

WILEY



Fire and Grazing Regulate Belowground Processes in Tallgrass Prairie

Author(s): Loretta C. Johnson and John R. Matchett

Source: *Ecology*, Vol. 82, No. 12 (Dec., 2001), pp. 3377-3389

Published by: Wiley on behalf of the Ecological Society of America

Stable URL: <https://www.jstor.org/stable/2680159>

Accessed: 20-02-2019 18:51 UTC

JSTOR is a not-for-profit service that helps scholars, researchers, and students discover, use, and build upon a wide range of content in a trusted digital archive. We use information technology and tools to increase productivity and facilitate new forms of scholarship. For more information about JSTOR, please contact support@jstor.org.

Your use of the JSTOR archive indicates your acceptance of the Terms & Conditions of Use, available at <https://about.jstor.org/terms>



JSTOR

Wiley, Ecological Society of America are collaborating with JSTOR to digitize, preserve and extend access to *Ecology*

FIRE AND GRAZING REGULATE BELOWGROUND PROCESSES IN TALLGRASS PRAIRIE

LORETTA C. JOHNSON^{1,3} AND JOHN R. MATCHETT²

¹*Division of Biology, Kansas State University, Manhattan, Kansas 66506-4901 USA*

²*USDA-NRCS, Lakota, North Dakota 58344 USA*

Abstract. In tallgrass prairie, belowground processes are even more important than in forested systems because aboveground biomass and standing dead litter are periodically removed by frequent fires or grazers. Thus, studies that address factors regulating belowground processes are especially relevant for tallgrass prairie. We predicted that effects of grazing and burning differ belowground and that changes in root productivity caused by burning or grazing provide feedback that affects ecosystem fluxes of C and N. These differences in belowground response should be driven largely by changes in N dynamics and the degree to which burning and grazing affect the pathway and magnitude of N loss and the degree of N limitation in these systems. Fire, the major pathway of N loss in ungrazed tallgrass prairie, should result in reduced net N mineralization and N availability. We expected plants to compensate for increased N limitation by increasing their allocation to roots, as manifested in increased soil respiration and C cycling belowground. In contrast, grazing conserves N in the ecosystem by redistributing the N once contained in grass to labile forms in urine and dung. Thus, we predicted that grazing should increase N cycling rates and N availability to plants. Consequently, grazed plants should be less N limited and should allocate less C to roots and more to shoots. This, in turn, should decrease belowground C cycling, manifested as reduced soil CO₂ flux.

We explored the roles of grazing and burning on root growth in experimental watersheds at Konza Prairie, Kansas, USA. To assess effects of fire on root productivity, we installed root ingrowth cores in two watersheds without grazers that differ in fire frequency: annually vs. infrequently burned (four years since the last fire). To assess effects of grazing, we installed root ingrowth cores in an annually burned watershed grazed by bison and in fenced controls (exclosures). Within bison “grazing lawns,” root ingrowth cores were installed in lightly and heavily grazed patches. Concurrently, we measured in situ rates of net N mineralization and soil respiration as indices of soil N and C cycling.

Annual burning resulted in a 25% increase in root growth compared to the unburned watershed (four years since last fire), as plants compensated for N limitation by increasing allocation to roots. Grazing had the opposite effect: it decreased root growth, especially in heavily grazed patches (~30% less than in fenced controls). Grazing by ungulates increased N cycling and availability. Therefore, grazed plants, instead of being N limited, experienced C limitation as shoots regrew and plants allocated less C to roots. Interestingly, root ingrowth on the long-term unburned watershed was as low as in lightly grazed patches in the grazed watershed. Thus, seemingly disparate treatments such as infrequent burning (characterized by accumulation of detritus aboveground) and grazing (periodic biomass removal) both had higher levels of N availability than annually burned prairie in the absence of grazers. Root growth in unburned and grazed watersheds must be limited by resources other than N (e.g., C in grazing lawns or light in infrequently burned prairie).

Burning and grazing also altered root tissue chemistry in contrasting ways that further accentuated the root growth differences caused by these treatments. Frequent fires lowered substrate quality of roots (C:N = 60), thus increasing N limitation. In contrast, grazing and infrequent burning improved root tissue quality (C:N = 40), promoting faster cycling of N. These large differences in root growth and tissue chemistry can result in profound ecosystem-level changes. Grazing increased net N mineralization rates from 87% to 617% compared to watersheds without grazers, whereas annual burning decreased it by ~50% compared to unburned prairie. Although grazing speeded up N cycling, it reduced soil respiration by 50% compared to fenced controls, presumably because of reduced root mass. On the other hand, annual burning increased soil respiration, presumably because of increased root biomass. Ultimately, differences in the quantity and quality of roots provide feedback to affect C and N cycling and help to maintain and even promote the fundamental differences in N cycling between burning and grazing in tallgrass prairie.

Key words: burning; grazing; Konza Prairie, Kansas; N cycling; net N mineralization; root growth; root ingrowth cores; soil respiration; tallgrass prairie; tissue chemistry.

Manuscript received 21 January 2000; revised 11 August 2000; accepted 22 August 2000; final version received 4 January 2001.

³ E-mail: johnson@ksu.edu

INTRODUCTION

In almost all terrestrial ecosystems, a dearth of knowledge exists about belowground processes, in general, and root growth and productivity, in particular. Recent reviews by Canadell et al. (1996) and Jackson et al. (1996, 1997) summarize what is presently known about root distributions, rooting depths, and global budgets of fine-root biomass, and highlight how much we still need to learn about belowground processes. This gap in our understanding of belowground processes is especially relevant for tallgrass prairie. Although the early works of Weaver (1919, 1954) were largely descriptive, they were instrumental in setting the stage for much of the grassland research in the second half of the 20th century. However, belowground processes still remain understudied in grasslands. Belowground biomass has been reported to be three to four times greater than aboveground biomass (Jackson et al. 1996), although few studies have documented root biomass (Weaver and Darland 1949, Hayes and Seastedt 1987, Benning and Seastedt 1997, Blair 1997, Derner and Briske 1999), and especially root productivity (Dahlman and Kucera 1965, Hayes and Seastedt 1987) in tallgrass prairie.

In the subhumid tallgrass prairie, belowground biomass plays an even more important role than in forested systems because aboveground biomass and standing dead litter are periodically removed, either by frequent fire or grazers. Thus, the main organic matter and carbon (C) inputs to these grassland soils are from belowground productivity (roots). Indeed, grasslands contain some of the largest stocks of soil organic C (~ 20 kg C/m²), rivaling soil C stocks in arctic tundra (Schlesinger 1997) and comprising nearly 15% of the terrestrial (non-wetland) global C stocks. Yet we know little about controls over belowground productivity in tallgrass prairie, where belowground processes probably regulate ecosystem structure and function.

Frequent fires (Hulbert 1969, Old 1969), large ungulate grazers (Collins et al. 1998, Knapp et al. 1999) and climatic variation, especially precipitation (Briggs and Knapp 1995), can all affect tallgrass prairie ecosystem structure and function, both above- and belowground. Because these three factors induce water, nitrogen, and light availability to shift in space and time in tallgrass prairie, it is difficult to identify a single limiting resource affecting plant community dynamics and ecosystem processes. According to the conceptual model of Burke et al. (1998), these subhumid grasslands exhibit "indeterminate dominance," i.e., no single resource limits plant-soil processes. The "indeterminate dominance" of the subhumid grassland is in sharp contrast to shortgrass steppe, in which plant-soil interactions exhibit a single limitation, such as water (Burke et al. 1998). Obviously, we expect belowground processes to differ along these temperature and precipitation gradients. In this paper, we focus on below-

ground processes taking place at the humid end of the precipitation gradient in grasslands.

This paper deals with fire and grazing and their effects on root growth and soil N and C cycling in tallgrass prairie. Both fire and grazing have been hypothesized to act similarly (Knapp and Seastedt 1986, Seastedt and Knapp 1993, Ojima et al. 1994); they result in reduced aboveground biomass, reduced aboveground detritus accumulation, and an altered physiological state of the remaining leaf area (Knapp and Seastedt 1986). Decreasing the amount of surface detritus and standing dead plant material relieves energy limitation to live plants by increasing light penetration, and results in higher aboveground productivity than in unburned prairie (Knapp and Seastedt 1986). On the other hand, burning and grazing have some dissimilar effects: spring burning removes detritus in one pulse at a time that directly benefits aboveground productivity (Blair 1997, Turner et al. 1997), but it also results in large combustion losses of N (Blair et al. 1998). In contrast, grazing removes live biomass periodically during the growing season, and the N once contained in the grass biomass is redeposited on the prairie in urine and dung patches, thus conserving N in the ecosystem. We expect that burning and grazing may have contrasting effects on belowground processes and root productivity. Although the effects of fire on belowground processes and root biomass have been examined (Hayes and Seastedt 1987, Ojima et al. 1994, Blair 1997, Turner et al. 1997), there have been few field studies of belowground response to grazing in tallgrass prairie, or of the interactions between grazing and fire (Hobbs et al. 1991, Benning and Seastedt 1997). Clearly, a knowledge of the belowground responses to grazing and fire is essential because it is likely that both strongly influence root inputs to soils (Benning and Seastedt 1997) and, ultimately, soil C and N accumulation in these systems.

