



Prescribed fire and grazing effects on carbon dynamics in a northern mixed-grass prairie[☆]

M.D. MacNeil^{*}, M.R. Haferkamp¹, L.T. Vermeire, J.M. Muscha

USDA-ARS, Fort Keogh Livestock and Range Research Laboratory, Miles City, MT 59301, USA

ARTICLE INFO

Article history:

Received 17 December 2007
Received in revised form 29 February 2008
Accepted 29 February 2008
Available online 8 April 2008

Keywords:

Abiotic environmental variation
Burning
Carbon flux
Grazing

ABSTRACT

Rangelands are complex systems that occupy more than 50% of the land area in the world. Carbon cycling on rangelands is generally understood, but details concerning agricultural management practices of prescribed fire and grazing are not well defined. Field experiments were conducted on northern mixed-grass prairie in eastern Montana with undisturbed, burned, and grazed treatments established in 2003. Designated plots were burned during the dormant season (December) in 2003. Grazing occurred in 2004 and 2005, removing 45–50% of then currently available leaf area. Responses were evaluated monthly from April to October of 2004 and 2005. Abiotic measurements included: precipitation, soil water content, photosynthetically active solar radiation, and temperatures of soil and leaves. Biotic responses were: standing crop, leaf area, root mass to a soil depth of 30 cm, and CO₂ fluxes above the mixed-grass prairie canopy and bare soil. Moisture available to the northern mixed-grass prairie system at this location was the primary identifiable factor that either directly or indirectly controlled much of the CO₂ flux. Treatment effects on seasonal changes in soil water content were consistent across years, with grazed and undisturbed plots being similar. Burned plots had less soil water content than grazed or undisturbed plots in late spring and early summer with soil water content becoming similar across all treatments in late summer and into autumn. Despite differences in soil water content, CO₂ fluxes above either burned or undisturbed plots were dynamically similar. However, peak CO₂ flux of grazed plots was shifted one month earlier in 2004 and was decreased in 2005, relative to the undisturbed and burned plots. Over the course of this experiment, cumulative CO₂ flux on the grazed plots was 72% of that on the burned and undisturbed plots. Depending on conditions during the growing season, C removed from northern mixed-grass prairie rangeland may not be re-sequestered during the growing season immediately post-burning. We conclude that the studied ecosystem is unlikely to sequester considerable C, irrespective of imposed agricultural practices, due to the relatively low CO₂ flux and the small magnitude of treatment observed.

Published by Elsevier B.V.

1. Introduction

Rangelands (i.e., unimproved grasslands, shrublands, savannas, and deserts) represent about 50% of the earth's land area (Allen-Diaz, 1996), and temperate grassland ecosystems contain 32% of the earth's natural vegetation (Adams et al., 1990). Rangelands also contain more than 33% of above- and below-ground terrestrial C reserves (Allen-Diaz, 1996; Follett et al., 2001). Inherent in all

rangeland ecosystems are both diurnal and seasonal variation in CO₂ fluxes, with the direction of the flux controlled by the balance between photosynthesis and respiratory processes (Verma et al., 1989). Precipitation or soil water content is frequently the most limiting resource affecting these processes (Meyers, 2001; Flanagan et al., 2002; Suyker et al., 2003) and ultimately net primary production (e.g., Sala et al., 1988; Sims and Singh, 1978), especially in arid and semi-arid ecosystems.

Rangelands are grazed by both wildlife and domestic livestock which are integral components of these production systems (Samson and Knopf, 1996; Williams and Diebel, 1996). Grazing may affect ecosystem processes both directly and indirectly through redistribution of biomass and nutrients (Frank et al., 2002). Several studies (e.g., Frank et al., 1995; Risch and Frank, 2006; Owensby et al., 2006) have shown grazing, at appropriate intensities, to be a carbon storage-neutral management practice. Reeder and Schuman (2002) found grazing increased C sequestration in semi-arid

[☆] This paper is a contribution from the USDA ARS and Montana Agricultural Experiment Station (MAES), Miles City, MT, USA. Mention of any trade names or proprietary products does not constitute a guarantee or warranty by the authors, USDA-ARS, or MAES nor does it imply approval of the products to the exclusion of others.

^{*} Corresponding author at: 243 Fort Keogh Road, Miles City, MT 59301, USA.
E-mail address: mike.macneil@ars.usda.gov (M.D. MacNeil).

¹ Retired.

mixed-grass and short-grass prairies. Allard et al. (2007) also found intensively grazed and managed grassland to be a slightly larger C sink than similar grassland that was less intensively grazed and managed.

Rangelands are also subjected to both prescribed and wild fires (White and Currie, 1983). Burning decreases standing dead biomass and surface litter, thus potentially increasing photosynthetically available radiation (Knapp and Seastedt, 1986). Prater et al. (2006) and Bradley et al. (2006) also indicate burning of Great Basin sagebrush communities may lead to invasion by non-native plants and degrade carbon storage capacity in these systems. However, similar invasion of burned sagebrush steppe by annual grasses was not observed in Eastern Oregon (Davies et al., 2007). Burning also results in a large combustion loss of N (Blair et al., 1998). Fire can potentially increase production of green biomass on Northern Great Plains rangelands, but White and Currie (1983) recommend that prescribed fire not be used when precipitation is limiting.

The extent of rangelands, their potential as a C reserve, and the varied activities that occur on them in agricultural production systems make understanding effects of management on CO₂ exchange necessary. Intrinsic differences among rangeland ecosystems compromise development of a consensus understanding of managerial effects on CO₂ flux and consequent C sequestration in them (Johnson and Matchett, 2001; Reeder and Schuman, 2002).

Thus, our primary objective was to determine the effects of fire and grazing on CO₂ fluxes and other measures of the biotic and abiotic state of a northern mixed prairie site. Secondly, we sought to quantify cause–effect relationships responsible for variation in CO₂ flux above the canopy and bare soil of northern mixed prairie.

