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Fluxes of CO_2 From Grazed and Ungrazed Tallgrass Prairie

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Abstract

To determine the impact of seasonal steer grazing on annual CO_2 fluxes of annually burned native tallgrass prairie, we used relaxed eddy accumulation on adjacent pastures of grazed and ungrazed tallgrass prairie from 1998 to 2001. Fluxes of CO_2 were measured almost continuously from immediately following burning through the burn date the following year. Aboveground biomass and leaf area were determined by clipping biweekly during the growing season. Carbon lost because of burning was estimated by clipping immediately prior to burning. Soil CO_2 flux was measured biweekly each year using portable chambers. Steers were stocked at twice the normal season-long stocking rate (0.81 ha $steer^{-1}$) for the first half of the grazing season (~ May 1 to July 15) and the area was left ungrazed the remainder of the year. That system of grazing is termed "intensive-early stocking." During the early growing season, grazing reduced net carbon exchange relative to the reduction in green leaf area, but as the growing season progressed on the grazed area, regrowth produced younger leaves that had an apparent higher photosynthetic efficiency. Despite a substantially greater green leaf area on the ungrazed area, greater positive net carbon flux occurred on the grazed area during the late season. Net CO_2 exchange efficiency was greatest when grazing utilization was highest. We conclude that with grazing the reduced ecosystem respiration, the open canopy architecture, and the presence of young, highly photosynthetic leaves are responsible for the increased net carbon exchange efficiency. Both GR and UG tallgrass prairie appeared to be carbon-storage neutral for the 3 years of data collection (1998 ungrazed: -31 g $C \cdot m^{-2}$, 1998 grazed: -5 g $C \cdot m^{-2}$; 1999 ungrazed: -40 g $C \cdot m^{-2}$, 1999 grazed: -11 g $C \cdot m^{-2}$; 2000 ungrazed: $+66$ g $C \cdot m^{-2}$, 2000 grazed: 0 g $C \cdot m^{-2}$).

Resumen

Para determinar el impacto del apacentamiento estacional sobre los flujos de CO_2 de praderas de zacates nativos altos quemadas anualmente, usamos la técnica "relaxed eddy accumulation" en potreros adyacentes apacentados (GR) y sin apacentar (UG) de pastizal de zacates altos, el estudio se realizó de 1998 al 2001. Los flujos de CO_2 fueron medidos casi continuamente inmediatamente después de la quema hasta la fecha de quema del siguiente año. La biomasa aérea y el área foliar fueron determinados mediante cortes cada dos semanas durante la estación de crecimiento. La pérdida de carbón debida a la quema fue estimada cortando inmediatamente antes del fuego, El flujo de CO_2 del suelo fue medido cada dos semanas durante los años de estudio, para ello se utilizaron cámaras portátiles. En la primera mitad de la estación de apacentamiento (1 de Mayo al 15 de Julio) la carga animal de novillos fue el doble de la normal para el apacentamiento continuo (0.81 ha $novillo^{-1}$), posteriormente el área se quedo sin apacentar el resto del año, este sistema de apacentamiento es llamado "carga intensiva temprana". A inicios de la estación de crecimiento, el apacentamiento redujo el intercambio de carbón neto en relación a la reducción del área foliar verde, pero conforme la estación de crecimiento progresó en el área apacentada, el rebrote produjo hojas jóvenes que aparentemente tuvieron una mayor eficiencia fotosintética. A pesar del área foliar verde substancialmente mayor en el área sin apacentar, en el pastizal apacentado, a finales de la estación, ocurrió el mayor flujo positivo de carbón neto. La eficiencia de intercambio de CO_2 neto fue mayor cuando la utilización por apacentamiento también fue mayor. Concluimos que con el apacentamiento, la reducida respiración del ecosistema, la arquitectura de copa abierta y la presencia de hojas jóvenes altamente fotosintéticas son responsables del aumento en la eficiencia de intercambio de carbón neto. En los tres años de colección de datos, tanto el pastizal de zacates altos apacentado como sin apacentar aparentaron ser un almacén neutro de carbón (1998: UG -31 $gC \cdot m^{-2}$, GR -5 $gC \cdot m^{-2}$; 1999: UG -40 $gC \cdot m^{-2}$, GR -11 $gC \cdot m^{-2}$; 2000: UG $+66$ $gC \cdot m^{-2}$, GR 0 $gC \cdot m^{-2}$).

Key Words: carbon balance, net ecosystem carbon exchange, carbon dioxide, aboveground biomass, leaf area, grazing optimization hypothesis

INTRODUCTION

Atmospheric CO_2 has increased dramatically during the past 150 years from 280 ppm in 1846 to 368 ppm in 1996 (Keeling and Whorf 2001) and may impact climate globally (Hansen et al. 1998). Increasing concentrations of atmospheric CO_2 and the potential for climatic and ecophysiological changes have made the global carbon balance an important scientific and political topic (Tans and Bakwin 1995). Agreements among nations to reduce greenhouse gas emissions have created a need

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to estimate the ability of agro-ecosystems to store carbon in soil and biomass. Knowledge of the potential for natural and agricultural ecosystems to sequester carbon and landscape-level data on carbon fluxes are needed to parameterize regional models that are used to predict carbon stores under different land management schemes. Currently, there are several landscape-level projects measuring carbon and water vapor fluxes, i.e., the FLUXNET network (Baldocchi et al. 2001). Measures of management impacts on annual net carbon exchange and water use of grassland ecosystems with domesticated ungulate herbivory have been sparingly assessed. In systems with domestic livestock, removal of half or more of the leaf area during the growing season occurs.

Grassland ecosystems and drylands are widespread in both hemispheres and may have the potential to sequester or release CO_2 in response to climate change, increasing CO_2, and land management (Thornley et al. 1991; Glenn et al. 1993; Ojima et al. 1993; Fisher et al. 1994; Seastedt et al. 1994). There have been several studies that used aerodynamic techniques for measuring carbon, water, and energy fluxes on central Great Plains grasslands (Verma et al. 1992; Kim et al. 1992; Frank and Dugas 2001; Meyers 2001; Sims and Bradford 2001; Suyker and Verma 2001; Frank 2004). Essentially all natural grasslands are grazed by wild and/or domestic ungulate herbivores during some period of the year. The impact that ungulate herbivory has on carbon and water vapor fluxes must be known in order to scale fluxes from measured sites to larger terrestrial entities. Ungulate grazing produces very different biomasses, leaf areas, and canopy structures. The impact of ungulate grazing on the acquisition of carbon through photosynthesis and the loss of carbon to the atmosphere in grassland ecosystems is mediated by climatic and ecophysiologic phenomena. In general, the greater the leaf area, the greater is carbon acquisition by the ecosystem. However, a relatively closed canopy structure and older leaves on ungrazed grasslands compared to grazed may reduce the ability of the ecosystem to fix carbon. Bremer et al. (2001) outlined the impacts of grazing on water balance and ecophysiological responses to grazing. Leaf area is reduced by grazing, which changes the partitioning of energy between the soil surface and the plant canopy, ultimately affecting evapotranspiration and carbon acquisition and loss by the grassland ecosystem. Grazing also affects soil CO_2 flux, the major pathway for ecosystem carbon transfer to the atmosphere, and is controlled by soil temperature, soil water content, and allocation of photosynthate to roots. Boone et al. (1998) and Craine et al. (1999) indicated that carbon availability played an important role in control of soil CO_2 flux rates. Bremer et al. (1998) reported that both clipping and grazing by cattle reduced soil CO_2 flux. There may be a confounding influence of grazing when soil water is conserved by removal of transpiring tissue. Bremer et al. (2001) showed that grazing reduced evapotranspiration, thereby maintaining higher soil water levels. Increased soil water likely sustained microbial action for a longer period, which would increase soil CO_2 flux.

The effect of grazing on productivity of grassland ecosystems has been discussed extensively, particularly in the past 20–25 years. The hypothesis that there is an optimum level of herbivory to sustain maximum productivity was proposed by McNaughton (1979) and termed by him the "grazing optimization hypothesis." That hypothesis was tested by Williamson et al. (1989) using grasshoppers as the herbivore, and they concluded that there was an optimal grazing intensity for maximum aboveground net primary production (net primary productivity) in a blue grama (*Bouteloua gracilis* [H.B.K.] lag. Ex Griffiths) grassland. Little or no utilization of grassland communities, as well as high utilization rates, resulted in less than optimum net primary productivity. Numerous mechanisms have been proposed for the increased net primary production on grazed areas compared to ungrazed. As early as 1952, Weaver and Rowland (1952) showed that excessive mulch accumulations would retard net primary productivity. Knapp and Seastedt (1996) reaffirmed that phenomenon. Nutrients sequestered in the aboveground litter were unavailable for plant use. The presence of a thick litter layer also affects photosynthetic efficiency of leaves, which must grow through that layer. Knapp (1985) reported that photosynthetic efficiency of big bluestem (*Andropogon gerardii* Vitman) leaves was greater on burned areas compared to unburned, which he attributed to the litter on the unburned area.

Because grasses regrow following top removal, there are leaves of different ages in the canopy. As leaves mature, their photosynthetic capacity declines (Parsons et al. 1988; Gold and Caldwell 1990). Grazing increases photosynthesis on a unit leaf-area basis (Gold and Caldwell 1990). Wallace (1990) indicated that there was an increase in photosynthetic rate of big bluestem under grazing compared to either clipped or control plants. Grazing also affects plant canopy structure and light penetration to leaves lower in the canopy. Gold and Caldwell (1990) reported that by reducing the upper leaves of grasses in the canopy through clipping, sunlit leaf percentage in the canopy was increased. In ungrazed grassland canopies, the upper leaves intercept a high proportion of the sunlight, thereby reducing the potential for energy capture by lower leaves. Because of the mechanisms listed above, the concept that there is a linear increase in carbon capture by grassland canopies as leaf area increases is not universally true. King et al. (1988) concluded that gross photosynthesis increased more rapidly than did leaf area index (LAI) when the plants were released from continuous stocking management. They attributed that response to an increasing proportion of young photosynthetic leaves near the top of the canopy.