This study on belowground processes quantified the controls of fire and grazing (by native grazers) over root productivity. We hypothesized that any changes in root productivity brought on by burning or grazing would feed back to affect ecosystem fluxes of C and N. Therefore, concurrent with the study of root productivity, we measured *in situ* net N mineralization and soil respiration as indices of N and C cycling, respectively. We hypothesized that, even though burning and grazing both result in aboveground biomass removal, their effects will differ below ground. These differences in belowground response should be driven largely by changes in N dynamics and the degree to which burning and grazing affect the pathway and magnitude of N loss and the degree of N limitation in these systems. Fire is the major pathway of N loss in ungrazed tallgrass prairie (Blair et al. 1998); frequent fires should result in reduced net N mineralization and N availability. We expect plants to compensate for increased N limitation by increasing allocation to roots (Ojima

et al. 1994). This should be manifested in increased soil respiration and C cycling belowground due to greater root mass. In contrast, grazing by ungulates should increase N cycling rates and N availability due to re-deposition of N in urine and dung and/or changes in tissue quality. Therefore, grazed plants will be less N limited and will allocate less C to roots while allocating more C for shoot regrowth, as demonstrated in early pot studies (Biswell and Weaver 1933, Jameson and Huss 1959). We expect that lower C allocated to roots should decrease belowground C cycling and should be manifested as reduced soil CO₂ flux.

MATERIAL AND METHODS

Konza site description

This study was carried out at the Konza Prairie Research Natural Area (KPRNA), a 3487-ha tallgrass prairie preserve located in the Flint Hills near Manhattan, Kansas, USA. Konza Prairie, an NSF-funded LTER (Long Term Ecological Research site), is an ideal location for this study because it provides an array of experimental burning and grazing regimes at the watershed scale. Konza Prairie is representative of the northern Flint Hills tallgrass prairie, a dissected upland with chert and flint-bearing limestone layers. The Flint Hills is the largest remaining tract of these once vast, but now diminishing (Samson and Knopf 1994), grasslands. Upland plateaus are flat, with rocky, shallow soils. The steep-sided hills and soils prevented much of the Flint Hills from being developed for row crop agriculture. Konza Prairie is dominated by native prairie species, especially big bluestem (*Andropogon gerardii*), Indian grass (*Sorghastrum nutans*), little bluestem (*Schizachyrium scoparius*), and switch grass (*Panicum virgatum*). More detailed site descriptions can be found in Knapp et al. (1998a).

Fire as a key ecological driver of aboveground processes has been well studied at Konza Prairie (Hulburt 1969, Knapp and Seastedt 1986, Briggs and Knapp 1995) and other tallgrass sites (Old 1969). In this paper, we evaluate the belowground effects of annual and infrequent burning (last burn four years before the study) on root growth and tissue quality. Effects of fire on N cycling (Blair 1997) and soil respiration (Knapp et al. 1998b) have been studied previously.

Bison have played a keystone role in tallgrass prairie (Knapp et al. 1999). Bison at Konza Prairie, free-ranging within a 1100-ha fenced area, are able to choose between recently burned and unburned prairie and among various topographic/physiographic conditions. The bison consume, on average, an estimated 20% of aboveground net primary production (D. Hartnett, Director of Konza Prairie, *personal communication*). The grazing activities of bison are distinctly patchy (Catchpole 1996), occurring mainly in "grazing lawns" (sensu McNaughton 1984, Knapp et al. 1999) on uplands of recently burned watersheds. In this paper, we eval-

uate grazing as a key ecological driver affecting root growth and tissue quality in grasslands. Grazing-mediated changes in N and C cycling remain poorly studied in tallgrass prairie and in many grasslands; to fill this gap in our understanding, we carried out measurements of in situ net N mineralization rates and soil respiration in grazed and ungrazed prairie.

The climate of KPRNA is characterized as temperate mid-continental. Yearly mean air temperature is 13°C and the growing season begins in April and extends through October. Average annual precipitation is 835 mm, of which ~75% occurs in the growing season. In 1996, the year of the root ingrowth study and first year of net N mineralization measurements, annual precipitation was 783 mm and growing season precipitation was 564 mm. In 1997, the second year of the net N mineralization studies and the year of the soil respiration measurements, the annual precipitation was 674 mm. Therefore, precipitation during the period of this study was close to the average and well within the extremes of precipitation. Thus, we can expect that the results reported in this study should reflect the average climatic and precipitation conditions on Konza Prairie.

Fire and grazing experimental regimes

The fire frequency regimes evaluated in this study of the Konza Prairie were as follows:

1) *Annually burned*. This experimental watershed has been burned annually in the spring for at least 10 yr before the start of this study;

2) *Unburned*. This experimental watershed had remained unburned for four years before the study. Several studies from Konza (Knapp and Seastedt 1986, Blair 1997) indicate that after four years without burning, litter has accumulated on the surface to as much as 1000 g/m² (Knapp and Seastedt 1986), such that it resembles a long-term unburned regime.

To avoid confusion, the reader should note that when reference is made to annually burned or unburned sites, this means *without grazers* unless otherwise specified.

The grazed experimental watershed used in this study has been grazed by bison since 1992; it was burned annually for at least 10 yr before the bison were reintroduced and remains annually burned. "Grazing lawns" were identified early in the spring before annual burning. Grazing lawns are >400 m², within which are smaller 4-m² grazed patches (Knapp et al. 1999). Lawns are characterized by foliage removal to ~5 cm above the soil. The lawns cover ~30% of uplands of the annually burned watershed area. Three grazing regimes were identified within this watershed:

1) *Lightly grazed patches* of grazing lawn. These were identified prior to burning in the spring, and were distinguished from heavily grazed patches because of the greater amount of senesced foliage and leaf litter present on the surface.

2) *Heavily grazed patches* of grazing lawn. These were identified prior to burning in the spring and were

clearly distinguished because they do not carry a fire due to low fuel load (Hobbs et al. 1991, Knapp et al. 1999). Heavily grazed patches are grazed to within a few centimeters of the soil surface and are devoid of any litter. We studied heavily and lightly grazed patches separately because intensity of grazing may lead to strong differences in root productivity and C and N cycling. Heavily and lightly grazed patches were in close proximity in the same experimental watershed.

3) *Bison exclosures* (fenced control). These permanently fenced areas (5×5 m, $n = 4$) are located within the grazed watershed but exclude bison grazing. They were established in 1991 before bison were introduced to the watershed. These exclosures allow evaluation of the effects of grazers on the same watershed, soil type, and burn regime. Root productivity should be similar in the ungrazed, annually burned watershed and in the fenced exclosures, because both are burned annually and lack grazers.

When reference is made to grazing regime in this paper, we mean *under the imposed annual burning conditions*.

In each watershed, the root productivity measurements and N and C cycling studies were carried out in the same areas on the flat upland plateaus, which are common to the grazed, annually burned, and infrequently burned watersheds. Topography and soil type are similar in this upland area. Soil depth to limestone bedrock varies from 10 cm to ~30 cm. The Florence soils are classified as a clayey-skeletal, montmorillonite, mesic Uderitic Argiustoll. The surface layer of these soils is typically silt loam or silty clay loam (Ransom et al. 1998).

Root ingrowth core technique: preparation, installation, and analysis

Root ingrowth cores (Jordan and Escalante 1980, Persson 1983, Cuevas and Medina 1988, Neill 1992, Fisk et al. 1998, Derner and Briske 1999) were used as an index of root production. Clearly, root production is a difficult process to quantify, and each available method requires assumptions. Given the objective of our study, we chose the root ingrowth method as the most appropriate and feasible. In the shallow, rocky soils of Konza Prairie, minirhizotrons are difficult to install; we are presently installing them on deeper soils of the lowland prairie. A second complication is the damage to the tubes from herds of grazers. Sequential coring can be unreliable because of concurrent growth and death of roots. Because of these constraints, we decided to use root ingrowth cores, but we are aware of the limitations of this technique: (1) enhanced root proliferation due to disturbance and altered nutrient availability in disturbed root-free soils (we used the native soil to minimize this effect); and (2) underestimation of root growth because of disappearance of roots over the measurement period (Fahey and Hughes 1994). We assume that errors associated with root in-

growth are constant over the burning and grazing regimes, and that the root ingrowth technique should provide, at the least, a suitable index of relative differences in root productivity in tallgrass prairie.

