Grazing and ecosystem carbon storage in the North American Great Plains

Justin D. Derner[1,3], Thomas W. Boutton[2] & David D. Briske[2]

[1] High Plains Grasslands Research Station, USDA-ARS, 8408 Hildreth Road, Cheyenne, WY, 82009, USA. [2]Department of Rangeland Ecology and Management, Texas A&M University, College Station, TX, 77843-2126, USA. [3]Corresponding author*

Abstract

Isotopic signatures of ^{13}C were used to quantify the relative contributions of C_3 and C_4 plants to whole-ecosystem C storage (soil + plant) in grazed and ungrazed sites at three distinct locations (short-, mid- and tallgrass communities) along an east–west environmental gradient in the North American Great Plains. Functional group composition of plant communities, the source and magnitude of carbon inputs, and total ecosystem carbon storage displayed inconsistent responses to long-term livestock grazing along this gradient. C_4 plants [primarily *Bouteloua gracilis* (H.B.K.) Lag ex Steud.] dominated the long-term grazed site in the shortgrass community, whereas the ungrazed site was co-dominated by C_3 and C_4 species; functional group composition did not differ between grazed and ungrazed sites in the mid- and tallgrass communities. Above-ground biomass was lower, but the relative proportion of fine root biomass was greater, in grazed compared to ungrazed sites at all three locations. The grazed site of the shortgrass community had 24% more whole-ecosystem carbon storage compared to the ungrazed site (4022 vs. 3236 g C m^{-2}). In contrast, grazed sites at the mid- and tallgrass communities had slightly lower (8%) whole-ecosystem carbon storage compared to ungrazed sites (midgrass: 7970 vs. 8683 g C m^{-2}; tallgrass: 8273 vs. 8997 g C m^{-2}). Differential responses between the shortgrass and the mid- and tallgrass communities with respect to grazing and whole-ecosystem carbon storage are likely a result of: (1) maintenance of larger soil organic carbon (SOC) pools in the mid- and tallgrass communities (7476–8280 g C m^{-2}) than the shortgrass community (2517–3307 g C m^{-2}) that could potentially buffer ecosystem carbon fluxes, (2) lower root carbon/soil carbon ratios in the mid- and tallgrass communities (0.06–0.10) compared to the shortgrass community (0.20–0.27) suggesting that variation in root organic matter inputs would have relatively smaller effects on the size of the SOC pool, and (3) the absence of grazing-induced variation in the relative proportion of C_3 and C_4 functional groups in the mid- and tallgrass communities. We hypothesize that the magnitude and proportion of fine root mass within the upper soil profile is a principal driver mediating the effect of community composition on the biogeochemistry of these grassland ecosystems.

Abbreviations: A. gerardii – Andropogon gerardii; ANPP – annual net primary productivity; *B. gracilis – Bouteloua gracilis*; C – carbon; *P. smithii – Pascopyrum smithii*; *S. scoparium – Schizachyrium scoparium*; SOC – soil organic carbon

* FAX No: + 307-637-6124.
E-mail: Justin.Derner@ars.usda.gov

Introduction

Rangelands cover approximately 40% of the earth's land surface, and are responsible for a comparable proportion of the carbon (C) flux associated with terrestrial net primary productivity (Scurlock and Hall, 1998). In addition, rangelands store > 10% of terrestrial biomass C, 10–30% of global soil organic carbon (SOC), and they have been estimated to sequester C in soil at a rate of 0.5 Pg C yr^{-1} (Olson et al., 1985; Schlesinger, 1997; Scurlock and Hall, 1998). This implies that modest changes in C storage in rangeland ecosystems have the potential to modify the global C cycle and indirectly influence climate (Conant et al., 2001; Ojima et al., 1993; Schimel et al., 1990). Despite this significance, our understanding of land use effects on the storage of C in rangelands remains limited (Reeder and Schuman, 2002; Schuman et al., 2002).

Livestock grazing is one of the most prevalent land uses of the world's rangelands, and has the potential to substantially alter C storage in those ecosystems by: (1) Modifying the magnitude and relative allocation of C to above- and below-ground biomass (Briske and Richards, 1995; Briske et al., 1996); (2) Altering microclimate and the availability of light, water, and nutrients (Archer and Smeins, 1991; Ruess, 1987); and (3) Influencing the quantity and quality of C inputs by modifying the species composition and functional diversity of plant communities (Pastor and Cohen, 1997; Ritchie et al., 1998). Although these grazing-induced processes collectively appear to accelerate rates of C cycling processes in grazed ecosystems (Bardgett et al., 1998; Ruess and Seagle, 1994), their influence on ecosystem C storage is often inconsistent and difficult to predict (Milchunas and Lauenroth, 1993; Reeder and Schuman, 2002).

The influence of livestock grazing on the C cycle of rangelands would intuitively be greatest where herbivory has induced changes in the functional composition of plant communities that alter the use and availability of key resources (Chapin et al., 1997). In various rangeland communities, grazing may modify functional group composition by altering the relative abundance of C_3 and C_4 plant species. Species with these distinct photosynthetic pathways differ markedly in their functional attributes, especially with respect to C-, nutrient-, and water-use characteristics (Pearcy and Ehleringer, 1984; Sage and Monson, 1999). Consequently, the relative proportion of C_3 and C_4 plants may have a profound influence on the rate and magnitude of various ecosystem processes, including evapotranspiration, primary productivity, decomposition and soil C storage (Epstein et al., 1999; Seastedt et al., 1994; Tilman, 1998; Wedin, 1995).

In the North American Great Plains, livestock grazing has been shown to be an important determinant of the C_3–C_4 composition of rangeland plant communities, along with mean annual precipitation, mean annual temperature and soil texture (Epstein et al., 1997). The effect of livestock grazing on C_3–C_4 composition varies with grazing regime, the relative combination of plant growth forms and climatic conditions (Parton and Risser, 1979; Sims et al., 1978; Sims, 1988). For example, 20 years of intensive livestock grazing in a southern tallgrass prairie reduced the relative proportion of C_4 grass biomass from > 70 to < 30% (Boutton et al., 1993). In contrast, 80 years of intensive livestock grazing in northern mixed-grass prairie increased the relative cover of C_4 grasses from approximately 15 to 86% (Frank et al., 1995). However, it is also well established that the relative grazing resistance of C_3 and C_4 functional groups is associated with growth form contrasts (caespitose vs. rhizomatous) as well as distinctions between photosynthetic pathways (Briske and Richards, 1995).