2. Materials and methods

2.1. Site description

Research was conducted during 2004 and 2005 at the USDA-ARS Fort Keogh Livestock and Range Research Laboratory (lat 46°22'N long 105°5'W) near Miles City, MT, USA. General climatic conditions at this location are illustrated in Fig. 1. Annual precipitation averages 340 mm with approximately 60% received from April through September. Daily temperature extremes range from >38 °C during summer to <−40 °C during winter. The average frost-free growing season is 150 d and typically begins in early May. Temperature,

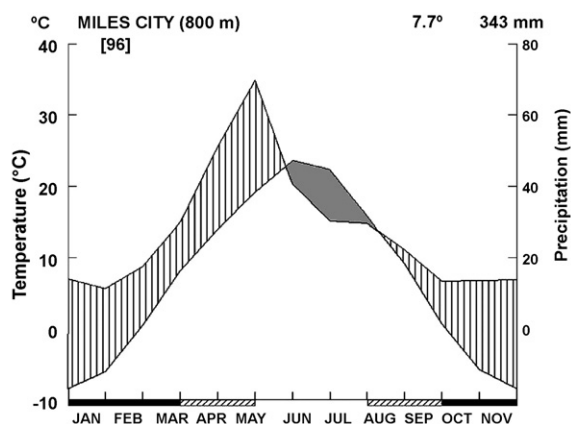


Fig. 1. Climate diagram developed for a 96-year period from data collected at Miles City, MT. Mean monthly temperature (°C) and precipitation indicate mesic spring, early summer and autumn periods interrupted by late summer and early autumn drought. Winter precipitation occurs as snow. Months shaded in black have average minimum daily temperature <0 °C, and those with diagonal lines have one or more days minimum temperatures <0 °C. Figure follows the standard form of Walter (1985).

precipitation, and photosynthetically active radiation (PAR, $\mu\text{mol}/\text{m}^2/\text{s}$) reported herein were measured at the study site.

2.2. Experimental design

Four replicate plots were established on a representative mixed prairie site with Epa fine loam soil (Haplic Regosols) located about 25 km west of Miles City, MT. Each replication was divided into three adjacent 15 m × 39 m plots which were randomly assigned to be either undisturbed, burned or grazed. Prior to imposing the treatments, there were no significant ($P > 0.1$) differences among plots in the quantity of above-ground biomass (567 kg/ha) present near the time of peak standing crop (8 July 2003) and carbon content of the above-ground biomass averaged 44.9%. Inter-plot coefficients of variation for above-ground biomass and carbon content were 13 and 1%, respectively. Burned plots were treated during the dormant season (December) prior to data collection. Grazed plots were stocked with yearling ewes during May and June of the years during which measurements were taken with the intent of harvesting 50% of currently available biomass. The grazing bouts occurred on a single day each month and were of 1–2 h in duration.

2.3. Measurements

An open-chamber gas exchange system was used to measure CO₂ flux ($\mu\text{m}/\text{m}^2/\text{s}$) above the plant canopy. Within each plot a permanent circular plot was centrally located, and a metal ring was installed that served as a base for the chamber. At 30-d prior to each day of data collection, a second chamber base was installed at a randomly selected point in each plot. At this second point, 1 d after measurement of atmospheric CO₂ flux, above- and below-ground biomass was determined as described below. At about 1000 and 2400 h, the open chamber was set on the previously installed metal ring, ventilation and mixing fans were started to insure near-ambient conditions within the chamber, and data recording was initiated after the differential between CO₂ concentrations at inlet and outlet ports became constant. The CO₂ concentration inside the chamber was measured every 30 s for a 5-min interval using a LI-COR 6400 (LI-COR Inc., Lincoln, NE, USA). The flux ($\mu\text{m}/\text{m}^2/\text{s}$) was calculated as the rate of change in CO₂ concentration. Measurements of photosynthetically active radiation and chamber temperature were recorded concurrently with measurements of CO₂. For inference to a 24-h period, the 1000 and 2400 h samples at each sample time were weighted by the number of hours of daylight and darkness, respectively, and averaged. At each sample time and across treatments, dynamic response in 24-h CO₂ flux was similar at the permanent and transient chamber base locations in each plot (data not shown). Thus, to provide greater precision in determining responses to treatment and temporal effects, the two concurrent CO₂ flux measures from each plot were averaged, and the average value was used to represent the plot.

Above-ground biomass was clipped to the soil surface at the second chamber base, described above, and sorted into herbaceous, half-shrub and cactus components. Herbaceous and half-shrub components were further sorted into live or green, current dead (tissue senesced during the current year) and old dead (previously senesced tissue) components. Leaf area was determined on live components with a photoelectric leaf area meter (LI-COR 3050-A; LI-COR Inc., Lincoln, NE, USA).

Each month, two soil cores (4.2 cm diameter × 30 cm deep) were obtained. Roots were washed from each soil core using a hydro-pneumatic root washer, dried at 60 °C for 48 h, weighed, and ground prior to laboratory analysis. For determination of soil C, soil samples were gently ground and sieved through a 1 mm screen. Small root particles passing through the screen were removed by

hand. A TR 100 soil moisture probe with a 20 cm wave guide (DYNAMAX INC, Houston, TX) was inserted at a 45° angle in each plot and buried just below the soil surface. Soil water content was measured in the field by connecting the soil probe to a Tektronix 1502C Metallic Time Domain Reflectometry (TDR) Cable Tester (DYNAMAX, INC, Houston, TX), connected to a laptop computer. The software TACQbeta was used to calculate soil water content and is available as freeware at <http://www.cprl.ars.usda.gov/programs/index.htm>.

For measurement of soil respiration, two 10.4-cm diameter by 3.5 cm PVC rings were installed in each plot at the beginning of each year. When installed, the rings projected 1 cm above the soil surface. At 4 d before each measurement, all vegetation was manually removed from the interior of each ring. Carbon dioxide concentration above the bare soil was measured using a 1 L LI-COR 6000-09 soil respiration chamber (LI-COR Inc., Lincoln, NE, USA) connected to a LI-COR 6200 (LI-COR Inc., Lincoln, NE, USA) infrared gas analyzer. The CO₂ concentration was recorded during four 15-s or three 20-s measurement cycles across a 5-min interval. Prior to each measurement cycle, the CO₂ concentration in the chamber was drawn below ambient concentration. Flux (μm/m²/s) was determined from the rate of change in CO₂ concentration using samples that spanned the ambient condition. Temperature of the soil at a depth of 8 cm was recorded concurrently.