Soil cores (5 cm diameter) were collected from all sites in early March 1996. Each soil core was kept associated with the hole from which it originally came. In the laboratory, all living roots and rhizomes were removed to prevent regrowth from within the core. The unsieved soils were subsequently inserted into a fiberglass screen mesh bag (mesh size 1.0 mm), sealed at the bottom, and put back into their original holes. The cores, on average, extended to 20 cm (range 10–30 cm) and generally to bedrock in these shallow soils. Any gaps between the core and the surrounding hole were filled with native soil from that site. All ingrowth cores were installed by mid-March 1996. They were installed in four locations in each of the following: annually burned and unburned watersheds, lightly grazed patches, heavily grazed patches, and fenced exclosures in the grazed watershed. Each location contained five randomly located ingrowth cores.

The cores were left in place until November 1996. At that time, the cores and surrounding soil were excavated with shovel, transported to the laboratory, and refrigerated (4°C) until processing (within a week of collection time). The cores were processed in the following manner: extraneous soil was removed from the exterior of the mesh core, without removing roots from inside the mesh core. Each ingrowth core was then cut in 5 cm depth segments in order to quantify changes in root productivity with depth. All live roots (easily identified by their white color) that had grown through the 1-mm core mesh and into the soil were manually extracted and sieved from each 5-cm soil segment. We also separated new rhizomes growing into the mesh, but these were not included in the root mass estimate. The roots were wet-sieved (250- μ m mesh) with de-ionized water to remove mineral soil particles, dried at 60°C and weighed. The roots were ground on a multisample ballmill grinder and analyzed for C and N on a Carlo Erba CN Analyzer (CE Instruments, Milan, Italy). Data were expressed on a per square meter basis for each root ingrowth core. Because most roots were concentrated in surface layers, e.g., mainly within the top 10 cm, slight variations in core depth due to shallow soils and the presence of bedrock had little effect on root productivity expressed on an areal basis.

We also calculated N and C inputs from plants to soils from the root ingrowth cores. This assumes that N and C are not resorbed from senescing roots, a reasonable assumption according to Nambiar (1987) and Aerts et al. (1992), and that N and C inputs from live roots are a realistic estimate of the N and C in dead roots.

Soil N cycling: in situ nitrogen mineralization and net nitrification

We determined net N mineralization and net nitrification rates in situ using a modification of the intact

TABLE 1. Significance (*P* values) of differences in measures of belowground root productivity and N and C inputs in response to fire and grazing treatments.

ANOVA factors, by treatment	Root ingrowth	Root N conc.	Root C:N	Root N input	Root C input
Fire					
Burned vs. unburned	0.05	0.016	0.0006	NS	NS
Burned vs. exclosures	NS	NS	NS	NS	NS
Grazing					
Lightly grazed vs. exclosures	NS	0.0003	0.0004	0.0082	NS
Heavily grazed vs. exclosures	0.0061	0.0001	0.0011	NS	0.01
Lightly vs. heavily grazed	0.0105	NS	NS	0.0085	0.02

Notes: For all five root parameters, *n* = 12–15; NS indicates nonsignificant values of *P*. Units of measurement are given in Figs. 1 and 2.

buried soil core technique (Raison et al. 1987). These cores were installed in heavily grazed patches of grazing lawns that can be easily identified because bison graze in distinct patches over the growing season (Fahnestock and Knapp 1993). Measurements could not be made within grazing exclosures due to their small size and the destructive nature of N mineralization sampling. For this portion of the study, therefore, we compared heavily grazed patches with the annually burned regime (no grazers). Because annually burned (no grazers) and fenced exclosures were similar in all respects (Table 1), we feel confident that this in no way affected our conclusions on the role of grazers on N cycling.

The N mineralization tubes were installed in three locations (~20 × 40 m) in each of the regimes (annually burned and heavily grazed patches). Each location contained 20 randomly located mineralization tubes. The N mineralization tubes were in close proximity (within 10–20 m, as close as possible) to the root ingrowth cores. For the net N mineralization analyses, we removed an initial soil core (5 cm diameter × 14 cm deep) and placed an incubation tube (5 cm diameter × 14 cm deep, polyvinyl chloride) at a location adjacent to the initial soil core. Lids placed on incubation tubes prevented leaching losses, and small holes placed near the top of each tube allowed for gas exchange. Measurements were made beginning on 18 June 1996 and 30 May 1997, using ~30-d incubation periods. Prior to laboratory analyses, soil samples were passed through a 4-mm mesh sieve to remove roots and rocks. Soil inorganic N was extracted from a subsample of ~10-g using 50 mL of 2 mol/L KCl, and N concentrations (NH₄⁺-N and [NO₃⁻-N + NO₂⁻-N]) were determined colorimetrically using an Alpkem Flow-Solution analyzer (Alpkem, Milwaukie, Oregon, USA). Additional soil subsamples were dried at 105°C to determine gravimetric moisture content, so that N could be expressed as mass per gram of dry soil. Daily net N mineralization rates were calculated by subtracting initial core total inorganic N values from incubation tube total inorganic N values, and then dividing by the incubation period. Daily net nitrification rates were calculated in a similar manner, using extractable NO₃⁻

Soil bulk density was determined from incubation tubes, and these values were used to calculate soil N mineralized per unit area.

Soil C cycling: in situ soil respiration

Soil respiration rates were measured in four locations in each of the following: heavily grazed patches and fenced exclosures in the grazed watershed, and in the annually burned watershed for comparison with the fenced exclosures. Each location contained four randomly located sites in which soil respiration was measured during summer and fall of 1997. Again, these sites were in close proximity (within 10–20 m) to the root ingrowth core area and the net N mineralization study area.

Respiration rates were determined using a LI-COR 6200 portable photosynthesis IRGA (infrared gas analyzer) fitted with a soil respiration chamber (LI-COR, Lincoln, Nebraska; Norman et al. 1992). Litter was removed before the gas flux measurement following the soil respiration methods of Knapp et al. (1998b). Three consecutive 30-s measurements were taken and then averaged prior to statistical analyses. Measurements were made on seven dates between 10 July and 30 October 1997, during midday (from 1000 to 1400 local time) to minimize diurnal temperature change influences, and were repeated at the same four permanent points each time.

Statistics

For the root ingrowth core study in each of the fire and grazing regimes, there were four sites (blocks) with three or four root ingrowth cores per block, for a total of 12–15 root ingrowth cores per regime. There was a total of 65 ingrowth cores for all regimes combined. The original experimental design had five root ingrowth cores per site (block), but time and personnel constraints permitted us to analyze only three or four out of the five cores. Because differences among blocks within the same regime were not significant (ANOVA, *P* > 0.05), results from all cores were pooled for each regime. Differences in root productivity, tissue chemistry, and distribution were assessed using one-way

ANOVA (Abacus Concepts 1989). Means were compared using Fisher's Protected LSD.

For the N-cycling study, treatment differences for net N mineralization, net nitrification were determined using ANOVA tests. Multiple comparisons of treatment means were made with Fisher's Protected LSD tests. For grazed and ungrazed treatments, N-cycling data were analyzed separately for each year because the main effects of year and treatment were significant. For the C-cycling studies, grazing treatment effects on soil respiration were determined by repeated-measures ANOVA. For both the C- and N-cycling studies, there were no significant block effects.

RESULTS

Fire and grazing as regulators of root growth and tissue quality

Annual burning stimulated root growth, increasing root productivity by nearly 25% compared to the long-term unburned treatment (Fig. 1A, Table 1). Grazing had the opposite effect; it decreased root productivity compared to both fenced exclosures in the grazed watershed and the ungrazed, annually burned watershed. Furthermore, the heavily grazed patches within grazing lawns had the lowest root productivity: ~35% less than the exclosures, and nearly 50% less than the ungrazed, annually burned treatment. Likewise, the heavily grazed patches contained 30% less root mass than did adjacent lightly grazed patches within the same grazing lawns.

Interestingly, root productivity in the long-term unburned treatment (not burned for four years) was as low as in some grazed patches (Fig. 1A). These contrasting regimes differ greatly in the amount of above-ground biomass and detritus accumulation (as much as 3 times the NPP; Knapp and Seastedt 1986), yet responded similarly belowground by producing few roots.

