouri tallgrass prairie. Mowing altered the proportional depth distribution of roots, generally increasing the proportion of roots in the upper 20 cm in both burned and unburned prairie, and significantly lowering the proportion of roots at 60–90 cm in mowed and burned prairie. Changes in both root biomass and depth distribution may be due to a combination of factors, including shifts in species composition in response to long-term mowing treatments (Gibson et al. 1993; Collins et al. 1998), and changes in belowground C allocation and/or root system architecture in response to altered soil resource availability (Fransen et al. 1998; McCulley et al. 2004) or aboveground biomass removal (Dickinson and Polwart 1982; Rodriguez et al. 1996). For example, the unexpected increase in fine root biomass in response to mowing unburned plots may be due to a reduction in forbs with tap roots or coarser root architecture, and an increase in cover of perennial grasses (Gibson et al. 1993). Likewise, the reduction in fine root biomass with mowing in burned plots, and the shallower root distribution, may simply reflect lower C allocation below ground in response to repeated defoliation. However, it was not possible in the present study to distinguish changes in root dynamics related to shifts in community composition from those resulting from altered biomass and nutrient allocation.

There were only minor treatment effects on root C concentration (%). However, both burning and mowing reduced root tissue N concentration (Fig. 2a), as reported in previous studies (Benning and Seastedt

1997; Ojima et al. 1994; Turner et al. 1993), leading to increased root C:N ratios at various depths. The reduction in N content with long-term annual burning presumably reflects cumulative N losses from annual burning, decreased soil N availability, and increased nitrogen use efficiency of plants in frequently burned grasslands (Blair 1997; Fynn et al. 2003; Ojima et al. 1994). We expected that the additional removal of N associated with combined burning and mowing would be additive and further reduce root N concentration as compared to burning or mowing alone, but this response was not apparent at most depths (Fig. 3a). In contrast, root N concentration in the 60–90 cm depth increment increased in response to mowing in burned plots, though the reason for this is not clear.

A number of studies have reported a positive response of root tissue quality, as well as N cycling rates, to grazing (Frank et al. 1998, 2002; Johnson and Matchett 2001; McNaughton et al. 1997). However, a key difference between grazing and mowing with aboveground biomass removal is the removal of nutrients and lack of redeposition of any of the N contained in biomass, as occurs with grazing. In this regard, biomass removal by annual mowing is likely to affect the system in a way more similar to annual burning. Annual burning and mowing with concurrent removal of aboveground biomass are similar in that both result in the loss of nutrients (Ojima et al. 1994; Seastedt et al. 1991), both alter the microenvironment due to removal of the litter layer and/or standing biomass (Knapp and Seastedt 1986), and both are spatially uniform in their impact, unlike the results of selective herbage removal by grazers (Hartnett et al. 1997; Knapp et al. 1999; Vinton et al. 1993). However, there are important differences that likely influence soil and root responses. First, the timing of the treatments differs with respect to plant phenology. Prescribed burning is typically conducted in the spring prior to the initiation of plant growth, and removes mostly senescent plant material which is typically low in nutrients. Spring burning also accelerates soil warming, which enhances plant productivity via more rapid plant development and a more favorable light and energy environment (Knapp and Seastedt 1986). An increase in total plant productivity under conditions of reduced nutrient availability should result in a greater quantity of lower quality (higher C:N) roots, as observed in the burned only plots in this study. In contrast, mowing was done in late June/early July, which is the peak growth period for the dominant C_4 grasses. Defoliation by mowing at this time removes nutrients contained in aboveground biomass, and may increase relative growth rates (Oesterheld 1992) or production of aboveground tissues (Loeser et al. 2004; Turner et al. 1993), compared to unburned treatments, though this may occur at the expense of C allocation to roots (Detling et al. 1979; Noy-Meir 1993; Turner et al. 1993). This is consistent with our observations of reduced total root biomass with mowing in burned plots.

Soil responses

The total C content of soil results from the balance of inputs of organic C (i.e., plant root and shoot 'litter') and losses of C due to microbial mineralization. Because root inputs constitute the largest contribution to soil organic C pools in grasslands where fire and grazing are frequent, reductions in root biomass may result in decreased soil C content. Alternatively, increases in soil organic matter (SOM) C mineralization by microbes could also lead to decreased total soil C content. It is possible that the observed reduction in total soil C content in the top 10 cm in response to mowing or burning (Fig. 4a) may be due to greater losses of SOM via microbial respiration. Burning does stimulate total soil CO_2 flux (Knapp et al. 1998c), but mowing or clipping most often reduce soil CO_2 flux (Bremer et al. 1998), suggesting that enhanced soil C mineralization doesn't underlie reductions in C storage in response to mowing. Reduced soil C with burning and/or mowing may also reflect the greater potential importance of surface litter inputs in the absence of fire and the reduction in surface litter inputs as a function of mowing.

