



Importance of Early Season Conditions and Grazing on Carbon Dioxide Fluxes in Colorado Shortgrass Steppe[☆]



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ARTICLE INFO

Article history:

Received 23 October 2015

Received in revised form 20 May 2016

Accepted 23 May 2016

Keywords:

Bowen ratio

carbon

NDVI

NEE

net ecosystem CO₂ exchange

semiarid rangeland

ABSTRACT

Understanding the influence of grazing management and environmental drivers on net ecosystem exchange of CO₂ (NEE) is essential for optimizing carbon (C) uptake in rangelands. Herein, using 15 treatment-years (two 3-yr experiments, one with three grazing treatments, the other two) and Bowen ratio flux towers, we evaluated the influence of grazing intensity, soil water content (SWC), and plant cover (Normalized Difference Vegetation Index, or NDVI) on NEE in Colorado shortgrass steppe. Among several soil water and plant cover traits evaluated over 6-yr, early season (April, DOY 91–120) SWC and early season (DOY 130) NDVI were most highly correlated with NEE (−0.96 and −0.98, respectively) during the second quarter (April to June) of the year and also over the entire growing season (April to September; −0.97 and −0.96). Due to the strong effect of early-season SWC, an average of 166 g m^{−2} CO₂ were lost in 2 yr with dry spring weather, compared with an average annual uptake of 218 g m^{−2} CO₂ in 4 yr with more abundant early-season precipitation and plant cover. Grazing effects on NEE were also apparent. In one experiment, moderate grazing resulted in annual CO₂ uptake of 267 g m^{−2} CO₂ over 3 yr compared with essentially zero NEE in heavily grazed pasture. However, that treatment difference in annual NEE was only half that experienced between dry and wet years. Similar trends were observed in a second experiment, although results were insignificant. Results suggest that the recommended moderate grazing intensity for the Colorado shortgrass steppe is near optimal for CO₂ uptake under season-long continuous grazing, with annual climatic variability sometimes being more influential. To enhance C sequestration in the western Great Plains of North America, grazing management strategies should emphasize flexible and adaptive practices that consider early-season SWC and promote vegetation cover during the key early spring growth period.

Published by Elsevier Inc. on behalf of The Society for Range Management.

Introduction

The need to understand biogeochemical cycles involving greenhouse gases is increasing as atmospheric concentrations of those gases continue to rise (Parton et al. 2015). The carbon (C) cycle remains a critical factor in this regard, with soil being the largest terrestrial reservoir, storing more than twice the C contained in Earth's atmosphere (Chapin et al. 2009; Morgan et al. 2010). A central question for agro-ecosystems worldwide is whether or not soil organic C has reached equilibrium or whether further soil C storage is possible, thereby partially off-setting greenhouse gas emissions into Earth's atmosphere. Rangelands cover

up to 50% of Earth's terrestrial surface and provide forage for much of the world's domestic livestock (Sims and Risser 1999). Soils of rangelands represent a large terrestrial reservoir of stored soil organic C (Lal 2004). Although primary production in these ecosystems has long been known to be controlled by water limitations (Noy-Mier 1973), less is known about the impacts of soil water dynamics and grazing on rangeland C balance in semiarid and arid environments.

Direct measurement of ecosystem-level fluxes of CO₂ using chamber or micrometeorological methods (Baldocchi et al. 1988) provides an essentially instantaneous measurement of the net ecosystem exchange of CO₂ (NEE) that can enhance our understanding of ecosystem C dynamics. Accurate measurements of NEE can be associated with correspondingly dynamic environmental attributes like weather and soil water content and evaluated over short time periods for examining mechanisms that underlie C cycle dynamics. Such measurements have revealed that CO₂ uptake in Great Plains rangelands occurs primarily over an approximate 3- to 4-month period during the most active part of the growing season and is approximately neutral or displays a slight

[☆] USDA-ARS Global Change Research Program provided funds for all phases of the research, and the NSF-funded Shortgrass Steppe LTER Project provided funds (DEB-1027319) for data processing, analysis, and manuscript preparation.

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net loss of CO₂ for the remainder of the year, when respiratory processes dominate NEE (Flanagan et al. 2002; Haferkamp and MacNeil 2004; Owensby et al. 2006; Svejcar et al. 2008; Polley et al. 2010; Liebig et al. 2013). As a result, long-term NEE on rangelands of this region appear to be close to neutral, with wet periods leading to CO₂ uptake and droughts to CO₂ loss (Zhang et al. 2010; Chimner and Welker 2011; Rigge et al. 2013; McGinn et al. 2014).

Rangeland NEE and its components, photosynthesis and plant and soil respiration, can respond to grazing. Not surprisingly, livestock grazing, which removes substantial leaf area, temporarily reduces canopy photosynthesis, thereby reducing canopy CO₂ uptake (LeCain et al. 2000, 2002; Haferkamp and MacNeil 2004; Owensby et al. 2006). However, because grazing stimulates initiation and growth of new photosynthetically efficient leaves (Ernst et al. 1980; King et al. 1984a, 1984b; Parsons et al. 1988), grazing often enhances photosynthetic capacity in rangelands, thus off-setting (LeCain et al. 2000, 2002; Haferkamp and MacNeil 2004; Owensby et al. 2006) and sometimes overcoming (Klumpp et al. 2011; Kang et al. 2013) the temporary negative effect of grazing on canopy photosynthesis. Greater CO₂ uptake, especially under light to moderate grazing (Kang et al. 2013), is consistent with the notion of compensatory plant growth in response to herbivory (McNaughton 1983; Owensby et al. 2006). Grazing can also affect NEE through impacts on soil respiration, although the responses are variable and potentially complex (Bremer et al. 1998; Craine et al. 1999; LeCain et al. 2000, 2002; Risch and Frank 2006; Klumpp et al. 2011; Kang et al. 2013). Heavy grazing, which drastically reduces canopy leaf area, can lead to net losses of CO₂ to the ambient atmosphere, especially during periods of low soil water content (SWC) (Chimner and Welker 2011; Otieno et al. 2011) and when rangelands are degraded (Zhu et al. 2015).