Burning and grazing also had opposing effects on root tissue quality, i.e., N concentration (Fig. 1B, Table 1) and C:N ratio (Fig. 1C, Table 1). Both lightly and heavily grazed patches in the grazing regime had similarly high root tissue N concentrations (0.9%), which averaged 30% higher than in the fenced exclosures. This suggests that the presence of grazing improves tissue quality relative to that in exclosures, regardless of whether a grazed patch has been heavily or lightly grazed. (Note that whether a grazed patch is lightly or heavily grazed has a large effect on root productivity.) In contrast, plants in the annually burned, but ungrazed, regime had low root N concentrations (0.6%), i.e., 30% lower than the unburned regime (Fig. 1B). This indicates that annual burning acts to decrease root tissue quality, with potential consequences for decomposition.

An unanticipated result was that the N concentration of roots from lightly and heavily grazed areas were

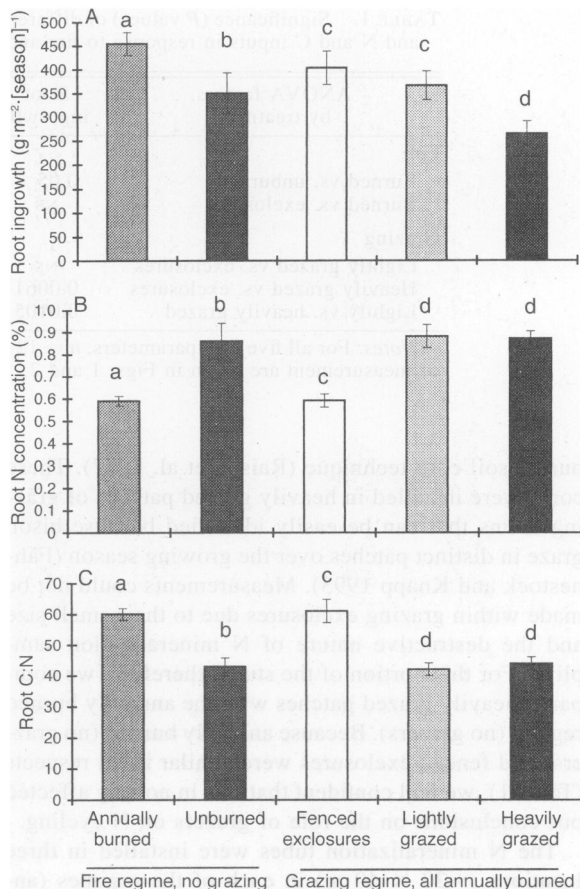


FIG. 1. (A) Root productivity per growing season, measured using the root ingrowth bag technique. Depth of the root ingrowth core averaged 20 cm (range 10–30 cm, depending on depth to bedrock). (B) Root N concentration as a percentage of root dry mass (g/g) of roots from the root ingrowth cores. (C) Root C:N (g C/g N) of roots from the root ingrowth cores. (Note that root C:N ratios are only presented for the 0–5 cm depth but do not change significantly with depth.) Values are means \pm 1 SE. Different letters within a grazing or burning regime indicate significant differences in treatment responses. All sampling occurred in 1996. See Table 1 for more details.

similar to those of the long-term unburned regime (Fig. 1B). Therefore, grazing and fire exclusion increased the concentration of root tissue N and thus improved tissue quality. This highlights that, in these two regimes with very different aboveground biomass and detritus accumulation, plants nevertheless had a similar belowground response in both root tissue quality (Fig. 1B,C) and productivity (Fig. 1A).

The C concentration of roots did not differ significantly across regimes or with depth (range 34.8–37.7%, data not shown). However, there were large differences in tissue quality expressed as C:N ratio, an index of the decomposability of a substrate. Thus, the differences in C:N ratios of roots were driven by changes in N, but not in C. The annually burned regime had root C:N ratios of 60, nearly 30% higher than the unburned

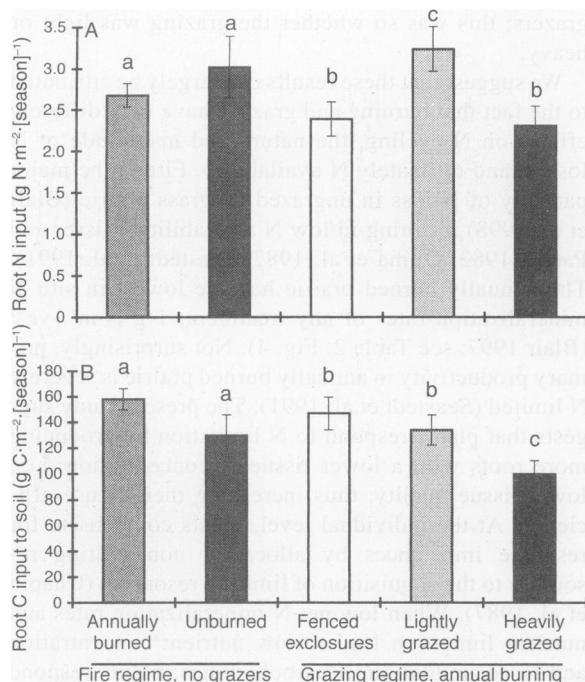


FIG. 2. (A) Root N mass per growing season of roots from the root ingrowth cores. N mass was calculated as the mass of roots (in g/m² per growing season) multiplied by the N concentration of the roots. (B) Root C mass per growing season of roots from the root ingrowth cores. C mass was calculated as the mass of roots (in g/m² per growing season) multiplied by the C concentration of the roots. Values are means \pm 1 SE. Different letters within a grazing or burning regime indicate significant differences in treatment responses. All sampling occurred in 1996.

regime (Fig. 1C). (Note that tissue C:N ratios are only presented for the 0–5 cm depth but do not change significantly with depth.) On the other hand, grazing acted to narrow the C:N ratio. Plants in either the lightly or heavily grazed areas had root C:N of 40, nearly 30% lower than the fenced exclosures. The wide C:N ratio of the roots in the annually burned and fenced exclosures indicates that N will be immobilized in the microbial biomass to a greater extent than on sites where the root tissue C:N ratio is narrower, i.e., grazed and unburned regimes.

Moreover, the similarities in root ingrowth, N concentrations, and C:N between the annually burned and the fenced exclosures provide additional evidence that these two regimes are indeed very similar and responded similarly to burning (Table 1), although in different, but adjacent watersheds.

Root N and C mass

The amount of N present in roots (Fig. 2A) is a function of root mass (Fig. 1A) and N concentration of those roots (Fig. 1B). Roots in the lightly grazed regime as well as the long-term, unburned regime tended to contain the greatest mass of N per unit area ($P = 0.07$). This suggests that light grazing (along with

annual burning) and the long-term unburned regime both enhance root N inputs to soil. In contrast, heavily grazed patches, annually burned regime, and fenced exclosures all had lower N masses that will result in lower N inputs to these soils. However, in the heavily grazed patches, low root mass drives the low N mass, whereas in the fenced exclosures and annually burned regime, low tissue N concentration drives the low N mass. Carbon inputs from roots were significantly lower in the heavily grazed patches than in exclosures or even lightly grazed patches (Table 1, Fig. 2B).

Rooting-depth distributions

When we combined all fire and grazing regimes, the distribution of new root growth in the cores declined exponentially ($r^2 = 0.96$, $y = 191.57e^{-0.3401x}$) with depth (Fig. 3). Therefore, new root production is concentrated in the surface layer, i.e., one-third of the ingrowth roots occurred in the top 0–5 cm, 55% in the top 0–10 cm, and 72% in the top 20 cm (Fig. 3).

N and C cycling

Grazing substantially enhanced N cycling. Daily net N mineralization rates were significantly higher in grazed lawns in 1996 and 1997, with increases of 87% and 617%, respectively (Fig. 4). Net nitrification was also significantly higher in grazed areas during both years, with increases of 153% in 1996 and 96% in 1997 (Fig. 4). Strong differences in N mineralization rates and nitrification rates between 1996 and 1997 were probably a result of large differences in precipitation. Total precipitation over the incubation period was 63% lower in 1997 than 1996 (26 mm vs. 71 mm). Precipitation occurring in the 30 d immediately prior to sampling was also substantially lower in 1997 than 1996 (71 mm vs. 157 mm).

Despite wide variation among dates attributed to seasonal moisture and temperature differences, soil respiration rates in grazed areas were usually about half those in ungrazed and exclosure areas (Fig. 5). Soil respiration averaged across all dates was 47% lower in

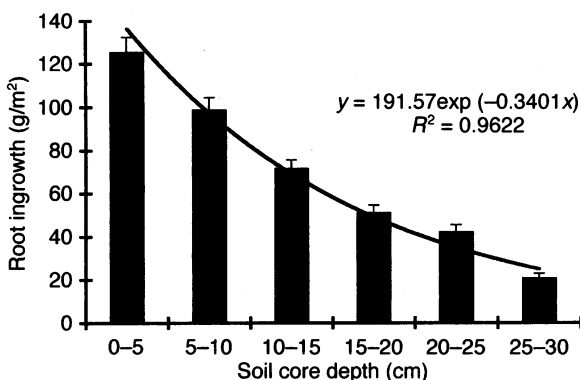


FIG. 3. Root productivity by 5 cm depth increment. All treatment regimes are combined; samples were taken in 1996.