2.4. Statistical analysis

To determine treatment effects on biotic and abiotic variables and the temporal consistency of those effects, all data were initially analyzed using PROC MIXED of SAS 9.1 (SAS Institute, Inc., Cary, NC). The linear model included fixed classification effects of year, month within year, treatment, and interactions of treatment with year and month within year. When the treatment by month within year interaction was significant, this effect was partitioned into treatment by year, treatment by month, and treatment by month by year interaction components to aid in interpretation. Random effects included in the model were replication and the replication by treatment interaction. Error variances for hypothesis testing and calculation of standard errors were: replication by treatment for treatment effects, and residual for treatment by month and treatment by month within year effects. To interpret the results, we used 3 threshold levels of significance: $P > 0.20$ as indicating no effect, $0.20 \leq P \leq 0.10$ as a region of uncertainty with respect to the existence of an effect, $0.10 > P > 0.05$ as indicating a noteworthy trend, and $P \leq 0.05$ as indicating a significant effect.

Path analysis (Wright, 1934) was used to better understand the interrelationships that affect CO₂ flux on northern mixed prairie rangeland. All variables describing the state of the northern mixed prairie system were adjusted for the fixed effects described above, and residual variances and covariances were calculated. The path diagram was structured such that measures of CO₂ flux were the ultimate response variables. A concurrently measured biotic or abiotic variable was assumed to cause variation in flux when their correlation was significant ($P < 0.05$). Abiotic measures from the preceding month were also evaluated for their potential causative contribution to the current state of the system.

3. Results

3.1. Abiotic variables

Temperatures and photosynthetically active radiation measures (Table 1) differed among months within years ($P < 0.01$), but were unaffected by treatments or interactions of treatment by year or treatment by month within year ($P > 0.20$). With the exception of

Table 1

Temperatures and photosynthetically active radiation (PAR, μmol/m²/s) measured concomitantly with CO₂ fluxes above a northern mixed prairie

	Temperatures (°C)				PAR
	Day		Night		
	Chamber	Soil	Chamber	Soil	
2004					
April	19.1	9.3	7.7	12.5	1122
May	19.3	13.8	8.8	14.7	967
June	26.8	17.9	12.4	20.5	1368
July	32.3	24.2	21.2	26.9	1308
August	28.5	22.8	16.0	24.1	1236
September	19.6	12.1	9.2	13.6	920
October	10.3	5.5	1.5	5.4	575
2005					
April	17.3	7.6	3.8	9.2	1266
May	24.0	15.3	14.0	17.1	1591
June	28.8	21.1	19.9	24.0	1549
July	34.6	26.1	21.9	29.0	1529
August	33.1	22.4	20.1	25.2	1337
September	24.9	15.9	14.4	18.1	839
October	15.8	9.4	8.8	10.5	597
S.E.	1.3	0.8	1.3	0.8	68

April, 2005 was warmer than 2004, with maximum temperatures recorded in July of each year. The decrease in temperature from August through October was also more rapid in 2004 than 2005. Photosynthetically available radiation was also greater in April through August of 2005 than in the corresponding period of 2004.

Treatments affected temporal changes in soil water content ($P < 0.01$). Seasonal dynamics of soil water content differed markedly between 2004 and 2005 ($P < 0.01$) with soils substantially drier in April, May and June of 2004 than in the same months of 2005 and the trend across years reversed for July, August and September. However, treatment effects on seasonal changes in soil water content were consistent across years. Seasonal changes in soil water content were similar for grazed and undisturbed plots. Burned plots, however, had less soil water content than grazed or undisturbed plots in late spring and early summer with soil water content becoming similar across all treatments in late summer and into autumn (Fig. 2).

3.2. Primary production

Seasonal dynamics of biomass production were markedly different between 2004 and 2005 with substantially greater biomass being produced in 2005 than 2004 ($P < 0.01$, Fig. 3A).

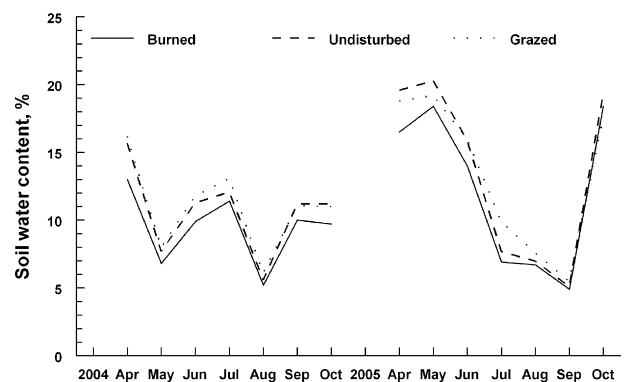


Fig. 2. Temporal changes in soil water content (S.E. = 0.91, calculated from pooled residual variance) of northern mixed-grass prairie sites that were burned, grazed, or left undisturbed.

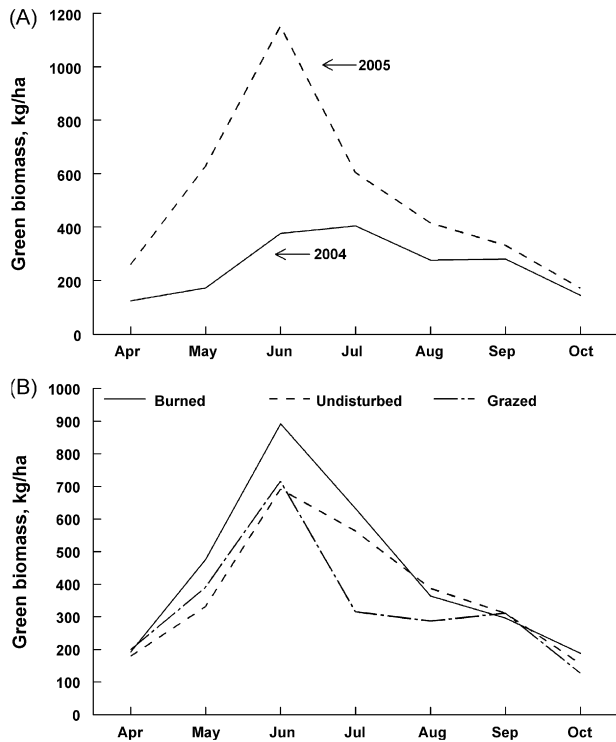


Fig. 3. Seasonal changes in the amount of green biomass on northern mixed-grass prairie sites: (A) in 2004 and 2005 (S.E. = 38), and (B) averaged over years on plots that were burned, grazed, or left undisturbed (S.E. = 47). The 3-factor interaction of treatment-month-year did not approach significance ($P > 0.20$). Standard errors (S.E.) were derived from pooled residual variance for the respective variable.