Previous studies on livestock grazing have focused largely on changes in above-ground ecosystem properties. By comparison, relatively little is known regarding the effects of grazing on the distribution and abundance of roots, and on the storage and dynamics of SOC. However, the isotopic C composition of roots and soil organic matter can provide unique and quantitative insights regarding the effects of grazing on the belowground system. More specifically, the C isotope signatures of C_3 ($\delta^{13}C \approx -27\%_0$) and C_4 ($\delta^{13}C \approx -13\%_0$) plants can be utilized to quantify grazing-induced changes in functional group composition in communities that possess a mixture of C_3 and C_4 plants. These isotopic signatures can be used to estimate the relative proportions of C_3 and C_4 plant C in above- and below-ground biomass and in the SOC pool by

depth, and they can provide evidence for long-term changes in the relative productivity of C_3 and C_4 plants in grazed grasslands (Boutton, 1996; Frank et al., 1995; Svejcar and Boutton, 1985).

The goals of this study were to assess the impact of long-term livestock grazing on the functional composition of rangeland plant communities, and to quantify differences in ecosystem C storage that may have resulted from those compositional changes at three locations in the North American Great Plains (Derner et al., 1997). Stable C isotope techniques were used to identify changes in functional composition of aboveground biomass and roots, and sources of SOC. Our specific objectives were to: (1) Evaluate the impact of long-term livestock grazing on the relative proportion of C_3 and C_4 functional groups; (2) Estimate the relative contributions of C_3 and C_4 plant sources to soil and root C; and (3) Quantify the influence of grazing-induced shifts in the functional composition of rangeland plant communities on whole-ecosystem C storage. To our knowledge, this is the first study to utilize $\delta^{13}C$ to quantify the relative contributions of C_3 and C_4 plants to whole-ecosystem C storage in grazed and ungrazed sites at three distinct locations along an environmental gradient in the North American Great Plains.

Materials and methods

Study areas

The tallgrass community, Konza Prairie Research Natural Area, was located on a midslope topographical position in the Flint Hills of eastern Kansas, near Manhattan (39°05′ N, 96°35′ W). Mean annual precipitation is 835 mm, and mean annual temperature is 12.8 °C (Bark, 1987). Vegetation is dominated by *Andropogon gerardii* Vitman, *Sorghastrum nutans* L. Nash, *Schizachyrium scoparium* (Michx.) Nash, and *Panicum virgatum* L. with a mean annual net primary productivity (ANPP) of 400 g m^{-2}. Soils were silty clay loams (Aquic Argiudoll; fine, montmorillonitic, mesic). The midgrass community was located on a midslope topographical position in west-central Kansas at Fort Hays State University (38°52′ N, 99°23′ W), where *S. scoparium*, *A. gerardii*, and

Bouteloua curtipendula (Michx.) Kunth comprise the dominant species, and mean ANPP is 220 g m^{-2}. This location has a mean annual precipitation of 588 mm, and mean annual temperature of 11.9 °C (Hulett and Tomanek, 1969). Soils were silt loams (Entic Haplustoll; loamy-skeletal, carbonatic, mesic). The shortgrass community was located on a swale topographical position at the Central Plains Experimental Range (CPER) in north-central Colorado (40°49′ N, 107°46′ W). Mean annual precipitation is 321 mm, and mean annual temperature is 8.6 °C (Lauenroth and Sala, 1992). Vegetation is predominately *B. gracilis* (H.B.K.) Lag ex Steud. (Milchunas et al., 1989), and mean ANPP is 100 g m^{-2}. Soils were sandy loams (Ustollic Haplargid; fine-loamy, mixed, mesic). At all three locations, long-term ungrazed sites (since 1969, 1908, and 1939 for the tallgrass, midgrass and shortgrass communities, respectively), ranging from 1 to 100 ha were compared with adjacent sites (i.e., fence line contrasts) that had been subjected to moderate, continuous season-long (May–October) grazing by cattle that removed approximately 40–60% of ANPP. For each location, grazed/ungrazed sites were positioned on the same soil series with similar aspect and slope.

Unfortunately, it was not possible to replicate grazing treatments at each of the three locations. Therefore, we acknowledge that our experimental design is potentially limited because the fence-lines technically define only one formal replicate within each treatment; however, we suggest that these fenceline contrasts are extraordinarily valuable because of the long-term consistent management at each location. In addition, both grazed and ungrazed treatments occurred on the same soil series at each of the three locations, and soil characteristics such as soil pH (Derner et al., 1997) and bulk density (Table 1) did not differ between the grazed and ungrazed sites at each location. Although there were some statistically significant differences in soil particle size [sand (<2000–50 μm), silt (<50–2 μm), clay (<2 μm)] distributions using the hydrometer method (Gee and Bauder, 1986) between some of the grazing treatments (Table 1), these differences were of insufficient magnitude to result in differences in soil texture class, and were unlikely large enough to account for any of the differences in response variables noted in this study.

Table 1. Mean soil bulk density and texture [sand (<2000–50 μm), silt (<50–2 μm), clay (<2 μm)]

	Shortgrass		Midgrass		Tallgrass	
	Ungrazed	Grazed	Ungrazed	Grazed	Ungrazed	Grazed
Bulk density (g cm^{-3})						
0–5 cm	1.23 (0.03)	1.20 (0.03)	0.85 (0.02)	0.88 (0.02)	0.88 (0.02)	0.90 (0.02)
5–15 cm	1.23 (0.02)	1.20 (0.02)	1.00 (0.02)	1.01 (0.01))	1.10 (0.01)	1.12 (0.02)
15–30 cm	1.27 (0.03)	1.27 (0.02)	0.96 (0.03)	0.99 (0.02)	1.23 (0.02)	1.23 (0.01)
Sand (%) 0–5 cm	76.6 (1.1)*	71.2 (1.4)	30.9 (1.6)	27.5 (1.7)	17.9 (0.9)	17.3 (0.9)
5–15 cm	73.2 (1.5)	70.6 (1.2)	34.0 (2.4)*	27.1 (1.0)	14.6 (0.7)	15.0 (0.6)
15–30 cm	64.8 (2.6)	67.1 (1.7)	28.9 (4.3)	25.0 (1.6)	13.3 (0.6)	12.0 (0.5)
Silt (%) 0–5 cm	12.6 (1.1)	19.5 (1.3)*	53.6 (2.2)	59.6 (1.2)*	57.2 (1.2)	58.8 (1.1)
5–15 cm	12.0 (0.9)	18.2 (1.4)*	46.5 (1.3)	54.5 (1.1)*	52.2 (0.9)	56.9 (1.0)*
15–30 cm	14.4 (1.4)	19.9 (0.9)*	38.7 (1.4)	47.3 (2.3)*	43.5 (1.0)	48.9 (1.3)*
Clay (%) 0–5 cm	10.8 (0.5)*	9.3 (0.4)	15.5 (1.1)*	12.8 (0.4)	24.9 (1.0)	23.9 (0.5)
5–15 cm	14.8 (1.3)*	11.2 (0.4)	19.4 (1.6)	18.4 (0.6)	33.2 (1.2)*	28.2 (1.0)
15–30 cm	20.8 (1.6)*	13.9 (1.2)	26.3 (3.0)	27.7 (2.7)	43.2 (1.1)*	39.1 (1.1)

Data are mean ± SE, $n = 10$. Asterisks indicate significant ($P < 0.05$) differences between grazing treatments within a community.

