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Carbon dioxide efflux from long-term grazing management systems in a semiarid region

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ABSTRACT

Grazing management can affect grassland carbon (C) dynamics, yet limited information is available documenting management effects on carbon dioxide (CO_2) efflux. A study was conducted to quantify the role of long-term grazing management to affect CO_2 efflux within the semiarid northern Great Plains of North America. Grazing management systems evaluated in the study included two native vegetation pastures differing in stocking rate [moderately grazed pasture (MGP), heavily grazed pasture (HGP)] and a fertilized, grazed crested wheatgrass [*Agropyron desertorum* (Fisch. ex. Link) Schult.] pasture (CWP) near Mandan, ND, USA. Carbon dioxide efflux was measured on 1–2 week intervals for three years using static chamber methodology. Supplemental assessments of soil temperature and water content, aboveground live biomass, root biomass, and soil microbial biomass C were conducted during each growing season. Carbon dioxide efflux did not differ between native vegetation pastures differing in stocking rate. However, mean hourly CO_2 efflux was greater in CWP ($100.1\,\text{mg C m}^{-2}\,\text{h}^{-1}$) than HGP ($81.1\,\text{mg C m}^{-2}\,\text{h}^{-1}$) ($P = 0.03$), a result attributed to prevalence of cool-season grass and high available N in CWP. Carbon dioxide efflux differed among grazing treatments during spring (March–May) and fall (September–November), but not winter (December–February) and summer (June–August). Associations between CO_2 efflux and abiotic factors were seasonally dependent, with positive associations between efflux and soil temperature during spring ($r = 0.71$, $P \leq 0.01$) and fall ($r = 0.45$, $P \leq 0.01$) and efflux and water-filled pore space (WFPS) during summer ($r = 0.46$, $P \leq 0.01$). In this study, increased stocking rate did not contribute to elevated CO_2 efflux within native vegetation pastures. Given strong weather-dependence on grassland productivity, long-term monitoring is necessary to confidently discern grazing management effects on C dynamics.

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1. Introduction

Grasslands represent the largest land resource in the world, and are responsible for regulating multiple ecosystem services for long-term societal benefit (Wedin and Fales, 2009). Grasslands in semiarid regions have been shown to sequester atmospheric carbon dioxide (CO_2) as soil organic C (SOC) (Svejcar et al., 2008; Derner et al., 2006; Frank, 2002). Accrual of CO_2 by semiarid grasslands is characterized by two to three month periods of high CO_2 uptake during active plant growth, followed by CO_2 balance or small losses during the remainder of the year (Derner and Jin, 2012; Svejcar et al., 2008). The net flux of CO_2 within semiarid grasslands is strongly controlled by abiotic factors affecting plant productivity (e.g., temperature, soil water status) (Frank et al., 2002), and accordingly, fluctuates considerably from year to year due to variations in weather (Zhang et al., 2010). Such attributes underscore the importance of understanding factors contributing to dynamics of CO_2 efflux, which refers to the net CO_2 flux from an ecosystem to the atmosphere from microbial and plant root emissions. Small increases in temperature and/or shifts in precipitation patterns have the potential to alter CO_2 efflux dynamics such that semiarid grasslands could be transformed from net C sinks to sources (Pendall et al., 2011; Knapp et al., 2002; Rustad et al., 2001).

Limited evaluations have been undertaken in grasslands for elucidating management effects on CO_2 efflux, particularly during dormant (non-growing season) periods over multiple years (Allard et al., 2007; Soussana et al., 2004). Also, published reports have found mixed effects of use and management of grasslands on CO_2 efflux. Grazing, N fertilization, and plant diversity manipulation have each been found to increase, decrease, or not affect CO_2 efflux (Adair et al., 2009; Liebig et al., 2008; Risch and Frank, 2006;

Knapp et al., 1998). Such mixed outcomes underscore the inherent complexity associated with identifying mechanisms contributing to CO_2 efflux in semiarid grasslands.

Understanding management effects on CO_2 efflux is important for elucidating ecosystem contributions to the global C cycle (Schlesinger, 1997). Limited evaluations of CO_2 efflux in semiarid grasslands, along with divergent outcomes of management, underscore the need for additional research. Given this context, we sought to evaluate CO_2 efflux dynamics over a three year period for three long-term grazing treatments located in the semiarid northern Great Plains, USA. Two management-related hypotheses were postulated to help guide this research: (1) CO_2 efflux will increase under grazed native vegetation with increasing stocking rate, and (2) an intensively-managed seeded forage will possess greater CO_2 efflux than grazed native vegetation.

2. Materials and methods

2.1. Description of site and grazing treatments

Grazing treatments were located at the USDA-ARS, Northern Great Plains Research Laboratory near Mandan, ND, USA (46° 46′ 12″N, 100° 55′ 59″W). The site possesses a semiarid continental climate, with evaporation typically exceeding precipitation in any given year (Bailey, 1995). Long-term (90 yr) mean annual precipitation at the site was 410 mm. Mean annual temperature was 4 °C, though daily averages range from 21 °C in the summer to −11 °C in the winter. The site is characterized by gently rolling topography (0–3% slope) with a silty loess mantle overlying Wisconsin age till. Predominant soils were Temvik-Wilton silt loams (FAO: Calcic Siltic Chernozems; USDA: Fine-silty, mixed, superactive, frigid Typic and Pachic Haplustolls) (Soil Survey Staff, 2012; Liebig et al., 2006).