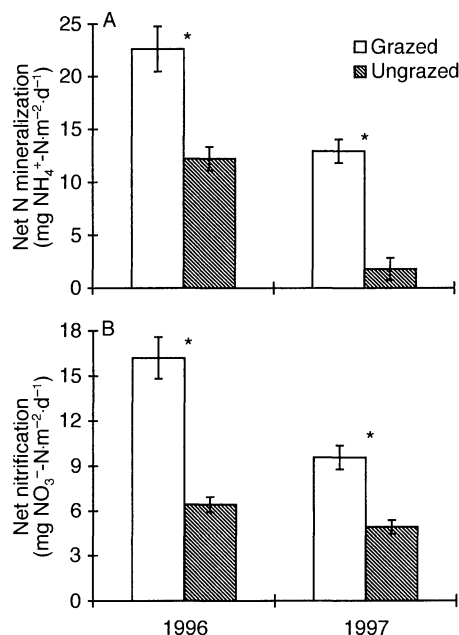


FIG. 4. One-month in situ (A) net N mineralization and (B) net nitrification rates for grazed vs. ungrazed areas in 1996 and 1997. Values are means \pm 1 SE (n = 60 per grazing regime). Asterisks (*) denote significant differences between grazed and ungrazed areas (P < 0.05, ANOVA).

grazed areas ($3.92 \mu\text{mol CO}_2\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) vs. ungrazed areas ($7.34 \mu\text{mol CO}_2\cdot\text{m}^{-2}\cdot\text{s}^{-1}$). Fenced enclosures ($7.43 \mu\text{mol CO}_2\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) were significantly greater than grazed areas but not significantly different than ungrazed areas of the annual burning regime. Averaged across treatments, soil respiration also differed significantly between dates, gradually decreasing throughout the season (Fig. 5), presumably in response to seasonal changes in temperature and moisture.

DISCUSSION

Contrasting effects of grazing and annual burning on belowground processes

Knapp and Seastedt (1986) hypothesized that burning and grazing may have similar effects on tallgrass prairie primary productivity and detritus accumulation. Although they both reduce aboveground biomass and detritus accumulation, these two key ecological drivers also differ in important ways; burning of detritus occurs as a discrete event, usually in the spring, whereas grazing of live biomass occurs in pulses as bison periodically revisit grazing lawns. These fundamental ecological differences in the effects of burning and grazing also extend belowground. Belowground response to grazing (lightly or heavily grazed patches) was opposite the response to fire (annually burned regime and fenced enclosures). Fewer roots (Fig. 1A) of a higher tissue quality (Fig. 1B,C) were produced in grazed patches compared to annual burned prairie without

grazers; this was so whether the grazing was light or heavy.

We suggest that these results can largely be attributed to the fact that burning and grazing have very different effects on N cycling, the nature and magnitude of N losses, and ultimately N availability. Fire is the major pathway of N loss in ungrazed tallgrass prairie (Blair et al. 1998) resulting in low N availability (Risser and Parton 1982, Ojima et al. 1987, Seastedt et al. 1991). The annually burned prairie had the lowest in situ N mineralization rates of any treatment, $1 \text{ g N}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$ (Blair 1997; see Table 2, Fig. 4). Not surprisingly, primary productivity in annually burned prairie is severely N limited (Seastedt et al. 1991). The present study suggests that plants respond to N limitation by producing more roots with a lower tissue N concentration, i.e., lower tissue quality, thus increasing their N use efficiency. At the individual level, plants compensate for resource imbalances by allocating non-limiting resources to the acquisition of limiting resources (Chapin et al. 1987). When low net N mineralization rates and nutrient limitation lead to low nutrient concentration and to accumulation of carbohydrates, plants respond by increasing their energy and C allocation to root growth, leading to a more favorable plant carbon : nutrient balance (Chapin et al. 1987, Chapin 1991).

In contrast to burning, grazing has been shown to accelerate cycling of N in grasslands (Coughenour 1991, Singh et al. 1991, Frank et al. 1994, Shariff et al. 1994, McNaughton et al. 1997) and to enhance N availability (Holland and Detling 1990). This study on Konza Prairie confirms that grazers induce faster N cycling in tallgrass prairie as well (Fig. 4, Table 2). Indeed, the grazing lawns where the root ingrowth cores were located had three times higher net N mineralization rates during the growing season than did the annually burned regime. This demonstrates that

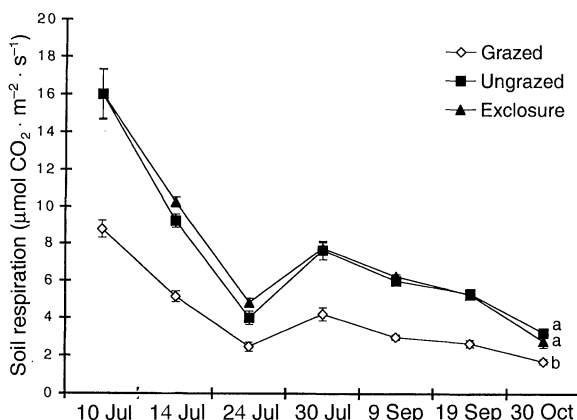


FIG. 5. In situ soil respiration rates in grazed, ungrazed, and enclosure areas for each sampling date. Values are means \pm 1 SE (n = 16 per grazing treatment). Different letters indicate significantly different values overall (P < 0.05, repeated-measures ANOVA). Sampling occurred between July 1996 and October 1997.

TABLE 2. Contrasting controls of fire and grazing over N and C cycling in tallgrass prairie.

N and C cycling variables	Fire regime		Grazing regime		
	Annual burning†	Unburned‡	Grazing lawn‡	Exclosures‡	Annual burning (no grazers)‡
Soil net N mineralization (mg N·m ⁻² ·d ⁻¹)	15 ^a	35 ^b	28 ^a (1996) 12 ^a (1997)	NA NA	12 ^b 2 ^b
Soil respiration (μmol CO ₂ ·m ⁻² ·s ⁻¹)	14 ^a	11 ^b	9.5 ^a	16 ^b	16 ^b

Notes: To make the data more comparable, the data subset is from early in the growing season. Different letters within a study indicate significant differences at $P \leq 0.05$.

† Data for N cycling are from Blair (1997); 10 May–13 June 1994. Data for C cycling are from Knapp et al. (1998); June–July 1996.

‡ Data on grazing effects are from the present study.

plants respond to grazing by reducing C allocation to roots (Fig. 1A) of an enhanced tissue quality (Fig. 1B,C), and presumably increasing allocation to shoot regrowth. Richards (1984) and Detling et al. (1979) also found reduced allocation to roots and increased allocation to shoots in clipping experiments. If plants become deficient in C (i.e., when herbivores remove photosynthetic tissue) or if they have a surplus of N, they compensate by producing proportionately more shoot and less root (Chapin 1980). The resulting decrease in root:shoot ratio reduces C stress, returning C and nutrient reserves to a balance more favorable for growth. Thus, shoot regrowth in grazing lawns is limited by C, not by N.

Similar effects of grazing and infrequent burning on belowground processes

A surprising result was that root ingrowth and tissue chemistry were similar in the unburned regime and in grazed patches (Fig. 1). Why do plants under these conditions have such similar belowground responses (i.e., reduced root production, high tissue N concentration)? We suggest that root growth in both regimes is not limited by N; instead, belowground production in these plants is limited by other resources, as has been suggested for aboveground production (Seastedt and Knapp 1993). In the unburned regime (last burned four years before the root ingrowth cores were installed), litter builds up on the soil surface and thus limits light penetration for new shoot growth, eventually reducing aboveground productivity (Knapp and Seastedt 1986). Because of the higher soil moisture (Knapp and Seastedt 1986), these unburned sites are characterized by N mineralization rates three times higher than in the annually burned regime (Blair 1997, Turner et al. 1997). Thus, total productivity in the unburned regime is limited by light for new shoot growth, not by N availability. Additionally, the fewer roots produced here have higher tissue N concentrations than do plants in the annually burned regime, reflecting greater N availability in the unburned regime. Similarly, grazing lawns are characterized by higher net N mineralization rates (Fig. 4), and thus greater N availability, than annually burned regimes. Therefore, seem-

ingly dissimilar aboveground conditions, such as infrequent burning and grazing, both result in higher levels of N availability than in annually burned prairie or fenced exclosures. This shows that root growth is secondarily limited by resources other than N in these treatments.