The potential impacts of alternate management on grassland soil C can be substantial. Seastedt et al. (1994) reported CENTURY model output that predicted gradual decline in soil C under the initial ~20 year of light grazing, while soil C was predicted to slowly increase in the absence of burning and grazing over the same time period. Differences between total soil C in the top 10 cm in long-term unburned vs. annually mowed plots in this study seem to be consistent with the predictions of the CENTURY model. In contrast, Seastedt et al. (1994) reported a predicted rapid decline in soil C under annual burning, and attributed this decline to fire-induced losses of N, while Ojima et al. (1994) suggested that changes in N use efficiency (NUE) under annual burning could ultimately maintain productivity and soil C levels despite N losses. Understanding the relationships between root dynamics and soil organic matter will be key to better predictive models.

Conclusions

This study demonstrated that long-term fire and mowing treatments have important independent and interactive effects on belowground biomass and nutrient content, as well as soil C and N storage. Sampling to a depth of 90 cm also revealed important root responses at depths rarely sampled in similar studies. These findings highlight the need to consider plant and soil responses to aboveground environmental variation beyond the 15–30 cm depth generally examined in belowground investigations.

Given the historic and ongoing loss of grasslands, and increasingly intense land use and other global changes, there is a growing need to develop sustainable management practices that will maintain important ecosystem functions, such as plant and soil C and N storage. More effective management of tallgrass prairie and other mesic grasslands will require a better understanding of the effects of fire, grazing, and mowing on grassland roots and soils, and the linkages between below- and above-ground processes. As more is learned about root and soil responses to fire, mowing, and grazing, the ability to predict impacts of future land-use change on ecosystem functioning will be improved.

Acknowledgements Support for this research was provided by the NSF-supported Konza Prairie Long-Term Ecological Research program, and by the Division of Biology at Kansas State University. We are grateful for field and laboratory assistance from A. Silletti, M. Stone, J. Nutt, K. Page, and the KPBS staff. This is publication 09-248-J from the Kansas Agricultural Experiment Station.

References

Archibald S, Bond WJ, Stock WD, Fairbanks DHK (2005) Shaping the landscape: fire-grazer interactions in an African savanna. Ecol Appl 15:96–109 doi:10.1890/03-5210

Benning TL, Seastedt TR (1997) Effects of fire, mowing and nitrogen additions on root characteristics in tallgrass prairie. J Veg Sci 8:541–546 doi:10.2307/3237205

Blair JM (1997) Fire, N availability, and plant response in grasslands: a test of the transient maxima hypothesis. Ecology 78:2359–2368

Blair JM, Seastedt TR, Rice CW, Ramundo R (1998) Terrestrial nutrient cycling in tallgrass prairie. In: Knapp AK, Briggs JM, Hartnett DC, Collins SL (eds) Grassland dynamics: Long-term ecological research in Tallgrass Prairie. Oxford University Press, New York, pp 222–243

Bond WJ, Keeley JE (2005) Fire as a global 'herbivore': the ecology and evolution of flammable ecosystems. Trends Ecol Evol 20:387–394 doi:10.1016/j.tree.2005.04.025

Bremer DJ, Ham JM, Owensby CE, Knapp AK (1998) Responses of soil respiration to clipping and grazing in a tallgrass prairie. J Environ Qual 27:1539–1548

Briggs JM, Knapp AK (1995) Interannual variability in primary production in tallgrass prairie: climate, soil moisture, topographic position and fire as determinants of aboveground biomass. Am J Bot 82:1024–1030 doi:10.2307/2446232

Briggs JM, Knapp AK, Brock BL (2002) Expansion of woody plants in tallgrass prairie: a15-year study of fire and fire-grazing interactions. Am Midl Nat 147:287–294 doi:10.1674/0003-0031(2002)147[0287:EOWPIT]2.0.CO;2

Chapin FS III (1980) The mineral nutrition of wild plants. Annu Rev Ecol Syst 11:233–260 doi:10.1146/annurev.es.11.110180.001313

Collins SL (1987) Interaction of disturbances in tallgrass prairie: a field experiment. Ecology 68:1243–1250 doi:10.2307/1939208

Collins S, Knapp AK, Briggs JM, Blair JM, Steinauer EM (1998) Modulation of diversity by grazing and mowing in tallgrass prairie. Science 280:745–747 doi:10.1126/science.280.5364.745