Carbon fixed by the plant canopy can be converted to above- and belowground biomass, can be respired, or can leak from the root system through exudation. Measures of photosynthesis through single leaf chambers or whole plant estimates fail to measure the carbon retained by the plant and that lost from belowground and canopy respiration. A study was initiated in 1998 to measure landscape-level net carbon exchange (NCE) of grazed and ungrazed tallgrass prairie using relaxed-eddy aerodynamic techniques. Our objective in this study was to determine how grazing affected ecosystem NCE and soil CO_2 fluxes from grazed and ungrazed tallgrass prairie.

MATERIALS AND METHODS

Study Area

Research was conducted from 1998 to 2001 on the Rannells Flint Hills Prairie Preserve near Manhattan, KS (lat 39°8.472′N, long 96°31.525′W, 324 m above mean sea level). Vegetation on the site was a mixture of C_3 and C_4 species, dominated by the C_4 warm-season grasses, *Andropogon gerardii* Vitman, *Sorghastrum nutans* (L.) Nash., and *Andropogon scoparius* Michx. Total perennial grasses made up 85% of the plant composition. Members of the Cyperaceae grasslike plants, (C_3 cool-season monocots) made up 5–7% of the plants. Principal forbs (all C_3 warm-season) also made up 5–7% of the stand and included *Vernonia baldwinii* var. *interior* (Small) Schub., *Ambrosia psilostachya* DC., *Artemisia ludoviciana* Nutt., and *Psoralea tenuiflora* var. *floribunda* (Nutt.) Rydb. The primary difference in the 2 areas was in cool-season grasses, with 5% in the grazed area and 1% in the ungrazed. The principal cool-season grass was *Poa pratensis* L. At this site, average peak aboveground biomass (dry weight) of 425 $\mathrm{g \cdot m^{-2}}$, of which 35 $\mathrm{g \cdot m^{-2}}$ is from forbs, usually occurs in early August (Owensby and Anderson 1967). The 30-year average annual precipitation was 840 mm, with 520 mm occurring during the growing season. Soils at the site were silty clay loams (Benfield series: fine, mixed, mesic, Udic Argiustolls). Depth to shale and limestone fragments ranged from 0.6 to 1.0 m. The upper 10 cm of the soil profile had a bulk density of 1.0 to 1.2 $\mathrm{g\ C \cdot m^{-3}}$ and an organic matter content of 4% to 6%. The area had been grazed by yearling steers during the summer and annually burned in spring for the past century or more. The flux measurement towers were located on a relatively flat ridgetop (< 3% slope in the primary wind direction) in 2 adjacent 31-ha grazing units. On the grazed site, no significant changes in topography or vegetation were observed within 600 m of the tower site in the direction of the prevailing wind. On the ungrazed site, the topography was more broken: a minimum of 50 to 370 m of uniform relief extended from the tower in the direction of the prevailing winds.

Grazing Scheme

Yearling steers (~ 250 $\mathrm{kg \cdot steer^{-1}}$) were placed on the grazed site during the first week of May each year and removed in mid-July (~ 340 $\mathrm{kg \cdot steer^{-1}}$) using an intensive-early stocking rate (0.81 $\mathrm{ha \cdot steer^{-1}}$) (Smith and Owensby 1978). The ungrazed site had been ungrazed since 1997. Both sites traditionally had been grazed and burned annually. Both grazing units were burned in the last 10 days of April during the 3 years of this study. A 2-strand electric fence was used to protect the flux measurement system. The sensors, sonic anemometer, and gas inlets were on masts which extended horizontally 1–2 m into the grazed area out of reach of the livestock.

CO_2 Flux Measurement

Net CO_2 exchange was measured using conditional sampling as proposed by Businger and Oncley (1990), following procedures similar to those of Baker et al. (1992) and Beverland et al. (1996). A detailed description of the instrumentation and procedures involved were reported by Ham and Knapp et al. (1998). Briefly, fluxes (F_c) of CO_2 were calculated every 30 minutes as

$$F_c = B\rho_w\theta(c_{up} - c_{dn}) \qquad [1]$$

where ρ_w is the standard deviation of the vertical wind component; θ is air density; ($c_{up} - c_{dn}$) is the time-averaged concentration difference between up- and down-moving eddies, expressed as mixing ratios; and *B* is an empirical relaxation factor (0.58). A 3-dimensional sonic anemometer (CSAT-3, Campbell Scientific, Logan, UT) mounted 2.5 m above the soil surface and operated at 10 Hz was used to measure ρ_w and control the gas sampling system. Air for the determination of ($c_{up} - c_{dn}$) for CO_2 was continuously sampled at 0.5 $\mathrm{L \cdot min^{-1}}$ through a 3.2-mm diameter (outer diameter) Teflon tube with the inlet positioned within 5 cm of the span of the anemometer. Air traveled through a 56-mm-long Teflon tube and barb fitting before reaching a 3-way solenoid valve (100 T, BioChem Valve, Boonton, NJ). The valve was controlled using the output from the anemometer so that up-moving and down-moving eddies were diverted into separate sample lines on the downstream side of the valve. The up- and down-moving air samples were filtered and routed through 9.5-mm diameter tubing to an environmental enclosure, and CO_2 and water vapor concentration of the samples was measured with an infrared gas analyzer (IRGA; LI-6262, Li-Cor Lincoln, NE) (see Ham and Knapp 1998, Fig. 1). Concentration differences were adjusted upward as a function of eddy reversal frequency using the method described by Beverland et al. (1996). IRGAs were automatically calibrated at midnight each night using a standard gas with ± 1% accuracy.

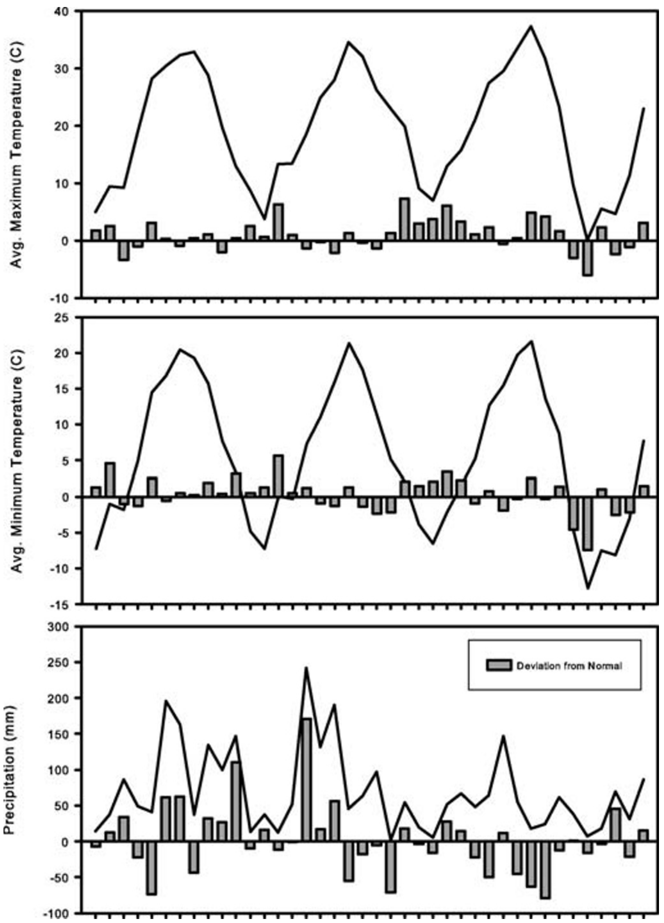

Figure 1. Average daily maximum and minimum air temperatures, monthly precipitation, and deviations from normal (1961–1990 averages) for the 3 carbon years of the study.

Ham and Knapp (1998), in an adjacent area, estimated the source area of the boundary-layer measurements using the method of Schmid (1994). Results showed that, under unstable and neutral boundary conditions, 90% of the total surface influence was in a 0.38-ha area extending 190 m upwind from the mast. Source area size was greater than 300 m under stable conditions. No significant spatial variations in vegetation or topography were observed within 300 m of the tower.

Wind speed and direction were measured with a wind monitor (R.M. Young, Traverse City, MI) positioned at 3 m on the flux tower. Winds were calm 0.10% of the time and averaged 4.5 $m \cdot s^{-1}$ over the course of the study and were generally from the southwest. Air temperature and humidity were measured on the tower at 2.5 m using a Vaisala HMP45C probe (Helsinki, Finland). Global irradiance was measured with a pyranometer (LI-200, Licor, Lincoln, NE), and photosynthetically active radiation (PAR) was measured with a quantum sensor (Li-190, Li-Cor), both on a tower located 4 m from each flux tower. Precipitation was obtained from a tipping range gauge at the ungrazed site. All data acquisition and control at the 2 towers were accomplished with 2 microloggers and accessories (CR10X, AM25T, AREL12, Campbell Scientific Inc, Logan, UT). Averages and other statistics were computed and stored on 30-minute intervals.

Soil-surface CO_2 flux was measured every 7 to 10 days using the closed-chamber method described by Norman et al. (1992) and used by Ham et al. (1995) and Bremer et al. (1998). Measurements were made at 10 locations within the source area near midday during the 3 years. The portable chamber had a diameter of 7.3 cm so measurements of soil CO_2 flux could be made between clumps of vegetation on a bare soil surface thereby providing only soil respiration. A Li-6200 portable photosynthesis system was used to measure the rates of change of CO_2 inside the chamber.