Ecosystem consequences: grazer-mediated changes in C and N cycling

Differences in the nature of limiting resources (N in annually burned, ungrazed prairie, C in grazing lawns, and light in infrequently burned prairie) cause plants to adjust their biomass and resource allocation. The effects of these large differences in root ingrowth and tissue chemistry (Fig. 1) transcend far beyond individual plant response and cause profound ecosystem-level changes. Ultimately, differences in the quantity and quality of roots provide feedback that affects C and N cycling (Hendricks et al. 1993). Litter tissue N concentration is a strong regulator of decomposition (Aber et al. 1990), and the C:N ratio of litter controls microbial N immobilization and net N mineralization dynamics (Holland et al. 1992). If we assume that N is not resorbed from fine roots before root senescence (Nambiar 1987, Aerts et al. 1992), then the tissue quality of live roots should be an estimate of the litter quality of dead, senesced roots. These differences in the quantity and quality of roots help to maintain and even promote the fundamental differences in N cycling and N limitation between burning and grazing regimes.

Several recent studies have documented substantially increased N mineralization in grazed systems, determined as either potentially mineralizable N using laboratory incubations (Frank and Groffman 1998, Tracy and Frank 1998), with in situ methods (McNaughton et al. 1997, Frank and Groffman 1998, Tracy and Frank 1998, but see Biondini et al. 1998), or inferred through ¹⁵N natural abundance data (Frank and Evans 1997). Similar results of increased N mineralization have been reported in grazed lands at Yellowstone National Park, Wyoming, USA: a 72–450% increase, depending on month (Frank and Groffman 1998). In this study of N cycling in grazed and ungrazed areas, grazers increased in situ N mineralization 87–617%, depending on year

(Fig. 4), and increased nitrification by 96–153%. Our N mineralization measurements in 1996 and 1997 suggest that the magnitude of difference between grazed and ungrazed areas may be greater at overall lower levels of mineralization. This study clearly shows that grazing can increase soil N cycling in at least two ways: through herbivore-mediated changes in tissue quality and decomposability (indirect effects), and through the re-distribution of N from recalcitrant forms (plant litter) to labile forms in urine and dung (direct effects).

To our knowledge, there are few reports of grazer-mediated changes in soil respiration in grasslands. Preliminary data from bison- and cattle-grazed pastures on two dates reveal that soil CO₂ efflux was 20–37% lower in grazed vs. ungrazed sites (Bremer et al. 1998). Similarly, Knapp et al. (1998b), in a preliminary study, also found a 30% reduction in grazed vs. ungrazed patches at Konza Prairie. Our season-long study of soil CO₂ fluxes from bison-grazed areas at Konza provides further evidence (Fig. 5). An obvious and large gap in our understanding of grazer effects on C cycling is the mechanism(s) by which grazers modify soil CO₂ flux or soil respiration. Soil respiration is derived from both root respiration and heterotrophic microbial respiration. Therefore, a reduction in soil respiration could be due to a reduction of either or both of these fluxes. One likely factor contributing to the low soil CO₂ flux in grazed areas relative to exclosures or annually burned sites is the reduced root growth there (Fig. 1A) compared to the high root mass in annually burned and fenced exclosures. However, it seems to be more complex than just a matter of finding fewer roots in grazed patches. Using clipping to simulate grazing, Bremer et al. (1998) found that soil CO₂ flux was highest in unclipped treatments and lowest in the most recently clipped plots. Only 6 d after clipping, soil CO₂ fluxes declined by 22–47% below those of unclipped controls. This suggests that the reduced soil CO₂ flux may be mediated by relatively quick, dynamic changes in root exudation subsequently driving associated changes in microbial respiration. We are continuing investigations into the mechanisms that may be controlling reduced soil C cycling in grazed areas.

Although fire and grazing are often studied as if they act separately, they occur and interact together (Hobbs et al. 1991). The root growth results presented here highlight the importance of this grazing–fire interaction in facilitating N cycling and inputs of N from roots to soil. For example, annual burning without grazing results in N immobilization, low net N mineralization, and severe N limitation. However, annual burning combined with grazing promotes faster cycling of N through the deposition of labile N contained in urine (Ruess and McNaughton 1984, McNaughton et al. 1988), and also, as this study clearly demonstrates, through enhancement of root tissue quality (Fig. 1B, C). Ultimately, this enhancement of tissue quality feeds back to affect N cycling. The higher quality root tissue

(with lower C:N) will lead to lower microbial immobilization of N in burned, grazed areas (compared to that in annually burned sites in the absence of grazers) and, ultimately, greater N availability. Additionally, there is also a trend toward greater N inputs from roots in the burned, grazed sites than in most other regimes (Fig. 2A). Infrequent fire also increases N availability (Fig. 1B,C) and N input from roots (Fig. 2A), but it is accompanied by lower aboveground productivity because of light limitation (Knapp and Seastedt 1986).

Root ingrowth, rooting distribution, and tissue quality compared to other studies

How do these estimates of root productivity, distribution, and root tissue quality compare with other tallgrass prairie and grassland studies? Indeed, our conservative estimates of fine root (≤ 1 mm) ingrowth are very similar to other estimates of root productivity in tallgrass prairie and grasslands in general (Table 3). The fact that results presented here (mean ± 1 SE of all regimes = 367 ± 31 g·m⁻²·growing season⁻¹) fall within the observed range (202–429 g·m⁻²·yr⁻¹) of measured tallgrass productivity is particularly encouraging. The good agreement suggests that, using a variety of methods (Table 3), we may be able to successfully constrain estimates of root productivity in tallgrass prairie. This study demonstrates that the root ingrowth core method is sensitive enough to detect ecologically important effects of fire and grazing on root productivity and tissue quality, in spite of potential problems.

This study differs from others in demonstrating ecologically important treatment effects on root tissue quality; other investigators have either not investigated or not found a treatment effect (Milchunas et al. 1995). At least some of the changes in root tissue quality may be due to shifts in species composition caused by the burning and grazing regimes (Hartnett et al. 1996, Collins et al. 1998; Konza LTER, *unpublished data*).⁴ However, we do not know the extent to which the changes in root tissue chemistry represent a change in tissue quality of the same species or shifts in species with differing tissue quality. C₃ grasses and forbs typically have higher N concentration in their tissues. Unfortunately, we did not quantify species composition in the exact vicinity of the root ingrowth cores. However, we do know that infrequent fires are known to favor C₃ over C₄ grasses (Hulbert 1969; Konza LTER, *unpublished data*), and that grazing increases the diversity and abundance of forbs (Hartnett et al. 1996, Collins et al. 1998). LTER species composition data (Konza LTER, *unpublished data*) from upland topographic locations on the same watersheds show that the C₃ grass *Poa pratensis* increased its cover (from <5% to as much as 25%) in the long-term unburned watershed compared to the annually burned regime (no graz-

⁴ URL: <http://www.ksu.edu/konza/lter/>

TABLE 3. Comparison of grassland root productivity in field settings.

Reference	Location	Type of grassland	Annual precipitation† (mm)	Depth (cm)	Method	Root productivity‡ (g·m ⁻² ·yr ⁻¹)
Hayes and Seastedt (1987)	Konza Prairie, Manhattan, Kansas, USA	tallgrass prairie	835	0–100	root windows	202 ^u , 1983 223 ^u , 1984
Sims and Singh (1978)	Osage Prairie, Oklahoma, USA	tallgrass prairie	(823)	not given	sequential coring	330 ⁺ (256–403)
	Cottonwood, South Dakota, USA	mixed grass prairie	(400)	not given	sequential coring	343 ⁺ (249–437)
	Pantex, Texas, USA	shortgrass	(423)	not given	sequential coring	453 ⁿ (437–468)
	Pawnee, Colorado, USA	shortgrass	(290)	not given	sequential coring	427 ⁿ (422–432)
Dahlman and Kucera (1965)	Missouri Prairie Res. Station, Missouri, USA	tallgrass prairie	1016	0–25	max–min biomass	429 ^u
This study	Konza Prairie, Manhattan Kansas, USA	tallgrass prairie	835	~0–20	root ingrowth cores	367 ⁻ (263–454)
Risser et al. (1981)	Osage Prairie, Oklahoma	tallgrass prairie	838	0–90	sequential coring	70–430 ⁿ (50–325 in top 20 cm)
McNaughton et al. (1998)	Serengetti, Africa	tallgrass, shortgrass	350–1200	0–20	max–min biomass	70–650 ⁿ
Pandey and Singh (1992)	Uttar Pradesh, India	tropical savanna	926–1145	0–10	sequential coring	404–838 ⁻
Shariff et al. (1994)	North Dakota, USA	mixed grass	432	0–10	sequential coring	176 ⁺ (50–400), 1989 65 ⁺ (10–175), 1990

Notes: Superscripts in the last column indicate grazing effects on root productivity: u, ungrazed; –, negative grazing effect; +, positive effect; n, neutral grazing effect.