Grazing treatments included two native vegetation pastures and one seeded forage pasture. The two native vegetation pastures included a moderately grazed pasture (MGP) and heavily grazed pasture (HGP), both established in 1916 and managed consistently without the application of fertilizer, herbicides, or fire (Frank et al., 2006). Ten point frames were used to estimate species composition in the summer of 2004 (Cook and Stubbendieck, 1986; Bonham, 1989). At 64% of the relative species composition, Kentucky bluegrass (*Poa pratensis* L.) was the dominant species in the MGP. The remaining species composition was comprised of sedges (*Carex filifolia* Nutt. and *Carex heliophila* Mack.), green needlegrass [*Nassella viridula* (Trin.) Barkworth] and blue grama [*Bouteloua gracilis* (H.B.K.) Lag. Ex Griffiths]. Lesser amounts of purple threeawn (*Aristida purpurea* Nutt), needle-and-thread [*Hesperostipa comata* (Trin. & Rupr.) Barkworth.], and western wheatgrass [*Pascopyrum smithii* (Rybd) Löve] were also present. The HGP was dominated by blue grama (40% of the species composition) and Kentucky bluegrass (30% of the species composition) while the remainder of the species were similar to that found in the MGP. A crested wheatgrass [*Agropyron desertorum* (Fisch. ex. Link) Schult.] pasture (CWP) represented the seeded forage, which was planted into native range in 1932. A majority of the species in this pasture was crested wheatgrass (50%) but blue grama and sedges also made significant contributions to the species composition. Blue grama is a native warm-season grass species and crested wheatgrass and Kentucky bluegrass are cool-season introduced grass species. The remaining species were cool-season native grasses.

Beginning in 1963, CWP was fertilized in the fall of each year with NH_4NO_3 at 45 kg N ha^{-1} to increase forage production. The moderately grazed pasture, HGP, and CWP occupied 15.4, 2.8, and 2.6 ha, respectively. None of the grazing treatments were replicated. While unfortunate, such a practice was common for field experiments prior to the common use of statistics (Sarvis, 1923).

Yearling steers were used to graze all three pastures from mid-May to early-October each year. Stocking rates for MGP and HGP were 2.6 and 0.9 ha steer^{-1} (0.39 and 1.1 animals ha^{-1}), respectively, while stocking rates within CWP were 0.4 ha steer^{-1} (2.3 animals ha^{-1}) in late-spring/early-summer and 0.9 ha steer^{-1} (1.2 animals ha^{-1}) for the remainder of the grazing season. Grazing has occurred on the pastures every year since establishment except during extreme drought. In such instances, grazing is either not allowed or the grazing season is abbreviated based on forage availability.

2.2. Experimental setup

The study was initiated on 6 October 2003 with the placement of six polyvinyl chloride (PVC) pipe anchors (19.6-cm i.d.; 15.2-cm height) in each grazing treatment. The anchors served as part of a two-piece opaque chamber system for GHG analyses (Liebig et al., 2010). Near the center of each grazing treatment, anchors were oriented in a hexagonal pattern with a distance between adjacent anchors of approximately 40 m in the MGP, and 10 m in the HGP and CWP. Anchors were inserted into soil to a depth of approximately 10 cm. Once inserted, headspace within each anchor was measured by volume displacement with water. Vegetation in each anchor was not removed throughout the study unless grazed by livestock.

2.3. Carbon dioxide efflux

Carbon dioxide efflux was measured in the grazing treatments from 21 October 2003 to 24 October 2006 employing static chamber methodology as outlined by Hutchinson and Mosier (1981). Within each treatment, gas samples were collected from duplicate two-part chambers consisting of six anchors (outlined above) each with a PVC cap (20.3-cm i.d.; 10.0-cm height), vent tube, and sampling port. Gas samples from inside the chambers were collected with a 20 ml syringe at 0, 15, and 30 min after installation (approximately 10:00 a.m. each sampling day). After collection, gas samples were injected into 12 ml evacuated Exetainer glass vials sealed with butyl rubber septa (Labco Limited, Buckinghamshire, UK).