Biomass and leaf area for grasses and herbaceous dicots were determined biweekly by harvesting 4 samples of 0.25 m^2 each in the source area of the tower during the first half of the growing season and monthly until the end of the growing season each year. Leaf area for grasses and herbaceous dicots were measured with an area meter (LI-3100, Li-Cor) and reported as LAI. Aboveground biomass was determined gravimetrically after samples had been dried for 72 hours at 55°C. Aboveground biomass was also determined just prior to the annual burn by harvesting 4 samples of 0.25 m^2 each in the source area of the tower. Carbon content of the aboveground biomass was measured using a Carlo Erba C/N Analyser (Milano, Italy). Carbon loss during the burn was determined by multiplying the carbon content of the aboveground biomass ($\sim$ 42%) by the total biomass. Black carbon left on the surface was minimal because burning occurred under conditions that left mostly white ash. We therefore did not measure the amount of carbon left on the surface. That may be a small source of error in the carbon balance calculations. Export of carbon from the system was estimated by multiplying the carbon content of beef cattle (Spector 1956) times the weight gain of the livestock on the grazed area.

Data Processing

Periods of time occurred when data were suspect or not available. Data were omitted when inadequate wind speed or direction, abrupt changes in boundary-layer stability, or precipitation disrupted the measurement. Data were also lost because of maintenance, calibration, and repair of the sensors and supporting equipment. Missing sections of data were estimated using a combination of interpolation and empirical modeling, an approach that has been widely employed in similar studies (Wofsy et al. 1993; Vermetten et al. 1994; Baldocchi 1997; Falge et al. 2001). The measurement of NCE and water vapor fluxes by conditional sampling was examined to eliminate data when wind speed was less than 0.4 $m \cdot s^{-1}$ or when wind direction placed the sonic anemometer in the lee of the support tower. Data were also eliminated when the stability of the boundary layer was in transition, which sometimes occurred for brief periods near sunrise or sunset. Winds on the upland prairie were very consistent, in both magnitude and direction, which improved long-term data quality.

Over the course of the 3 years, about 15% of the NCE data were missing or rejected. At night, intermittent missing NCE was estimated by assuming that the magnitude of the flux was equal to the previous 30-minute flux. If larger blocks of night data were missing, nightly respiration (sunset to sunrise) gaps were filled using the mean diurnal variation approach of Falge et al. (2001) with a 7-day data window. Missing daytime measurements of NCE were predicted from measurements of global PAR. Linear relationships between NCE and radiation, determined using data collected within 5 days of the missing segment, were used for the analysis. Others have used this approach to fill in missing data (e.g., Baldocchi 1997). If data were available for only one of the 2 tower sites, missing data were estimated using the ratio of the grazed and ungrazed for the different 30-minute time periods prior to and following the missing data period. Daily and yearly CO_2 fluxes were calculated by integrating (summing) the screened 30-minute NCE data over 24 hours and over the year. NCE 30-minute data were also averaged over 20-day periods for graphic presentation. Throughout the discussion, CO_2 fluxes toward the grassland surface are considered positive, whereas fluxes away from the surface are negative.

Net CO_2 exchange efficiency was calculated by dividing the 20-day average net CO_2 exchange rates for 30-minute periods by the aboveground biomass or green LAI during that period. Periods selected for this paper were chosen to reflect the greatest differences in net CO_2 exchange efficiency between grazed and ungrazed areas. Data for the other periods during the growing season are available from the authors.

RESULTS

With any type of long-term flux measurements, errors can multiply and accumulate over time. This is especially troublesome when attempting to integrate tower-based flux measurements over long periods (Goulden et al. 1996; Moncreif et al. 1996). However, the primary objective was to measure flux differences between grazed and ungrazed tallgrass prairie rather than quantify the yearly carbon budget. Because the differences between the grazed and ungrazed sites were large during the growing season, any slight bias in the flux data had a lessened impact on the conclusions. Data are presented for a carbon year, which is defined as the period from just after burning in one season until just before burning the following season. That is required to take into account the carbon lost

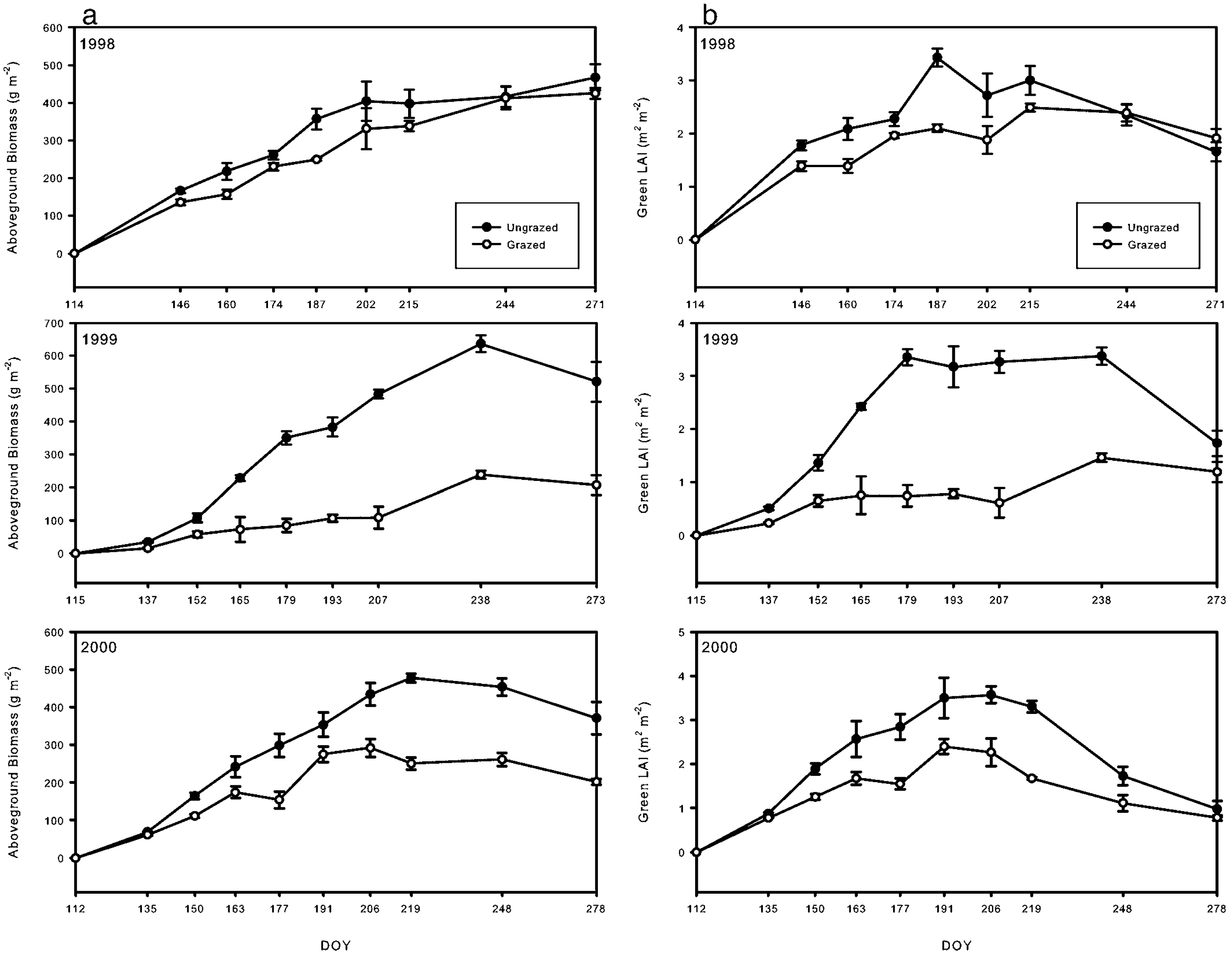

Figure 2. Aboveground biomass (**a**) and green leaf area index (LAI) (**b**) for the 1998–2000 growing seasons on grazed and ungrazed tallgrass prairie in the source area for the flux towers. Error bars are 1 SE ($n = 4$).

because of burning, which is not adequately measured by the flux system.

Environmental Conditions

Carbon fluxes were greatly affected by the differences among years in the environmental conditions. Deviations from normal temperature and precipitation are shown in Figure 1.

1998–1999. During the 1998–1999 carbon year, temperatures were near normal and precipitation above normal in the growing season. The winter period was generally warmer than normal, particularly in February.

1999–2000. Temperature was near normal during the growing season, but was much warmer than normal during the winter period. Precipitation was above normal early in the growing season, but was lower than normal in the late season. Winter precipitation was near normal.

2000–2001. Temperatures were above normal, particularly in the late summer, and much below normal in the winter period. Precipitation was much below normal during the growing season and near normal during the winter period.

Total yearly average precipitation for the 3-year period was 844 mm, which was 4 mm above the 30-year average.

Aboveground Biomass and Green Leaf Area

1998–1999. Peak aboveground biomass accumulation was near the long-term average during the 1998 growing season (Fig. 2). By midseason, the grazed area biomass was 70% (-108 g$\cdot$m^{-2}) of the biomass on the ungrazed area. By the end of the growing season, aboveground biomass was essentially the same for both the grazed and ungrazed areas. Green LAI on the grazed area was 61% (-1.3 m$^2\cdot$m^{-2}) of the LAI on the ungrazed area (Fig. 2). Green LAI was equal 1 month prior to the end of the growing season on both treatments.