Maximum green biomass was $404 \pm 38 \text{ kg ha}^{-1}$ in 2004 and $1154 \pm 38 \text{ kg ha}^{-1}$ in 2005. Temporal changes in green biomass were affected by treatment ($P < 0.01$, Fig. 3B), but treatment by year interaction effects on these seasonal dynamics did not approach significance ($P > 0.20$). During the May–June period, green biomass was greater on burned plots than on either grazed or undisturbed plots, which were similar to each other. From June to July, green biomass on the grazed plots declined precipitously and remained nearly the same until October. In contrast, green biomass on burned and undisturbed plots decreased more gradually. By October, the amount of green standing crop was similar across treatments.

Temporal variation among treatments in currently and previously senesced biomass is shown in Fig. 4. By definition, the amount of currently senesced biomass was near zero on all plots in April of both years. In 2004, quantities of currently senesced biomass followed similar patterns across all treatments, increasing modestly through autumn. In 2005, however, undisturbed and burned plots had much more currently senesced biomass remain standing than did the grazed plots. Quantities of previously senesced biomass followed generally similar patterns on grazed and undisturbed plots across both years. Burning effectively removed most biomass in late 2003. Thus, there was little previously senesced biomass on those plots during 2004. Greater amounts of previously senesced biomass were found on the burned plots in 2005.

Within years, temporal variation in the amount of litter was not influenced by treatment ($P > 0.20$). In 2004, the amount of litter was least on the burned plots ($2.8 \pm 3.2 \text{ kg/ha}$), intermediate on the undisturbed plots ($15.1 \pm 3.2 \text{ kg/ha}$), and greatest on the grazed plots ($31.3 \pm 3.2 \text{ kg/ha}$). In 2005, amount of litter was least on the burned plots ($6.6 \pm 3.2 \text{ kg/ha}$), but similar on plots that were either undisturbed or grazed (17.2 ± 3.2 and $15.5 \pm 3.2 \text{ kg/ha}$, respectively). There was 60% greater root mass to a depth of 30 cm in 2004 than in 2005 ($P = 0.03$). However, temporal changes in quantities of roots

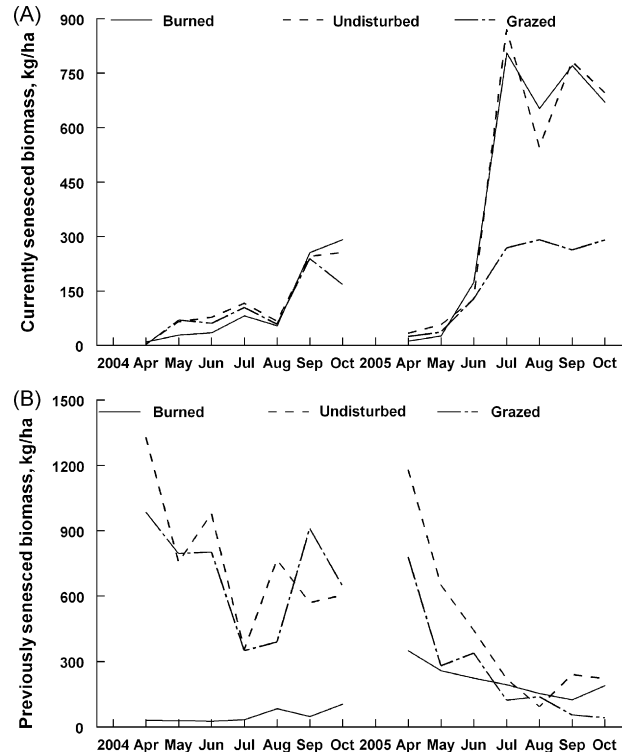


Fig. 4. Temporal changes in amounts of (A) currently senesced biomass (S.E. = 78), and (B) previously senesced biomass (S.E. = 128) on northern mixed-grass prairie sites that were burned, grazed, or left undisturbed. Standard errors (S.E.) were derived from pooled residual variance for the respective variable.

from the soil surface were not affected by treatments. Cactus was ubiquitous and invariant on the study area.

Leaf area index was affected by the interaction of year and treatment ($P < 0.01$). In 2004, leaf area index was similar across all treatments. Whereas in 2005, leaf area index was much greater than in 2004, and was greater in burned plots than in the grazed and undisturbed plots (Fig. 5). Within years, temporal variation in leaf area index was similar across treatments (data not shown).

3.3. CO_2 flux

Treatment effects on CO_2 flux above the rangeland canopy of northern mixed-grass prairie changed temporally across years and

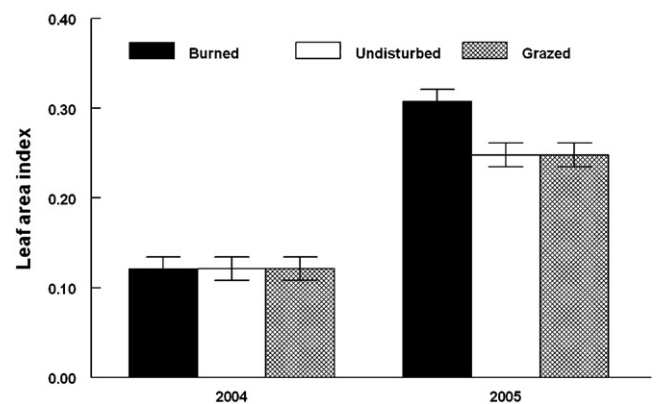


Fig. 5. Leaf area index of live biomass on northern mixed-grass prairie sites that were burned, grazed, or left undisturbed in 2004 and 2005. Standard errors of the means, calculated from pooled residual variance, are represented by the open brackets around the means.