Grazing impacts on NEE in the shortgrass steppe have been evaluated with closed chambers employed several times during the growing season (LeCain et al. 2002), but no reports have yet characterized how grazing impacts long-term, continuously measured NEE in this important semiarid rangeland ecosystem of the western Great Plains. Such long-term measurements are essential for evaluating ecosystem C dynamics. To determine how grazing management and environmental factors affect NEE on shortgrass steppe, Bowen ratio energy balance (BREB) towers equipped with infrared gas analyzers for continuously monitoring CO₂ fluxes were installed and operated continuously on pastures in the Colorado shortgrass steppe from 2001 to 2006. From 2001 to 2003, three BREB towers were installed at the US Department of Agriculture – Agriculture Research Service (USDA-ARS) Central Plains Experimental Range (CPER) in northeastern Colorado on three pastures: one ungrazed, one moderately grazed, and one heavily grazed. Two of the towers from this initial experiment were subsequently installed and operated in a second experiment conducted in two other CPER pastures continuously from 2004 to 2006, one with moderate grazing, the other heavy. Our objective was to use the NEE data from both experiments to contrast the effects of grazing intensity on NEE. We hypothesized that annual NEE would be zero or negative (indicating net CO₂ uptake) under moderate cattle grazing, whereas heavy grazing would reduce annual CO₂ uptake compared to moderately grazed or ungrazed pastures. We monitored precipitation and SWC to evaluate how these attributes plus plant cover or biomass, as represented in the Normalized Difference Vegetation Index, influenced NEE.

Materials and Methods

Site Description

The experiment was conducted at the USDA-ARS Central Plains Experimental Range (CPER), lat 40°50'N, long 104°43'W at the northern limit of the shortgrass steppe, a semiarid rangeland on the western edge of the North American Great Plains used extensively for livestock grazing. The CPER is about 12 km northeast of Nunn, Colorado. Mean

annual precipitation is 341 mm with 242 mm occurring during the spring and early summer growing season (April to August). Mean air temperatures are 15.6°C in summer and 0.6°C in winter with July maximum temperatures averaging 30.6°C.

Measurements were obtained from two consecutive experiments at the CPER. The first grazing experiment (Grazing Experiment 1, GE1) was conducted on an Olney soil (fine loamy) series on upland plains (Loamy Plains ecological site: R067BY002CO) for 3 years, 2001–2003. The C₄ grass blue grama, (*Bouteloua gracilis* [Willd. Ex Kunth] Lag. ex Steud) is the dominant species at this experimental site with needleleaf sedge (*Carex duriuscula* [C.A. Mey.] being the primary C₃ perennial graminoid. Plains pricklypear (*Opuntia polyacantha* Haw.) is an important succulent plant, and scarlet globemallow (*Sphaeralcea coccinea* [Nutt] Rydb.) is the dominant forb (Milchunas et al. 2008). Three Bowen ratio CO₂ energy balance (BREB) flux towers were installed in 2000 in a 129-ha pasture that had been moderately grazed (40% annual forage removal) over the prior 50 years. This pasture was subdivided in 2001 to create three grazing intensity treatments: 1) moderate grazing intensity (with stocking rate of 0.6 animal unit months, AUM, ha⁻¹, for the mid-May to early October grazing season; size was 62 ha); 2) heavy grazing intensity (60% annual forage removal with stocking rate of 0.9 AUM ha⁻¹; 29 ha) and 3) ungrazed (38 ha). A small enclosure was constructed around the BREB systems in each grazed pasture to protect them from cattle.

A second grazing experiment (GE2) was conducted on coarse-fine loamy soils of rolling plains (Sandy Plains ecological site: R067BY024CO) over 3 later years, 2004–2006. The plant community was similar to that of GE1, with the exception that the C₃ grass needlandthread (*Hesperostipa comata* [Trin. & Rupr.] Barkworth) was codominant with *B. gracilis*. Two BREB-CO₂ towers measured the effects of moderate (again 40% annual forage removal with stocking rate of 0.6 animal unit months, AUM, ha⁻¹, for the mid-May to early October grazing season; size was 65 ha) and heavy (60% annual forage removal with stocking rate of 0.9 AUM ha⁻¹; 65 ha) grazing treatment on CO₂ fluxes in pastures that had also been previously grazed for more than 50 years at moderate levels. There was no ungrazed treatment in this experiment. The moderately grazed pasture was on a Remmit soil (coarse-loamy) series and the heavily grazed pasture on a Zigweid soil (fine loamy) series.

Net Ecosystem CO₂ Exchange Fluxes

We followed the methods of Dugas (1993) and Dugas et al. (1999) to calculate fluxes of CO₂ using a BREB system (Model 023/CO₂ Bowen ratio system, Campbell Scientific Inc., Logan, UT, USA). Details of instrumentation, calibration and measurement protocol were the same as those described previously by Frank and Dugas (2001). Briefly, temperature and humidity gradients were measured every 2 s from two arms mounted on a micrometeorological mast positioned at 1 m and 2 m height above the shortgrass steppe canopy to determine the Bowen ratio. The Bowen ratio was in turn used with measurements of net radiation at 1 m above the canopy (Model Q*7 net radiometer, REBS, Seattle, WA), average soil heat flux from two heat flux plates (Model HFT, REBS), and soil temperature to determine sensible heat flux. Turbulent diffusivity was assumed equal for heat, water vapor, and CO₂ and was calculated using 20-min averages of sensible heat flux and air temperatures measured from the two tower arms. Twenty min average CO₂ fluxes were calculated as a product of the turbulent diffusivity and the 20 min averages of the CO₂ differential between the two measurement arms, corrected for vapor density differences at the two heights. When meteorological conditions were not suitable for the BREB method of calculating turbulent diffusivity, which was about 10% of the time and occurred mostly at night when fluxes were small, we calculated diffusivity according to the method of Dugas et al. (1999) using wind speed, atmospheric stability, and canopy height. Herein, the convention for CO₂ fluxes will be to refer to them as net ecosystem CO₂ exchange (NEE),

with positive numbers representing net CO₂ losses from the ecosystem to the ambient atmosphere and negative numbers representing net uptake of CO₂ by the ecosystem from the ambient atmosphere. Negative values of NEE are composed mostly of photosynthetic CO₂ assimilation but also include components of soil and plant respiration. Positive values of NEE comprise mostly soil and plant respiration but may also include some photosynthesis during the growing season.