Concentration of CO_2 inside each vial was measured by gas chromatography 1–3 d after collection using a Shimadzu GC-17A gas chromatograph (Shimadzu Scientific Instruments, Kyoto, Japan) attached to an ISCO Retriever IV autosampler (Teledyne Isco, Inc., Lincoln, NE). Using this system, each sample was auto-injected with 1 ml directed to a thermal conductivity detector (TCD) using ultra-pure He carrier gas. Prior to reaching the TCD, samples passed through a 4-m HayeSep D column (Hayes Separations, Inc., Bandera, TX). The gas chromatograph was calibrated with a commercial blend of CO_2 (350, 400, 1998.7 µL L^{-1}) balanced in N_2 from Scott Specialty Gases (Scott Specialty Gases, Plumsteadville, PA). Precision analysis expressed as coefficient of variation for 18 replicate injections of 350 µL CO_2 L^{-1} standard was 0.6%. Standard error associated with the precision analysis was ±1.93 µL CO_2 L^{-1}. Gas flux was calculated from the change in concentration in the chamber headspace over time (Hutchinson and Mosier, 1981). Utilization of the algorithm by Hutchinson and Mosier (1981) provides a correction to the calculated flux rate should CO_2 concentration in the chamber headspace increase such that the diffusion gradient is altered, resulting in a curvilinear response for CO_2 concentration vs. time. Changes in CO_2 concentration during measurement periods over the course of the study were typically small. Accordingly, most efflux rates were calculated following a linear response.

Measurements of CO_2 efflux were made one to two times per week when near-surface soil depths were not frozen or during mid-winter thawing periods. Otherwise, CO_2 efflux was measured every other week. Over the course of the evaluation, CO_2 efflux was measured 126 times.

2.4. Weather, plant, and soil attributes

Precipitation, air temperature, and solar radiation were monitored at a North Dakota Agricultural Weather Network (NDAWN) station within 1 km of the grazing treatments. Daily data were downloaded following each CO_2 efflux measurement from the NDAWN website (NDAWN, 2012).

Aboveground live biomass was measured in the grazing treatments by clipping four representative 0.25 m^2 quadrats every 2–3 week during each growing season. Locations of quadrats were approximately equidistant between anchors 1 and 2, 1 and 6, 3 and 4, and 4 and 5. Green plant material was separated from dead material, oven dried at 70 °C for 48 h, and weighed. Due to variation in plant growth between years, aboveground live biomass was measured 12, 9, and 5 times in 2004, 2005, and 2006, respectively.

Near-surface soil temperature and water content were measured concurrently with CO_2 efflux when the soil was not frozen. Soil temperature was measured at a 6 cm depth with an Omega HH81A handheld digital thermometer attached to a heavy-duty T type thermocouple probe (Omega, Inc., Stamford, CT). Volumetric water content was measured in the surface 12 cm of soil using a time-domain reflectometry technique with a Campbell CS620 HydroSense System (Campbell Scientific, Inc., Logan, UT). One measurement of soil temperature and three measurements of soil water content were made within 30 cm of each anchor during the 15 min gas sampling period. Values for volumetric water content were converted to water-filled pore space (WFPS) using field-measured soil bulk density for the surface 10 cm (Linn and Doran, 1984).

Soil microbial biomass C was measured in the grazing treatments during peak aboveground biomass each year. Eight soil cores were collected from four locations (as outlined above) in each treatment at 0–5 cm using a 3.5-cm (i.d.) step-down probe. Cores within a location were composited, transferred to a double-lined plastic bag, placed in cold storage at 5 °C, and analyzed within 1-week of collection. Samples were processed by sieving through a 2.0-mm sieve at field moisture content and subsampled for estimation of microbial biomass using the microwave irradiation method (Islam and Weil, 1998). Briefly, fifty grams of field moist soil was incubated 10-d at 55% water-filled pore space in the presence of 10 ml of 2.0 M NaOH. Carbon dioxide content was determined by single end-point titration with 0.1 M HCl (Paul et al., 1999). Flush of CO_2-C following irradiation was calculated without subtraction of a 10-d control as suggested by Franzluebbers et al. (1999). Data were expressed on a volumetric, oven-dry basis using soil bulk density values derived from the same cores used for microbial biomass determination (Blake and Hartge, 1986).

Root biomass was determined at the same time as microbial biomass C by collecting a separate set of six cores to a 30 cm depth following the same soil sampling protocol outlined above. Roots were separated from soil using a hydropneumatic elutriation system (Smucker et al., 1982), dried at 70 °C for 48 h, and weighed. Live and dead roots were not separated, but non-root organic material was removed during processing.

2.5. Data analyses

Due to the lack of replication of grazing treatments, anchors and sampling locations served as pseudo-replicates for measurements of CO_2 efflux, aboveground biomass, root biomass, and soil properties (Gomez, 1984). While far from ideal, use of this approach may be justified given the value of the grazing treatments, which are rare even among long-term ecosystem studies (Richter and Markewitz, 2001). Collected data were analyzed using PROC MIXED in SAS (Littell et al., 1996) with grazing treatments and pseudo-replicates considered fixed and random effects, respectively. A significance criterion of $P \leq 0.05$ was used to discriminate differences among means, and variation of means was documented using standard error or standard deviation. Associations between measured parameters were identified using Pearson correlation analysis.