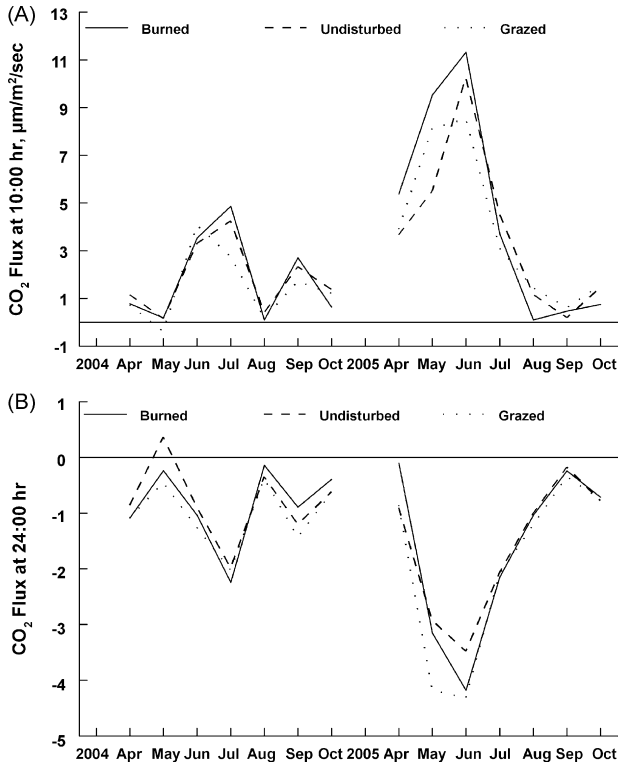


Fig. 6. Temporal changes in CO₂ flux at 10:00 h ((A) S.E. = 0.4) and 24:00 h ((B) S.E. = 0.03) above northern mixed-grass prairie sites that were burned, grazed, or left undisturbed. The standard errors (S.E.) were derived from pooled residual variance for the respective variables.

months ($P \approx 0.04$, Fig. 6). The CO₂ fluxes above either burned or undisturbed plots followed similar patterns throughout 2004 and 2005. However, a significant treatment by month within year interaction resulted from peak CO₂ flux of grazed plots being shifted one month earlier in 2004 and decreased in 2005, relative to the undisturbed and burned plots. The 24-h CO₂ flux was qualitatively similar to CO₂ flux measured at 1000 h. The CO₂ flux measured at 2400 h was invariant to treatments, but mirrored temporal changes at 1000 h. Over the course of this experiment, cumulative CO₂ flux on the grazed plots was 72% of that on the burned and undisturbed plots.

Temporal effects affected CO₂ flux above soil from which the vegetation had been removed ($P < 0.01$). Treatments may have also affected this CO₂ flux ($P = 0.07$). However, no treatment or temporal effects on biomass of roots or amount of carbon stored in soil were observed ($P > 0.20$). Burned plots released less CO₂ to the atmosphere than undisturbed plots (-1.35 ± 0.07 vs. -1.53 ± 0.07) with grazed plots being intermediate (-1.40 ± 0.07). The CO₂ fluxes were similar above the rangeland canopy at 2400 h and over bare soil (Fig. 7).

Intra-day variation in CO₂ flux over the canopy was driven by variation in the amounts of cactus and green biomass, and most importantly by the leaf area of the green biomass (Fig. 8). Interpretation of this specific result hinges on the recognition of the very large correlation ($r = 0.88$) between the amount of green biomass and leaf area. The simple correlations of leaf area and green biomass with CO₂ flux were both substantial and positive (0.67 and 0.51, respectively). However, as indicated by the significant path coefficients, with leaf area held constant a significant effect of green biomass remains and conversely with the amount of green biomass held constant a significant effect of leaf area also persists. Thus, with fixed leaf area, an increase in green biomass would be expected to reduce the C sequestered.

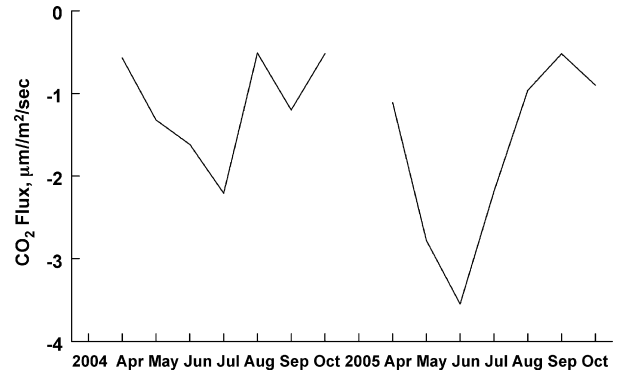


Fig. 7. Temporal changes in CO₂ fluxes above bare soils (S.E. = 0.2, calculated from pooled residual variance) of northern mixed-grass prairie sites.

Whereas, if green biomass was held constant, then increased leaf area would be expected to increase C sequestered. Thus, it may be concluded that both the amount of live biomass and its morphology contribute to the flux. As indicated by the positive path coefficients, a greater amount of soil water present the previous month had significant positive effects on the amount of leaf area, green biomass, and cactus. Effects of senesced biomass and litter on CO₂ flux above the canopy of this northern mixed-grass prairie were both indirect and relatively small.

The CO₂ flux above bare soil was concurrently affected by soil water content and the amounts of root biomass and current standing dead on the plot (Fig. 8). As expected, the current amount of soil water was positively associated with the amount of soil water present the previous month. All three direct effects on CO₂ flux were of approximately equal magnitude. Increasing the

