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# Carbon exchange and species composition of grazed pastures and exclosures in the shortgrass steppe of Colorado

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## Abstract

Grasslands comprise approximately 40% of the world's terrestrial surface. Consequently, grassland ecosystems are a significant component of the global carbon cycle. In order to better understand how grazing affects the carbon cycle of grasslands, this study measured CO<sub>2</sub> exchange rate (CER) and soil respiration rate (SRR) on 130 ha pastures with a 56-year history of heavy (60% removal) and light (20% removal) grazing, and their accompanying 0.8 ha exclosures, on the shortgrass steppe of northeastern Colorado, USA. A CER chamber that covered 1 m<sup>2</sup> of native grassland was used on five plots in each of the four areas. Mid-day CER and SRR were measured during the growing seasons of 1995–1997, along with green vegetation index (GVI, similar to leaf area index) and plant species composition.

When averaged over each growing season, there was no significant difference in CER of grazed pastures versus exclosures. However, there were seasonal differences in CER, which varied over the 3 years. Differences in CER between grazed pastures and exclosures were not related to GVI, which rarely differed between treatments. Grazing treatment differences in CER were driven by climate variability and species composition differences resulting from long-term grazing and exclusion from grazing. Exclosures had more cool-season (C<sub>3</sub>) grasses and forbs than grazed plots, which contained more warm-season (C<sub>4</sub>) grasses (primarily *Bouteloua gracilis* (H.B.K.) Lag. Ex Steud.). The somewhat unique, cool spring of 1995 was favorable to cool-season plant metabolism and resulted in higher CER in exclosures compared with grazed pastures. Warm, dry conditions in spring of 1996 favored warm-season species, resulting in higher CER in the heavily-grazed pasture. In 1997, there was little difference in CER between grazed pastures and exclosures. There were very few sampling dates when SRR was different in grazed pastures and exclosures. This study suggests that these intensities of cattle grazing do not alter the photosynthetic and soil respiration components of the carbon cycle of the US shortgrass prairie. It appears that cattle grazing can be a sustainable component of managing this ecosystem for maximum global carbon sequestration.

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**Keywords:** Carbon cycling; Carbon exchange; Grazing; Photosynthesis; Shortgrass steppe; Soil respiration; Species composition

## 1. Introduction

Concerns about increasing atmospheric CO<sub>2</sub> and global climate change have increased the need for data and information on the global carbon cycle. The

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forests of the world have been the focus of most of the research on terrestrial carbon sequestration, while arid ecosystems have received less research attention, due to their relatively low productivity (Cole, 1996; Glenn et al., 1993). However, since approximately 40% of the world's land surface is grassland, these ecosystems are a significant component of the global carbon cycle (Frank et al., 2000; Glenn et al., 1993; World Resources, 1986). Understanding the carbon cycle of the major grassland ecosystems of the world is critical for developing accurate and predictive global carbon cycle models (Glenn et al., 1993; Ojima et al., 1993; Schimel, 1995).

Restoration of degraded grasslands and management for maximum carbon uptake may offset part of the increase in global CO<sub>2</sub> (Glenn et al., 1993; Keller and Goldstein, 1998). Understanding how management (grazing, fire, weed control) affects carbon cycling of grasslands is needed before land managers can incorporate carbon-related criteria into decisions. Overgrazing of grasslands by domestic livestock has been implicated in reduced global carbon uptake (Keller and Goldstein, 1998; Ojima et al., 1993). Since much of the grasslands of the world are grazed by domestic livestock, the effect of grazing on the carbon cycle of grassland ecosystems needs to be better understood.

Ecosystem CO<sub>2</sub> exchange (photosynthesis, and plant and soil respiration) is a major component of the carbon cycle of grasslands. Many studies have investigated the photosynthetic response of individual plants to grazing or simulated grazing (Painter and Detling, 1981; Wallace, 1990). Clipping improves tillering in grazing-tolerant grass species and typically stimulates photosynthesis in remaining leaves (Coughenour, 1985; Painter and Detling, 1981). However, there have been few reports where photosynthesis of grazed plants was measured on a native plant community (McNaughton et al., 1996). A reduction in above-ground phytomass from grazing would presumably reduce net carbon uptake of grasslands (Frank et al., 2000). However, when CO<sub>2</sub> exchange rate (CER) was measured on sods from pastures with different stocking densities of sheep, it was found that a moderate stocking rate had higher CERs than a light or heavy stocking rate (Vickery, 1972). In another study, canopy photosynthesis was measured on cultivated bermudagrass (*Cynodon dactylon*)

swards which were defoliated at varying frequencies (Morgan and Brown, 1983). While defoliation caused a temporary decline in canopy photosynthesis, swards which were completely defoliated on a monthly basis had canopies with younger leaves and consequently higher photosynthesis rates than swards partially defoliated each week. In the mixed-grass prairie of Wyoming, USA, grazed pastures had higher community photosynthesis rates than ungrazed plots in the spring due to earlier "green-up" (LeCain et al., 2000). However, on a seasonal basis there was very little effect of cattle grazing on photosynthesis rates.

In addition to above-ground CO<sub>2</sub> exchange, grazing has direct and indirect effects on the below-ground components of the carbon cycle. Grazing reduced annual soil respiration by 18% in the US tallgrass prairie (Bremer et al., 1998). Clipping was found to reduce root respiration in blue grama (*Bouteloua gracilis* (H.B.K.) Lag. Ex Steud.) plants, although rates recovered in as little as 3 days following the cessation of clipping (Detling et al., 1979). The initial reduction in translocation of carbohydrates from removed photosynthetic tissue is directly related to lower root respiration, but the long-term effects of grazing on root and soil respiration are influenced by many factors (Bremer et al., 1998).

Understanding how grazing by livestock affects CO<sub>2</sub> exchange is also critical to the long-term planning and management of grasslands. Few studies have measured CO<sub>2</sub> exchange of grazed rangelands, but many have assessed primary productivity. In many ecosystems, grazing reduces above-ground net primary productivity (ANPP), but there are examples where grazing actually increases ANPP (Milchunas and Lauenroth, 1993; Sims and Singh, 1978). McNaughton (1979) maintains that an optimal level of grazing will maximize ANPP in most rangeland ecosystems, so most of the reported negative effects of grazing may be examples of overgrazing for a particular ecosystem.

The objectives of this study are to investigate the effects of grazing by domestic cattle on the photosynthetic and soil respiratory components of the carbon cycle of the shortgrass steppe of the Great Plains of North America. This semiarid ecosystem covers approximately 280,000 km<sup>2</sup>, stretching north to south from the Colorado–Wyoming border to western Texas, and west to east from the foothills of the Rocky Mountains to the Oklahoma panhandle. Because of

its large size, the shortgrass steppe may be a significant component of the terrestrial carbon cycle of North America (Fan et al., 1998; Frank et al., 2000). Since 45% of the shortgrass steppe remains in native grassland, and most of this is utilized for grazing by livestock, it is important to know how grazing affects carbon cycling in this region (Lauenroth et al., 1994).