Flux Tower Data Processing and Gap-Filling

Standard correction procedures and outlier detection algorithms recommended for rangeland ecosystems were applied to the raw data sets of both experiments (Dugas et al. 1997, 2001; Falge et al. 2001). Observations from the BREB systems were then processed to provide continuous time series of meteorological and flux data. Interpolation and regression analysis were then used in GE1 to gap fill. In cases where lack of data precluded regression analysis, observations from another BREB tower from the experiment were used. The total percentage of missing data over all variables (22), sites (3), and years (3), after outliers were removed, was 10.4%. See Parton et al. (2012) for more details. In GE2, data files containing 20-min aggregated values of the net CO₂ fluxes (F) and the ancillary variables (incoming photosynthetically active radiation Q , air temperature T_a , soil temperature (5 cm depth) T_s , air relative humidity RH , vapor pressure deficit VPD , and others) were used as inputs for the procedure of partitioning F into gross photosynthesis (P_g) and ecosystem respiration (R_e) components as described by Gilmanov et al. (2013, 2014). The basic equations of the partitioning scheme are:

$$P_g(Q, T_s, VPD) = \frac{\varphi(VPD)}{2\theta} \left(\alpha Q + A_{max} - \sqrt{(\alpha Q + A_{max})^2 - 4\alpha A_{max} \theta Q} \right) \quad (1)$$

$$\varphi(VPD) = \begin{cases} 1, & VPD \leq VPD_{cr} \\ \exp\left(-\left(\frac{VPD - VPD_{cr}}{\sigma_{VPD}}\right)^2\right), & VPD > VPD_{cr} \end{cases} \quad (2)$$

$$R_e(T_s) = r_0 \exp(k_T T_s), \quad (3)$$

$$F_{CO_2}(Q, T_s, VPD) = P_g(Q, T_s, VPD) - R_e(T_s), \quad (4)$$

where α is the apparent quantum yield (initial slope), A_{max} is the photosynthetic capacity (plateau) of the light-response, θ is the convexity parameter (Thornley and Johnson 2000), r_0 and k_T are the coefficients of the exponential temperature response ($r_0 = R_e[0]$), and the normalized VPD -response function $\varphi(VPD)$ depends on two parameters: the critical VPD value, VPD_{cr} , below which water deficit doesn't affect photosynthesis ($\varphi = 1$ for $VPD \leq VPD_{cr}$), and the curvature parameter, σ_{VPD} ($1 \leq \sigma_{VPD} \leq 30$), lower values describing strong water-stress effect, and the higher values – weak effect (Gilmanov et al. 2013).

Parameters α , A_{max} , θ , r_0 , k_T , VPD_{cr} , and σ_{VPD} of Eqs. (1–4) describing diurnal dynamics of the CO₂ exchange were numerically fitted to the datasets of individual measurement days of each measurement year (2004, 2005, 2006) and treatment (moderately and heavily grazed). Interpolation and extrapolation of the seasonal patterns demonstrated by these parameters to days with missing measurements were used as major tools of gap-filling (in addition to statistical interpolation of short—a few 20-min. intervals—data gaps). Using the diurnal data for meteorological drivers (Q , T_{air} , T_{soil} , RH , VPD) allowed generation of the diurnal rates ($\text{mg CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) of P_g , R_e , and F based on equations (1–4).

Numerical 24-hr integration of these rates $NEE(t) = \int_{t-1}^t F(\tau) d\tau$ provided the year-round daily series of $NEE(t)$ values in $\text{g m}^{-2} \text{ d}^{-1}$ ($t = 1, 2, \dots, 365$) for corresponding years of study.

Precipitation and Soil Water Content

Tipping rain bucket rain gauges (Model TE 525 mm, Texas Electronic, Dallas, TX) and snowfall adapters were used to monitor precipitation.

Volumetric soil water content (SWC) was measured at 0–15 cm depth using calibrated water content reflectometers (Model CS615, Campbell Scientific Inc., Logan, UT). Annual precipitation during GE1 (2001–2003) was 105% (2001, 356 mm), 71% (2002, 243 mm), and 95% (2003, 322 mm) of the long-term average of 340 mm (Fig. 1). As a result, soil water content (SWC) in 2001 and 2003 was generally above 0.1 and as high as 0.2 during the spring-early summer, when net primary production in this rangeland is most responsive to soil moisture (Fig. 1A, C), and then declined later in the growing season. In contrast, SWC in 2002 stayed below 0.07 until a precipitation event on DOY 140 (May 20) pushed SWC above 0.1, although it declined to low values a few weeks later (Fig. 1B). Sustained moderate to high SWC was not achieved until DOY 238 (August 26) in 2002, too late to substantially affect plant production. As in GE1, annual precipitation during Grazing Experiment 2 (GE2; 2004–2006) varied among years, with 86% (2004, 293 mm) 109% (2005, 370 mm), and 89% (2006, 301 mm) of the long-term average (Fig. 2).

NDVI and Aboveground Plant Biomass

Seasonal patterns of remotely sensed Normalized Difference Vegetation Index (NDVI) were calculated for all pastures using MODIS data. We used 7-day 250-m resolution NDVI composites from the expedited Moderate Resolution Imaging Spectroradiometer (eMODIS) product (Jenkerson et al. 2010). Values of NDVI reported herein were all corrected by subtracting initial NDVI values (background) before the start of the growing season from observed NDVI values during the growing season.

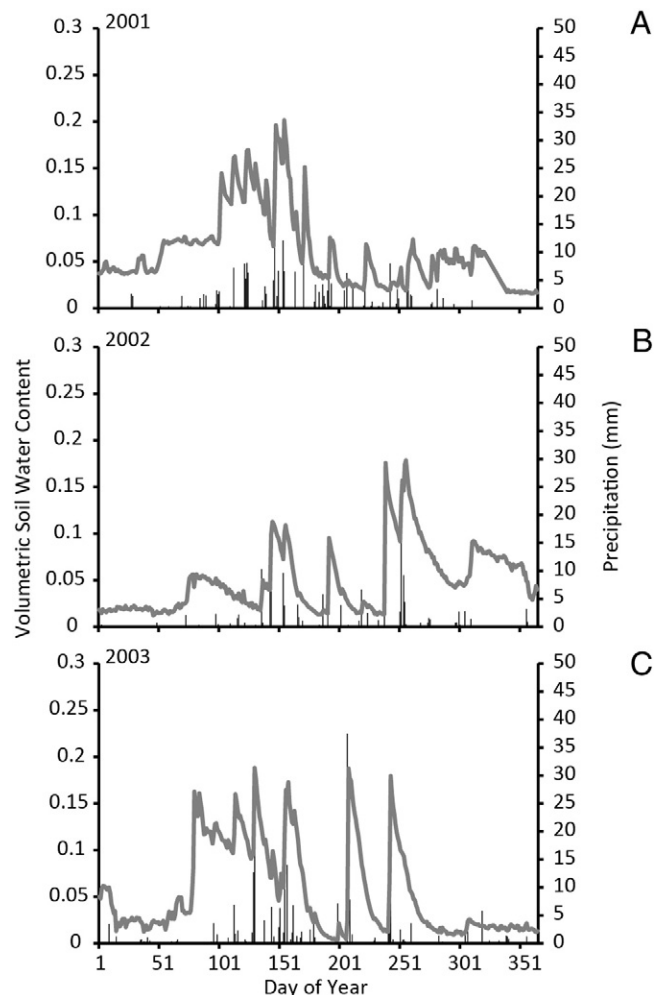


Figure 1. Daily volumetric soil water content and precipitation in Grazing Experiment 1 (GE1) for years 2001–2003. Data averaged across grazing treatments.