Plant and soil collection and processing

Above-ground biomass of herbaceous species, excluding litter, was determined by clipping at peak biomass in July 1994. Ten, 0.5×0.5 m plots were clipped at ground level in each long-term grazed and ungrazed site in the three communities. Plots were located at 2 m intervals along a randomly located transect. Biomass was separated into major functional groups (Table 2), dried at 60 °C and weighed. Above-ground tissue samples from dominant plant species ($n = 3$–5 individual plants/species) in each functional group were taken from the tall- and shortgrass communities in July 1998, and the midgrass community in September 1999. Tissue samples were dried at 60 °C, pulverized, and analyzed for δ^{13}C (Table 2).

A soil core (2×30 cm) was taken from the center of each plot that was sampled for above-ground biomass; no effort was made to locate cores either beneath or between plants. Soil cores were divided into three depth increments (0–5, 5–15, and 15–30 cm), then passed through a 2-mm sieve to remove coarse roots (>2 mm). Subsamples of sieved (but otherwise untreated) soil were retained for organic C analyses by combustion/gas chromatography (Carlo-Erba NA-1500, Fisons Instruments, Danvers, Massachusetts, USA) using methods described by Nieuwenhuize et al. (1994). Coarse roots were then placed in 40 mL of 1 M HCl to remove CaCO$_3$, washed thoroughly with distilled water, dried at 60 °C, weighed, and pulverized. Fine roots (<2 mm) were removed from soils by flotation in 500 mL 1 M HCl. This procedure also served to volatilize CaCO$_3$ in preparation for C isotope analyses of roots and soils. Fine roots and soil were then washed with distilled water, dried at 60 °C, weighed, and pulverized. Acid pretreatment has no effect on δ^{13}C of roots and SOC (Midwood and Boutton, 1998). Live and dead roots could not be distinguished for either fine or coarse root fractions; hence, root biomass values include both live and dead roots.

Isotopic and elemental analyses

Above-ground biomass, coarse and fine roots, leaf tissue samples, and soils were ground with a ring pulverizer (Model TE250, Angstrom, Inc., Belleville, Michigan, USA) and analyzed for C concentration (g kg^{-1}) and δ^{13}C using a Carlo-Erba EA-1108 elemental analyzer interfaced with a Delta Plus (Finnigan MAT, Bremen, Germany) isotope ratio mass spectrometer operating in continuous flow mode. The isotopic composition is expressed as a δ^{13}C value where:

$$\delta^{13}C(‰) = \frac{(^{13}C/^{12}C)_{sample} - (^{13}C/^{12}C)_{standard}}{(^{13}C/^{12}C)_{standard}} \times 10^3$$

(1)

Table 2. δ^{13}C values for plant species within functional groups found in above-ground biomass

	Shortgrass Community		Midgrass Community		Tallgrass Community	
	Species	δ^{13}C (‰)	Species	δ^{13}C (‰)	Species	δ^{13}C (‰)
C$_4$ grass	Aristida longiseta	−13.15 (0.42)	Andropogon gerardii	−12.70 (0.14)	Andropogon gerardii	−12.51 (0.20)
	Bouteloua gracilis	−13.26 (0.33)	Bouteloua curtipendula	−13.98 (0.10)	Panicum virgatum	−12.46 (0.13)
	Buchloë dactyloides	−14.28 (0.52)	Bouteloua gracilis	−14.06 (0.15)	Schizachyrium scoparium	−12.50 (0.03)
	Schedonnardus paniculatus	−13.48 (0.07)	Schizachyrium scoparium	−12.92 (0.14)	Sorghastrum nutans	−12.91 (0.17)
	Sporobolus cryptandrus	−14.70 (0.21)	Sporobolus asper	−12.89 (0.09)	Sporobolus heterolepis	−13.38 (0.08)
C$_3$ grass	Pascopyrum smithii	−27.98 (1.58)	Elymus canadensis	−26.63 (1.31)	Koeleria pyramidata	−27.97 (0.74)
	Stipa comata	−25.89 (0.57)	Poa pratensis	−26.70 (0.55)	Poa pratensis	−27.11 (0.34)
C$_3$ forbs	Sphaeralcea coccinea	−27.30 (1.64)	Ambrosia psilostachya	−26.93 (0.25)	Ambrosia psilostachya	−28.67 (0.11)
			Brickellia grandiflora	−29.34 (0.16)	Artemisia ludoviciana	−27.59 (1.34)
			Euphorbia bicolor	−28.05 (0.30)	Aster ericoides	−28.12 (1.23)
			Schrankia uncinata	−28.30 (0.18)	Dalea purpurea	−26.10 (0.23)
C$_3$ shrubs	Artemisia frigida	−27.17 (2.05)	Amorpha canescens	−28.07 (0.34)	Amorpha canescens	−27.75 (0.83)
	Ceratoides lanata	−27.08 (0.39)			Rosa arkansana	−27.85 (0.45)

Data are mean ± SD, n=2–6.

All δ^{13}C values were expressed relative to V-PDB (Coplen, 1995). Repeated measurements ($n = 5$) of a laboratory soil standard (Leco 502-062, Leco, St. Joseph, MI, USA) yielded a precision of <0.1‰ for δ^{13}C, and <0.15 g kg^{-1} for C concentration.

The proportion of C derived from C$_4$ sources in above-ground biomass, roots, and SOC was estimated by the mass balance equation:

$$\delta^{13}\text{C} = (\delta^{13}\text{C}_{C4})(x) + (\delta^{13}\text{C}_{C3})(1 - x) \qquad (2)$$

where δ^{13}C is the δ^{13}C value of the whole sample, δ^{13}C$_{C4}$ is the average δ^{13}C value of the C$_4$ species at the site, x is the proportion of C from the C$_4$ species, δ^{13}C$_{C3}$ is the average δ^{13}C value of the C$_3$ species at the site, and $1-x$ is the proportion of C from the C$_3$ species. Mass of C in roots and above-ground biomass (g C m^{-2}) was calculated as the product of C concentration (g kg^{-1}) and biomass (g m^{-2}). Soil C mass (g C m^{-2}) was computed as the product of SOC concentration (%), bulk density (g cm^{-3}, from Derner et al., 1997), and soil depth (cm).