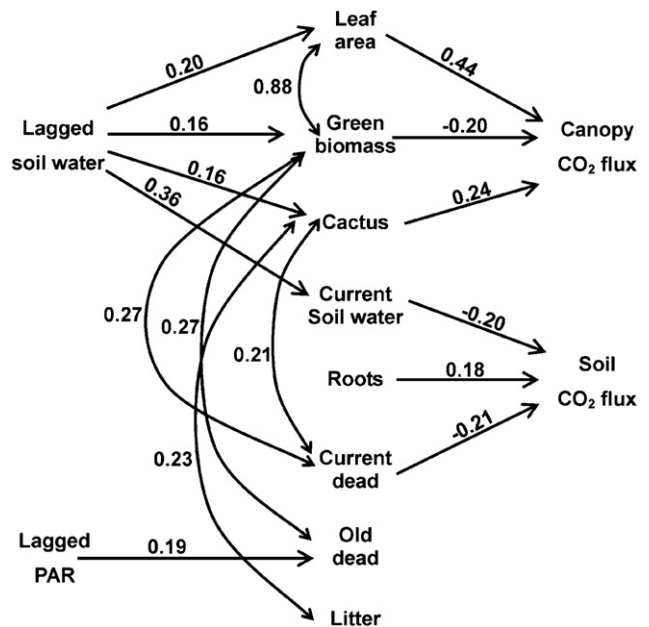


Fig. 8. Path diagram illustrating relationships of abiotic and biotic factors and their influence on CO₂ fluxes above northern mixed-grass prairie. Following Wright (1934), variables considered dependent are connected with those of which they are functions by single-headed arrows. Values above the single-headed arrows indicate the fraction of the standard deviation of the dependent variable directly attributable to factor indicated at the tail of the arrow. Values adjacent to the curved and double-headed arrows indicate residual correlations between the variables. Lagged variables indicate measurements made one month prior to the others. For simplicity non-significant relationships and unidentified residual effects have been omitted from the diagram.

amount of root biomass increased the CO₂ flux, while increases in soil water content and amount of current dead biomass decreased the amount of CO₂ lost to the atmosphere.

4. Discussion

Despite the relatively short duration of this study, seasonal changes in the state of this northern mixed-grass prairie rangeland ecosystem observed between the 2 years and within years were substantially greater than the effects of either imposed disturbance. For rangelands, as in our study, precipitation or soil water content is frequently the most limiting resource affecting primary production (e.g., Sala et al., 1988; Sims and Singh, 1978). Annual patterns of precipitation and biomass produced over the 2 years studied also conform to the prediction of Heitschmidt and Vermeire (2006) that more abundant precipitation after July 1 cannot mitigate the loss of biomass due to lack of precipitation earlier in the growing season.

The CO₂ flux values observed in this study were relatively small compared to more productive locations with 2.5 times (Knapp et al., 1998) to 4.3 times (Byrne et al., 2005) greater precipitation and those dominated by woody shrubs (e.g., Bradley et al., 2006; Prater et al., 2006). For example, Knapp et al. (1998) observed soil flux values for June that were of approximately 3- to 4-fold greater magnitude than those reported here. Further, McCulley et al. (2005) found the sensitivity of CO₂ flux to precipitation increased from short-grass steppe (345 mm mean annual precipitation) to subhumid tallgrass prairie. Hunt et al. (2004) observed the northern mixed prairie to be in carbon balance, with sagebrush steppe located within 200 km to be a net carbon sink from 1995 to 1999. Wylie et al. (2007) also estimated annual CO₂ assimilated in plants through photosynthesis and emitted back into the atmosphere through soil microbial, plant and animal respiration to be in approximate equilibrium for the Northern Great Plains rangelands during the period from 1998 to 2001. Many studies have also shown reduced CO₂ flux with the onset of drought (e.g., Verma et al., 1989; Kim et al., 1992; Meyers, 2001; Sims and Bradford, 2001).

The path diagram (Fig. 8) illustrates the primary driving variables that influenced CO₂ flux in the ecosystem being studied. Increased soil water content positively affected leaf area, green biomass production and the amount of cactus and thus it indirectly influenced CO₂ flux above the canopy of a northern mixed-grass prairie. The relative importance of leaf area among biotic variables that drive CO₂ flux was consistent with observations of Prater et al. (2006) in the Great Basin, and Suyker and Verma (2001) in the tallgrass prairie. Increased soil water content also reduced the amount of CO₂ lost to the atmosphere. This agrees with Frank and Dugas (2001) and Wylie et al. (2007), who found the C dynamics of the northern mixed-grass prairie were primarily controlled by precipitation. Despite having affected primary production in a mesic grassland (Heisler et al., 2004), the lack of any effect of litter on CO₂ flux was noted in our study. This may result from the small and relatively invariant amount of litter present on the plots. The CO₂ flux observed here above bare soil was substantially less than was observed by Knapp et al. (1998) in the much more productive sub-humid tallgrass prairie.

Wild fire is common during summer and early autumn in the northern mixed-grass prairie. However, prescribed fire is infrequently used as a management tool in this region. We found CO₂ flux over burned and unburned plots for the most part remarkably similar, despite increased green biomass on the burned plots in this northern mixed prairie. In the more productive tallgrass prairie, where prescribed fire is routinely used to increase aboveground primary production (Briggs and Knapp, 1995), fire has been shown to increase soil CO₂ flux (Knapp et al., 1998).

Ansley et al. (2002) suggested that carbon uptake following a fire might offset the initial carbon loss from combustion within 1 year. We did not measure CO₂ released to the atmosphere during burning, but note that all plots had similar quantities of above-ground biomass and litter prior to imposition of the treatments and thus carbon content of the available fuel was approximately 283 kg/ha. Based on the observed between-year differences in green biomass, any estimation of time required to re-sequester carbon released by burning in this region is critically dependent upon the abiotic state following the fire. In this study growing conditions were relatively poor immediately following the fire (i.e., in 2004). Thus, we hypothesized the time required to re-sequester carbon released by burning would be significantly extended relative to times when post-fire conditions are better. In contrast to Ansley et al. (2002), we estimated that carbon released to the atmosphere in the present study would not be replenished on the rangeland until the second year following the burn. Further, because unburned control plots continue to sequester carbon as well, there is an opportunity cost that should be considered in carbon balance calculations. The carbon released to the atmosphere by burning should be replaced by that increment of carbon sequestration from the burned area over and above the carbon sequestered by unburned rangeland. Our data collection was not of sufficient duration to ascertain the time required for the incremental increase in carbon sequestration on burned plots to offset carbon released by burning.