1999–2000. Grazing in the tower footprint was much greater in 1999 because the steers had free choice of where to graze. Aboveground biomass accumulation on the grazed area was greatly reduced compared to the ungrazed (Fig. 2). By

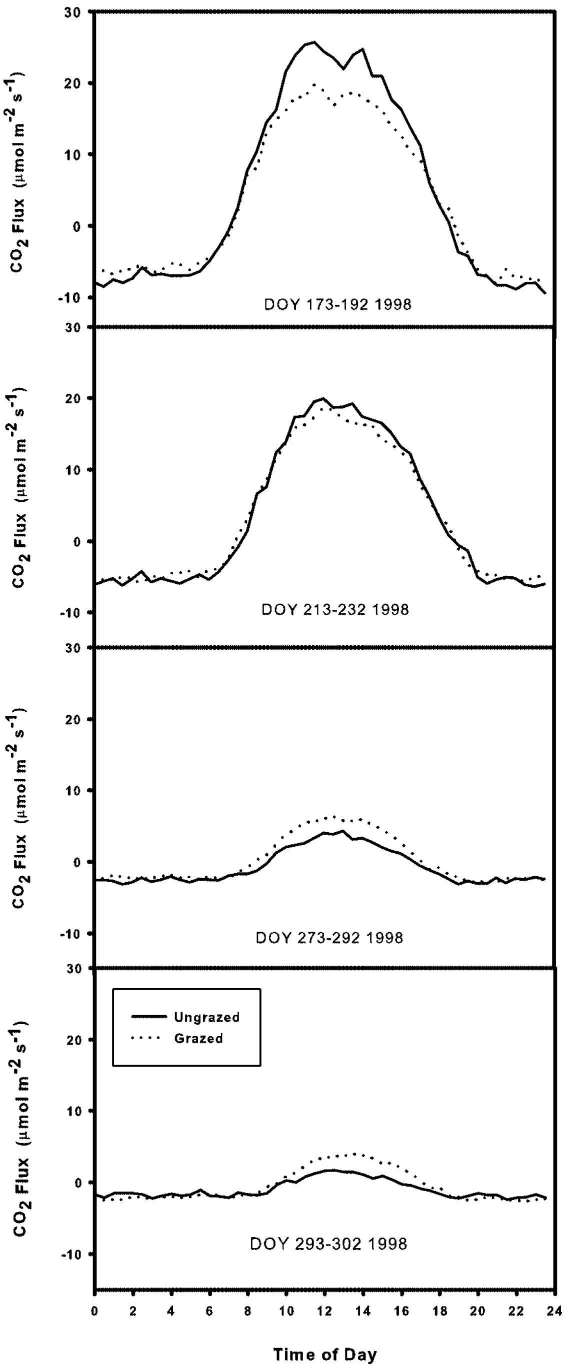

Figure 3. Daily net carbon dioxide flux (30-minute average) on grazed and ungrazed areas averaged over a 20-day period for the 1998–1999 carbon year.

midseason, the grazed area biomass was 24% (−265 g•m^{-2}) of the biomass on the ungrazed area. By the end of the growing season, aboveground biomass was still much lower on the grazed area than the ungrazed. Green LAI on the grazed area was 22% (−2.61 m^{2}•m^{-2}) of the LAI on the ungrazed area (Fig. 2). Green LAI was equal by the end of the growing season on both treatments.

2000–2001. Grazing in the tower footprint in 2000 was similar to that in 1998, but because of the below-normal precipitation, regrowth was minimal during the late season (Fig. 2). By midseason, the grazed area biomass was 78% (−78 g•m^{-2}) of the biomass on the ungrazed area. By the end of the growing season, aboveground biomass was still much lower on the grazed area than on the ungrazed because of the lack of regrowth in the late season. Green LAI on the grazed area was 68% (−1.1 m^{2}•m^{-2}) of the LAI on the ungrazed area (Fig. 2). Green LAI was equal by the end of the growing season on both treatments, a condition caused mainly by leaf senescence in the ungrazed area.

Net Carbon Flux

The data for boundary-layer fluxes are presented as 20-day averages for the 30-minute data and as total cumulative fluxes of carbon for the 20-day periods. For brevity, graphical analysis of the diurnal patterns is presented for 4 20-day periods in each year (Figs. 3–5). Because weather variables affect phenology greatly in different seasons, different periods were chosen to represent the impact of grazing and regrowth on carbon fluxes among years.

Diurnal Net Carbon Flux. *1998–1999.* Fluxes for the day of year (DOY) 173 to DOY 192 period showed an increasingly greater net carbon flux on the ungrazed compared to the grazed. By the DOY 173–192 period, 30-min fluxes showed that carbon loss during the nighttime period was slightly, but consistently, greater on the ungrazed area compared to the grazed (Fig. 3). During the daytime hours, there was a greater net carbon fixation on the ungrazed than the grazed area. By the DOY 213–232 period, the difference between the grazed and ungrazed treatments began to narrow and by the DOY 273–292 period, there was a consistently greater daytime NCE on the grazed than on the ungrazed. During the remainder of the growing season, there was an increasingly greater net CO_2 flux on the grazed than on the ungrazed area.

1999–2000. Following the burn in 1999–2000, the initial 20-day averages showed a net carbon loss with the grazed and ungrazed areas having similar losses. Compared to 1998–1999, the differences in net CO_2 fluxes between the grazed and ungrazed areas were much greater which reflected the greater grazing use in the tower footprint. As the season progressed there was an increasingly greater net CO_2 flux on the ungrazed area compared to the grazed, with daytime fluxes on the grazed area being less than half those of the ungrazed (Fig. 4). Following livestock removal, there was still greater net CO_2 flux on the ungrazed area during the DOY 190–209 period, but by the DOY 210–229 period, fluxes were similar for the 2 areas. During the rest of the growing season, there was an increasingly greater net CO_2 flux on the grazed area compared to the ungrazed.

2000–2001. In 2000–2001, fluxes for the DOY 112–211 periods showed an increasingly greater carbon flux on the ungrazed compared to the grazed (Fig. 5). There was a slight but consistently greater carbon loss during the nighttime period on the ungrazed compared to the grazed. During the daytime hours, there was a greater net carbon fixation on the ungrazed than the grazed area. By the DOY 212–231 period, the difference between the grazed and ungrazed was negligible, and by DOY 232, there was a slightly greater net CO_2 flux on the grazed than on the ungrazed. During the remainder of the growing season, there was an increasingly greater net CO_2 flux

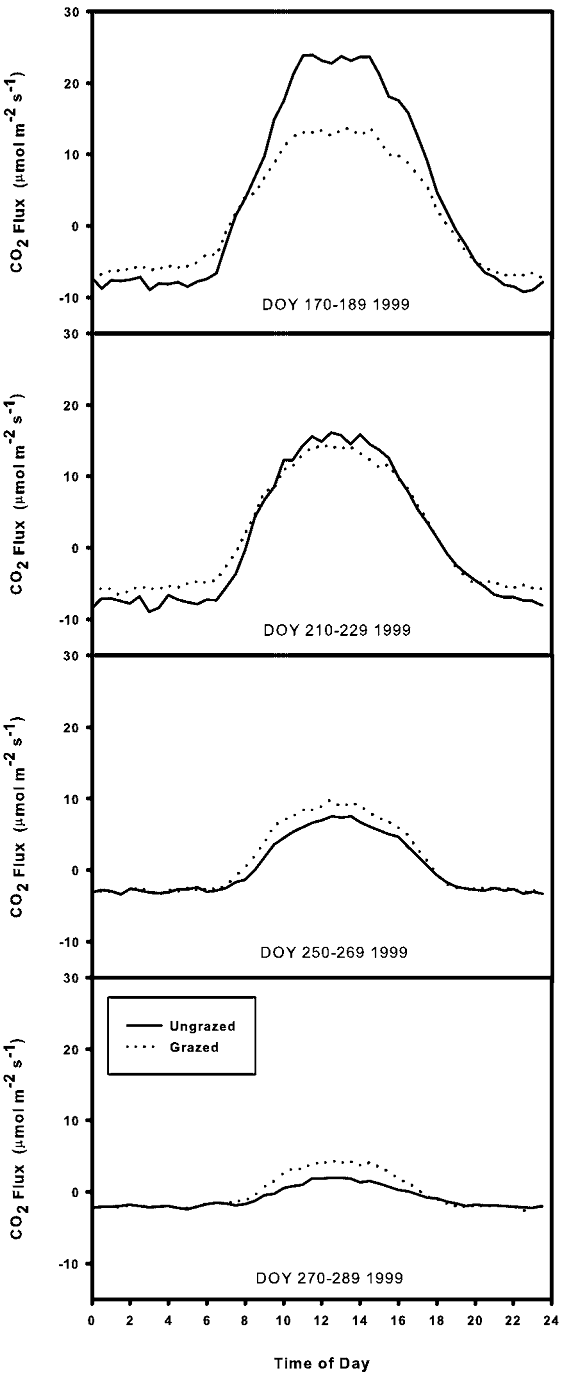

Figure 4. Daily net carbon dioxide flux (30-minute average) on grazed and ungrazed areas averaged over a 20-day period for the 1999–2000 carbon year.