## 2. Materials and methods

The study site is at the US Department of Agriculture-Agricultural Research Service (USDA-ARS) Central Plains Experimental Range (CPER) (40°49'N, 104°46'W) in the shortgrass steppe of northeastern Colorado, USA. Long-term annual precipitation averages 32 cm, 70% of which occurs during the April through September growing season. Maximum July temperatures average 30.6 °C and January minimums average -11.0 °C (Milchunas et al., 1994). Vegetation is primarily composed of C<sub>4</sub> grasses, mostly blue grama (*Bouteloua gracilis* (H.B.K.) Lag. Ex Steud.) and buffalo grass (*Buchloe dactyloides* (Nutt) Engelm.), mixed with varying amounts of C<sub>3</sub> grasses, cactus, shrubs and forbs (Milchunas et al., 1989). Adjacent, lightly- and heavily-grazed pastures (130 ha), established in 1939, were used in this study (Klippel and Costello, 1960; Hart, 2001). Pastures were grazed by cattle from May through October with stocking rates targeted at removing 20% (0.12 heifers/ha; lightly-grazed) and 60% (0.26 heifers/ha; heavily-grazed) of the forage (Hart, 2001). Each pasture contained a 0.8 ha enclosure, which was also established in 1939 in areas which represented the dominant vegetation community of the larger pastures (Klippel and Costello, 1960). The soil type of both pastures was classified as an Ascalon fine sandy loam (mixed, mesic, Aridic, Arjjustoll). However, evaluation of the soil profile during the experiment revealed that the clay content in the B horizon of the heavily-grazed pasture was 5–11% higher than the lightly-grazed pasture (Reeder, personal communication).

CO<sub>2</sub> exchange techniques were used to nondestructively assess plant community photosynthesis and soil respiration. Metal, angle-iron frames that enclose 1 m<sup>2</sup> of ground were driven into the soil along transects crossing the grazed and enclosed areas of the heavily- and lightly-grazed pastures. The frames were level

with the soil surface and had no apparent effect on cattle activity. Five frames per treatment, spaced 5 m apart, were installed (total = 20). Canopy CER was measured with a 40 cm (height) × 100 cm × 100 cm 'Lexan' (Regal Plastics, Littleton, Colorado)<sup>1</sup> chamber, that has a closed-cell foam gasket on the base to form a seal with the frame. The air in the chamber is mixed by small fans and a sample of air is pumped to a portable infrared gas analyzer (Analytical Development Co., LCA-2, Hoddesdon, UK). CER is estimated from the rate of CO<sub>2</sub> depletion within the chamber and is calculated on a ground surface area basis. Measurements were performed rapidly (about 2 min) to minimize changes in the microclimate caused by the chamber. CER measurements were performed from 1000 to 1300 h (mountain daylight time) approximately every 3 weeks during the growing seasons of 1995, 1996, and 1997. Diurnal measurements (data not shown) showed that maximum daily CER occurred during this time of day. The order of measurements among the pastures was varied each date to avoid problems relating to time of sampling. In 1995, measurements could only be performed on six dates due to many overcast days, since measurements were only made on nearly cloud-free days.

Soil respiration rate (SRR) was measured at the same time as CER on five small plots (82 cm<sup>2</sup>) near the CER frames (PP Systems—Soil Respiration Chamber; Hertfordshire, UK). Plastic rings that form a tight seal with the soil respiration chamber were inserted about 2.5 cm into the ground. All above-ground vegetation was clipped from within each ring prior to each measurement. Since continual clipping of the vegetation could make these small areas unrepresentative of the pastures, the rings were moved twice during each growing season. In 1995, the soil respiration equipment was not available until the latter part of the season. Plant community CER was corrected for soil respiration by subtracting SRR, both calculated on a ground surface area basis. Therefore, CER comprises above-ground plant photosynthesis and plant respiration only.

On each measurement date, the point frame method was used to determine the relative photosynthetic

<sup>1</sup> Mention of a trademark or manufacturer by the USDA does not imply its approval to the exclusion of other products or manufacturers that may also be suitable.

surface area and species composition (Warren-Wilson, 1963). Although the point frame method has limitations when used to measure leaf area index (Hazlett, 1992), it was ascertained to be the best method of nondestructively measuring green surface area and species composition on repeatedly sampled plots. Green leaf, stem, and sheath “hits” (where the point of the wire touches a plant) were recorded since all three are significant contributors to photosynthesis (Caldwell et al., 1981). The point frame has 10 wires and sampling was done at 10 locations in each 1 m<sup>2</sup> frame. The total number of “hits” as these 100 wires were passed through the canopy was divided by 100 to obtain a “green vegetation index” (GVI, similar to leaf area index) for each of the 20 plots. The species of each “hit” was identified to assess species contribution to GVI. Each species was categorized into one of six functional types; C<sub>3</sub> grass, C<sub>4</sub> grass, C<sub>3</sub> forb, C<sub>4</sub> forb, shrub or crassulacean acid metabolism (CAM) species. Soil water content at the time of CER measurement was determined gravimetrically from 0 to 30 cm soil cores taken near the CER frames and converted to volumetric soil water content using soil bulk density of each plot. Air (10 cm) and soil (2.5 cm) temperatures at the time of CER measurement were also measured. Seasonal precipitation and air temperature were obtained from a nearby weather station.

Treatment mean ( $n = 5$ ) comparisons of soil water content, GVI, CER, and SRR were analyzed within each sampling date using the SAS analysis of variance procedure (SAS Institute Inc., Cary, NC). Mean CER for the growing season of each year was analyzed with the SAS analysis of variance procedure by averaging CER over all the measurement dates within each replicate frame ( $n = 5$ ). Correlations between variables were analyzed using the SAS PROC CORR procedure (Table 3). The conclusions from this analysis need to be evaluated within the limitation that there is only one true replication. A similar approach was used in previous studies with these same pastures (Hazlett, 1992; Hart, 2001).

### 3. Results

Growing season precipitation and temperature varied over the 3 years of the study (Fig. 1). Spring (April, May, June) of 1995 was uncharacteristically wet and

cool compared with long-term averages at the CPER, and was followed by a dry summer. Spring of 1996 was warmer and drier than in 1995, and was followed by a fairly typical summer and autumn. Spring of 1997 was similar to long-term averages, but a significant drought occurred from mid-June to late-July. This is not apparent in Fig. 1 as early-June and late-July precipitation were greater than normal, but can be seen in the soil water content data (Fig. 2). There were no grazing treatment differences in soil temperature taken at the time of CER measurement. Therefore, soil and air temperature data were averaged over all treatments (Fig. 3). These data again reveal the relatively cool spring of 1995 compared with 1996.