Grazing is the predominant agricultural land use in the rangeland ecosystems that we studied. Grazing removed green biomass and reduced the amount of currently senesced biomass in our study. A portion of this carbon was certainly translocated to the soil surface through manure and trampling, although we did not detect significant treatment effects on litter. Here, and in Haferkamp and MacNeil (2004) and Owensby et al. (2006) some differences in seasonal pattern of CO₂ flux was observed on grazed sites relative to ungrazed sites. While this variation results in the treatment by month within year effects being significant, much of this effect appears to result from differences between grazed and ungrazed plots in one or two months, near the time of peak green biomass, being asynchronous across years. In this study and to a greater degree in Haferkamp and MacNeil (2004), grazing was intense but of very limited duration offering limited opportunity for diet selection. In contrast, LeCain et al. (2000, 2002) removed similar percentages of forage from mixed-grass prairie and short-grass steppe with season-long grazing by cattle, but half the leaf blades were never grazed. Thus, while LeCain et al. (2000, 2002) observed generally increased CO₂ flux on grazed pastures relative to ungrazed pastures, the opposite effect was observed following the grazing bouts in our study and in the study of Haferkamp and MacNeil (2004). Liebig et al. (2006) found, under long-term grazing, that soils of heavily grazed northern mixed prairie accumulated more C than those that were simultaneously stocked at a lower level. This tendency for greater C sequestration with grazing than without grazing has also been observed by others (Reeder and Schuman, 2002; Allard et al., 2007). However, Frank et al. (1995), Risch and Frank (2006), and Owensby et al. (2006) among others suggested grazing, at appropriate intensities, to be a carbon storage-neutral management practice. The present results are consistent with the conclusion of Biondini and Manske (1996) that precipitation is more important than grazing or grazing system in control of ecosystem processes in Northern Great Plains grasslands. However, we are not aware of any direct comparison of grazing system effects on CO₂ flux and it does seem any statement about grazing effects on CO₂ flux should be tempered by consideration of the grazing system.

5. Conclusion

Soil water availability was the primary identifiable factor that either directly or indirectly controlled much of the CO₂ fluxes for the studied northern mixed-grass prairie. However, despite burned plots being generally drier during the growing season, burned and undisturbed plots had similar patterns of CO₂ flux above the canopy. Grazing altered the seasonal pattern of CO₂ flux relative to the undisturbed and burned plots. Depending on conditions during the growing season, C removed from northern mixed-grass prairie rangeland by fire may not be re-sequestered during the growing season immediately post-burning. Thus, the studied ecosystem is unlikely to sequester considerable C, irrespective of imposed agricultural practices, due to the relatively low CO₂ flux and the small magnitude of observed treatment effects.