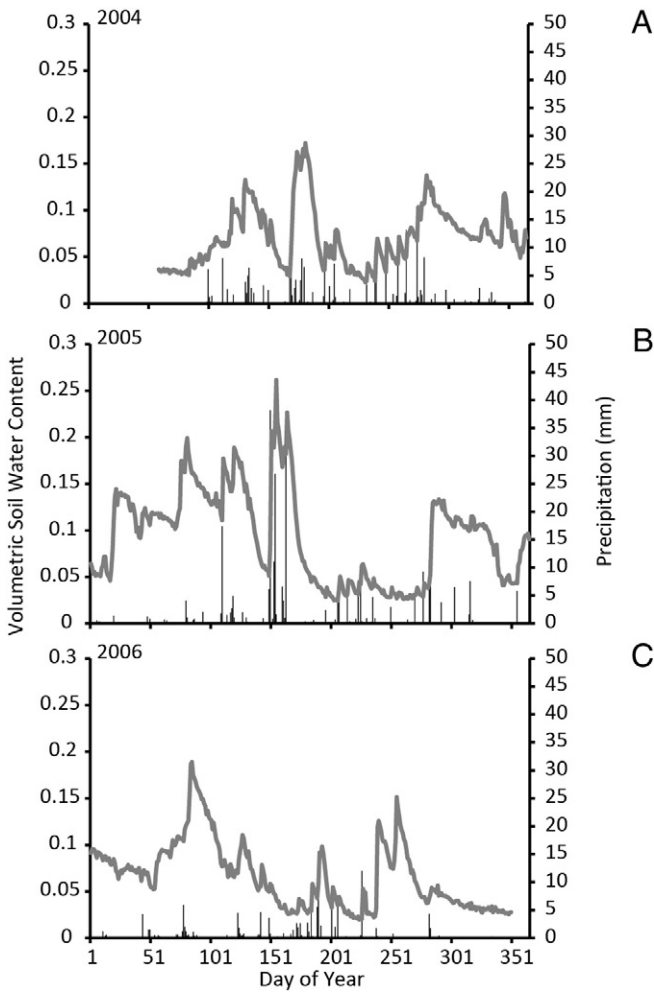


Figure 2. Daily volumetric soil water content and precipitation in Grazing Experiment 2 (GE2) for years 2004–2006. Data averaged across grazing treatments.

Seasonal patterns of standing live (green) and dead (brown or gray) plant aboveground biomass (AGB) were also measured periodically during the growing season (April to September) for the ungrazed, moderately grazed, and heavily grazed pastures from GE1 (2001–2003) (Parton et al. 2012). Measurements were determined within a 30 × 30 m sampling area that surrounded each of the BREB towers. On each sampling occasion, 1 m² quadrats were randomly located within each of the nine 10 × 10 m grids in each sampling area. Aboveground plant biomass in the quadrats was clipped by plant functional groups to the base of the vegetation (crown), separated into standing live and dead, oven-dried at 60°C, and weighed to obtain AGB. Biomass is presented as live (green, current year) materials and as totals (standing live and dead) of AGB and AGB – cactus.

Periodic measurements of plant biomass were not collected in GE2. However, we correlated the seasonal patterns in NDVI with observed green AGB for all of the grazing treatments from 2001 to 2003 and obtained a strong relationship (Fig. 3A). We therefore used these NDVI values as a surrogate for aboveground biomass or plant cover from 2001 to 2006 since we measured AGB only during 2001–2003.

Statistics

Within each of the two experiments, we first evaluated interactions of grazing treatments (*n* = 3 for GE1, *n* = 2 for GE2) by year (2001–2003 for GE1, 2004–2006 for GE2). Analyses of variance (ANOVA) (SAS, version 9.2, GLM Procedure) for grazing treatment by year interactions on NEE were assessed for both GEs over the entire year (annual), and within 3-month increments: 1) Quarter 1: January

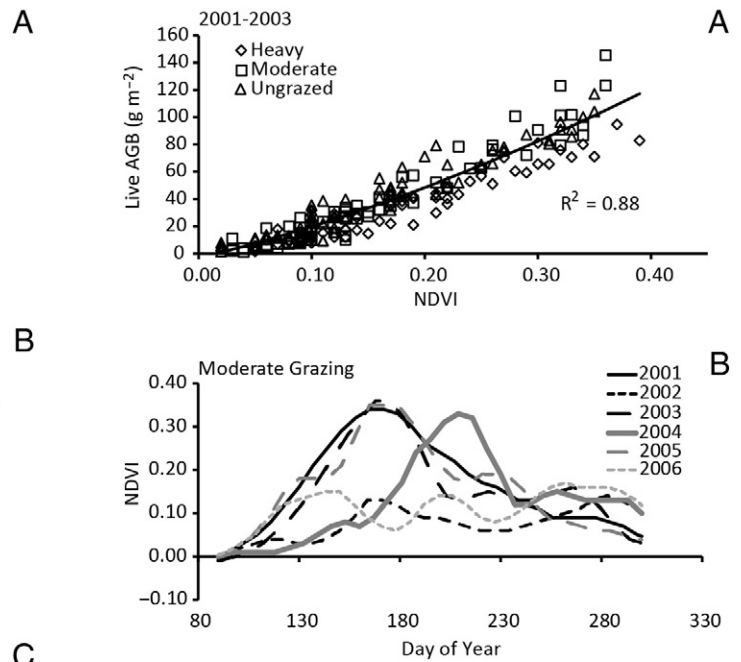


Figure 3. Relationships between A, Normalized Difference Vegetation Index (NDVI) and live aboveground biomass (AGB) in heavily, moderately, and ungrazed pastures (season-long grazing from mid-May to early October) (GE1) and B, Day of Year and NDVI for moderately grazed pastures in years 2001–2003 (GE1) and 2004–2006 (GE2). NDVI measures are corrected (see Materials and Methods).

to March, 2) Quarter 2: April to June, 3) Quarter 3: July to September, and 4) Quarter 4: October to December, as well as the approximate growing (April to September, combination of Quarters 2 and 3) and dormant (January to March and October to December, combination of Quarters 1 and 4) seasons. Among all analyses, only one significant grazing treatment by year interaction was observed, as there was considerable amount of variability. Lack of replicated pastures in both GEs necessitated the use of years or treatments as replicates, provided that there were no year-by-treatment interactions. We therefore ran the analyses again, using years as replications for determining grazing treatment effects, and grazing treatments as replications for determining year effects (Tables 1 and 2 and S1 and S2). Due to the cost and footprint of micro-meteorological measurements, replications in such experiments are typically not done. A limitation of this analysis is that it precludes discussion of possible treatment-by-year effects. LSD means comparison tests (*P* < 0.05) were conducted only when ANOVA indicated significant year or treatment effects (*P* < 0.05).