Over the 3 years of this study, there were only a few dates when a significant difference in soil water content was observed between grazed pastures and exclosures (Fig. 2). However, soil water content was often greater in the heavily-grazed pasture and it is exclosure. This was attributed to a higher water holding capacity in the heavily-grazed pasture because of higher clay content in the B horizon. Unfortunately, this limits making direct comparisons between the two grazing intensities.

Growing season patterns of CER and SRR were well associated with GVI and soil moisture. GVI increased nearly linearly from near zero in April to a maximum of about 1.5 during July of 1995 and 1996 (Figs. 4B and E, and 5B and E). The drought in July 1997 delayed peak GVI until later in the season (Fig. 6B and E). Plant community CER paralleled GVI in 1995 and 1996, and reached a maximum of about 17  $\mu\text{mol}/\text{m}^2/\text{s}$  (Figs. 4A and D, and 5A and D). The drought during July of 1997 greatly reduced CER, but plants recovered with late-season rains (Fig. 6A and D). SRR reached a maximum of about 12  $\mu\text{mol}/\text{m}^2/\text{s}$ , and coincided well with the period of highest soil moisture (Fig. 7). After the point of peak productivity, CER, SRR and GVI declined with declining soil moisture until October or November, when most vegetation was senescent.

Though seasonal trends in CER were similar over the 3 years, seasonal differences in CER in grazed pastures versus exclosures were variable across years. In 1995, CER was higher in the exclosures, compared with both grazed pastures, during the early part of the growing season (May and June; Fig. 4A

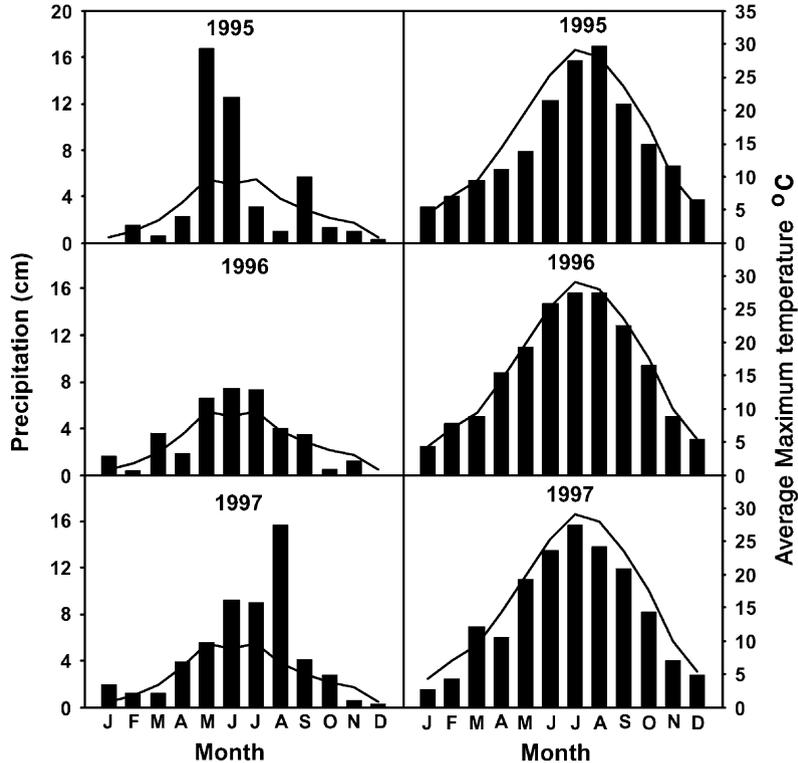


Fig. 1. Monthly total precipitation and average maximum monthly temperature at the USDA-ARS Central Plains Experimental Range during 1995–1997. The lines are long-term averages over the period 1964–1997.

and D). Differences in CER between grazed pastures and their exclosures then diminished by mid-July through September. By contrast early-season GVI did not differ significantly due to grazing (Fig. 4B and E). Early-season differences in CER between grazed pastures and exclosures were associated with the proportion of cool-season ( $C_3$ ) and warm-season ( $C_4$ ) species in these pastures (Fig. 4C and F). In the spring, the ratio of  $C_3$ – $C_4$  species was several times greater in the exclosures than in the grazed pastures. This ratio declined with the advancing growing season, as increased temperatures supported growth of  $C_4$  species.

Contrary to treatment differences in 1995, in 1996 the heavily-grazed pasture had higher CER than its exclosure during the first half of the season (Fig. 5A). GVI did not differ between the heavily-grazed pasture and exclosure during nearly the entire season of 1996 (Fig. 5B). Consistent with the 1995 data, the exclosure had a higher percentage of  $C_3$  species than

the heavily-grazed pasture in 1996, especially in the spring (Fig. 5C). However, this ratio was lower in the exclosure than in 1995 and more similar to a previous report (Hazlett, 1992).

In 1996, seasonal trends in CER in the lightly-grazed pasture were different from the heavily-grazed pasture (Fig. 5A and D). There was no difference in CER due to light-grazing early in the season, compared with its exclosure. However, the lightly-grazed pasture had higher CER on two mid- to late-season dates. There was very little difference in GVI between the lightly-grazed pasture and its exclosure, but the exclosure again had a greater percentage of  $C_3$  species (Fig. 5E and F).

In 1997, there were no significant differences in CER in the heavily-grazed pasture and exclosure during the entire season (Fig. 6A). There was a relatively rapid increase in GVI in the heavily-grazed pasture, compared with the exclosure, from days 156 to 204 (Fig. 6B). This was caused by a severe hail storm prior