Dahlman RC, Kucera CL (1965) Root productivity and turnover in native prairie. Ecology 46:84–89 doi:10.2307/1935260

Detling JK, Dyer MI, Winn DT (1979) Net photosynthesis, root respiration, and regrowth of *Bouteloua gracilis* following simulated grazing. Oecologia 41:127–134 doi:10.1007/BF00344997

Dickinson NM, Polwart A (1982) The effect of mowing regime on an amenity grassland ecosystem: above- and belowground components. J Appl Ecol 19:569–577 doi:10.2307/2403489

Field CB, Campbell JE, Lobell BD (2008) Biomass energy: the scale of the potential resource. Trends Ecol Evol 23:65–72 doi:10.1016/j.tree.2007.12.001

Frank DA, McNaughton SJ, Tracy BF (1998) The ecology of the Earth's grazing ecosystems. Bioscience 48:513–521 doi:10.2307/1313313

Frank DA, Kuns MM, Guido DR (2002) Consumer control of grassland plant production. Ecology 83:602–606

Fransen B, de Kroon H, Berendse F (1998) Root morphological plasticity and nutrient acquisition of perennial grass species from habitats of different nutrient availability. Oecologia 115:351–358 doi:10.1007/s004420050527

Fynn RWS, Haynes RJ, O'Connor TG (2003) Burning causes long-term changes in soil organic matter content of a South African grassland. Soil Biol Biochem 35:677–687 doi:10.1016/S0038-0717(03)00054-3

Gao YZ, Giese M, Lin S, Sattelmacher B, Zhao Y, Brueck H (2008) Belowground net primary productivity and biomass allocation of a grassland in Inner Mongolia is affected by grazing intensity. Plant Soil 307:41–50 doi:10.1007/s11104-008-9579-3

Gibson DJ, Seastedt TR, Briggs JM (1993) Management practices in tallgrass prairie: large- and small-scale experimental effects on species composition. J Appl Ecol 30:247–255 doi:10.2307/2404626

Harris D, Horwath WR, van Kessel C (2001) Acid fumigation of soils to remove carbonates prior to total organic carbon or carbon-13 isotopic analysis. Soil Sci Soc Am J 65:1853–1856

Hartnett D, Hickman KR, Fischer-Walter LE (1996) Effects of bison grazing, fire, and topography on floristic diversity in tallgrass prairie. J Range Manage 49:413–420 doi:10.2307/4002922

Hartnett DC, Steuter AA, Hickman KR (1997) Comparative ecology of native versus introduced ungulates. In: Knopf F, Samson F (eds) Ecology and conservation of great plains vertebrates. Springer-Verlag, New York, pp 72–101

Hobbs NT, Schimel DS, Owensby CE, Ojima DS (1991) Fire and grazing in the tallgrass prairie: contingent effects on nitrogen budgets. Ecology 72:1374–1382 doi:10.2307/1941109

Johnson LC, Matchett JR (2001) Fire and grazing regulate belowground processes in tallgrass prairie. Ecology 82:3377–3389

Knapp AK, Seastedt TR (1986) Detritus accumulation limits productivity of tallgrass prairie. Bioscience 36:662–668 doi:10.2307/1310387

Knapp AK, Briggs JM, Blair JM, Turner CL (1998a) Patterns and controls of aboveground net primary production in tallgrass prairie. In: Knapp AK, Briggs JM, Hartnett DC, Collins SL (eds) Grassland dynamics: Long-term ecological research in tallgrass prairie. Oxford University Press, New York, pp 193–221

Knapp AK, Briggs JM, Hartnett DC, Collins SL (1998b) Grassland dynamics: Long-term ecological research in tallgrass prairie. Oxford University Press, New York

Knapp AK, Conard SL, Blair JM (1998c) Determinants of soil CO_2 flux from a sub-humid grassland: effect of fire and fire history. Ecol Appl 8:760–770

Knapp AK, Blair JM, Briggs JM, Collins SL, Hartnett DC, Johnson LC, Towne EG (1999) Keystone role of bison in North American tallgrass prairie. Bioscience 49:39–50 doi:10.2307/1313492

Kucera CL, Dahlman RC (1968) Root-rhizome relationships in fire-treated stands of big bluestem, *Andropogon gerardii* Vitman. Am Midl Nat 80:268–271 doi:10.2307/2423615

Loeser MR, Crews TE, Sisk TD (2004) Defoliation increased above-ground productivity in a semi-arid grassland. J Range Manage 57:442–447 doi:10.2307/4003972