Results

Plant Cover

Some initial comments on substantial yearly differences in plant cover are discussed first, given the importance of the ecosystem photosynthetic surface in determining NEE. The effects of variable precipitation and SWC dynamics among years (see Figs. 1 and 2) on plant cover are most easily visualized from annual tracings of NDVI, presented in Fig. 3B throughout the 6 years of experiments. Results are shown for moderately grazed pastures, although patterns were similar in other pastures (data not shown). Years 2001, 2003, and 2005 indicated a common pattern of plant cover for this rangeland ecosystem (Fig. 3B), with sufficient spring moisture (see Figs. 1 and 2) to support canopy development, which peaked in late June. For the remaining years, either delayed spring precipitation (2002 and 2004), or periodic and significant dry periods of low SWC (2002, 2004, and 2006; see Figs. 1 and 2) altered the seasonal NDVI dynamics (see Fig. 3B). As a result, spring green-up was

Table 1

Cumulative yearly net ecosystem exchange (NEE) of Grazing Experiments 1 and 2, summed across grazing treatments for the dormant and growing seasons and the entire year. Bold numbers indicate means comparisons of year effects were observed at $P < 0.05$. Means with different letters following were significantly different at $P < 0.05$

Time period	Experiment	Yr	NEE ($\text{g CO}_2 \text{ m}^{-2}$)
Dormant season Jan-Mar & Oct-Dec	GE1	2001	259
		2002	160
		2003	211
	GE2	2004	208
		2005	217
		2006	60
Growing season Apr-Sep	GE1	2001	-332
		2002	-35
		2003	-399
	GE2	2004	-1 a
		2005	-534 b
		2006	-354 b
Annual Jan-Dec	GE1	2001	-73
		2002	124
		2003	-188
	GE2	2004	207 a
		2005	-317 b
		2006	-294 b

subdued in 2006 and delayed in 2004, while periodic periods of low SWC prevented significant accumulation of plant cover in years 2002 and 2006 (Fig. 3B). Significant late-spring precipitation in 2004 substantially increased SWC in July and resulted in a late but substantial growth peak near DOY 210 (July 29), more than a month later than occurred in the nominal precipitation years (2001, 2003, and 2005) at approximately DOY 170 (June 19).

NDVI measurements were unable to discern effects of cattle grazing and so are not presented. Further discussion of this and additional comments about measurements and implications of aboveground biomass evaluated in GE1 may be found in the Supplemental Materials (Figs. S1 and S2).

Year and Grazing Treatment Responses of NEE

The highest quarterly rates of CO_2 uptake (negative NEE; see *Net Ecosystem CO_2 Exchange Fluxes* section in Materials and Methods for details on NEE nomenclature) were observed from April to June (Fig. 4) in the 3

Table 2

Cumulative grazing treatment. Net ecosystem exchange (NEE) of Grazing Experiments 1 and 2, summed across study years (2001–2003 for GE1 and 2004–2006 for GE2) over the dormant and growing seasons, and the entire year. Bold numbers indicate means comparisons of treatment effects were observed at $P < 0.05$. Means with different letters following were significantly different at $P < 0.05$

Time period	Experiment	Treatment	NEE ($\text{g CO}_2 \text{ m}^{-2}$)
Dormant season Jan-Mar & Oct-Dec	GE1	U ¹	180 b
		M	131 b
		H	319 a
	GE2	M	129
		H	195
		H	-316
Growing season Apr-Sep	GE1	U	-322
		M	-316
		H	-128
	GE2	M	-396
		H	-197
		H	-142
Annual Jan-Dec	GE1	U	-186
		M	192
		H	-267 b
	GE2	M	-2 a
		H	
		H	

¹ U indicates ungrazed; M, moderately; H, heavily grazed season-long from mid-May to early October.

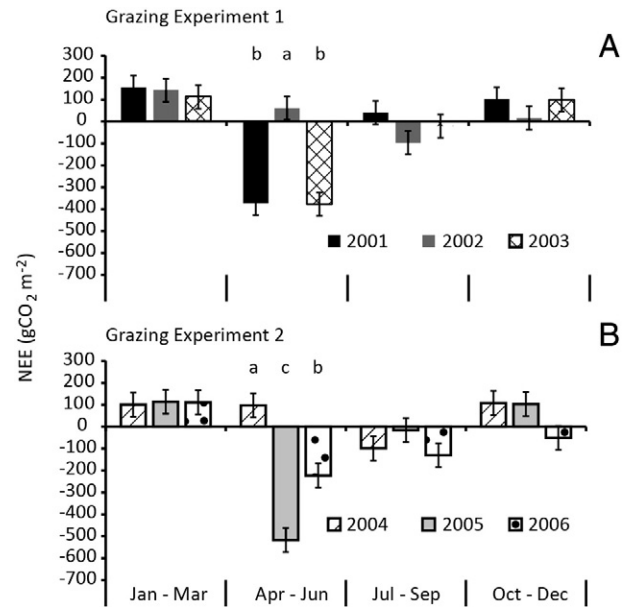


Figure 4. Quarterly (January to March; April to June; July to September; October to December) average net ecosystem CO_2 exchange (NEE) averaged across grazing treatments for each of the years in Grazing Experiment 1 (GE1; 2001–2003) and Grazing Experiment 2 (GE2; 2004–2006). See Tables S1 and S2 for ANOVA results and Figs. S3 and S4 for daily flux data (Supplemental Materials). Different letters above histograms indicate significant mean differences among years at $P < 0.05$.

years (2001, 2003, 2005) with ample spring SWC (see Figs. 1 and 2) and plant cover (see Fig. 3B), illustrating the potential dominance of photosynthetic CO_2 assimilation at this time of year. April to June CO_2 uptake was also evident in 2006, although mean values were lower than the other 3 years (see Fig. 4). Soil water constraints in 2006 (see Fig. 2C) that limited the development of plant cover (Fig. 3B) also apparently limited April to June CO_2 uptake that year. In contrast, net losses of CO_2 (positive NEE) were observed from April to June in the 2 years (2002, 2004) with low spring SWC (generally < 0.1 , see Figs. 1 and 2) and low plant cover (see Fig. 3B).