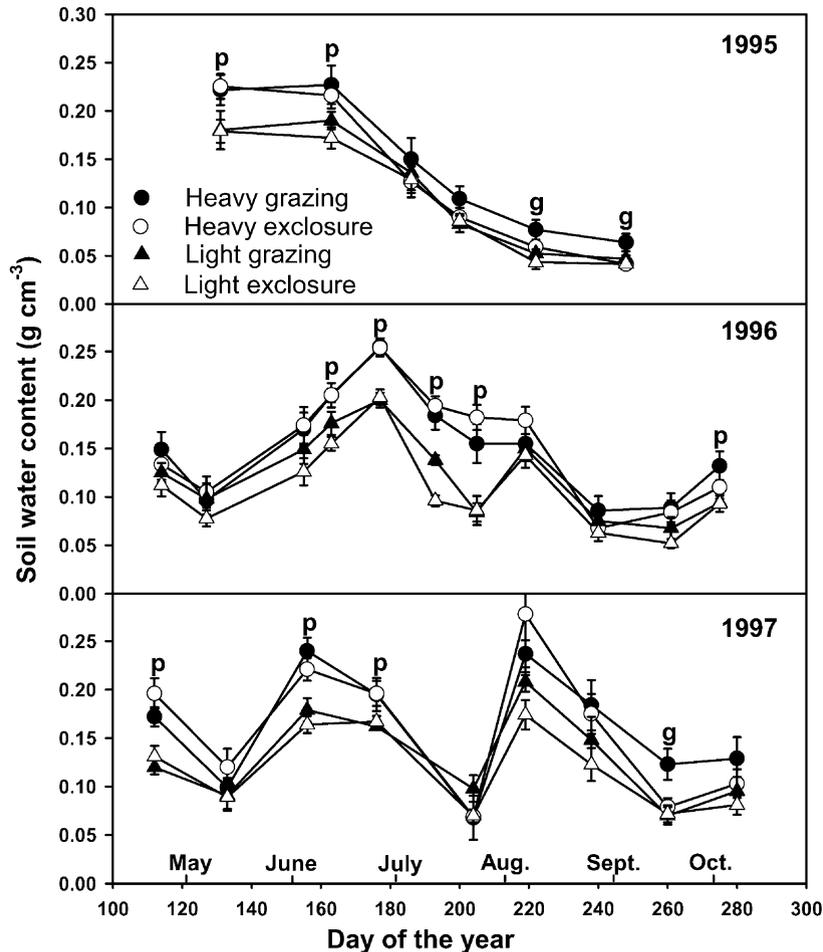


Fig. 2. Volumetric soil water content in the upper 30 cm in heavily- and lightly-grazed pastures and their accompanying exclusions during 1995–1997. The X-axis has the first day of each month marked. Data are means of three soil cores  $\pm$  S.E. 'P' denotes a significant difference due to the pasture (heavy grazed and its enclosure vs. light grazed and its enclosure) by analysis of variance ( $P \leq 0.05$ ); 'g' denotes a difference due to grazing.

to day 156, which apparently affected the plants (or the measurement technique) in the enclosure more than in the grazed plots. However, no treatment differences in CER were detected on these dates. The data from year 1997 were unique when compared with 1995 and 1996 in that the ratio of C<sub>3</sub> and C<sub>4</sub> species did not differ in the heavily-grazed pasture versus enclosure (Fig. 6C).

In 1997, the CER results from the lightly-grazed pasture (Fig. 6D) were similar to 1996 (Fig. 5D). There was little early-season difference in CER between the pasture and its enclosure, but CER of the lightly-grazed pasture was higher than the enclosure

on three mid- and late-season dates. Again, treatment differences in CER were not related to GVI (Fig. 6E).

Contrary to the CER data, there were few sampling dates where a difference in SRR was seen in grazed pastures versus exclusions. Early in the season, when most differences in CER were seen, there was no consistent difference in SRR of grazed pastures and exclusions. In 1995 there was one mid-July sampling date when the lightly-grazed pasture had higher SRR than the enclosure (Fig. 7D). In 1996 both the heavily-grazed and lightly-grazed pastures had one or two mid-season dates when SRR was higher in grazed

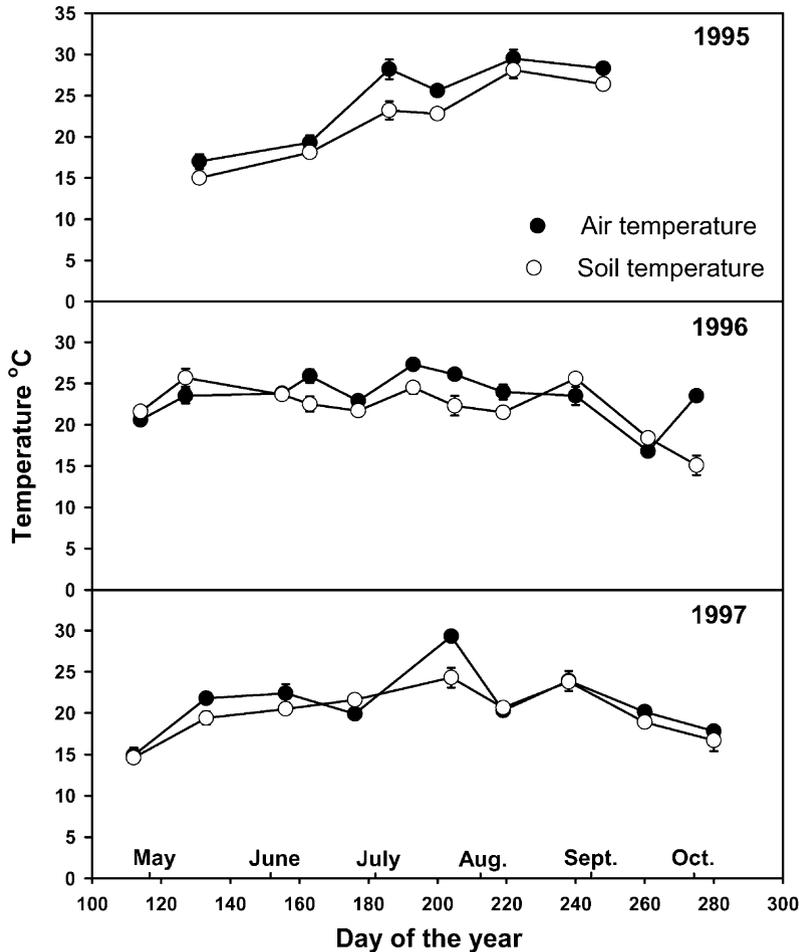


Fig. 3. Air and soil (2.5 cm) temperatures on each date of CO<sub>2</sub> exchange rate measurement in heavily-grazed and lightly-grazed pastures and their accompanying enclosures during 1995–1997. There were no differences due to grazing treatment. Therefore, data are averaged over all the treatments ( $n = 20$ ;  $\pm$ S.E).

pastures versus enclosures (Fig. 7B and E). In 1997 only the first sampling date had a treatment difference in SRR (Fig. 7C and F). There was no apparent relationship between the occasional treatment difference in SRR and the other response variables.

The data do not allow calculation of net primary productivity, but are useful for making comparisons of the efficiency of CO<sub>2</sub> assimilation in long-term grazed pastures and enclosures on the shortgrass steppe. By averaging the CER data over each season, overall trends in carbon exchange resulting from 56 years of grazing can be evaluated (Table 1). This analysis shows that there is no difference in the

mid-day, growing season carbon exchange rate in these long-term grazed pastures versus enclosures. Average CER of the heavily-grazed pasture and enclosure were slightly higher than that of the lightly-grazed pasture and its enclosure. This was likely a response to higher soil water content in the heavily-grazed pasture, rather than a response to different grazing intensity.