Statistical analyses

Root and soil variables were analyzed using a split-plot design with grazing the main factor and soil depth designated as the split factor. Above-ground biomass and total ecosystem C storage were analyzed using a one-way Analysis of Variance (ANOVA) using grazing as the single factor. Communities were not replicated so analyses were performed separately for each community. Although we assume that the ten samples within each grazing treatment constitute replicate samples, we recognize that this sampling scheme could be perceived as pseudoreplication. The potential statistical consequences and limitations of pseudoreplication have been discussed (see Heffner et al., 1996; Hurlbert, 1984).

Results

Above-ground biomass

Above-ground biomass in the ungrazed sites was almost four-fold greater in the tallgrass community (441 g m^{-2}) than in the shortgrass community (118 g m^{-2}) (Table 3). Grazed sites had

Table 3. Mean above-ground biomass by functional group

Functional group	Above-ground biomass (g m^{-2})					
	Shortgrass		Midgrass		Tallgrass	
	Ungrazed	Grazed	Ungrazed	Grazed	Ungrazed	Grazed
C$_4$ grass	52.4 (3.4)	74.4 (5.0)*	185.6 (17.6)	100.0 (7.5)*	340.7 (33.1)	200.4 (10.8)*
C$_4$ total	52.4 (3.4)	74.4 (5.0)*	185.6 (17.6)	100.0 (7.5)*	340.7 (33.1)	200.4 (10.8)*
C$_3$ grass	64.7 (12.7)	7.2 (1.5)*	0	0.3 (0.3)	18.1 (4.2)	24.9 (2.8)
C$_3$ forbs	1.3 (0.4)	4.2 (0.8)*	22.2 (6.4)	20.5 (4.8)	65.2 (14.2)	38.2 (5.0)*
C$_3$ shrubs	0	4.3 (4.3)	0	0	17.4 (13.3)	0.3 (0.3)*
C$_3$ total	66.0 (12.8)	15.7 (3.8)*	22.2 (6.4)	20.8 (4.7)	100.6 (20.1)	63.4 (5.6)*
Total	118.4 (12.5)	90.1 (5.6)*	207.8 (19.3)	120.8 (9.2)*	441.3 (31.7)	263.8 (14.5)*
From biomass (% C$_4$)	48 (5)	83 (3)*	90 (3)	83 (3)	77 (4)	76 (1)
From δ^{13}C of biomass (% C$_4$)	44 (4)	82 (5)*	93 (3)	77 (3)*	76 (4)	66 (2)*

Data are mean ± SE, *n* = 10. Asterisks indicate significant (*P* < 0.05) differences between grazing treatments within a community.

approximately 24–42% less biomass than their ungrazed counterparts at all three locations.

Biomass of C$_4$ grasses was 41–46% lower in grazed than in the ungrazed sites in the tall- and midgrass communities, but it was 42% higher in the grazed than in the ungrazed site in the short-grass community (Table 3). Biomass of the C$_3$ functional groups was 76% lower in the grazed than ungrazed site of the shortgrass community, and 37% lower in the grazed than ungrazed site of the tallgrass community; however, there was no difference in C$_3$ biomass between grazing treatments in the midgrass community.

Biomass of the tall- and midgrass communities consisted of 76–90% C$_4$ biomass, regardless of grazing treatment (Table 3). Biomass in the grazed site in the shortgrass community also consisted of primarily (83%) C$_4$ species, but C$_3$ species comprised a significant proportion (52%) of the biomass in the ungrazed shortgrass community.

δ^{13}C values of bulk above-ground biomass were significantly higher in the ungrazed sites of the tall- and midgrass communities, while the opposite response occurred in the shortgrass community (Figure 1a–f). The relative composition of C$_3$ and C$_4$ species in above-ground biomass as estimated by isotopic mass balance (Eq. 2) was generally in good agreement with direct assessments of biomass in those functional groups (Table 3). However, the isotopic mass balance approach indicated that ungrazed sites of the tall- and midgrass communities had a significantly higher proportion of C$_4$ grass

biomass than the grazed sites, whereas the direct biomass approach did not show a significant difference.

Root biomass

Contrary to results for above-ground biomass, total root biomass (0–30 cm, fine + coarse roots) was 60–78% greater in the shortgrass community than in the tallgrass community (Figure 2). Total root biomass (0–30 cm) in the ungrazed sites ranged from 1369 ± 210 g m^{-2} in the tallgrass community to 2188 ± 165 g m^{-2} in the shortgrass community. As a result of these differences in above- and belowground biomass, root/shoot ratios were higher in the shortgrass community (ungrazed = 18:1, grazed = 25:1) than in the tallgrass community (ungrazed = 3:1, grazed = 5:1).