McCulley RL, Jobbágy EG, Pockman WT, Jackson RB (2004) Nutrient uptake as a contributing explanation for deep rooting in arid and semi-arid ecosystems. Oecologia 141:620–628 doi:10.1007/s00442-004-1687-z

McNaughton SJ, Banyikwa FF, McNaughton MM (1997) Promotion of the cycling of diet-enhancing nutrients by African grazers. Science 279:1798–1800 doi:10.1126/science.278.5344.1798

McNaughton SJ, Banyikwa FF, McNaughton MM (1998) Root biomass and productivity in a grazing system. Ecology 79:587–592

Milchunas DG, Lauenroth WK (1993) Quantitative effects of grazing on vegetation and soils over a global range of environments. Ecol Monogr 63:327–366 doi:10.2307/2937150

Noy-Meir I (1993) Compensating growth of grazed plants and its relevance to the use of rangelands. Ecol Appl 3:32–34 doi:10.2307/1941787

Oesterheld M (1992) Effect of defoliation intensity on aboveground and belowground relative growth rates. Oecologia 92:313–316 doi:10.1007/BF00317456

Ojima DS, Schimel DS, Parton WJ, Owensby CE (1994) Long- and short-term effects of fire on nitrogen cycling in tallgrass prairie. Biogeochemistry 24:67–84 doi:10.1007/BF02390180

Reynolds HL, D'Antonio C (1996) The ecological significance of plasticity in root weight ratio in response to nitrogen: Opinion. Plant Soil 185:75–97 doi:10.1007/BF02257566

Risser PG, Birney CE, Blocker HD, May SW, Parton WJ, Weins JA (1981) The true prairie ecosystem. US/IBP Synthesis Series 16. Hutchinson Ross, Stroudsburg

Rodriguez MA, Alvarez J, Gomez-Sal A (1996) Vertical distribution of below-ground biomass in intensively grazed mesic grasslands. J Veg Sci 7:137–142 doi:10.2307/3236427

SAS Institute (1999) SAS/STAT user's guide, version 8.0. SAS Institute, Cary

Seastedt TR, Ramundo RA (1990) The influence of fire on belowground processes of tallgrass prairie. In: Collins SL, Wallace LL (eds) Fire in North American tallgrass prairies. University of Oklahoma Press, Norman, pp 99–117

Seastedt TR, Briggs JM, Gibson DJ (1991) Controls of nitrogen limitation in tallgrass prairie. Oecologia 87:2–79 doi:10.1007/BF00323782

Seastedt TR, Coxwell CC, Ojima DS, Parton WJ (1994) Controls of plant and soil carbon in a semihumid temperate grassland. Ecol Appl 4:344–353 doi:10.2307/1941938

Snaydon RW (1987) Ecosystems of the world. 17B. Managed grasslands: Analytical studies. Elsevier, Amsterdam

Tix D, Charvat I (2005) Aboveground biomass removal by burning and raking increases productivity in tallgrass prairie. Restor Ecol 13:20–28 doi:10.1111/j.1526-100X.2005.00004.x

Todd TC (1996) Effects of management practices on nematode community structure in tallgrass prairie. Appl Soil Ecol 3:235–246 doi:10.1016/0929-1393(95)00088-7

Todd TC, James SW, Seastedt TR (1992) Soil invertebrate and plant responses to mowing and Carbofuran application in a North American tallgrass prairie. Plant Soil 144:117–124 doi:10.1007/BF00018852

Towne EG, Kemp KE (2003) Vegetation dynamics from annually burning tallgrass prairie in different seasons. J Range Manage 56:185–192 doi:10.2307/4003903

Turner CL, Seastedt TR, Dyer MI (1993) Maximization of aboveground grassland production: the role of defoliation frequency, intensity, and history. Ecol Appl 3:175–186 doi:10.2307/1941800 van der Maarel E, Titlyanova A (1989) Above-ground and below-ground biomass relations in steppes under different grazing conditions. Oikos 56:364–370 doi:10.2307/3565622

Van Dyke F, Van Kley SE, Page CE, Van Beek JG (2004) Restoration efforts for plant and bird communities in tallgrass prairies using prescribed burning and mowing. Restor Ecol 12:575–585 doi:10.1111/j.1061-2971.2004.00352.x

Vinton MA, Hartnett DC, Finck EJ, Briggs JM (1993) Interactive effects of fire, bison (*Bison bison*) grazing, and plant community composition in tallgrass prairie. Am Midl Nat 129:10–18 doi:10.2307/2426430

Weaver JE (1954) North American prairie. Johnsen, Lincoln