Species composition, indicated by the total number of species in each functional group and the percentage contribution to GVI, was averaged over all sampling dates from the 3-year study (Table 2). There is no difference in the number of grass species in the grazed and enclosed portions of these pastures. However,

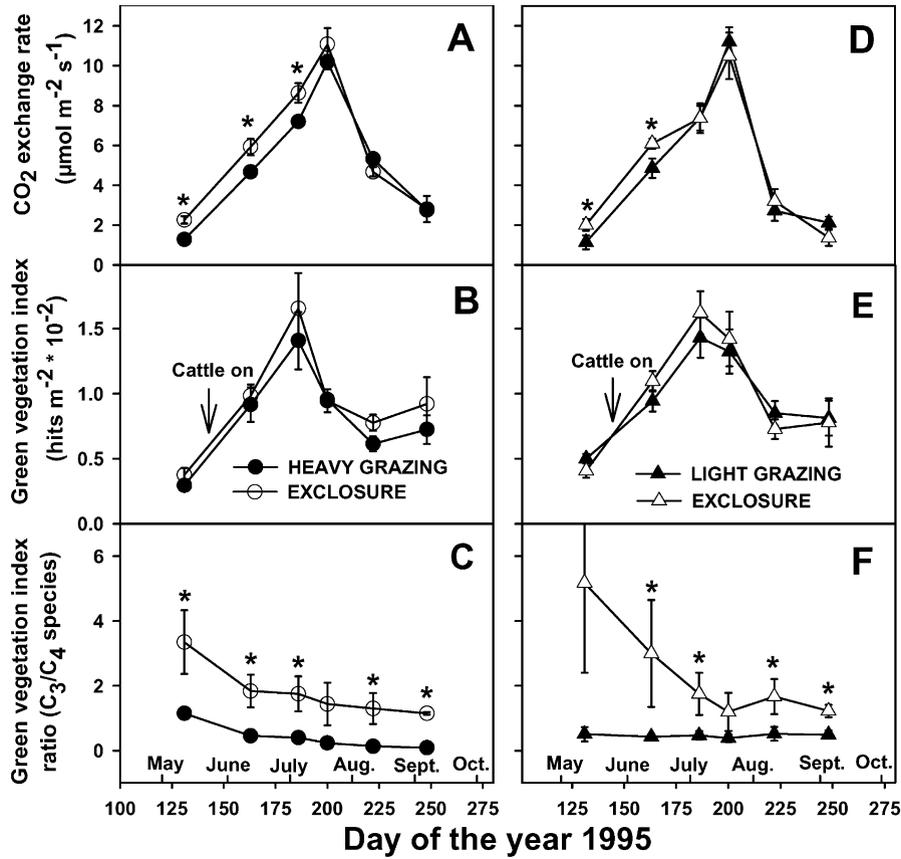


Fig. 4. The 1995 data of CO<sub>2</sub> exchange rate (corrected for soil respiration) on a ground surface area basis, green vegetation index (point frame) and the ratio of C<sub>3</sub> and C<sub>4</sub> species comprising the green vegetation index in heavily-grazed (A, B, C) and lightly-grazed (D, E, F) pastures and their accompanying enclosures. The X-axis has the first day of each month marked. Data are means of five plots ± S.E. An asterisk over the means denotes a significant difference by analysis of variance ( $P \leq 0.05$ ).

Table 1

Mid-day CO<sub>2</sub> exchange rates of grazed pastures and enclosures on the shortgrass steppe of eastern Colorado, averaged over three growing seasons<sup>a</sup>

Treatment	Year		
	1995	1996	1997
Heavily-grazed (μmol CO <sub>2</sub> m <sup>-2</sup> s <sup>-1</sup> )	5.06 ± 0.5	7.71 ± 0.6	8.24 ± 0.4
Exclosure (μmol CO <sub>2</sub> m <sup>-2</sup> s <sup>-1</sup> )	6.12 ± 0.6	6.66 ± 0.6	8.08 ± 0.8
<i>P</i>	0.206	0.226	0.872
Lightly-grazed (μmol CO <sub>2</sub> m <sup>-2</sup> s <sup>-1</sup> )	4.90 ± 0.6	6.58 ± 0.7	7.65 ± 0.5
Exclosure (μmol CO <sub>2</sub> m <sup>-2</sup> s <sup>-1</sup> )	5.15 ± 0.6	5.98 ± 0.6	7.12 ± 0.4
<i>P</i>	0.791	0.503	0.391

<sup>a</sup> Means are the average CO<sub>2</sub> exchange rate from all the measurement dates within each grazing treatment and replication over the year ( $n = 5$ ; ±S.E.). 'P' is the probability that the null hypothesis is true by analysis of variance.