Grazing had a significant effect on total root biomass only in the midgrass community (Table 4; Figure 2). Total root biomass in the upper 30 cm of the soil profile was 1970 ± 209 g m^{-2} in the ungrazed site and 1249 ± 116 g m^{-2} in the grazed site of this community. This overall decrease in total root biomass is the net result of 72% less coarse root biomass and 60% greater fine root biomass in the upper 30 cm of the profile in the grazed site (Figure 2). In the short- and tall-grass communities, there was a significant grazing×soil depth interaction in the fine root component (Table 4). Grazing increased fine root biomass in the 0–5 cm depth interval, but decreased it at depths >5 cm in both communities
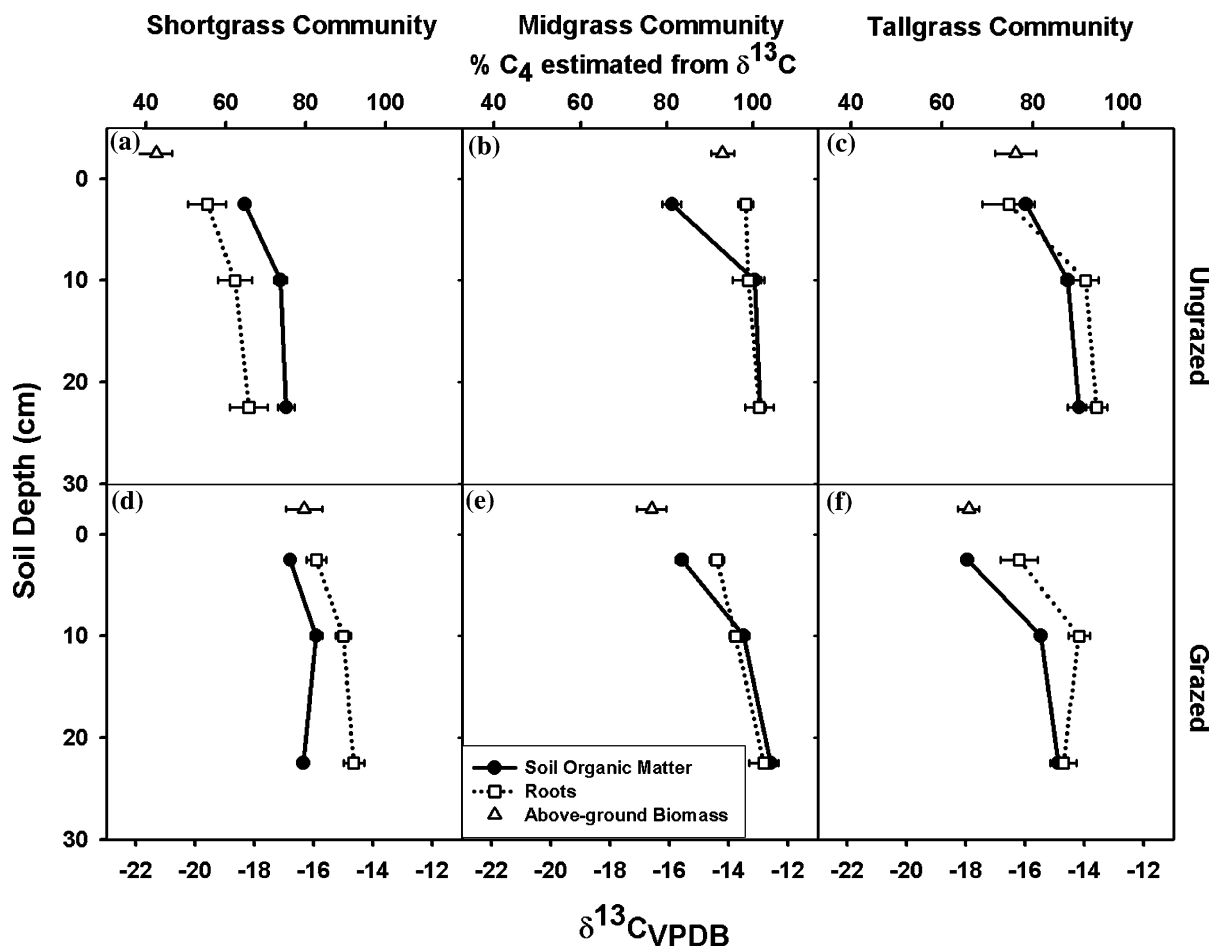
Figure 1. $\delta^{13}C$ values of above-ground biomass ($\triangle$), roots ($\square$), and SOC ($\bullet$) in ungrazed (a–c) and grazed (d–f) sites in short-, mid-, and tallgrass prairie ecosystems. Data are means $\pm$ S.E. ($n = 10$), and values for roots and soil carbon are plotted at the mid-point of each soil depth increment (0–5, 5–15, and 15–30 cm). The upper x-axis provides an estimate of the proportion of carbon derived from C_4 sources, and is based on Eq. 2.

(Figure 2). Fine, coarse, and total root biomass decreased significantly with increasing soil depth in all three communities.

The relative biomass of fine roots (i.e., fine root biomass/total root biomass), summed across soil depths, was greater in the grazed (65–73%) compared to the ungrazed (27–65%) sites in all three communities (Figure 2). Conversely, coarse root biomass as a proportion of total root biomass was lower in grazed sites (27–35%) than in ungrazed sites (35–73%) in all three communities.

Roots in the grazed site of the shortgrass community had significantly higher $\delta^{13}C$ values (−16 to −14‰) at all soil depths than roots in the ungrazed site (−20 to −18‰) (Figure 1a, d),

indicating an increase in relative biomass of C_4 grass roots in the grazed site. In contrast, grazing had no effect on root $\delta^{13}C$ values in the midgrass (Figure 1b, e) and tallgrass (Figure 1c, f) communities.

Mass balance calculations (Eq. 2) based on the isotopic composition of root tissue revealed significantly higher proportions of C_4 species roots at all soil depths in grazed (80–90%) than in the ungrazed (57–68%) site of the shortgrass community (Figure 1). In contrast, grazing had no significant effect on the relative proportion of C_4 root biomass in the mid- and tallgrass communities. C_4 grass roots generally comprised >75% of the root biomass in all communities, grazing treatments and soil depths. The only
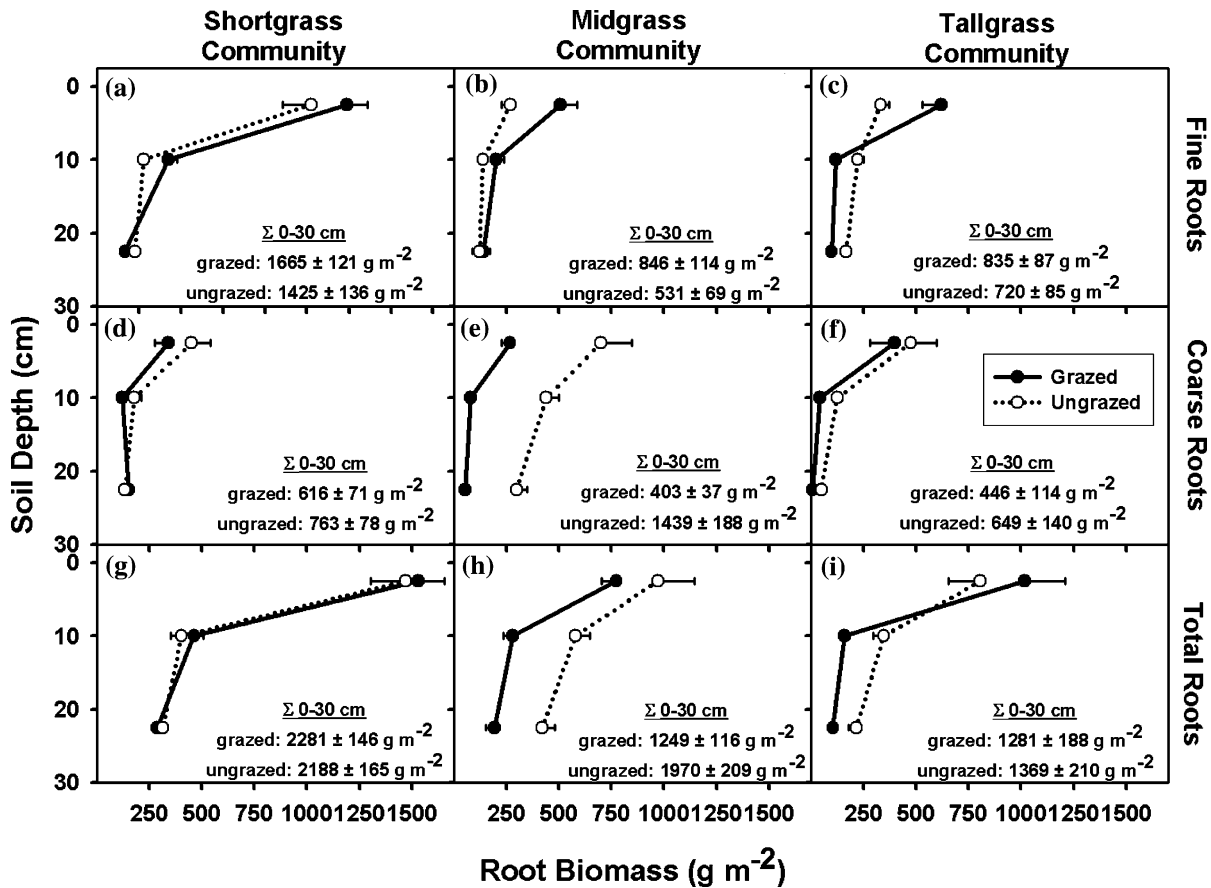
84