Carbon dioxide efflux data were tested for normality using skewness, kurtosis, and Kolmogorov–Smirnov coefficients before and after data were log-transformed. Data transformation did not improve data normality, so original data were used for statistical analyses. A mixed repeated measures model was used to analyze the effects of year, quarterly period (1 December–28/29 February, 1 March–31 May, 1 June–31 August, and 1 September–30 November), and grazing treatment on CO_2 efflux. Effects of soil temperature and WFPS on CO_2 efflux were also evaluated using a repeated measures model, but with a limited data set including only sampling times when soil temperature and WFPS were measured. Both analyses utilized a time series covariance structure in the repeated measures model, where correlations decline over time (Phillips et al., 2009). Cumulative CO_2 efflux for each grazing treatment was calculated by linearly interpolating data points and integrating the underlying area (Gilbert, 1987).

3. Results

3.1. Weather, soil temperature, water content, and aboveground biomass

Precipitation beginning and ending in mid-October of each year was 132 mm in 2003–2004, 450 mm in 2004–2005, and 216 mm in 2005–2006, with 96% of precipitation events totaling <5 mm event^{-1}. Precipitation received as snow was minimal, with continuous snow cover only from December 2003 to March 2004. Mean air temperature and sums of solar radiation during the study were 6.7 ± 12.0 °C and 14.0 ± 8.2 MJ m^{-2} d^{-1}, respectively. During periods when the soil was not frozen, soil temperature at 6 cm ranged from 1.0 to 25.2 °C with a mean of 14.7 ± 0.2 °C (Fig. 1A). Mean soil temperature did not differ among grazing treatments ($P = 0.73$; data not shown). Water-filled pore space at 0–10 cm ranged from 10% to 75% (Fig. 1B). Mean WFPS was significantly lower in CWP (32%) and MGP (32%) compared to HGP (36%) ($P = 0.03$; data not shown), presumably due to greater available water holding capacity in the latter (Lorenz and Rogler, 1967) and/or differences in transpiration losses among treatments. Soil bulk density at 0–10 cm in HGP was lowest among the grazing treatments (1.03 Mg m^{-3} vs. 1.04 and 1.18 Mg m^{-3} for MGP and CWP, respectively; data not shown). Accordingly, calculation of mean WFPS in HGP would be lower than the other treatments based on lower soil bulk density (i.e., contributing to lower volumetric water content and higher total porosity) (Linn and Doran, 1984). Additional detail regarding weather and soil attributes over the course of the study may be found elsewhere (Liebig et al., 2010).

Production of live aboveground biomass was strongly associated with annual precipitation ($r = 0.79$; $P = 0.01$). Aboveground biomass was greatest in 2005 (Mean = 1176 kg ha^{-1}) and substantially reduced during 2004 and 2006 when growing season precipitation was limiting (Mean = 549 and 504 kg ha^{-1}, respectively). Mean aboveground biomass differed among treatments each year, with observed trends similar in 2004 and 2006. In 2004, mean aboveground biomass was greatest in MGP (644 kg ha^{-1}), intermediate in CWP (546 kg ha^{-1}), and least in HGP (457 kg ha^{-1}) ($P = 0.02$), whereas in 2006, mean aboveground biomass was again greatest in MGP (710 kg ha^{-1}), but intermediate in HGP (450 kg ha^{-1}) and least in CWP (352 kg ha^{-1}) ($P = 0.04$). Under more normal precipitation conditions in 2005, mean aboveground biomass was greatest under CWP (1571 kg ha^{-1}), intermediate in MGP (1147 kg ha^{-1}) and least in HGP (810 kg ha^{-1}) ($P = 0.02$) (data not shown). Differences in
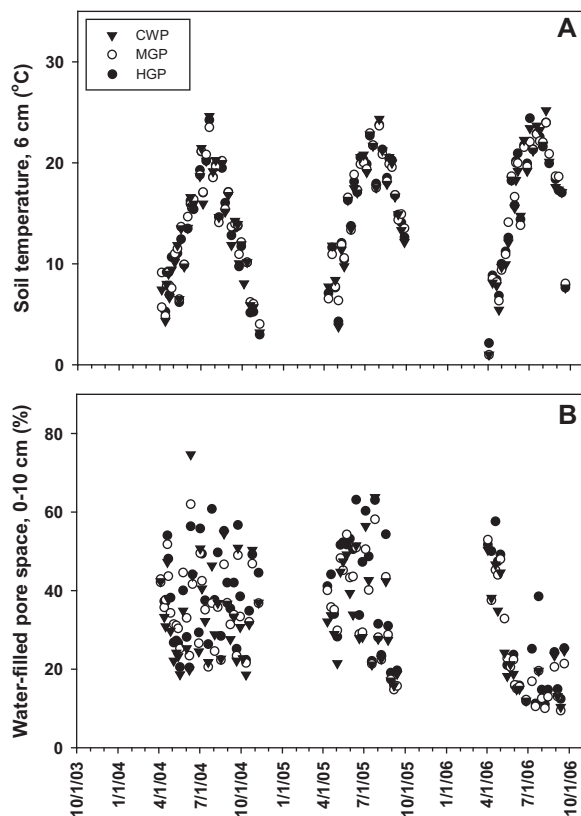
Fig. 1. Near-surface soil temperature (A) and water-filled pore space (B) within the crested wheatgrass pasture (CWP), heavily grazed pasture (HGP), and moderately grazed pasture (MGP) from October 2003 through October 2006 when the soil was not frozen.

aboveground biomass production between treatments were likely a function of plant diversity and soil N availability. Diverse grassland plant communities, such as that found in MGP, are capable of producing greater aboveground biomass in drought-like conditions compared to grassland communities lacking plant diversity (De Boeck et al., 2008; Pfisterer and Schmid, 2002). However, when growing conditions are adequate (as they were in 2005), accumulated soil N following drought can significantly boost aboveground biomass production (Chen et al., 2011; Bonanomi et al., 2006).