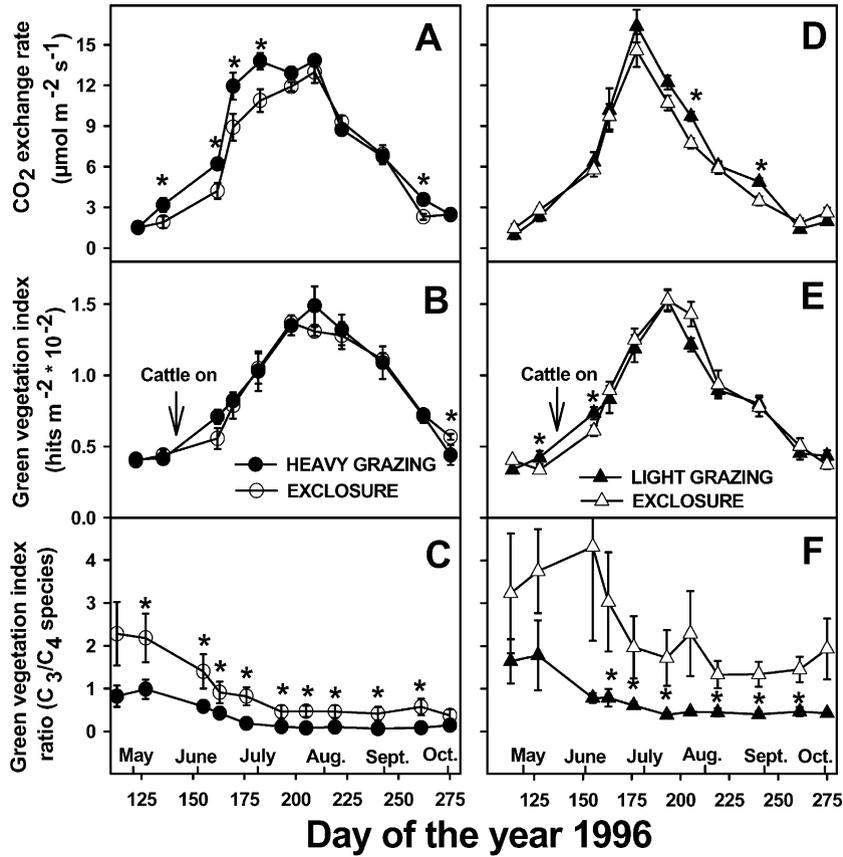


Fig. 5. The 1996 data of CO<sub>2</sub> exchange rate (corrected for soil respiration) on a ground surface area basis, green vegetation index (point frame) and the ratio of C<sub>3</sub> and C<sub>4</sub> species comprising the green vegetation index in heavily-grazed (A, B, C) and lightly-grazed (D, E, F) pastures and their accompanying enclosures. The X-axis has the first day of each month marked. Data are means of five plots ± S.E. An asterisk over the means denotes a significant difference by analysis of variance ( $P \leq 0.05$ ).

Table 2

Number of plant species and percentage of green vegetation index<sup>a</sup> (in parenthesis) of different functional types in Colorado shortgrass steppe pastures with differing cattle grazing histories

Functional type	Heavily-grazed	Exclosure	Lightly-grazed	Exclosure
C <sub>3</sub> grass	6 (10%)	6 (21%)	6 (9%)	6 (29%)
C <sub>3</sub> forb	17 (4%)	20 (8%)	15 (19%)	18 (23%)
C <sub>4</sub> grass	5 (83%)	5 (62%)	5 (66%)	5 (41%)
C <sub>4</sub> forb	1 (<1%)	1 (<1%)	1 (<1%)	1 (<1%)
Shrub	1 (<1%)	3 (6%)	2 (2%)	4 (3%)
CAM <sup>b</sup>	1 (3%)	1 (3%)	1 (5%)	2 (4%)
Total species	31	36	30	36

<sup>a</sup> Data are the mean of 130 observations averaged over the 3-year study.

<sup>b</sup> Crassulacean acid metabolism species.

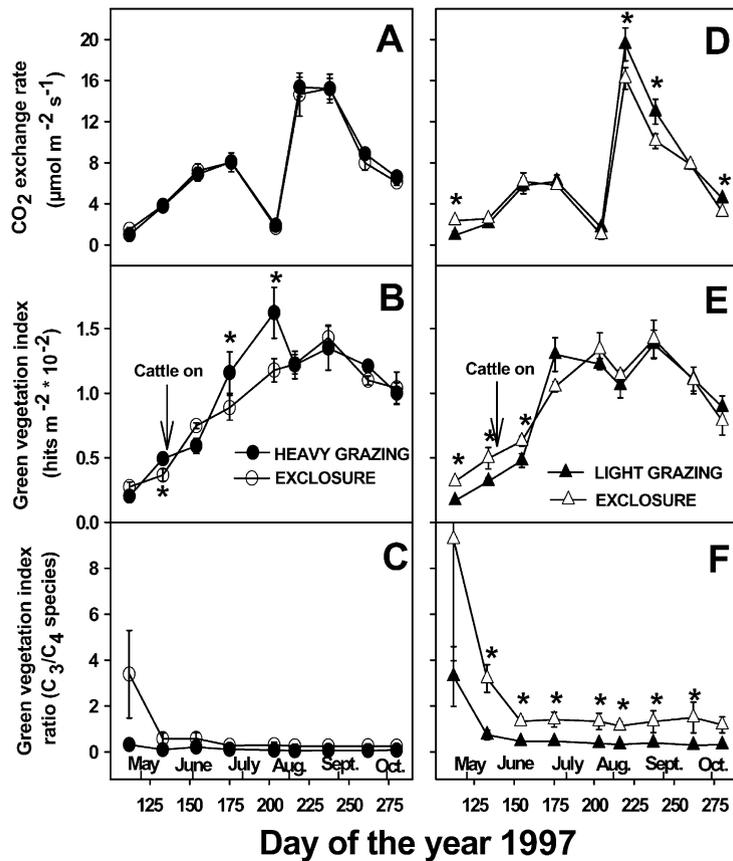


Fig. 6. The 1997 data of CO<sub>2</sub> exchange rate (corrected for soil respiration) on a ground surface area basis, green vegetation index (point frame) and the ratio of C<sub>3</sub> and C<sub>4</sub> species comprising the green vegetation index in heavily-grazed (A, B, C) and lightly-grazed (D, E, F) pastures and their accompanying enclosures. The X-axis has the first day of each month marked. Data are means of five plots ± S.E. An asterisk over the means denotes a significant difference ( $P \leq 0.05$ ) by analysis of variance.

both lightly- and heavily-grazed pastures have a lower percentage of C<sub>3</sub> grasses than the enclosures, and a greater percentage of C<sub>4</sub> grasses. There is also a slight reduction in the number of C<sub>3</sub> forbs and shrubs in the grazed pastures and therefore a slight reduction in total number of species.

## 4. Discussion

### 4.1. Plant community CO<sub>2</sub> exchange and soil respiration

Overall, there were only small and seasonal differences in plant community CERs between these grazed pastures and enclosures. When the data are

averaged over each growing season, there is no significant difference in CER in grazed and enclosed areas of this shortgrass steppe ecosystem (Table 1). This is not surprising given that the total photosynthetic surface area (GVI) was not reduced by grazing. These results agree with others who have documented only minor effects of grazing on the productivity of the North American shortgrass prairie (Milchunas and Lauenroth, 1993; Milchunas et al., 1994). Similar results were also reported in the mixed-grass prairie of Wyoming (LeCain et al., 2000). By contrast, leaf area is significantly reduced by grazing in mid-to tall-grasslands and can result in greatly reduced canopy photosynthesis and productivity (Bremer et al., 1998).