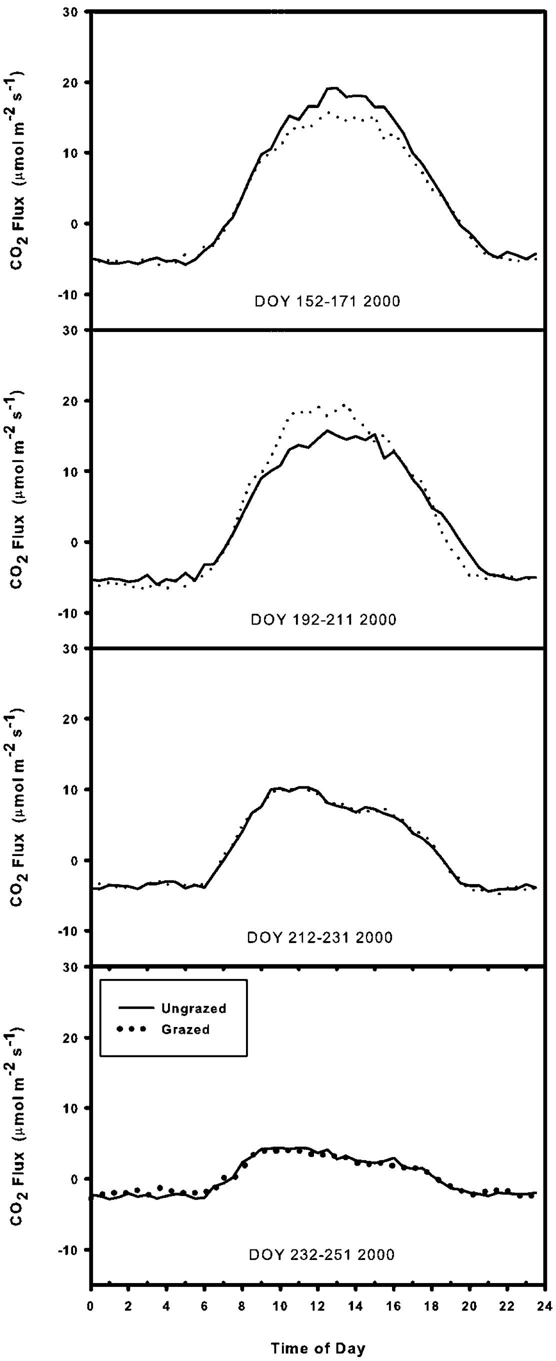

Figure 5. Daily net carbon dioxide flux (30-minute average) on grazed and ungrazed areas averaged over a 20-day period for the 2000–2001 carbon year.

on the grazed than on the ungrazed area. Net CO_2 fluxes in the late season were much lower than the during previous 2 years because of the dry late summer.

Total Cumulative Net Carbon Flux. *1998–1999.* Cumulative total carbon fluxes reflected the change in net CO_2 flux (Fig. 6). From the beginning of the carbon year until DOY 173, there was a greater amount of net carbon accumulated on the ungrazed area compared to the grazed. Following livestock removal, there was more carbon accumulated on the grazed area than the ungrazed until the end of the growing season. After the first killing frost (DOY 306), net carbon fluxes from the grazed and ungrazed areas were similar.

Net carbon flux was partitioned into daytime and nighttime fluxes for 3 different 20-day periods (Fig. 7). During the DOY 173–192 period, which is just prior to the middle of the growing season, NCE was greater in the ungrazed area in the daytime and lower in the nighttime. Total flux was greater during that period. By the middle of the late growing season (DOY 213–232), nighttime, daytime, and total fluxes were

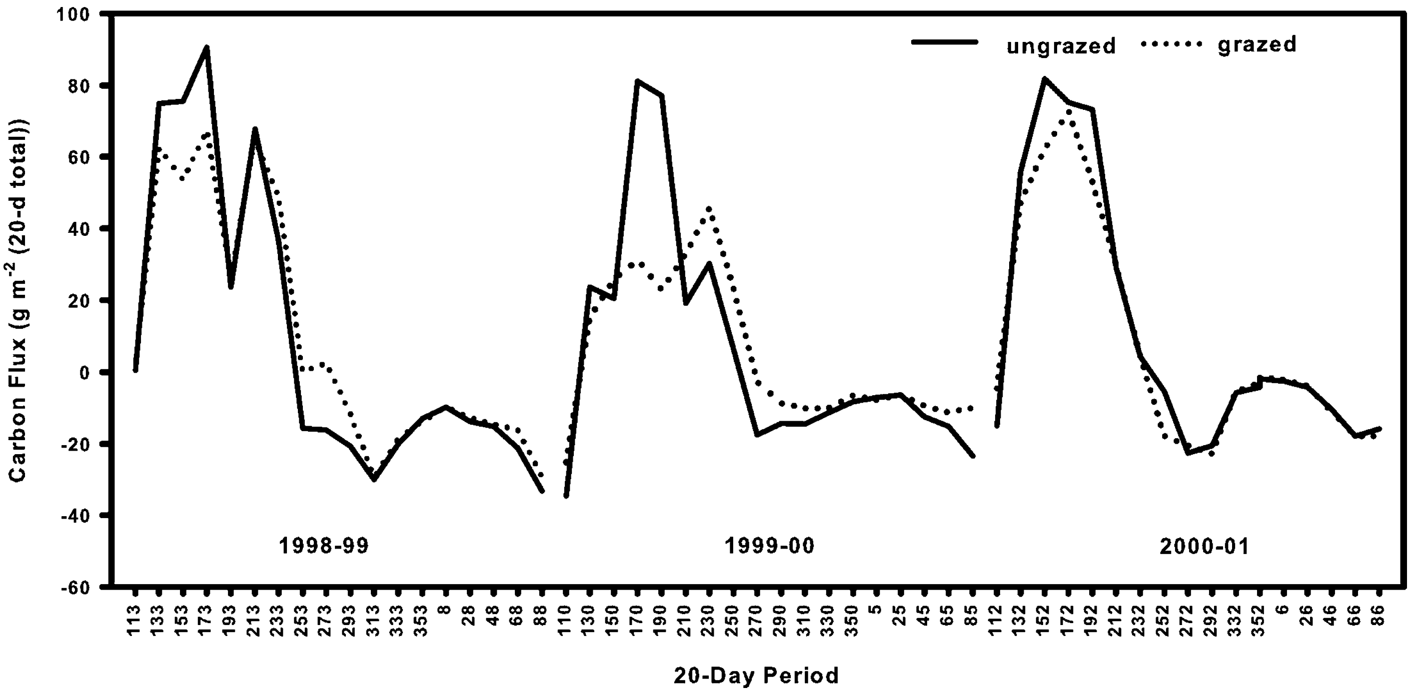

Figure 6. Net carbon exchange for grazed and ungrazed tallgrass prairie for the 1998–2001 carbon years. Values are 20-day accumulations.

similar. In the latter portion of the growing season (DOY 273–292), daytime fluxes were greater and nighttime fluxes lower on the grazed compared to the ungrazed. Total NCE was negative for the ungrazed and essentially zero for the grazed.

1999–2000. As in 1998–1999, cumulative total carbon fluxes reflected the change in net CO_2 flux (Fig. 6), but because of the increased grazing use the accumulations were much greater on the ungrazed compared to the grazed. By DOY 210, the grazed area had a greater net carbon accumulation or lower loss than did the ungrazed and that continued until the end of the growing season. After frost, net carbon fluxes from the grazed and ungrazed areas were similar.

During the DOY 170–189 period, which is just prior to the middle of the growing season, NCE for the ungrazed area was twice that of the grazed in the daytime (Fig. 7). During the nighttime there was a greater loss of carbon from the ungrazed than from the grazed. Total carbon retention by the ecosystem was much greater during that period. By the middle of the late growing season (DOY 210–229), daytime fluxes were similar on ungrazed and grazed areas, but nighttime loss of carbon was greater on the ungrazed area, which resulted in a greater carbon retention by the ecosystem on the grazed area. In the latter portion of the growing season (DOY 270–289), daytime fluxes were greater and nighttime fluxes similar on the grazed compared to the ungrazed. Total NCE was negative for the ungrazed and essentially zero for the grazed.

2000–2001. Cumulative total carbon fluxes reflected the change in net CO_2 flux (Fig. 6). From the beginning of the carbon year until DOY 212, there was a greater amount of net carbon accumulated on the ungrazed area compared to the grazed. Contrary to the previous years, following livestock removal, there was not more carbon accumulated on the grazed area than on the ungrazed until the end of the growing season. After DOY 271, net carbon fluxes from the grazed and ungrazed areas were similar.

During the DOY 172–191 period, which is just prior to the middle of the growing season, NCE was slightly greater in the ungrazed in the daytime and lower by an equal amount in the nighttime (Fig. 7). Total flux was essentially equal on the grazed and ungrazed during that period. By the middle of the late growing season (DOY 212–231), nighttime, daytime, and total fluxes were similar. In the latter portion of the growing season (DOY 272–291), daytime fluxes and nighttime were similar on the grazed compared to the ungrazed. Total NCE was negative and similar for the ungrazed and grazed areas.

Soil CO_2 Fluxes. *1998–1999.* Soil CO_2 fluxes rose during the most active growth period, peaked in midseason, and declined to a midwinter low (Fig. 8). During the late winter and early spring, fluxes varied depending on the temperatures, with cold periods reducing them. Soil CO_2 fluxes between the grazed and ungrazed areas were similar at the beginning of the growing season, but as the season progressed, the ungrazed area had greater fluxes. By DOY 233, the grazed area had fluxes equal to that on the ungrazed. For a period of time the fluxes were greater on the grazed than the ungrazed, but from DOY 321 to 363 fluxes were again higher on the ungrazed compared to the grazed. During the remainder of the winter and spring, fluxes were similar on the 2 areas.

1999–2000. Soil CO_2 fluxes followed the same pattern as in the 1998 grazing season (Fig. 8). As in 1998, soil CO_2 fluxes between the ungrazed and grazed areas were similar at the beginning of the growing season, but as the season progressed the difference between grazed and ungrazed was much greater than in 1998. By DOY 245, the grazed area had fluxes equal to that on the ungrazed. After DOY 245, fluxes were similar on the 2 areas.

2000–2001. Again, soil CO_2 fluxes rose during the most active growth period, peaked in midseason, and declined to a midwinter low. Fluxes were much lower in the winter period in 2000, likely because of the extended period of frozen soil in the winter of 2000–2001. Soil fluxes between the grazed and ungrazed areas were similar at the beginning of the growing season, but as the season progressed, the ungrazed area had greater fluxes (Fig. 8). On DOY 203, the grazed area had fluxes equal to that on the ungrazed, but for the remainder of the growing season, fluxes were greater on the ungrazed than the grazed. After DOY 265, fluxes were similar on the 2 areas.