† Mean values; parentheses indicate values during the years of this study.

‡ Mean and range (in parentheses; where available); the estimate excludes rhizomes. Years are given where available.

ers). The rest of the cover was contributed by *C*₄ tallgrass species (*Andropogon gerardii* and *Sorghastrum nutans*). Grazing had the effect of decreasing grass cover and increasing forb cover and diversity (Collins et al. 1998). Cover of the dominant tallgrass big bluestem (*A. gerardii*) decreased from 55% in the exclosures to 35% in grazed areas in the same watershed (Hartnett et al. 1996). Therefore, at least some of the changes in root tissue quality may be due to shifts in species composition caused by the burning and grazing regimes.

Whatever the cause for the changes in tissue quality, it clearly is of profound importance in feedbacks to, and maintenance of, the patterns of C and N cycling observed in tallgrass prairie (Blair et al. 1998). It also demonstrates that further study of ecological controls over root tissue chemistry and production is warranted, especially in grassland systems that are largely dominated by belowground biomass.

Our study is one of the first to clearly demonstrate that grazing reduces allocation to roots in subhumid tallgrass prairie, which is manifested in reduced soil CO₂ efflux. Because bison graze patchily (Catchpole 1996) and their activities are not evenly distributed across watersheds or among topographic locations

(Knapp et al. 1999), additional studies are underway to investigate the temporal and spatial dynamics of grazer impacts on root productivity and belowground processes. Although the effects of grazing on decreased root productivity in Konza grazing lawns appear to be *unequivocal*, effects of grazing on root productivity in a variety of grassland ecosystems are *equivocal* at best (Milchunas and Lauenroth 1993). Much evidence comes from greenhouse pot experiments (Biswell and Weaver 1933, Jameson and Huss 1959) and studies of short-term effects following clipping (Detling et al. 1979, Richards 1984) rather than a consensus of field studies (Milchunas and Lauenroth 1993). If the analysis is restricted to field studies of the effects of grazers on root productivity in grasslands (Table 3), no clear pattern of grazer effect emerges. Of nine studies of root productivity in grazed grasslands, three show a positive grazing effect, four a neutral grazing effect, and this study and one other show a negative grazing effect. The reason underlying this lack of congruence of grazer effects highlights an intriguing area of research as well as an obvious gap in our ability to predict the ecosystem consequences of grazers across a range of grassland ecosystems.

ACKNOWLEDGMENTS

Konza LTER provided support for this study. Thanks to numerous root pluckers: Jesse Nippert, Melissa Hill, Connie Briggs, Sarah Glaser, Dixie Smith, Cheryl Balaun, Kathy Gai-tros, Jake Goheen, and Bryan Stork. Thanks to the following persons for helpful comments: Ton Damman, Alan Knapp, John Blair, and John Briggs; reviewers Justin Derner and one anonymous reviewer; and subject-matter editor Joseph B. Yavitt. This is contribution number 01-152-J from the Kansas Agricultural Experiment Station.

LITERATURE CITED

- Abacus Concepts. 1989. Superanova. Abacus Concepts, Berkeley, California, USA.
- Aber, J. D., J. Melillo, and C. McClaugherty. 1990. Predicting long-term patterns of mass loss, nitrogen dynamics, and soil organic matter formation from initial fine litter chemistry in temperate forest ecosystems. *Canadian Journal of Botany* **68**:2201–2208.
- Aerts, R. C., C. Bakker, and H. DeCaluwe. 1992. Root turnover as a determinant of the cycling of C, N, and P in a dry heathland ecosystem. *Biogeochemistry* **15**:175–190.
- Benning, T., and T. Seastedt. 1997. Effects of fire, mowing, and nitrogen addition on root characteristics in tall-grass prairie. *Journal of Vegetation Science* **8**:541–546.
- Biondini, M. E., B. D. Patton, and P. E. Nyren. 1998. Grazing intensity and ecosystem processes in a northern mixed grass prairie, USA. *Ecological Applications* **8**:469–479.
- Biswell, H. H., and J. E. Weaver. 1933. Effect of frequent clipping on the development of roots and tops of grasses in prairie sod. *Ecology* **14**:368–390.
- Blair, J. M. 1997. Fire, N availability, and plant response in grasslands: a test of the transient maxima hypothesis. *Ecology* **78**:2359–2368.
- Blair, J. M., T. R. Seastedt, C. W. Rice, and R. Ramundo. 1998. Terrestrial nutrient cycling in tallgrass prairie. Pages 222–243 in A. K. Knapp, J. M. Briggs, D. C. Hartnett, and S. L. Collins, editors. *Grassland dynamics: long-term ecological research in tallgrass prairie*. Oxford University Press, New York, New York, USA.
- Bremer, D. J., J. M. Ham, C. E. Owensbys, and A. Knapp. 1998. Responses of soil respiration to clipping and grazing in a tallgrass prairie. *Journal of Environmental Quality* **27**:1539–1548.
- Briggs, J. M., and A. K. Knapp. 1995. Interannual variability in primary production in tallgrass prairie: climate, soil moisture, topographic position, and fire as determinants of aboveground biomass. *American Journal of Botany* **82**:1024–1030.
- Burke, I., W. Lauenroth, M. A. Vinton, P. B. Hook, R. H. Kelly, H. E. Epstein, M. R. Aguiar, M. D. Robles, M. O. Aguilera, K. L. Murphy, and R. A. Gill. 1998. Plant–soil interactions in temperate grasslands. *Biogeochemistry* **42**:121–143.
- Canadell, J., R. B. Jackson, J. R. Ehleringer, H. A. Mooney, O. E. Sala, and E.-D. Schulze. 1996. Maximum rooting depth of vegetation types at the global scale. *Oecologia* **108**:583–595.
- Catchpole, F. E. 1996. The dynamics of bison (*Bos bison*) grazing patches in tallgrass prairie. Thesis. Kansas State University, Manhattan, Kansas, USA.
- Chapin, F. S., III. 1980. The mineral nutrition of wild plants. *Annual Review of Ecology and Systematics* **11**:233–260.
- Chapin, F. S., III. 1991. Effects of multiple environmental stresses on nutrient availability and use by plants. Pages 67–88 in H. A. Mooney, W. E. Winner, and E. J. Pell, Response of plants to multiple stresses Academic Press, San Diego, California, USA.
- Chapin F. S., III, A. J. Bloom, C. B. Field, and R. H. Waring. 1987. Plant responses to multiple environmental factors. *BioScience* **37**:49–57.
- Collins, S., A. K. Knapp, J. M. Briggs, J. M. Blair, and E. M. Steinauer. 1998. Modulation of diversity by grazing and mowing in tallgrass prairie. *Science* **280**:745–747.
- Coughenour, M. B. 1991. Biomass and nitrogen responses to grazing of upland steppe on Yellowstone's northern winter range. *Journal of Applied Ecology* **28**:71–82.
- Cuevas, E., and E. Medina. 1988. Nutrient dynamics within Amazonian forests. II. Fine root growth, nutrient availability, and leaf litter decomposition. *Oecologia* **76**:222–235.
- Dahlman, R. C., and C. L. Kucera. 1965. Root productivity and turnover in native prairie. *Ecology* **46**:84–89.
- Detling, J. K., M. I. Dyer, and D. T. Winn. 1979. Net photosynthesis, root respiration, and regrowth of *Bouteloua gracilis* following simulated grazing. *Oecologia* **41**:127–134.
- Derner, J., and D. Briske. 1999. Does a tradeoff exist between morphological and physiological root plasticity? A comparison of growth forms. *Acta Oecologia* **20**:519–526.
- Fahey, T. J., and J. W. Hughes. 1994. Fine root dynamics in a northern hardwood forest ecosystem, Hubbard Brook Experimental Forest, NH. *Journal of Ecology* **82**:533–548.
- Fahnestock, J. T., and A. K. Knapp. 1993. Water relations and growth of tallgrass prairie forbs in response to selective grass herbivory by bison. *International Journal of Plant Sciences* **154**:432–440.
- Fisk, M. C., S. K. Schmidt, and T. R. Seastedt. 1998. Topographic patterns of above- and belowground production and nitrogen cycling in alpine tundra. *Ecology* **79**:2253–2266.
- Frank, D. A., and R. D. Evans. 1997. Effects of native grazers on grassland N cycling in Yellowstone National Park. *Ecology* **78**:2238–2248.
- Frank, D. A., and P. M. Groffman. 1998. Ungulate vs. landscape control of soil C and N processes in grasslands of Yellowstone National Park. *Ecology* **79**:2229–2241.
- Frank, D. A., R. S. Inouye, N. Huntly, G. W. Minshall, and J. E. Anderson. 1994. The biogeochemistry of a north-temperate grassland with native ungulates: nitrogen dynamics in Yellowstone National Park. *Biogeochemistry* **26**:163–188.
- Hartnett, D., K. R. Hickman, L. E. Fischer-Walter. 1996. Effects of bison grazing, fire, and topography on floristic diversity in tallgrass prairie. *Journal of Range Management* **49**:413–420.
- Hayes, D. C., and T. R. Seastedt. 1987. Root dynamics of tallgrass prairie in wet and dry years. *Canadian Journal of Botany* **65**:787–791.
- Hendricks, J. J., K. J. Nadelhoffer, and J. D. Aber. 1993. Assessing the role of fine roots in carbon and nutrient cycling. *Trends in Ecology and Evolution* **8**:174–178.
- Hobbs, N. T., D. S. Schimel, C. E. Owensby, and D. S. Ojima. 1991. Fire and grazing in the tallgrass prairie: contingent effects on nitrogen budgets. *Ecology* **72**:1374–1382.
- Holland, E. A., and J. K. Detling. 1990. Plant response to herbivory and belowground nitrogen cycling. *Ecology* **71**:1040–1049.
- Holland, E. A., W. J. Parton, J. K. Detling, and D. L. Coppock. 1992. Physiological response of plant populations to herbivory and their consequences for ecosystem nutrient flow. *American Naturalist* **140**:685–706.
- Hulbert, L. C. 1969. Fire and litter effects in undisturbed bluestem prairie in Kansas. *Ecology* **50**:874–877.
- Jackson, R. B., J. Canadell, J. R. Ehleringer, H. A. Mooney, O. E. Sala, and E.-D. Schulze. 1996. A global analysis of root distributions for terrestrial biomes. *Oecologia* **108**:389–411.
- Jackson, R. B., H. A. Mooney, and E.-D. Schulze. 1997. A