Production dynamics of live aboveground biomass were variable across years (Fig. 2). Peak aboveground biomass in 2004 occurred on day of year (DOY) 187 for all grazing treatments, with
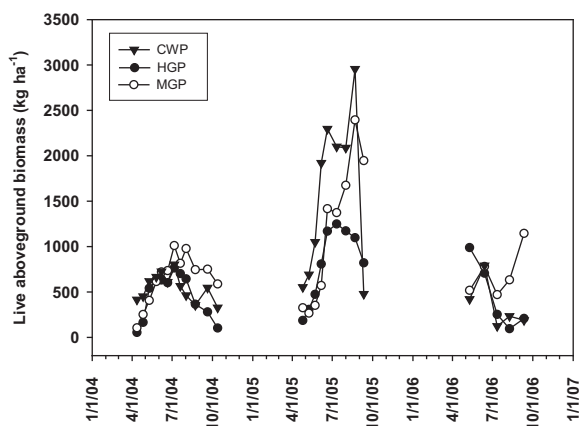

Fig. 2. Aboveground green biomass within the crested wheatgrass pasture (CWP), heavily grazed pasture (HGP), and moderately grazed pasture (MGP), 2004–2006.

Table 1
Mean hourly CO_2 efflux partitioned by grazing treatment, year, and quarterly period. *F* statistics and *P* values for comparisons within an effect are provided below listed means.

Effect	CO_2 efflux mg CO_2-C m^{-2} h^{-1}
Grazing treatment	
Crested wheatgrass (CWP)	100.1 (3.6)[a]
Heavily grazed (HGP)	81.1 (3.3)
Moderately grazed (MGP)	91.1 (3.3)
F statistic	*3.7*
P value	*0.0257*
Year[b]	
1	78.5 (2.2)
2	129.4 (4.7)
3	64.2 (2.2)
F statistic	*43.3*
P value	*<0.0001*
Quarterly period	
December–February	9.4 (0.4)
March–May	79.2 (2.6)
June–August	174.6 (4.0)
September–November	56.9 (1.9)
F statistic	*202.1*
P value	*<0.0001*

[a] Values in parentheses reflect the standard error of the mean.
[b] Values for year effect determined using beginning and ending dates in mid-October.

values of 1011, 802, and 764 kg ha^{-1} for MGP, CWP, and HGP, respectively ($P = 0.4938$). In 2005, peak aboveground biomass was reached on DOY 192 in HGP (1292 kg ha^{-1}) and DOY 234 in CWP and MGP (2956 and 2395 kg^{-1}, respectively). Peak aboveground biomass in 2006 was reached early in the season for HGP (DOY 130; 989 kg ha^{-1}) and CWP (DOY 164; 791 kg ha^{-1}), but toward the end of the growing season for MGP (DOY 254; 1145 kg ha^{-1}) (data not shown).

3.2. Carbon dioxide efflux

Carbon dioxide efflux was affected by grazing treatment, year, and quarterly period (Table 1). Mean hourly CO_2 efflux was greatest in CWP (100.1 mg C m^{-2} h^{-1}), intermediate in MGP (91.1 mg C m^{-2} h^{-1}), and least in HGP (81.1 mg C m^{-2} h^{-1}). Mean CO_2 efflux was nearly twice that in Year 2 compared to Years 1 and 3, an outcome resulting from superior growing conditions due to adequate growing season precipitation in Year 2. Grazing treatment responses across years due to annual variation in growing conditions were similar, with mean CO_2 efflux ranging from 79.4–100.5 mg C m^{-2} h^{-1} in Year 1, 154.7–181.7 mg C m^{-2} h^{-1} in Year 2, and 68.5–90.1 mg C m^{-2} h^{-1} in Year 3. Summer months were characterized by greatest mean CO_2 efflux (174.6 mg C m^{-2} h^{-1}), which corresponded to periods of warm soil temperatures (15–25 °C) (Fig. 1). Carbon dioxide efflux in spring and fall were similar (range = 56.9–79.2 mg C m^{-2} h^{-1}), and least during winter when soil was frozen (9.4 mg C m^{-2} h^{-1}).