Figure 2. Root biomass (fine, coarse, and total) in ungrazed (○) and grazed (●) sites in short-, mid-, and tallgrass prairie ecosystems. Data are means ± S.E. ($n = 10$), and plotted at the midpoint of each soil depth increment (0–5, 5–15, and 15–30 cm). The sum of root biomass in the upper 30 cm of the soil profile is also indicated within each panel.

exception was the high proportion of C_3 root biomass in the ungrazed site of the shortgrass community.

Soil organic carbon

SOC (g C m^{-2}) to a depth of 30 cm was more than three-fold greater in the tallgrass community (8280 g C m^{-2}) than in the shortgrass community (2517 g C m^{-2}) (Figure 3). The grazing treatment×soil depth interaction was significant for SOC mass in both the short- and midgrass communities (Table 4). In the shortgrass community, SOC at 0–5 and 5–15 cm was greater in the grazed compared to the ungrazed site, but there was not a significant effect at 15–30 cm. SOC at 0–5 cm was lower in the grazed compared to ungrazed site of

the midgrass community, but it was greater at 15–30 cm (Figure 3). Grazing treatment had no effect on SOC mass in the tallgrass community.

$\delta^{13}C$ values of soil organic matter were generally greater than −16‰ in the mid- and tallgrass communities, indicating that >80% of SOC was derived from C_4 species (Figure 1). In contrast, $\delta^{13}C$ values of soil organic matter were less than −16‰ in the shortgrass community, suggesting that approximately 60–80% of SOC was derived from C_4 species. Grazing treatment had no effect on $\delta^{13}C$ values of soil organic matter in any community (Table 4; Figure 1). However, the grazing×soil depth interaction was significant in the tallgrass community, where $\delta^{13}C$ values of soil organic matter at 0–5 cm were lower (−18‰) in the grazed compared to the ungrazed (site −16‰).

Table 4. Summary of root and soil statistical results

Community	Variable	Grazing	Soil Depth	Grazing ×Depth
Shortgrass	Fine root biomass			**
	Coarse root biomass		*	
	Total root biomass		*	
	Root δ¹³C	*		
	SOC mass			*
	SOC δ¹³C			
Midgrass	Fine root biomass	**	*	
	Coarse root biomass	*	*	
	Total root biomass	*	*	
	Root δ¹³C			
	SOC mass			*
	SOC δ¹³C			
Tallgrass	Fine root biomass			*
	Coarse root biomass		*	
	Total root biomass		*	
	Root δ¹³C		*	
	SOC mass		*	
	SOC δ¹³C			**

$* = P < 0.10$ and $** = P < 0.05$.

Ecosystem carbon storage

Whole-ecosystem C storage was almost three-fold greater in the ungrazed tallgrass community (8997 g C m^{-2}) than in the shortgrass community (3236 g C m^{-2}) (Figure 4). SOC comprised the largest proportion of ecosystem C, representing 78–82% of whole-ecosystem C in the shortgrass community, and 90–94% in the mid- and tallgrass communities. Root C comprised 17–21% of whole-ecosystem carbon in the shortgrass community, with considerably lower values in the midgrass (6–9%) and tallgrass (6%) communities. In contrast, above-ground biomass C was a small fraction (0.6–2.1%) of whole-ecosystem C for all three communities. C derived from C$_4$ plant sources dominated whole-ecosystem C storage (71–95%) in all three communities (Figure 4).

Whole-ecosystem C storage was 24% greater in the grazed than in the ungrazed sites of the shortgrass community, and this increase was associated with a higher proportion of C$_4$-derived C (Figure 4). Greater C storage in this community was primarily due to greater SOC storage in the grazed (3307 ± 231 g C m^{-2}) than ungrazed (2517 ± 82 g C m^{-2}) site (Figure 2; Figure 4). In contrast, whole-ecosystem C storage was approximately 8% lower in the grazed compared to the ungrazed site in both the mid- and tallgrass communities, although these differences were only marginally significant ($P < 0.10$).

Discussion

Functional group composition, the source and magnitude of C inputs, and total ecosystem C storage displayed inconsistent responses to long-term livestock grazing at three locations in the North American Great Plains. C$_4$ plants
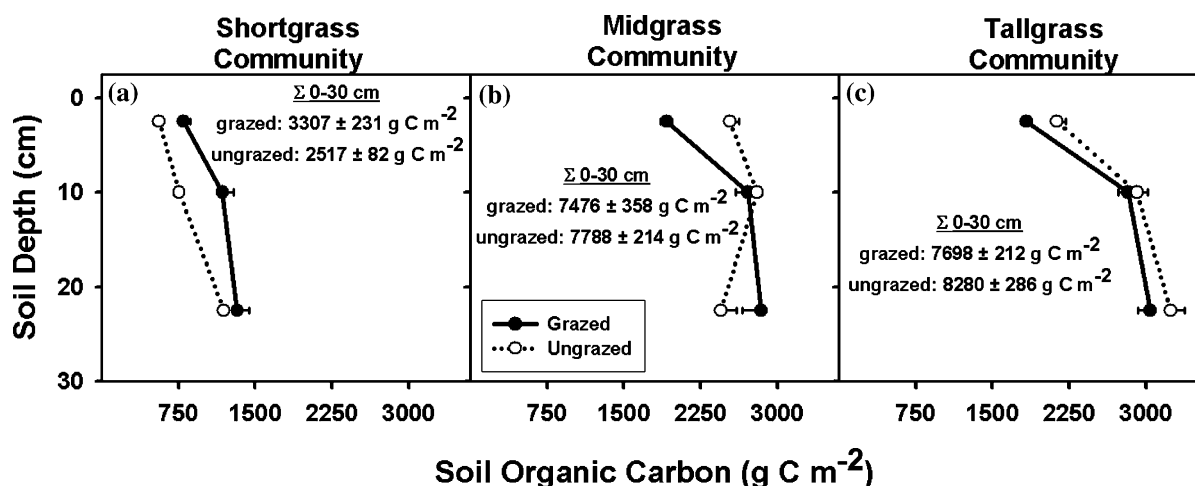