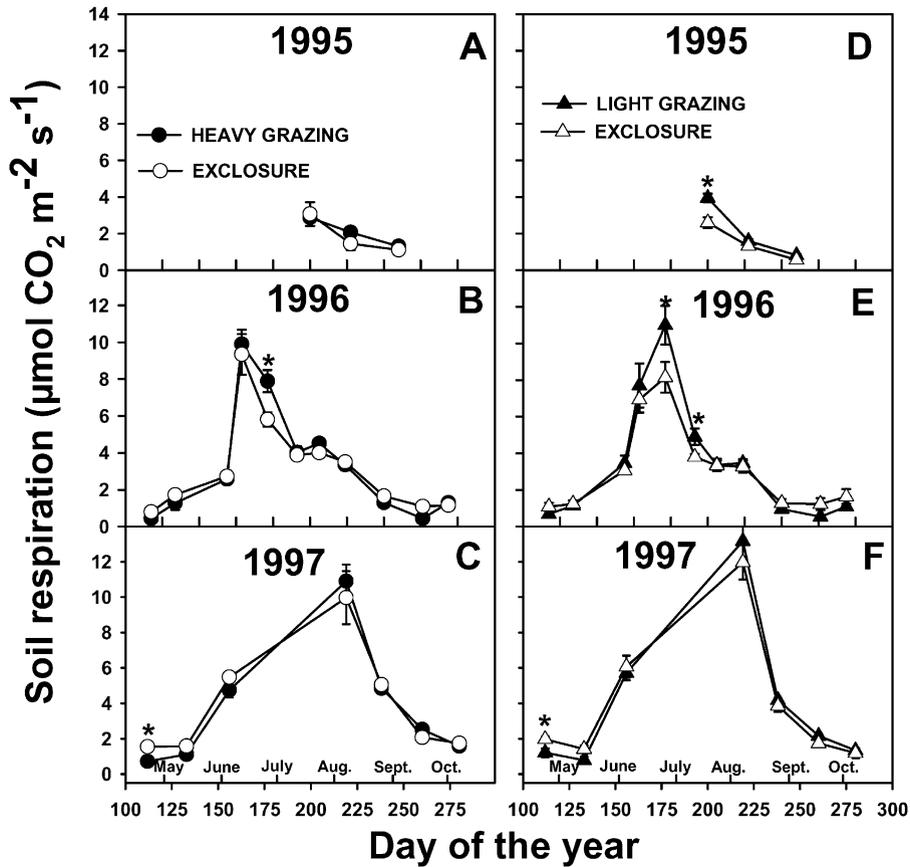


Fig. 7. Soil respiration on a ground surface area basis in heavily-grazed (A, B, C) and lightly-grazed (D, E, F) pastures and their accompanying exclosures during the growing seasons of 1995–1997. The X-axis has the first day of each month marked. Data are means of five plots  $\pm$  S.E. In 1995, the equipment was not available until the last three dates. An asterisk over the means denotes a significant difference by analysis of variance ( $P \leq 0.05$ ).

A closer look at seasonal trends in CER suggests that differences in CER are related to climate variation and the contrasting production of C<sub>3</sub> and C<sub>4</sub> species that result from long-term grazing and exclosures. The photosynthetic metabolism of warm- and cool-season species help explain the responses in the spring of the different years of the study. Optimum temperature for photosynthesis of blue grama is about 40 °C, while a maximum of 25 °C is characteristic of many C<sub>3</sub> species (Monson et al., 1983). An analysis using data from all the treatments shows that early-season (April, May, June) CER is well correlated with total GVI in all 3 years (Table 3). In 1996 and 1997, CER was well correlated with GVI of C<sub>4</sub> species, but not with GVI of C<sub>3</sub> species. This suggests that production of C<sub>4</sub> species

was primarily driving CER in the spring of these years. In the spring of 1995, CER was correlated with GVI of both C<sub>3</sub> and C<sub>4</sub> species (Table 3). Apparently, the uncharacteristic, cool conditions of spring 1995 favored the growth and photosynthetic pathway of cool-season species resulting in a greater proportion of the productivity as C<sub>3</sub> species (C<sub>3</sub>/C<sub>4</sub> GVI ratio) and greater CER in the exclosures in spring of 1995 (Fig. 4A and D). The warmer, drier climate in spring 1996 was more optimal for C<sub>4</sub> photosynthesis, resulting in favorable conditions for C<sub>4</sub> plants, and higher CER in the heavily-grazed pasture (Fig. 5A). Conditions during the spring of 1997 were such that there was no difference in C<sub>3</sub>/C<sub>4</sub> GVI ratio in the heavily-grazed and exclosed plots, and no difference in CER.

Table 3

The correlation<sup>a</sup> of CO<sub>2</sub> exchange rate with green vegetation index (GVI), air and soil temperature, and soil water content in grazed pastures and exclosures of the Colorado shortgrass steppe

Source of variation	Correlation with CO <sub>2</sub> exchange rate		
	1995	1996	1997
Total GVI	0.841 <0.0001	0.877 <0.0001	0.795 <0.0001
C <sub>3</sub> species GVI	0.632 <0.0001	-0.095 0.4339	0.189 0.0939
C <sub>4</sub> species GVI	0.6418 <0.0001	0.8986 <0.0001	0.831 <0.0001
Air temperature	0.729 <0.0001	0.6256 <0.0001	0.319 0.0038
Soil temperature	0.488 <0.0001	-0.281 0.0299	0.404 0.0014
Soil water content	-0.686 <0.0001	0.464 <0.0001	0.266 0.0086

<sup>a</sup> Pearson correlation coefficients, and probabilities that the null hypothesis is true ( $n \geq 60$ ).

Although differences in soil moisture prevent direct comparisons between heavily- and lightly-grazed pastures, the photosynthetic response of light grazing versus it is exclosure was different from that of heavy grazing versus exclosure in 1996 and 1997. The cool conditions in the spring of 1995 were atypical of this site, and therefore the growth and photosynthetic responses were somewhat unique. In the more typical years of 1996 and 1997, very little difference in CER between the lightly-grazed pasture and exclosure was seen in the spring. Warmer temperatures in the latter half of the growing season resulted in occasional higher CER in the lightly-grazed pasture due to greater percentage of C<sub>4</sub> species and senescence of C<sub>3</sub> species in the exclosed area.

Seasonal grazing treatment differences in CER could not be attributed to soil water content. Though variable across the 3 years of the study, there was little effect of grazing treatment on soil moisture. Spring-time soil water content was inconsistently correlated with CER (Table 3). Though precipitation is the primary factor influencing productivity in this ecosystem, soil moisture is typically favorable during the spring. Treatment differences in CER were also not directly related to soil or air temperature. There

was no effect of grazing treatment on soil temperature (data not shown). Seasonal trends in soil and air temperature are shown in Fig. 3. There was a fairly good correlation between early-season CER and air (all 3 years) and soil (1995 and 1997) temperature at the time of measurement (Table 3). These results suggest that early-season (when soil moisture is good) CER on this shortgrass steppe is primarily a function of photosynthetic surface area, temperature and the photosynthetic pathway of the dominate species.