Carbon dioxide efflux differed among grazing treatments during spring and fall but not winter and summer (Fig. 3). Within the March–May quarterly period, CO_2 efflux was 43% greater in CWP compared to HGP and MGP (98.9 vs. 69.3 mg C m^{-2} h^{-1}), a result likely driven by a burst of early-season plant growth typical of cool-season grasses, coupled with readily available N in soil (Chen et al., 2011; Bonanomi et al., 2006). During the September–November quarterly period, CO_2 efflux was 47% greater in CWP and MGP than HGP (67.9 vs. 47.4 mg C m^{-2} h^{-1}). Greater CO_2 efflux in the fall may have been caused by a similar plant species- and N-induced burst of growth in CWP, while aggressive growth of *Poa pratensis* – also a cool-season grass – may have been responsible for late-season
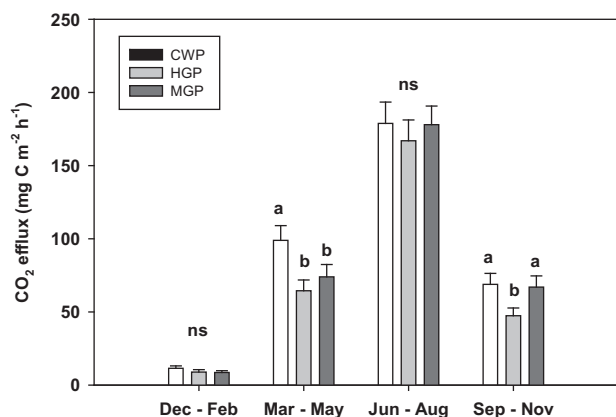
Fig. 3. Mean hourly CO_2 efflux rates partitioned into quarterly periods for crested wheatgrass pasture (CWP), heavily grazed pasture (HGP), and moderately grazed pasture (MGP). Error bars reflect ±1 standard error. Treatment values within a quarterly period assigned a different letter are significantly different at $P \leq 0.05$. ns, not significant at $P \leq 0.05$.

efflux in MGP. Overall, CO_2 efflux for year and quarterly period were adequately characterized by time series graphs for each treatment (Fig. 4), where dynamics of temperature and biomass production were visually similar to CO_2 efflux. Carbon dioxide efflux was positively associated with live aboveground biomass ($r = 0.86$; $P \leq 0.01$).

Cumulative CO_2 efflux over the three year period was 21.7, 19.0, and 17.2 Mg C ha^{-1} for CWP, MGP, and HGP, respectively, equating to mean annual efflux rates of 7.2, 6.3, and 5.7 Mg C ha^{-1} (Fig. 5). Cumulative CO_2 flux in MGP did not differ from the other grazing treatments, but was significantly greater in CWP than HGP ($P = 0.03$). Mean annual CO_2 efflux from each grazing treatment was less than that observed by Frank et al. (2006) (10 Mg C ha^{-1} yr^{-1}) from MGP between 2001 and 2003, but compared favorably to CO_2 efflux in the same study during a drought year (2002; 6.6 Mg C ha^{-1} yr^{-1}) when only 288 mm of precipitation was received.

Carbon dioxide efflux was strongly associated with near-surface WFPS and soil temperature (both $P \leq 0.01$; $n = 1359$). Within quarterly periods, correlation analyses identified associations between CO_2 efflux and soil temperature during March–May ($r = 0.71$; $P < 0.01$) and September–November ($r = 0.45$; $P \leq 0.01$) and CO_2 efflux and WFPS during June–August ($r = 0.46$; $P \leq 0.01$) (Table 2). Accordingly, soil temperature had an overriding influence on CO_2 efflux during periods of rapid growth or during plant senescence, an observation consistent with previous studies in grassland ecosystems (Frank et al., 2002; Mielnick and Dugas, 2000; Norman et al., 1992). During periods of warm but relatively stable soil temperature, soil water status was related to CO_2 efflux. Such a relationship has been observed in other studies where strong CO_2

Table 2
Pearson correlation coefficients for associations between mean quarterly CO_2 efflux and water-filled pore space (WFPS) and soil temperature.