Figure 3. SOC content in ungrazed (○) and grazed (●) sites in short-, mid-, and tallgrass prairie ecosystems. Data are means ± S.E. ($n = 10$), and plotted at the midpoint of each soil depth increment (0–5, 5–15, and 15–30 cm). The sum of SOC in the upper 30 cm of the soil profile is also indicated within each panel.
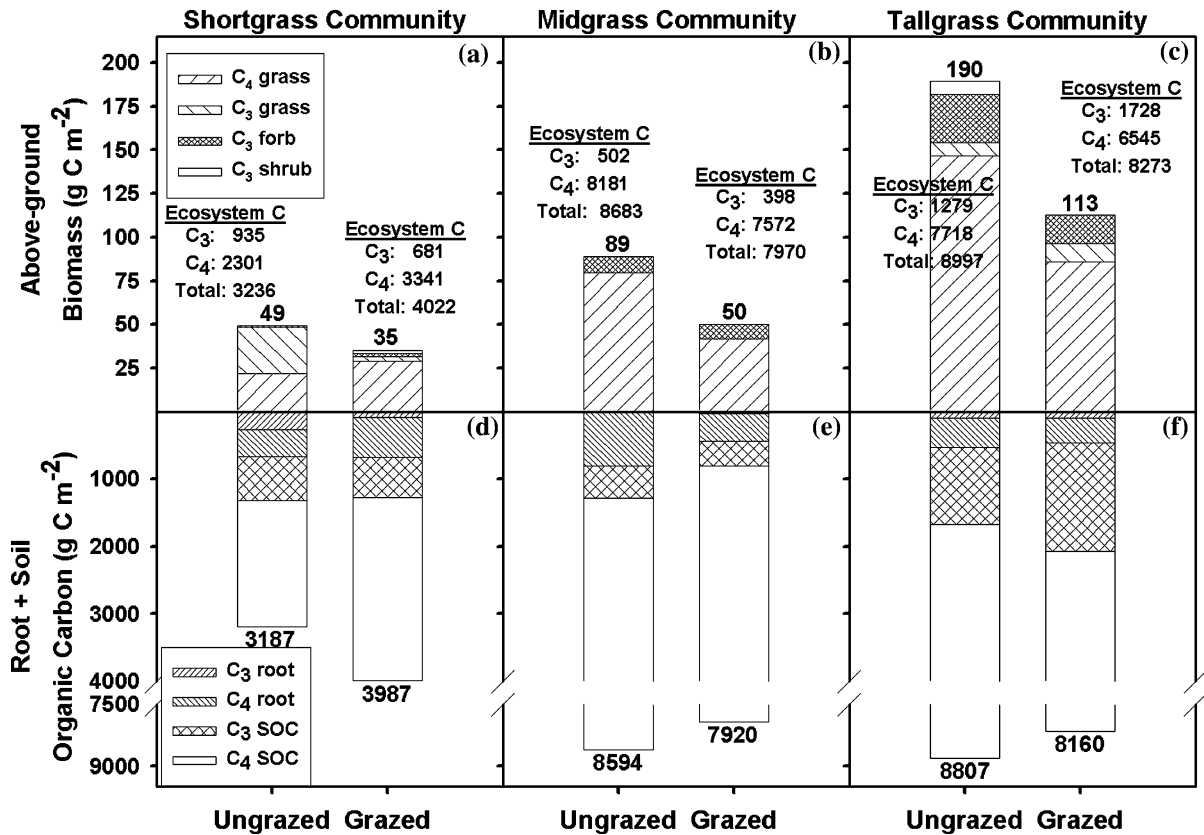
Figure 4. Whole-ecosystem carbon storage in ungrazed and grazed sites in short-, mid-, and tallgrass prairie ecosystems. The carbon content of above- and belowground biomass was computed as the product of dry biomass (Table 3 and Figure 2) and tissue carbon concentrations (data not shown). Root and soil carbon masses are for the upper 30 cm of the soil profile. C_3 and C_4 sources were determined by species identification for above-ground carbon, and by isotopic mass balance (Eq. 2) for belowground carbon (roots and soil organic carbon). Note the difference in scale between above- and belowground components.

dominated the long-term moderately grazed site in the shortgrass community, whereas the ungrazed site was co-dominated by C_3 and C_4 plants; functional group composition did not differ between grazed and ungrazed sites in the mid- and tallgrass communities (Objective 1). Above-ground biomass and the relative proportion of coarse root biomass were lower, while the relative proportion of fine root biomass was greater, in grazed compared to ungrazed sites at all three locations (Objective 2). The grazed site of the shortgrass community had 24% more whole-ecosystem C storage compared to the ungrazed site. In contrast, grazed sites at the mid- and tallgrass communities had 8% lower whole-ecosystem C storage compared to ungrazed sites (Objective 3).

Long-term moderate grazing was associated with a substantial change in functional group composition in only the shortgrass community where the C_4 shortgrass *B. gracilis* increased in abundance relative to several C_3 species, including *Pascopyrum smithii (Rydb.) A. Love.* This pattern of species replacement has been well documented in the shortgrass community (Hart and Ashby1998; Milchunas et al., 1989, 1990, 1998), and it is apparently initiated by the selective grazing of C_3 relative to C_4 species (Hart, 2001). This pattern of interspecific plant selection by herbivores may partially be a function of photosynthetic pathway (Caswell et al., 1973), but the contrasting herbivory resistance between these two species is probably more a function of growth form than of photosynthetic pathway. Compositional shifts between plant species with contrasting photosynthetic pathways were not observed in the mid- and tallgrass communities because they were initially dominated by C_4

grasses and species replacement patterns in these communities involve a high proportion of subordinate C_4 species (Branson and Weaver, 1953).