Carbon Balance

The carbon balance was derived solely from the eddy flux measurements by summing the flux estimates for the entire year and accounting for the carbon losses from burning and cattle export and were reported on a g $C \cdot m^{-2}$ basis. No adjustment for methane was done. Methane emissions from grazing animals were estimated using data from Ahlgrimm and Gadeken (1990) to be 0.34 g $C \cdot m^{-2}$ and did not take into account any correction for uptake by the soil. Because methane fluxes were so low, they were not included in the estimate. A greater concern was the point-source emissions of CO_2 from the grazing livestock. The proportion of those CO_2 emissions captured by the eddy flux system is unknown, consequently we did not attempt to include them in the carbon balance.

1998–1999. NCE in the 1998–1999 carbon year was slightly negative on the ungrazed and essentially zero on the grazed area (Table 1). When taken into context relative to the total amount of carbon fixed and lost during the year, neither grazed nor ungrazed tallgrass prairie could be considered a source or sink. The grazing impact on NCE measured by the eddy flux system during this year was minor with the difference between grazed and ungrazed tallgrass prairie primarily in the amount of carbon lost during the spring burn. Carbon export for the cattle on the grazed area (6 g $C \cdot m^{-2}$) was a small amount. The common practice of annual burning of steer-grazed tallgrass prairie (Anderson et al. 1970) resulted in a significant loss of carbon from the system in one event. In unburned areas, the loss would be spread over the entire growing season.

1999–2000. NCE in the 1999–2000 carbon year was similar to that of the previous year and neither grazed nor ungrazed tallgrass prairie was likely a source or sink (Table 1). Because grazing in the source area was much greater in 1999–2000 than during the previous year, NCE from flux measurement was much greater on the ungrazed than the grazed area and the amount of carbon lost during the spring burn was twice as great on the ungrazed area compared to the grazed.

2000–2001. NCE in the 2000–2001 carbon year was positive on the ungrazed area compared to negative in the previous 2 years and slightly positive on the grazed area (Table 1). NCE from flux measurement was much greater on the ungrazed area compared to the grazed, even though 2000–2001 had the least early-season precipitation of the 3 years. Burn biomass carbon loss was not greatly different on the grazed and ungrazed areas,

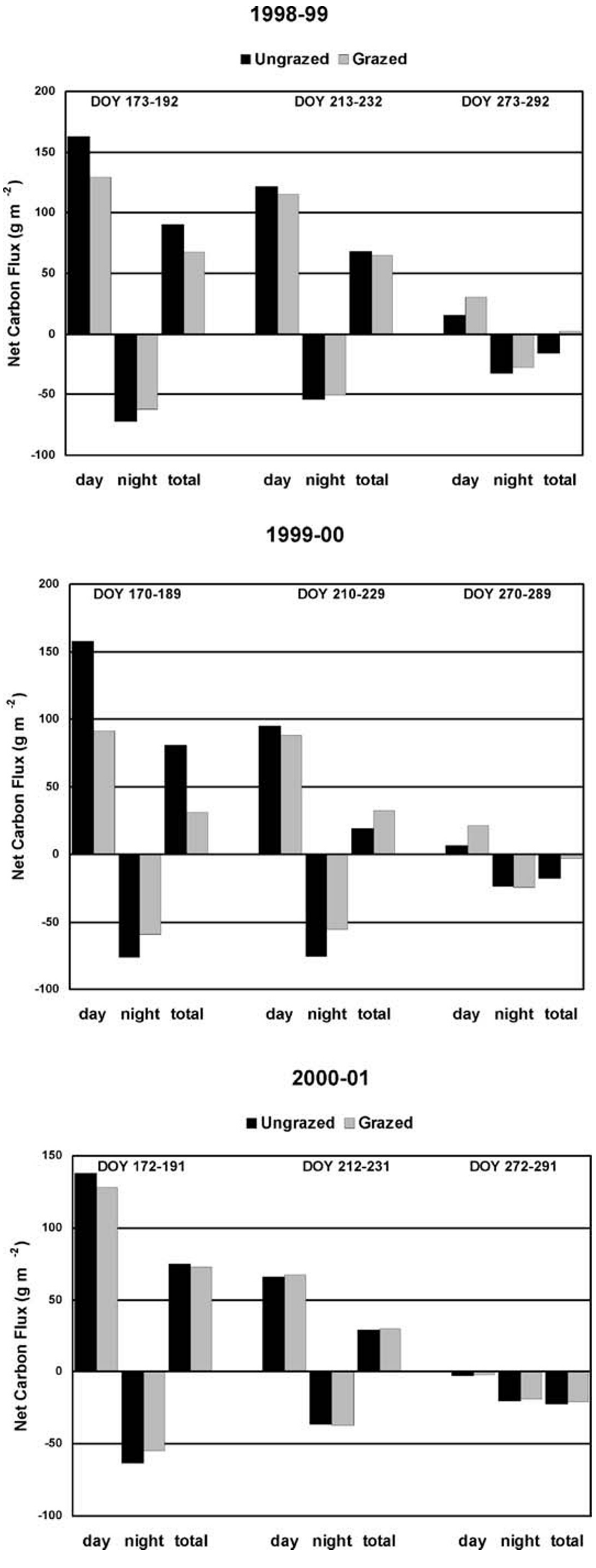

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Figure 7. Daytime, nighttime, and total net carbon exchange for grazed and ungrazed tallgrass prairie for the 1998–2001 carbon years. Values are 20-day accumulations.

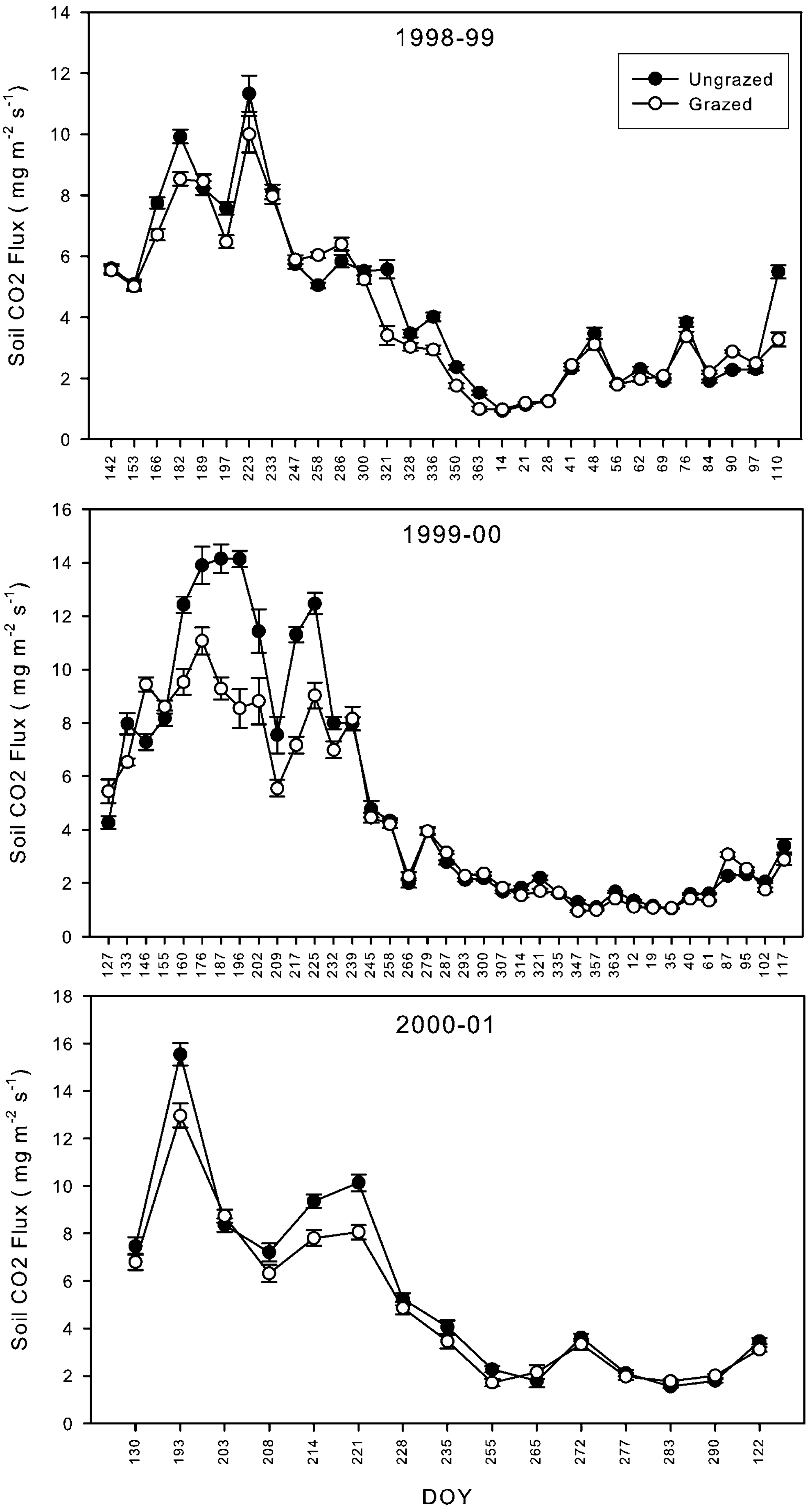
1998-99
Ungrazed
Grazed
Soil CO2 Flux (mg m^{-2} s^{-1})
0
2
4
6
8
10
12
14
142 153 166 182 189 197 223 233 247 258 286 300 321 328 336 350 363 14 21 28 41 48 56 62 69 76 84 90 97 110
1999-00
Soil CO2 Flux (mg m^{-2} s^{-1})
0
2
4
6
8
10
12
14
16
127 133 146 155 160 176 187 196 202 209 217 225 232 239 245 258 266 279 287 293 300 307 314 321 335 347 357 363 12 19 35 40 61 87 95 102 117
2000-01
Soil CO2 Flux (mg m^{-2} s^{-1})
0
2
4
6
8
10
12
14
16
18
130 193 203 208 214 221 228 235 255 265 272 277 283 290 122
DOY

Table 1. Cumulative CO_2 flux ($\mu mol \cdot m^{-2}$) on grazed and ungrazed areas during indicated 20-day periods for the 1998–2000 growing seasons.