These data show very little influence of these grazing intensities on soil respiration (Fig. 7). These results differ from earlier work that documented a significant reduction in soil respiration due to grazing in the US tallgrass prairie (Bremer et al., 1998). In this study, maximum SRR were about 3× of those of the tallgrass prairie, indicating very different soil microbial and root respiration activity between these two ecosystems. Since the root respiration component of soil respiration is directly affected by the translocation of assimilated carbon from the above-ground plant, and the CER data show that grazing has only minor influences on assimilation, there should be only temporary reductions in root respiration rate due to grazing in this ecosystem (Bremer et al., 1998; Detling et al., 1979). Considering data from the whole study there was a surprisingly weak correlation between SRR and soil temperature ( $r^2 = 0.25$ ;  $P = 0.09$ ), but a significant correlation with soil water content ( $r^2 = 0.76$ ;  $P = 0.0001$ ). Bremer et al. (1998) also showed a poor correlation between SRR and soil temperature, but a good correlation with soil water content.

#### 4.2. Species composition and green vegetation index

After the initial 14 years there was very little difference in the species composition of the exclosed and grazed areas of these pastures (Klippel and Costello, 1960). Averaging the data from the current study shows that after 56 years the grazed pastures had fewer C<sub>3</sub> grasses and forbs and a higher percentage of C<sub>4</sub> grasses compared to their exclosures (Table 2). Since this study sampled only a small portion of these large pastures, and the large pastures were not replicated, only limited conclusions about species

composition can be made. However, the results agree with Hazlett (1992), who performed a thorough vegetation study on these pastures. That study reported more cool-season grasses, more forbs, more litter and 20 times more standing dead biomass on the ungrazed than the grazed site. Cool-season grasses of the short-grass steppe are preferentially grazed due to their upright growth habit and early emergence (Caswell et al., 1973; Hart, 2001). In contrast, the low basal meristem of blue grama protects it from overgrazing by cattle (Knight, 1973).

Observed differences in species composition should not be attributed to “grazing” per se. The Great Plains of North America have an evolutionary history of grazing by large herbivores, in particular bison (*Bison bison* L.). Therefore, grazing by large mammals is not a disturbance, but is really the natural condition of much of the North American prairie (Hart, 2001; Milchunas et al., 1988). Species composition is actually more similar to pre-settlement conditions in the grazed pastures than in the exclosures (Hart, 2001).

GVI did not decline significantly under grazing, even in the heavily-grazed pasture (Figs. 4B, 5B and 6B). This is due to the dominance of blue grama in the heavily-grazed pasture, which was very productive under grazing (Knight, 1973; Milchunas et al., 1989). Grazing-tolerant species, such as blue grama, have adaptive traits, including basal meristems, low stature and the ability to reproduce vegetatively, that promote their survival and spread under grazing (Coughenour, 1985; Milchunas et al., 1988). By contrast, in sub-humid grasslands, where mid- to tall-grasses dominate, grazing greatly reduces photosynthetic surface area as tall-grasses are preferentially grazed by large herbivores.

Similar vegetative responses might be expected in other semiarid grasslands where limited resources (water and nitrogen) create strong competition among plant species. Plants which are grazing-tolerant have a competitive advantage when grazed and are therefore likely to increase in abundance. However, the vegetative response to grazing will be quite different in grasslands which have not evolved under grazing, such as ecosystems of the Great Basin and desert southwest of the US (Milchunas et al., 1988; Schlesinger et al., 1990). Grazing can greatly reduce the leaf area and the competitive ability of native,

grazing-intolerant species, allowing for the expansion of invader species (Mack, 1981).

#### 4.3. Global carbon cycle and management implications

Management decisions, such as grazing intensity, fire and weed control, can change a grassland from a carbon sink to a carbon source (Ojima et al., 1993). Nearly all the carbon that is utilized in an ecosystem initially enters through plant carbon assimilation. Therefore, plant community CER is a relative indicator of the productivity and “health” of the ecosystem. Soil respiration is also a relative indicator of the “health” of the soil system, being very dependent upon root respiration and soil biota activity, and the availability of organic matter. This study shows that the carbon assimilation and soil respiration components of the carbon cycle of the North American shortgrass prairie are not greatly affected by long-term cattle grazing. Whereas livestock grazing has been shown to reduce productivity and carbon sequestration in other grassland ecosystems, it appears that the shortgrass steppe can be utilized for cattle grazing without negative effects on the global carbon cycle (Keller and Goldstein, 1998; Milchunas and Lauenroth, 1993; Sims and Singh, 1978). These results agree with those of other researchers who have found this ecosystem to be quite resilient to cattle grazing (Coffin et al., 1998; Milchunas and Lauenroth, 1993; Milchunas et al., 1998). Since up to 90% of the plant-based carbon is below-ground, removal of even 60% of the above-ground plant material, as in the heavily-grazed pasture, has only minor effects on ecosystem functioning (Milchunas et al., 1998).

However, carbon exchange is only one aspect of the necessary considerations for rangeland management. Though the species composition data are limited by the small sample size, a reduction in C<sub>3</sub>, or cool-season species, was seen in the grazed pastures compared with exclosures (also see Hart, 2001 and Hazlett, 1992). Under heavy grazing, the pasture was 83% C<sub>4</sub> grasses (mostly blue grama). This decline in C<sub>3</sub> species may reduce the amount of forage available early in the season. Grazing at a light (or moderate) intensity would promote the best combination of species diversity and seasonal forage production,

with no apparent negative impact on the carbon cycle of the ecosystem (Hart, 2001).

Ultimately, the ability of grasslands to mitigate increasing global CO<sub>2</sub> depends on how much carbon is stored in the soil. A simulated annual carbon budget for blue grama suggests that up to 80% of the net carbon fixed above-ground is translocated and utilized below-ground (Detling et al., 1979). Speculation on soil carbon sequestration based on data from this study is limited due to the specific sampling conditions. Within this limitation, the data suggests that the carbon assimilation and soil respiration components of the CO<sub>2</sub> cycle are not greatly affected by cattle grazing at these intensities on the shortgrass steppe. These results agree with another shortgrass steppe study which compared NO, N<sub>2</sub>O and CH<sub>4</sub> exchange rates in grazed and ungrazed pastures (Hutchinson et al., 1997). These researchers found no effect of grazing on fluxes of these greenhouse gases. However, the observed changes in species composition resulting from grazing could alter the amount of organic carbon in the soil. Soil carbon in the 15–30 cm layer was higher in the heavily-grazed pasture compared with the enclosure (Reeder et al., 1998). This was attributed to the greater dominance, and the shallow root system of blue grama in the heavily-grazed pasture.

In conclusion, this research suggests that cattle grazing causes only small changes in plant community carbon exchange and soil respiration of the North American shortgrass steppe. These results should be useful to those attempting to characterize the components of the global carbon cycle and global climate change and also to those making rangeland land management decisions directed at maximizing carbon sequestration. Though the sample size was limited, these conclusions may provide information about other semiarid grasslands of the world, provided that the flora has evolved under grazing, where grazing-tolerant species will maintain ecosystem productivity when utilized by domestic livestock.

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