Summer (~July to September) NEEs generally indicated CO_2 uptake, but flux rates were considerably less in magnitude than observed in April to June, sometimes near zero, with net CO_2 losses observed in 2001 (see Fig. 4).

As expected, and with only one exception (October to December, 2006), the two dormant-season quarters (January to March and October to December) were characterized by CO_2 losses (positive NEE) (see Fig. 4), reflecting the dominance of respiratory CO_2 release into the atmosphere at this time of year.

Rates of NEE in the April to June quarter were reflected in the annual fluxes, with CO_2 losses of 124 and 207 $\text{g CO}_2 \text{ m}^{-2}$ measured in 2002 and 2004, and rates of uptake from 73 to over 300 $\text{g CO}_2 \text{ m}^{-2}$ in the remaining wetter years (Table 1). In GE2, significant NEE differences among years during April to June ($P = 0.02$, Table S2) plus marginal significance for year effects from July to September ($P = 0.08$, see Table S2) and the growing season ($P = 0.07$, see Table S2) resulted in significant ($P = 0.02$, see Table S2) annual differences in NEE (see Table 1). The year 2004 with the dry spring had annual NEE losses of 207 $\text{g CO}_2 \text{ m}^{-2}$ in contrast to gains averaging over 300 $\text{g CO}_2 \text{ m}^{-2}$ in years 2005 and 2006 (see Table 1).

In GE1, significant grazing treatment quarterly differences in NEE were detected only in January to March, with almost twice as high CO_2 losses occurring in heavily compared with moderately grazed or ungrazed pastures (Fig. 5A). As a result, dormant NEE fluxes differed with grazing intensity ($P = 0.007$, Table S1), with significantly greater CO_2 losses from heavily (319 $\text{g CO}_2 \text{ m}^{-2}$) compared with moderately grazed (131 $\text{g CO}_2 \text{ m}^{-2}$) or ungrazed (180 $\text{g CO}_2 \text{ m}^{-2}$) pastures

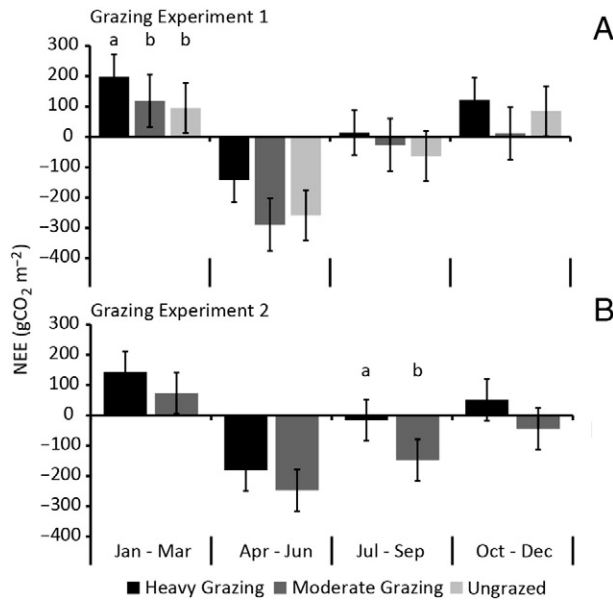


Figure 5. Quarterly (January to March; April to June; July to September; October to December) average net ecosystem CO₂ exchange (NEE) averaged across years (2001–2003 for Grazing Experiment 1, GE1; and 2004–2006 for Grazing Experiment 2, GE2) for heavily, moderately, and ungrazed pastures (season-long grazing from mid-May to early October; no ungrazed pasture in GE2). See Tables S1 and S2 for ANOVA results and Figs. S5 and S6 for daily flux data (Supplemental Materials). Different letters above histograms indicate significant mean differences among grazing treatments at $P < 0.05$.

(Table 2). Trends suggesting greater April to June CO₂ uptake under moderate grazing or ungrazed pastures compared with heavily grazed pastures were not significant (see Fig. 5A). Further, annual NEE for ungrazed ($-142 \text{ g CO}_2 \text{ m}^{-2}$) and moderately grazed ($-186 \text{ g CO}_2 \text{ m}^{-2}$) pastures indicated net uptake of CO₂, whereas the heavily grazed pasture exhibited net CO₂ losses ($192 \text{ g CO}_2 \text{ m}^{-2}$) (see Table 2). These large annual NEE treatment differences were not significant (see Table S1), due to high variability in the flux data.

In GE2, a trend suggesting greater April to June CO₂ uptake under moderate compared with heavy grazing became significant ($P = 0.02$, see Table S2) in July to September, when net CO₂ uptake under moderate grazing ($-147 \text{ g CO}_2 \text{ m}^{-2}$) was approximately 10-fold greater than that measured under heavy grazing ($-15 \text{ g CO}_2 \text{ m}^{-2}$) pastures (Fig. 5B). Growing season NEE under moderate grazing ($-396 \text{ g CO}_2 \text{ m}^{-2}$) indicated twice the rate of CO₂ uptake achieved under heavy grazing ($-197 \text{ g CO}_2 \text{ m}^{-2}$) (see Table 2); differences were marginally significant ($P = 0.07$, see Table S2). Annual NEE in GE2 was also affected by grazing treatment, with moderate grazing exhibiting significantly ($P = 0.04$, see Table S2) higher rates of annual CO₂ uptake (NEE = $-267 \text{ g CO}_2 \text{ m}^{-2}$) compared with heavy grazing, which was essentially neutral for NEE across years 2004–2006 (see Table 2). That said, the difference in NEE between these two grazing treatments ($269 \text{ g CO}_2 \text{ m}^{-2}$) was approximately half that ($524 \text{ g CO}_2 \text{ m}^{-2}$) measured between the driest (2004) and wettest (2005) years of GE2.

While there is evidence that grazing impacts on NEE in semiarid rangelands of the western Great Plains may be more evident in wet than dry years (Lecain et al. 2000; Chimner and Welker 2011), lack of significant year-by-treatment interactions for NEE in this experiment precluded any evaluation of such (see Materials and Methods).

Environmental Relationships

To better understand environmental and ecosystem effects on NEE, we evaluated relationships between cumulative NEE during the two spring-summer quarters (Q2, April to June; Q3, July to September)

and the full growing season (Q2 + Q3, April to September) to several temporal measurements of SWC, NDVI, precipitation, and number of rainfall events (Table S3). April to June (~spring) and April to September (~whole growing-season) NEE were best predicted by early growing season (May 10) NDVI and early growing season (April 1–31, DOY 91–120) SWC (Fig. 6; see Table S3). April to June NEE was also significantly associated with corresponding April to June measures of NDVI ($r = -0.93$) and SWC ($r = -0.83$), but not as significantly as the early growing-season measures (see Table S3). Whole growing-season measures of NDVI or SWC were moderately correlated with whole growing-season NEE ($r = -0.62$ and -0.77); in the case of NDVI the relationship was nonsignificant (see Table S3). In Q3 (July to September), correlations of NEE to environmental/ecosystem variables were, with one exception (SWC), nonsignificant (see Table S3).