	1998			1999			2000	
DOY	Ungrazed	Grazed	DOY	Ungrazed	Grazed	DOY	Ungrazed	Grazed
	($\mu mol \cdot m^{-2}$)							
113–132	23	23	110–129	−1 595	−1 165	112–131	−697	−216
133–152	3 464	2 900	130–149	1 691	564	132–151	2 582	2 193
153–172	3 497	2 479	150–169	3 445	1 688	152–171	3 781	2 868
173–192	4 186	3 116	170–189	3 748	1 452	172–191	3 476	3 364
193–212	1 100	1 229	190–209	3 568	1 127	192–211	3 384	2 463
213–232	3 137	3 157	210–229	883	1 514	212–232	1 354	1 368
233–252	1 689	2 261	230–249	1 402	2 117	232–251	197	206
253–272	−199	3	250–269	292	1 092	252–271	−251	−823
272–292	−753	115	270–289	−810	−129	272–291	−1 047	−951
293–312	−957	−546	290–309	−661	−405	292–311	−954	−1 056

which coupled with the greater NCE from flux measurement, led to the positive carbon balance on the ungrazed area.

Net CO_2 Exchange Efficiency

During 1998, grazing in the source area for the grazed treatment was minimal, as evidenced by the relatively small reductions in aboveground biomass and green leaf area (Fig. 2). Consequently, there was a corresponding similarity in the amount of CO_2 retained or lost by the ecosystem per unit of aboveground biomass and leaf area (Fig. 9). There was a slightly better efficiency on the ungrazed area early in the season compared to the grazed (DOY 173–192 and 213–233) and a slightly better efficiency in the late season on the grazed compared to the ungrazed (DOY 273–292). Cumulative CO_2 fluxes were greater on the ungrazed in the early season than on the grazed and lower in the late season (Table 2).

Grazing in the source area for the flux towers was much greater in the 1999 growing season. By midseason, there was 3 to 4 times as much aboveground biomass and green leaf area on the ungrazed as on the grazed (Fig. 2). During daylight hours throughout the growing season, there was a substantially greater amount of CO_2 retained by the ecosystem on the grazed area compared to the ungrazed per unit of biomass or green leaf area (Fig. 10). Conversely, there was more CO_2 lost from the system during nighttime hours on the grazed area compared to the ungrazed per unit of biomass or leaf area. The greatest differences in NCE efficiency came during the 20-day period following livestock removal in mid-July (DOY 210–229). Cumulative CO_2 flux response to grazing in 1999 was similar to that in 1998 (Table 2).

Grazing in the source area for the flux towers in 2000 was greater than that in the 1998 growing season but less than that in 1999. Midseason aboveground biomass and green leaf area on the ungrazed was twice that on the grazed (Fig. 2). NCE efficiency during daylight hours on the grazed area was only slightly higher than that of the ungrazed in the early and middle portions of the growing season (Fig. 11). During those periods, there was more carbon lost from the system during nighttime hours on the grazed area compared to the ungrazed per unit of leaf area, but net CO_2 exchange efficiency per unit of aboveground biomass did not differ greatly between treatments. In the late growing season, CO_2 retained by the ecosystem per unit of leaf area during daylight hours was greater on the ungrazed area than on the grazed, and CO_2 lost during nighttime hours was less per unit of leaf area. Cumulative CO_2 fluxes in 2000 were greater on the ungrazed in the early season than on the grazed and similar in the late season (Table 2).

DISCUSSION AND CONCLUSIONS

The primary focus of this research was to determine the impact of grazing on NCE of tallgrass prairie compared to ungrazed areas. Because essentially all grasslands are grazed, parameters used in models to predict the carbon fluxes and responses to elevated CO_2 must be derived from grazed areas. Almost all of the work that has been done in the carbon flux and elevated CO_2 area has been on ungrazed grasslands. Inputs into mechanistic models have relied heavily on LAI, soil water, energy, and climate to estimate ecosystem productivity. For a given climatic input, LAI has a large impact on productivity estimates and grazing reduces LAI. Therefore, modeled productivity estimates generally linearly decline with grazing because LAI is reduced. Our research has shown that there appear to be compensatory mechanisms which result in greater carbon acquisition at certain times during the growing season from grazed areas than from ungrazed even though LAI was much greater on the ungrazed area. That outcome was likely because of more photosynthetically efficient leaves on the grazed area because of leaf age and leaf canopy architecture, which attenuates light with depth in the canopy. Williamson et al. (1989) indicated that grasses are well adapted to regenerating biomass removed by grazing. Because apical meristems of grass tillers remain at or below the soil surface during most

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Figure 8. Soil CO_2 flux as measured with surface chambers at midday on grazed and ungrazed tallgrass prairie period for the 1998–2001 carbon years. Error bars are 1 SE ($n = 4$).

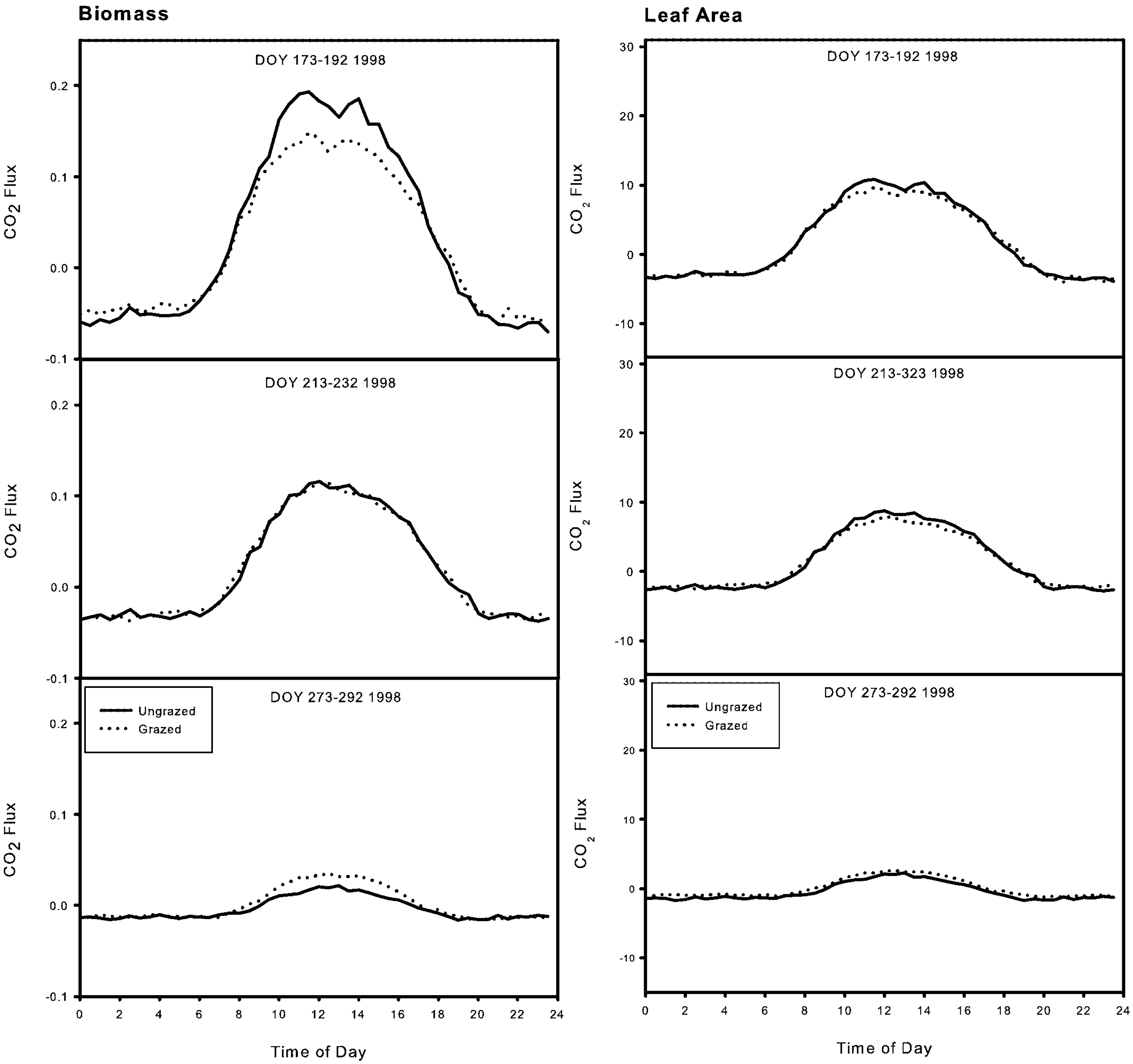

Figure 9. Net carbon dioxide capture efficiency reported as carbon exchange per unit of aboveground biomass (ABM) (μmol • m^{-2} • s^{-1} [g ABM]$^{-1}$) or green leaf area index (μmol • m^{-2} • s^{-1} [Green LAI m^2 • m^{-2}]$^{-1}$) (30-minute average) on grazed and ungrazed areas averaged over indicated 20-day periods for the 1998 growing season.

of the growing season (Dahl and Hyder 1977), leaf replacement continues under grazing because the apical meristem is not removed by the grazing animal. Also, grass leaves grow from their base from intercalary meristems (Hyder 1972) which, because of the lack of internode elongation of the grass stem, remain at a height that is normally not exposed to grazing animals, particularly cattle. Williamson et al. (1989) used grasshoppers to remove varying amounts of leaf biomass and found that in none of the 5 experiments they conducted did a short-duration grazing event reduce annual NPP of blue grama compared with ungrazed areas. Oosterheld (1992) reported that with 2 grass species, plants showed the same aboveground growth regardless of defoliation intensity because of an exponential stimulation of relative growth rate by defoliation. He concluded that exponential aboveground compensatory responses represent a key feedback process resulting in constant aboveground growth regardless of defoliation intensity. However, if defoliation is substantial and frequent, that conclusion is not valid. In the Williamson et al. (1989) study, when grazing was defined as heavy, there was a reduction in aboveground net primary productivity.