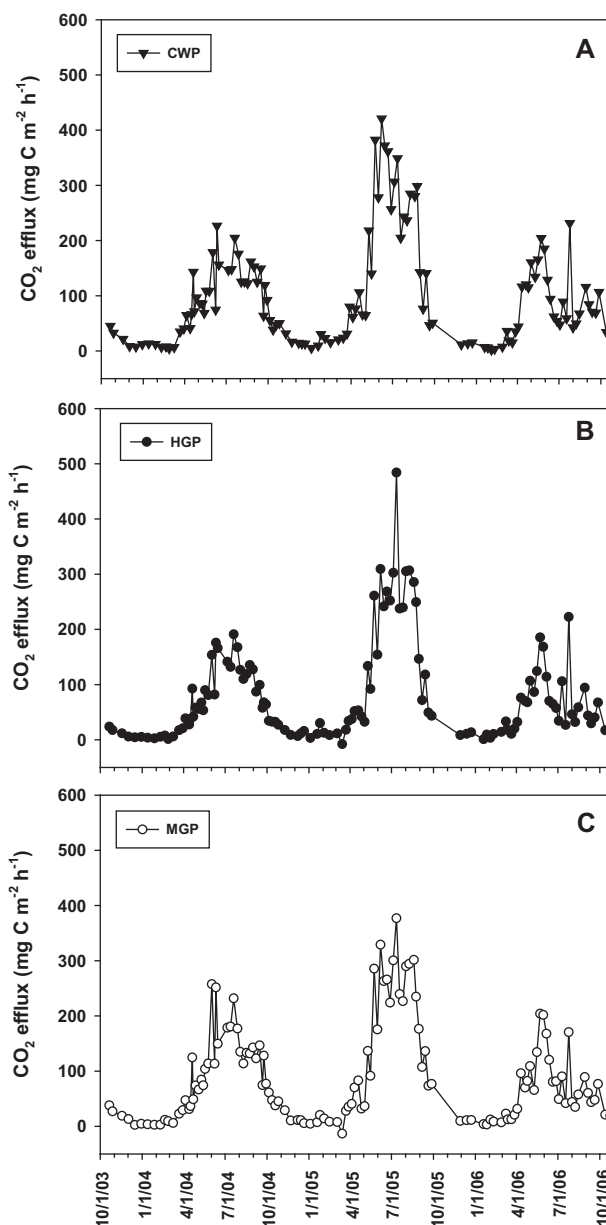| Quarter	CO_2 efflux
WFPS (%; 0–10 cm)	
December–February	–
March–May	0.04
June–August	0.46[a]
September–November	0.10
Soil temperature (°C; 6 cm)	
December–February	–
March–May	0.71[a]
June–August	−0.01
September–November	0.45[a]

[a] Correlation significant at $P < 0.01$.

Fig. 4. Daily CO_2 efflux for crested wheatgrass pasture (CWP; A), heavily grazed pasture (HGP; B), and moderately grazed pasture (MGP; C) from 21 October 2003 through 24 October 2006.

efflux responses followed precipitation pulses during warm summer months (Bahn et al., 2008; Xu and Wan, 2008; Wildung et al., 1975).

3.3. Microbial biomass C and root biomass

Microbial biomass C was significantly greater in native vegetation pastures compared to CWP each year, with numerical differences ranging from 2.4- to 4.7-fold greater in the former (Table 3). Within individual grazing treatments, however, microbial biomass C did not differ among years. Differences in vegetation morphology and soil chemical attributes may have served to depress microbial abundance and activity in CWP relative to the native vegetation pastures. Whereas exposed soil between plant crowns was commonly observed in CWP, vegetation in MGP and HGP created a continuous mat over the soil surface, which may act to buffer microbial communities in near-surface depths from

Table 3
Microbial biomass C at 0–5 cm and root biomass at 0–30 cm for grazing management treatments. Values presented for each year within a grazing treatment.

Year	Crested wheatgrass (CWP)	Heavily grazed (HGP)	Moderately grazed (MGP)	P-value[a]
Microbial biomass C, 0–5 cm (kg C ha^{-1})				
2004	201 (18)[b]	514 (94)	460 (83)	0.0308
2005	126 (55)	672 (124)	504 (53)	0.0037
2006	177 (8)	733 (65)	637 (64)	<0.0001
P-value	0.3194	0.3059	0.2098	
Root biomass, 0–30 cm (Mg ha^{-1})				
2004	4.69 (0.45)	3.58 (0.44)	2.96 (0.12)	0.0261
2005	4.60 (0.30)	3.87 (0.52)	2.70 (0.08)	0.0120
2006	3.53 (0.33)	3.55 (0.43)	3.18 (0.21)	0.6972
P-value	0.0968	0.8647	0.1301	

[a] Microbial biomass C and root biomass compared across grazing treatments within a year (row) and year within a grazing treatment (column).
[b] Values in parentheses reflect the standard error of the mean. Standard deviation = standard error × $\sqrt{4}$.

weather-related fluctuations (Wagai et al., 1998). Previously documented trends in soil pH have shown excess N contributed to accumulated acidity in CWP (Liebig et al., 2006). Increased soil acidification can narrow the spectrum of adaptable bacterial species (Rousk et al., 2010; Benizri and Amiaud, 2005) and has been associated with decreased microbial biomass in both natural and managed ecosystems (Watanabe et al., 2010; Malý et al., 2009; Aciego Pietri and Brookes, 2008). Alternatively, lower microbial biomass C may be attributed to greater humification of soil organic matter, or conversely, lower levels of labile organic matter in CWP (Bahn et al., 2008; Raiesi and Asadi, 2006). Across all grazing treatments, microbial biomass C was not associated with mean annual CO_2 efflux ($P = 0.36$) nor mean live aboveground biomass ($P = 0.50$).

Root biomass at peak aboveground biomass varied among grazing treatments in two of three years (Table 3). In 2004, significantly more root biomass was present in CWP (4.69 ± 0.90 Mg ha^{-1}) than MGP (2.96 ± 0.24 Mg ha^{-1}), while in 2005, root biomass was greater in CWP (4.60 ± 0.60 Mg ha^{-1} and HGP (3.87 ± 1.04 Mg ha^{-1}) compared to MGP (2.70 ± 0.16 Mg ha^{-1}) (*Note*: measure of variation in parentheses reflects standard deviation). Root biomass did not differ among years within grazing treatments. Similar to microbial biomass, root biomass was not associated with other measured parameters. Correlations between root biomass and CO_2 efflux, live aboveground biomass, and microbial biomass C were all nonsignificant ($P = 0.54$, 0.63, and 0.17, respectively).