Discussion

Environmental and Seasonal Responses

Previous reports indicate spring soil moisture is critical for promoting CO₂ uptake and plant production in rangelands of the North American Great Plains (Sims et al. 1978; Milchunas et al. 1994; Flanagan et al. 2002; Derner and Hart 2007; Derner et al. 2008; Svejcar et al. 2008; Polley et al. 2010; Zhang et al. 2010; Chimner and Welker 2011; Wiles et al. 2011; Parton et al. 2012; Rigge et al. 2013). Results from this experiment confirm the importance of spring soil moisture in determining not only the April to June rate of NEE, but also for the entire growing season (Fig. 6). Our results go further in indicating that, at least for the shortgrass steppe, early spring moisture, essentially the month of April, may be slightly more predictive for NEE than are conditions throughout the entire second quarter (April to June, ~spring, see Table S3). Early-spring moisture sets the potential for the entire and critical spring growth season and may be especially important for the shortgrass steppe (Polley et al. 2010). In addition to the direct benefits of soil moisture on plant growth, having adequate to optimal soil moisture in early spring (April) is important for promoting plant leaf area and nitrogen mineralization early in the growing season (Schimel and Parton 1986; Hook and Burke 2000), both of which enhance canopy photosynthesis and drive springtime CO₂ uptake, and can affect the entire growing season.

The importance of environmental attributes on NEE was less apparent in the second half of the growing season, the approximate summer months. While July to September NEE was also negatively correlated (CO₂ uptake) to average SWC of that quarter, correlations with NDVI and precipitation were positive (CO₂ loss) and not significant (see Table S3). An important implication of these relationships is that the occurrence of peak plant cover or biomass needs to occur in early spring to maximize CO₂ uptake. This is illustrated nicely in 2004 when significant plant cover was reached more than a month later than occurred in normal precipitation years, and a net loss of CO₂ still resulted. In contrast, an annual net CO₂ uptake was realized in 2006, a year of adequate spring plant cover, but a generally dry year in which NDVI values (e.g., plant cover) never reached half those measured in midsummer of 2004. Despite the importance of biomass and leaf area index in affecting the photosynthetic capacity of a stand (Flanagan et al. 2002; Frank 2002; Polley et al. 2010), our results suggest that early season moisture ensures peak plant cover occurs in spring when the conditions are generally most optimal for CO₂ uptake in the shortgrass steppe. Later in summer, warmer and drier conditions may lower photosynthetic performance, even when adequate biomass is present (Polley et al. 2010). Further, later-season precipitation can result in significant respirational losses in summer (Flanagan et al. 2002; Schwinning and Sala 2004; Munson et al. 2010; Parton et al. 2012; Zhu et al. 2015). All of this underscores the importance of achieving high leaf area early in the growing season for maximizing annual CO₂ uptake, especially in rangeland communities with dry summers.

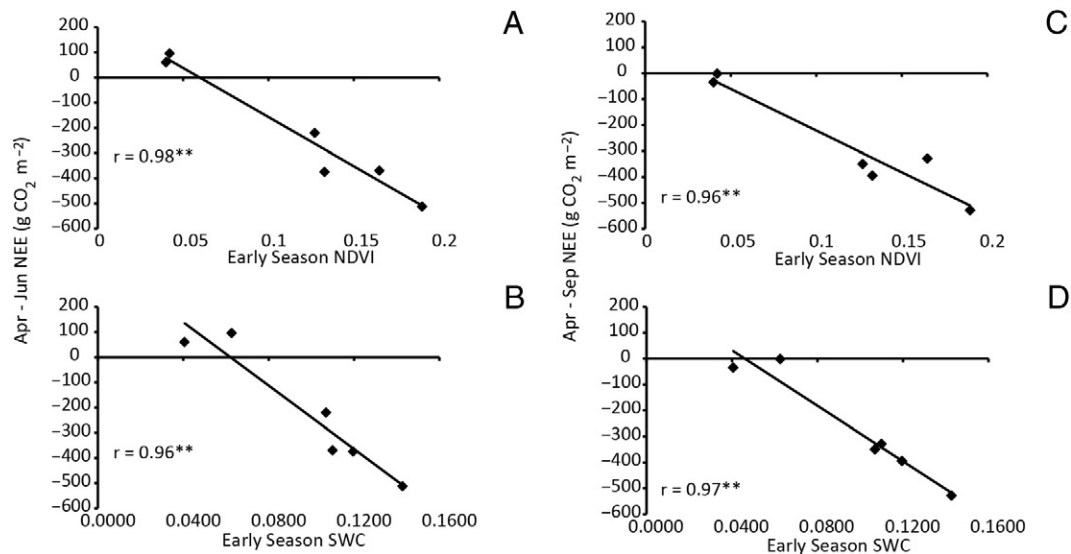


Figure 6. Effects of early growing season (DOY 91–120) soil water content (SWC) and NDVI (Day 130) on net ecosystem CO₂ exchange (NEE) determined for –spring quarter (April to June; DOY 91–181) and growing season (April to September; DOY 91–273) for 6 years (2001–2006). Data were averaged across moderate and heavy grazing treatments for Grazing Experiments 1 and 2. See Table S3 for more details (Supplemental Materials).

Grazing Responses

Although few significant effects of grazing treatment were observed in GE1, similar rates of NEE observed in moderately grazed and ungrazed pastures (see Fig. 5A, Table 2) support previous work that suggests moderate defoliation may have little long-term effect on canopy photosynthesis and may sometimes enhance it due, in part, to trade-offs between the loss of photosynthetic surface and the gain of more photosynthetically efficient leaves under grazing (LeCain et al. 2000, 2002; Haferkamp and MacNeil 2004; Owensby et al. 2006; Klump et al. 2011; Kang et al. 2013). In this experiment, these trade-offs appeared to be in balance, with no net effect of moderate grazing on NEE compared with the ungrazed pasture.

Results from both experiments indicate potentially negative effects of heavy grazing on CO₂ uptake. The grazing treatment response was clearest in GE2, with a trend suggesting 37% higher CO₂ uptake under moderate compared to heavy grazing during April to June, becoming significant with 10-fold higher July to September CO₂ uptake under moderate grazing (see Fig. 5B). While most CO₂ uptake generally occurs in the spring (see Fig. 4), grazing does not commence until mid-May. Thus, the accumulated effects of grazing practices became more apparent and easier to detect later in the growing season. Similar, but nonsignificant trends were observed in GE1. Important as this grazing effect was on an annual basis (see Table 2), it was only about half that due to yearly differences in net CO₂ uptake of over 500 g CO₂ m⁻² due to soil water availability.