- global budget for fine root biomass, surface area, and nutrient contents. *Proceedings of the National Academy of Sciences (USA)* **94**:7362–7366.
- Jameson, D. A., and D. L. Huss. 1959. The effect of clipping leaves and stems on number of tillers, herbage weights, root weights, and food reserves of Little Bluestem. *Journal of Range Management* **12**:122–126.
- Jordan, C. F., and G. Escalante. 1980. Root productivity in an Amazonian rain forest. *Ecology* **6**:14–18.
- Knapp, A. K., J. M. Blair, J. M. Briggs, S. L. Collins, D. C. Hartnett, L. C. Johnson, and E. G. Towne. 1999. Keystone role of bison in North American tallgrass prairie. *BioScience* **49**:39–50.
- Knapp, A. K., J. M. Briggs, D. C. Hartnett, and S. L. Collins, editors. 1998a. *Grassland dynamics: long-term ecological research in tallgrass prairie*. Oxford University Press, New York, New York, USA.
- Knapp, A. K., S. L. Conard, and J. M. Blair. 1998b. Determinants of soil CO₂ flux from a sub-humid grassland: effect of fire and fire history. *Ecological Applications* **8**:760–770.
- Knapp, A. K., and T. R. Seastedt. 1986. Detritus accumulation limits productivity of tallgrass prairie. *BioScience* **36**:662–668.
- McNaughton, S. J. 1984. Grazing lawns: animals in herds, plant form and coevolution. *American Naturalist* **124**:863–868.
- McNaughton, S. J., F. F. Banyikwa, and M. M. McNaughton. 1997. Promotion of the cycling of diet-enhancing nutrients by African grazers. *Science* **278**:1798–1800.
- McNaughton, S. J., F. F. Banyikwa, and M. M. McNaughton. 1998. Root biomass and productivity in a grazing system. *Ecology* **79**:587–592.
- McNaughton, S. J., R. W. Ruess, and S. W. Seagle. 1988. Large mammals and process dynamics in African ecosystems. *BioScience* **38**:794–800.
- Milchunas, D. G., and W. K. Lauenroth. 1993. Quantitative effects of grazing on vegetation and soils over a global range of environments. *Ecological Monographs* **63**:327–366.
- Milchunas, D. G., A. S. Varnamkhasti, W. K. Lauenroth, and H. Goetz. 1995. Forage quality in relation to long-term grazing history, current-year defoliation, and water resource. *Oecologia* **101**:366–374.
- Nambiar, E. K. S. 1987. Do nutrients retranslocate from fine roots? *Canadian Journal of Forestry Research* **17**:913–918.
- Neill, C. 1992. Comparison of soil coring and ingrowth methods for measuring belowground production. *Ecology* **73**:1918–1921.
- Norman, J. M., R. Garcia, and S. B. Verma. 1992. Soil surface CO₂ fluxes and the carbon budget of a grassland. *Journal of Geophysical Research* **97**:18845–18853.
- Ojima, D. S., W. J. Parton, D. S. Schimel, and C. E. Owensby. 1987. Stimulating the long term impact of burning on C, N, P cycling in tallgrass prairie. Pages 353–370 in G. Giovannozzi-Sermanni and P. Nannipieri, editors. *Current perspectives in environmental biogeochemistry*.
- Ojima, D. S., D. S. Schimel, W. J. Parton, and C. E. Owensby. 1994. Long- and short-term effects of fire on nitrogen cycling in tallgrass prairie. *Biogeochemistry* **24**:67–84.
- Old, S. M. 1969. Microclimate, fire, and plant production in an Illinois prairie. *Ecological Monographs* **39**:355–384.
- Pandey, C. B., and J. S. Singh. 1992. Rainfall and grazing effects on net primary productivity in a tropical savanna, India. *Ecology* **73**:2007–2021.
- Persson, H. 1983. The distribution and productivity of fine roots in boreal forests. *Plant and Soil* **71**:87–101.
- Raison, R. J., M. J. Connell, and P. K. Khana. 1987. Methodology for studying fluxes of soil mineral-N in situ. *Soil Biology and Biochemistry* **19**:521–530.
- Ransom, M., C. W. Rice, T. C. Todd, and W. A. Wehmuller. 1998. Pages 48–66 in A. K. Knapp, J. M. Briggs, D. C. Hartnett, and S. L. Collins, editors. *Grassland dynamics: long-term ecological research in tallgrass prairie*. Oxford University Press, New York, New York, USA.
- Richards, J. H. 1984. Root growth response to defoliation in two *Agropyron* bunchgrasses: field observations with an improved root periscope. *Oecologia* **64**:21–25.
- Risser, P. G., and W. J. Parton. 1982. Ecosystem analysis of the tallgrass prairie: nitrogen cycle. *Ecology* **63**:1342–1351.
- Ruess, R. W., and S. J. McNaughton. 1984. Urea as a promotive coupler of plant–herbivore interactions. *Oecologia* **63**:331–337.
- Samson, F., and F. Knopf. 1994. Roundtable: prairie conservation in North America. *BioScience* **44**:418–421.
- Schlesinger, W. 1997. *Biogeochemistry: an analysis of global change*. Second edition. Academic Press, New York, New York, USA.
- Seastedt, T. R., J. M. Briggs, and D. J. Gibson. 1991. Controls of nitrogen limitation in tallgrass prairie. *Oecologia* **87**:72–79.
- Seastedt, T. R., and A. K. Knapp. 1993. Consequences of nonequilibrium resource availability across multiple time scales: the transient maxima hypothesis. *American Naturalist* **141**:621–633.
- Shariff, A. R., M. E. Biondini, and C. E. Grygiel. 1994. Grazing intensity effects on litter decomposition and soil nitrogen mineralization. *Journal of Range Management* **47**:444–449.
- Singh, R. S., A. S. Raghubanshi, and J. S. Singh. 1991. Nitrogen-mineralization in dry tropical savanna: effects of burning and grazing. *Soil Biology and Biochemistry* **23**:269–273.
- Tracy, B. F., and D. A. Frank. 1998. Herbivore influence on soil microbial biomass and nitrogen mineralization in a North American grassland ecosystem: Yellowstone National Park. *Oecologia* **114**:556–562.
- Turner, C. L., J. M. Blair, R. J. Schartz, and J. C. Neel. 1997. Soil N and plant responses to fire, topography, and supplemental N in tallgrass prairie. *Ecology* **78**:1832–1843.
- Weaver, J. E. 1919. *The ecological relations of roots*. Carnegie Institution of Washington, Washington, D.C. Publication Number 286.
- Weaver, J. E. 1954. *North American prairie*. Johnsen Publishing, Lincoln, Nebraska, USA.
- Weaver, J. E., and R. W. Darland. 1949. Soil-root relationships of certain native grasses in various soil types. *Ecological Monographs* **19**:305–338.