References

- Adams, R.M., Rosenzweig, C., Peart, R.M., Ritchie, J.T., McCarl, E.A., Glycer, J.D., Curry, R.B., Jones, J.W., Boote, K.J., Allen Jr., L.H., 1990. Global climate change in U.S. agriculture. *Nature* 345, 219–224.
- Allard, V., Soussana, J.-F., Falcimagne, R., Berbigier, P., Bonnefond, J.M., Ceschia, E., D'hour, P., Hénault, C., Laville, P., Martin, C., Pinarès-Patino, C., 2007. The role of grazing management for the net biome productivity and greenhouse gas budget (CO₂, N₂O and CH₄) of semi-natural grassland. *Agric. Ecosyst. Environ.* 121, 47–58.
- Allen-Diaz, B., 1996. Rangelands in a changing climate: impacts, adaptations, and mitigation. In: Watson, R.T., Zinyowera, M.C., Moss, R.H. (Eds.), *Climate Change 1995, Impacts, Adaptation, and Mitigation of Climate Change: Scientific-Technical Analyses*. Cambridge Univ. Press, Cambridge, UK, pp. 131–158.
- Ansley, R.J., Dugas, W.A., Heuer, M.L., Kramp, B.A., 2002. Bowen ratio/energy balance and scaled leaf measurements of CO₂ flux over burned prosopis savanna. *Ecol. Appl.* 12, 948–961.
- Biondini, M.E., Manske, L., 1996. Grazing frequency and ecosystem processes in a northern mixed prairie, USA. *Ecol. Appl.* 6, 239–256.
- Blair, J.M., Seastedt, T.R., Rice, C.W., Ramundo, R., 1998. Terrestrial nutrient cycling in tallgrass prairie. In: Knapp, A.K., Briggs, J.M., Hartnett, D.C., Collins, S.L. (Eds.), *Grassland Dynamics: Long Term Ecological Research in Tallgrass Prairie*. Oxford Univ. Press, New York, NY, pp. 222–243.
- Bradley, B.A., Houghton, R.A., Mustard, J.F., Hamburg, S.P., 2006. Invasive grass reduces above ground carbon stocks in shrublands of the western US. *Global Change Biol.* 12, 1815–1822.
- Briggs, J.M., Knapp, A.K., 1995. Interannual variability in primary production in tallgrass prairie: climate, soil moisture, topographic position and fire as determinants of aboveground biomass. *Am. J. Bot.* 82, 1024–1030.
- Byrne, K.A., Kiely, G., Leahy, P., 2005. CO₂ fluxes in adjacent new and permanent temperate grasslands. *Agric. Forest Meteorol.* 135, 82–92.
- Davies, K.W., Bates, J.D., Miller, R., 2007. Short-term effects of burning wyoming big sagebrush steppe in southeast oregon. *Rangeland Ecol. Manage.* 60, 515–522.
- Flanagan, L.B., Wever, L.A., Carlson, P.J., 2002. Seasonal and interannual variation in carbon dioxide exchange and carbon balance in a northern temperate grassland. *Global Change Biol.* 8, 599–615.
- Follett, R.F., Kimball, J.M., Lal, R., 2001. The potential of U.S. grazing lands to sequester soil carbon. In: Follett, R.F., Kimball, J.M., Lal, R. (Eds.), *The Potential of U.S. Grazing Lands to Sequester Carbon and Mitigate the Greenhouse Effect*. Lewis Publishers, Boca Raton, FL, pp. 401–430.
- Frank, A.B., Dugas, W.A., 2001. Carbon dioxide fluxes over a northern, semi-arid, mixed-grass prairie. *Agric. Forest Meteorol.* 108, 317–326.
- Frank, A.B., Tanaka, D.L., Hofmann, L., Follett, R.F., 1995. Soil carbon and nitrogen of Northern great Plains grasslands and influenced by long-term grazing. *J. Range Manage.* 48, 470–474.
- Frank, D.A., Kuns, M.M., Guido, D.R., 2002. Consumer control of grassland plant production. *Ecology* 83, 602–606.
- Haferkamp, M.R., MacNeil, M.D., 2004. Grazing effects on carbon dynamics in the northern mixed-grass prairie. *Environ. Manage.* 33 (Suppl. 1), S462–S474.
- Heisler, J.L., Briggs, J.M., Knapp, A.K., Blair, J.M., Seery, A., 2004. Direct and indirect effects of fire on shrub density and aboveground productivity in a mesic grassland. *Ecology* 85, 2245–2257.
- Heitschmidt, R.K., Vermeire, L.T., 2006. Can abundant summer precipitation counter losses in herbage production caused by spring drought? *Rangeland Ecol. Manage.* 59, 392–399.
- Hunt Jr., R.E., Kelly, R.D., Smith, W.K., Fahnestock, J.T., Welker, J.M., Reiners, W.A., 2004. Estimation of carbon sequestration by combining remote sensing and net ecosystem exchange data for northern mixed-grass prairie and sagebrush-steppe ecosystems. *Environ. Manage.* 33 (Suppl. 1), S432–S441.
- Johnson, L.C., Matchett, J.R., 2001. Fire and grazing regulate below ground processes in tallgrass prairie. *Ecology* 82, 3377–3389.
- Kim, J., Verma, S.B., Clement, R.J., 1992. Carbon dioxide budget in a temperate grassland ecosystem. *J. Geophys. Res.* 97, 6057–6063.
- Knapp, A.K., Conrad, S.L., Blair, J.M., 1998. Determinants of soil CO₂ flux from a sub-humid grassland: effect of fire and fire history. *Ecol. Appl.* 8, 760–770.
- Knapp, A.K., Seastedt, T.R., 1986. Detritus accumulation limits productivity of tallgrass prairie. *Bioscience* 36, 662–668.
- LeCain, D.L., Morgan, J.A., Schuman, G.E., Reeder, J.D., Hart, R.H., 2000. Carbon exchange rates in grazed and ungrazed pastures of Wyoming. *J. Range Manage.* 53, 199–206.
- LeCain, D.L., Morgan, J.A., Schuman, G.E., Reeder, J.D., Hart, R.H., 2002. Carbon exchange rates and species composition of grazed and ungrazed pastures in the shortgrass steppe of Colorado. *Agric. Ecosyst. Environ.* 93, 421–435.
- Liebig, M.A., Gross, J.R., Kronberg, S.L., Hanson, J.D., Frank, A.B., Phillips, R.L., 2006. Soil response to long-term grazing in the northern Great Plains of North America. *Agric. Ecosyst. Environ.* 115, 270–276.
- McCulley, R.L., Burke, I.C., Nelson, J.A., Lauenroth, W.K., Knapp, A.K., Kelly, E.F., 2005. Regional patterns in carbon cycling across the Great Plains of North America. *Ecosystem* 8, 106–121.
- Meyers, T.P., 2001. A comparison of summertime water and CO₂ fluxes over rangeland for well watered and drought conditions. *Agric. Forest Meteorol.* 106, 205–214.
- Owensby, C.E., Ham, J.M., Auen, L.M., 2006. Fluxes of CO₂ from grazed and ungrazed tallgrass prairie. *Rangeland Ecol. Manage.* 59, 111–127.
- Prater, M.R., Obrist, D., Arrone III, J.A., DeLucia, E.H., 2006. Net carbon exchange and evapotranspiration in postfire and intact sagebrush communities in the Great Basin. *Oecologia* 146, 595–607.
- Reeder, J.D., Schuman, G.E., 2002. Influence of livestock grazing on C sequestration in semi-arid mixed-grass and short-grass rangelands. *Environ. Pollut.* 116, 457–463.
- Risch, A.C., Frank, D.A., 2006. Carbon dioxide fluxes in a spatially and temporary heterogeneous temperate grassland. *Oecologia* 147, 291–302.
- Sala, O.E., Parton, W.J., Joyce, L.A., Lauenroth, W.K., 1988. Primary production of the central grasslands region of the United States. *Ecology* 69, 40–45.
- Samson, F.B., Knopf, F.L., 1996. *Prairie Conservation*. Island, Washington, DC.
- Sims, P.L., Bradford, J.A., 2001. Carbon dioxide fluxes in a southern plains prairie. *Agric. Forest Meteorol.* 109, 117–134.
- Sims, P.L., Singh, J.S., 1978. The structure and function of ten western North American grasslands. III. Net primary production, turnover and efficiencies of energy capture and water use. *J. Ecol.* 66, 573–597.
- Suyker, A.E., Verma, S.B., 2001. Year-round observations of net ecosystem exchange of carbon dioxide in a native tallgrass prairie. *Global Change Biol.* 7, 279–289.
- Suyker, A.E., Verma, S.B., Burba, G.G.B., 2003. Interannual variability in net CO₂ exchange of a native tallgrass prairie. *Global Change Biol.* 9, 255–265.
- Verma, S.B., Kim, J., Clement, R.J., 1989. Carbon-dioxide, water-vapor and sensible heat fluxes over a tallgrass prairie. *Boundary-Layer Meteorol.* 46, 53–67.
- Walter, H., 1985. *Vegetation of the Earth and Ecological Systems of the Geobiosphere*, 3rd edition. Translated from the 5th revised German edition by O. Muise. Springer-Verlag, NY.
- White, R.S., Currie, P.O., 1983. Prescribed burning in the Northern Great Plains: yield and cover responses of 3 forage species in the mixed grass prairie. *J. Range Manage.* 36, 179–183.
- Williams, J.R., Diebel, P.L., 1996. The economic value of the prairie. In: Samson, F.B., Knopf, F.L. (Eds.), *Prairie Conservation*. Island, Washington, DC, pp. 19–35.
- Wright, S., 1934. The method of path coefficients. *Ann. Math. Stat.* 5, 161–215.
- Wylie, B.K., Fosnight, E.A., Gilmanov, T.G., Frank, A.B., Morgan, J.A., Haferkamp, M.R., Meyers, T.P., 2007. Adaptive data-driven models for estimating carbon fluxes in the Northern Great Plains. *Remote Sens. Environ.* 106, 399–413.