A compositional shift from C_3–C_4 co-dominance to C_4 dominance by *B. gracilis* has important implications for soil C inputs in the shortgrass community. The dominant C_3 species *P. smithii* has a uniform distribution of relatively coarse roots in the upper 30 cm of soil profile, whereas 85% of *B. gracilis* roots, which are mostly fine, are located in the upper 15 cm of the soil profile (Coupland and Johnson, 1965; Dormaar et al., 1995; Schuman et al., 1999). Frank et al. (1995) have previously recognized the ability of *B. gracilis* to maintain comparable SOC concentrations in intensively grazed compared to ungrazed midgrass communities. In fact, most investigations in the Great Plains that document constant or greater SOC concentrations in response to grazing have been associated with an increase in the relative composition of *B. gracilis* (Frank et al., 1995; Reeder et al., 2004; Reeder and Schuman, 2002; Schuman et al., 1999; Smoliak et al., 1972). Although a previous investigation found grazing to have little influence on SOC pools in a similar shortgrass community (Burke et al., 1999), soils were only sampled to 5 cm. These investigators did find higher particulate organic matter C and N, in grazed compared to ungrazed sites in this community (Burke et al., 1999), suggesting that recent C inputs were greater on grazed than on ungrazed sites. Particulate organic matter C represents relatively recent litter inputs as they are stabilized into humic material, and it is often used to draw inferences of early shifts in C dynamics and pools in response to land use management (e.g., Cambardella and Elliott, 1992).

Root:shoot ratios varied from 3–5:1 in the tallgrass community to 18–25:1 in the shortgrass community which are within the range of values previously reported along this gradient (Jackson et al., 1996; Schuman et al., 1999; Sims et al., 1978). Larger root:shoot ratios in the shortgrass community are likely due to the enhanced root production in this water-limited environment and are consistent with the occurrence of greater belowground constraints on plant–soil interactions in the shortgrass community compared to the tallgrass community (Burke et al., 1998). Root:shoot ratios were greater in the grazed com-

pared to ungrazed sites of all three communities because grazing decreased above-ground biomass proportionally more than belowground biomass.

The relative and total mass of fine roots was greater in grazed compared to ungrazed sites in all three communities despite no observed differences in total root biomass between the grazed and ungrazed sites in the short- and tallgrass communities. This greater proportion of fine root biomass in grazed areas suggests that root turnover and rates of nutrient cycling processes is likely accelerated in all three grazed sites as root turnover is greater for fine compared to coarse roots (Eissenstat and Yanai, 1997). The redistribution of root biomass into proportionally more fine roots in the 0–30 cm soil depth directly influences C turnover because decomposition rates of roots decrease with increasing soil depth. For example, the decomposition rate of *B. gracilis* roots in the shortgrass prairie decreased linearly from the soil surface to 1 m depth, thereby reducing the rate of decomposition by 50% at the greatest soil depth (Gill and Burke, 2002).

Reconciliation of inconsistent carbon storage in response to grazing

Why did C storage differ in response to long-term moderate grazing along the east–west environmental gradient in the North American Great Plains? Why was C storage greater in grazed compared to ungrazed sites only in the short-grass community and not in the mid- and tallgrass communities? As mentioned previously, differences in functional group composition and the source and magnitude of C inputs contributed to this inconsistency in ecosystem C storage in response to grazing. The grazed shortgrass community possessed several unique structural state variables: (1) greater proportion of C_4 plant composition (primarily *B. gracilis*), (2) greater amount and proportion of fine root biomass, and (3) higher root:shoot ratios. We infer from these unique state variables that greater C storage in the shortgrass community is primarily attributable to grazing-induced modifications in root architecture and dynamics. A grazing-induced increase in the abundance of *B. gracilis* is associated with greater SOC because of greater fine root production and greater root turnover in the upper portion of the soil profile.

In contrast to the observed results in the grazed site at the shortgrass community, soil and whole-ecosystem C storage were largely unaffected by long-term moderate grazing in the mid- and tallgrass communities, as both communities displayed slight (8%) decreases. The differential responses between the shortgrass and the mid- and tallgrass communities with respect to grazing and whole-ecosystem C storage are likely due to: (1) the possession of much larger SOC pools in mid- and tallgrass communities (three-fold greater than in the shortgrass community) that could potentially buffer total ecosystem C flux (Schuman et al., 1999), (2) lower root C/soil C ratios in the mid- and tallgrass communities (0.06–0.10) compared to the shortgrass community (0.20–0.27) suggesting that variation in organic matter inputs from roots would have relatively smaller effects on the SOC pool, and (3) the absence of grazing-induced variation in the relative proportion of the C_4 functional group to modify root architecture and dynamics in the mid- and tallgrass communities.

The observed difference in SOC between the grazed and ungrazed site in the shortgrass community was 790 g C m^{-2}, which represented a 31% increase, but the addition of this amount of SOC would have only resulted in a 9–10% in total ecosystem carbon storage in the mid- and tallgrass communities. Therefore, soils with larger pools of SOC would require either a greater change in the magnitude of C fluxes, or a longer duration of modified C inputs or losses to induce a significant modification in SOC storage. The higher ratios of root C/soil C in the shortgrass community may enable a grazing induced increase in fine root biomass to have a relatively rapid impact on the size of the SOC pool. Root C/soil C ratios for the 0–30 cm soil depth in long-term lightly and heavily grazed sites of the shortgrass community are 0.10 and 0.14, respectively, (Reeder et al., 2004) and 0.13 and 0.12, respectively, in northern mixed-grass prairie (Schuman et al., 1999).

Collectively, our findings of smaller SOC pools, higher root C/soil C ratios, and substantial variation in functional group composition between the ungrazed and grazed site in the shortgrass community, compared to the mid- and tallgrass communities, provide insight to at least partial reconcile the variable response of ecosystem C storage to grazing along this environmental gradient. We propose an alternative hypothesis to that of tissue chemistry (e.g., Vinton and Burke, 1995), as the predominant mechanism contributing to inconsistent patterns of ecosystem C storage. We hypothesize that the magnitude and proportion of fine root mass within the upper soil profile is the principal driver linking grazing-induced changes in species composition to the biogeochemistry of these grassland ecosystems. This response is less prevalent in the mid- and tallgrass communities because grazing-induced species replacement of dominant C_4 species by subordinate C_4 species (Branson and Weaver, 1953) is not sufficient to modify fine root production, subsequent root turnover, and the size of SOC pools. In contrast, a compositional shift from C_3–C_4 co-dominance to C_4 dominance by *B. gracilis* with increasing grazing intensity in the shortgrass community significantly alters root architecture and dynamics to increase SOC and whole-ecosystem C storage.

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