4. Discussion

Outcomes from this study did not support the hypothesis of greater CO_2 efflux under grazed native vegetation at higher stocking rates, as mean CO_2 efflux did not differ between HGP and MGP. Greater soil organic C (SOC) in HGP than MGP (Liebig et al., 2006, 2010) was anticipated to contribute to increased CO_2 efflux in the former, as SOC has been found to be positively associated with CO_2 efflux in North American and European grasslands (Bahn et al., 2008; Frank et al., 2006). Additionally, greater microbial and root biomass under grazing management with higher stocking rate would suggest increased potential for enhanced root and soil respiration in HGP. Other factors, such as compromised soil-atmosphere gas exchange due to trampling-induced changes in soil physical properties (Donkor et al., 2002; Knapp et al., 1998), a shorter plant canopy (Risch and Frank, 2006), and possible differences in labile vs. recalcitrant C in near-surface soil depths (Bahn et al., 2008) may have overshadowed differences in SOC and belowground biomass between grazing treatments, thereby contributing to similar CO_2 efflux between HGP and MGP.

Positive responses between available soil N, above- and belowground biomass production, and CO_2 efflux in grasslands are well documented (Peng et al., 2011; Xu and Wan, 2008; Verburg et al., 2004). In the context of this study, the growth habit of crested wheatgrass coupled with applied fertilizer N contributed to greater CO_2 efflux in CWP compared to the native vegetation pastures. Seasonal dynamics of CO_2 efflux suggest differences among grazing treatments were most pronounced in early spring (CWP > HGP = MGP) when readily available N and adequate soil moisture contributed to ideal conditions for biomass production of cool-season grasses. Moreover, greater SOC in CWP compared to HGP and MGP (Liebig et al., 2006, 2010) was anticipated to contribute to greater CO_2 efflux in CWP. Accordingly, the second hypothesis failed to be rejected given outcomes of this study.

In addition to management-related impacts, soil temperature and moisture status proved to be strongly associated with CO_2 efflux, though associations were seasonally dependent with temperature most relevant during spring and fall and moisture status most important in summer. Such information, while not new (Wildung et al., 1975), does underscore the importance of carefully accounting for precipitation pulses in summer months to adequately quantify C dynamics in semiarid grasslands.

Differences in microbial and root biomass suggest sources of CO_2 efflux likely varied among grazing treatments. While microbial and root respiration is inherently difficult to distinguish (Schlesinger, 1997), low microbial biomass and high root biomass in CWP suggest greater root-dominated contributions to CO_2 efflux relative to HGP and MGP. Such 'root dependence' on CO_2 loss in CWP may infer a stronger association between CO_2 efflux and plant growth compared to management systems with greater CO_2 contributions from microbial activity. Additional investigation is warranted to better understand the role of grazing management to affect microbial communities, and in turn, how microbial communities influence soil C dynamics in grasslands.
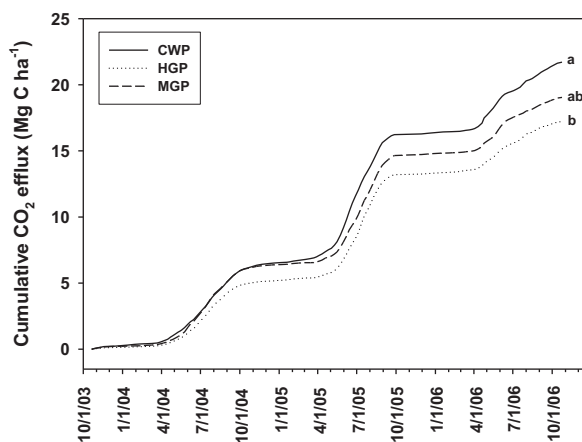

Fig. 5. Cumulative CO_2 efflux within the crested wheatgrass pasture (CWP), heavily grazed pasture (HGP), and moderately grazed pasture (MGP) from 21 October 2003 through 24 October 2006. Different letters to the right of the cumulative flux values signify treatment differences at $P \leq 0.05$.

Broadly, mean annual CO_2 efflux rates observed within this study fell within expected ranges for temperate grasslands (1.3–8.3 Mg C ha^{-1} yr^{-1}) (Raich and Schlesinger, 1992). However, it is important to acknowledge two of three study years were conducted under drought conditions. Sensitivity to drought can have an overriding effect on grassland productivity, and accordingly, can significantly alter C dynamics in grazing management systems (Derner and Jin, 2012). Long-term monitoring is needed to thoroughly document mechanisms contributing to C dynamics in semiarid grasslands in order to more confidently ascertain their role as CO_2 sinks, particularly given anticipated trajectory of future climate change.

Acknowledgments

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