The negative impact of heavy grazing on CO₂ uptake is likely a response to removing sufficient foliage as to diminish the photosynthetic surface of the rangeland for much of the growing season, thereby reducing stand photosynthetic capacity. Although no plant data were available for GE2 (and NDVI could not detect grazing responses throughout, see Supplemental Materials), grazing treatment reductions in July to September leaf area must have been sufficient to result in lower photosynthesis in the heavily grazed pasture (see Fig. 5B). Unlike the GE1 pastures that were dominated by the prostrate C₄ grass *B. gracilis*, GE2 pastures had a high abundance of more erect C₃ grasses (especially *H. comata*) that are easily defoliated under grazing, which could have resulted in significant leaf area differences between grazing treatments, increasing treatment differences in stand photosynthetic capacity and the ability to detect treatment effects on NEE.

Results from GE1 were important in illustrating that grazing practices may also affect dormant season (October to March) fluxes.

Significantly higher dormant season NEE (more CO₂ loss) ($P = 0.007$, see Table S1) under heavy grazing compared with moderately grazed or nongrazed (see Fig. 5A, January to March) was due to higher rates of ecosystem respiration, which in the dormant season is essentially soil respiration. While not significant, we observed the same trend of higher dormant season soil respiration under heavy grazing in GE2, due to higher NEE rates measured from January to March (see Fig. 5B). Chamber measurements of NEE conducted on a nearby rangeland showed a strong trend for greater soil respiration in the heavily grazed pasture early in the growing season (LeCain et al. 2000). Responses of soil respiration to grazing are a complex function of management effects on the abiotic and biotic environment (Balogh et al. 2011; Klump et al. 2011; Zhu et al. 2015). Possible reasons for higher soil respiration under heavy grazing in the dormant season include increases in soil temperature due to a more open canopy and less surface litter (LeCain et al. 2002; Chimner and Welker 2011), grazing-induced increases in root turnover that supply more carbon to belowground microbes (Dawson et al. 2000), and cattle excrement-stimulated microbial activity (Nichols et al. 2016). The shortgrass steppe is especially resilient to grazing (Milchunas et al. 1988; Augustine et al. 2012), which may explain why even heavy grazing in this rangeland ecosystem may not immediately lead to lower soil respiration. However, heavy grazing under a protracted drought can lead to C loss (Ingram et al. 2008) and presumably longer-term heavy grazing than the 3 years experienced by pastures in the present studies would eventually lead to lower respiratory losses in concert with lowered photosynthetic performance (Bremer et al. 1998; Craine et al. 1999; Owensby et al. 2006; Polley et al. 2010; Kang et al. 2013; Liebig et al. 2013).

Conclusions

These two experiments extend and elaborate on earlier studies that emphasized the importance of early-season NEE on the annual C balance of dry rangelands (e.g., Svejcar et al. 2008), particularly for the shortgrass steppe (Polley et al. 2010). Our results illustrate that annual NEE rates, which averaged 166 g CO₂ or 50 g C lost in each of 2 years with dry early seasons (2002 and 2006) and an average 218 g CO₂ or 59 g C gained in each of the 4 remaining years with wetter springs (2000, 2003–2005) (for a total of 540 g CO₂ or 147 g C gained over the 6 years), were driven primarily by differences in SWC, with April SWC levels being most predictive of spring and annual NEE fluxes. Ample spring soil moisture enhanced CO₂ uptake by establishing a plant

canopy of young, photosynthetically efficient leaves at a time of year when conditions were optimal for photosynthesis. Later growing season moisture was less effective for assimilating CO₂, even with substantial standing biomass. Heavy grazing decreased CO₂ uptake compared with moderately grazed pastures, although differences were only significant in GE2. Further, the magnitude of the grazing effect on annual NEE in GE2 was approximately half that experienced between dry and wet precipitation years, supporting previous experiments in the Great Plains indicating yearly differences in weather often have greater effects on NEE than do grazing practices (Flanagan et al. 2002; Chimner and Welker 2011). Pastures of GE2 were composed of a more balanced mixture of C₃ and C₄ perennial grasses compared with GE1, in which the C₄ *B. gracilis* dominated. These pasture differences in plant community may have been important in the clearer grazing response observed in GE2, although variable flux data in GE1 was certainly a factor as well. Results of the grazing treatments provide evidence that moderate grazing can often enhance annual CO₂ uptake over heavy grazing. Results are partially consistent with our hypothesis of greater CO₂ uptake under moderate compared with heavy grazing, but the lack of consistency between GE1 and GE2 and net losses of CO₂ in dry years indicates that even moderate grazing cannot ensure annual net CO₂ or C gain.

Implications

April (or spring) SWC and plant cover data can be used to predict seasonal, as well as annual, CO₂ uptake and forage production. Such information can be used to develop grazing management strategies on the basis of these important ecosystem attributes. Strategies for season-long grazing will likely not differ much from those already advanced toward optimizing livestock performance since the presently recommended moderate stocking rate appears near optimal for CO₂ uptake. However, adaptive grazing management involving seasonal changes in stocking density, as well as seasonal use of pastures that are rotated across years (Roche et al. 2015), should benefit from using early-season SWC and plant cover information. Such information can optimize seasonal livestock performance and promote high photosynthesis rates that will have the potential to further increase soil organic matter. For maximizing CO₂ uptake and enhancing soil organic C, stocking should be done in a manner that maintains leaf area as much as possible in the critical spring months. Increases in soil organic C can enhance pasture condition and future performance by increasing soil health and, perhaps most importantly, greater water-holding capacity. Further research involving adaptive grazing management is necessary to evaluate trade-offs between animal performance and both short-term (NEE) and longer-term (soil organic C) pasture responses to grazing strategies to determine to what extent such potential can be realized.

Acknowledgements

Thanks to Dan LeCain, Jeff Thomas, Mary Ashby, Lisa Van Amburg, and Agnes Przeszlowska for field data collection and sample processing; Susan Lutz for figure development; and Matt Mortenson for statistical assistance. Thanks to Dan LeCain for assistance with Bowen ratio flux measurements. Livestock used in the experiments was provided by the Crow Valley Livestock Cooperative, Inc.

Appendix A. Supplementary Data

Supplementary data to this article can be found online at <http://dx.doi.org/10.1016/j.rama.2016.05.002>.

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