In our study, when there was substantially reduced green leaf area because of grazing in the early growing season, there was a greatly reduced NCE during the daylight hours. Later in the season, lack of light penetration and older leaves on the ungrazed area likely caused reductions in NCE. Wuhlschleger and Oosterhuis (1992), working with cotton, concluded that leaf senescence contributed to reduced canopy photosynthesis when new leaf initiation could not compensate for increased leaf aging after canopy closure. As supply of assimilate from the upper canopy increased, lower canopy supply decreased dramatically. Lecain et al. (2000) found that there were higher CO_2 exchange rates in grazed pastures than in ungrazed exclosures in a Wyoming grassland early in the season. They concluded that there was better light penetration to newly emerging leaves and a warmer microclimate near the soil because of lack of litter. Canopy respiration is also greater with a greater leaf area. Because grazing reduces leaf area, canopy respiration would be reduced as well. Morris and Jensen (1998) indicated that there was an optimum canopy biomass under grazing and a supraoptimal canopy under nongrazing of *Spartina anglica* salt marshes. They concluded that because net ecosystem production was similar for grazed and ungrazed areas, it was likely because less of the assimilate was being used for canopy respiration under grazing. From our study, we conclude that under grazing the continual regeneration of new leaves i.e., greater leaf-level photosynthesis, and the open canopy architecture provided greater radiation use efficiency and reduced canopy respiration, which compensated for the lower leaf area. It appears that, as grazing utilization increases, there is an increased efficiency of CO_2 retention by the ecosystem during daylight hours per unit of biomass or green LAI during the late season. That likely occurs because there is active leaf initiation and growth on the grazed area compared to essentially no new leaf initiation or growth on the ungrazed. The greatest impact on net CO_2 exchange efficiency occurred during the 1999 growing season when biomass and green LAI were the least on the grazed area compared to the ungrazed. Because we measured ecosystem-level CO_2 flux, the effect of grazing on microbial and root respiration is reflected in net CO_2 flux. When grazing significantly reduced green leaf area, soil CO_2 flux rates were reduced to half that of the ungrazed. Because grazing greatly reduced the amount of carbon available for translocation below ground, root and microbial respiration were reduced. Craine et al. (1999) showed that both shading and clipping reduced soil CO_2 flux by 40% and 19% respectively in a Minnesota grassland. Bremer et al. (1998), studying Kansas tallgrass prairie, reported that both clipping and grazing reduced soil CO_2 flux.

Cumulative effects of grazing on CO_2 flux between grazed and ungrazed prairie are difficult to assess because of the large differences in grazing that occurred in the source area for the flux towers. Interannual comparisons are also difficult because of weather differences. Peak carbon acquisitions for the ungrazed area were similar among years (Fig. 6), but the length of time that the ungrazed maintained high flux rates was longer in years when adequate soil moisture supplies existed for extended periods. It appears that previous year's weather conditions are decoupled from the next season. Tallgrass prairie generally stores soil water from late summer until the beginning of the next growing season (Anderson 1965), therefore growth in the early season is usually not water limited. Flux rates among the 3 years of this study were similar early in the season and were affected by current weather later in the season. On grazed areas, flux rates were most affected by the amount of grazing in the source area.

Table 2. Net carbon exchange (NCE) for indicated periods in the growing season, carbon lost at burning time, carbon exported by livestock grazing, and a carbon balance. Early season extended from mid-April to mid-July (90 days), late season from mid-July to mid-October (90 days), and dormant season from mid-October to mid-April (185 days).

	Ungrazed	Grazed
1998–1999	--------------g $C \cdot m^{-2}$	-------------
NCE early season	239	185
NCE late season	76	133
NCE total growing season	315	318
NCE dormant season	−184	−194
Burn biomass C	−167	−123
Cattle export	0	−6
Carbon balance	−36	−5
1999–2000		
NCE early season	97	48
NCE late season	101	115
NCE total growing season	198	163
NCE dormant season	−74	−89
Burn biomass C	−159	−76
Cattle export	0	−7
Carbon balance	−35	−9
2000–2001		
NCE early season	193	176
NCE late season	65	26
NCE total growing season	258	202
NCE dormant season	−71	−73
Burn biomass C	−126	−116
Cattle export	0	−7
Carbon balance	61	6

The overall impact of the increased NCE efficiency on the grazed area compared to the ungrazed was that a greater amount of CO_2 was retained by the ecosystem in the late season on the grazed area in 1998 and 1999 (Table 1). Late-season water stress in 2000 was likely the reason that there was not a greater late-season retention of CO_2 or less loss on the grazed area compared to the ungrazed. Because the area was burned each year, NPP was not affected by litter buildup. Therefore, we conclude that the differences in net CO_2 exchange efficiency we have shown here are most likely because of reduced respiration losses and increased photosynthetic efficiency afforded by an open canopy and younger leaves. These data elucidate, in part, the mechanism by which grazed grasslands attain a maximum NPP at some optimal grazing rate McNaughton (1983). They lend support to the "grazing maximization hypothesis" proposed by McNaughton (1979).

Other factors that might have impacted NCE differentially between the grazed and ungrazed areas include soil and vegetation trampling effects and the fertilization effects of urine and fecal deposition. At the stocking densities in this study, trampling effects were likely minimal, with only 5–10% of the area trampled (extrapolated from Quinn and Hervey 1970). Any trampling likely had a negative effect on plant photosynthetic capacity by physically damaging the leaf, but

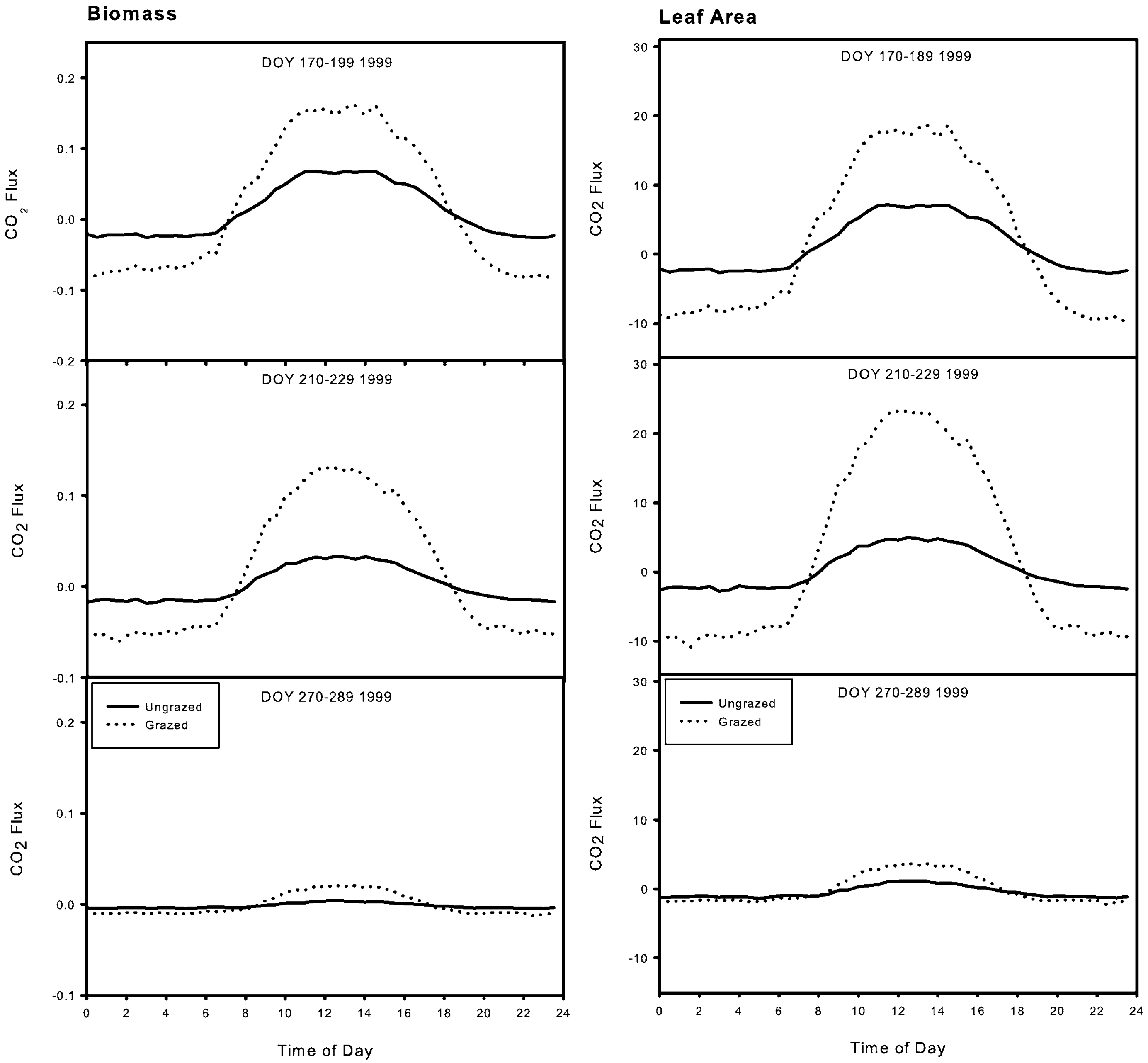

Figure 10. Net carbon dioxide capture efficiency reported as net carbon exchange per unit of aboveground biomass (ABM) (μmol•m^{-2}•s^{-1} [g ABM]$^{-1}$) or green leaf area index (μmol•m^{-2}•s^{-1} [Green LAI m^2•m^{-2}]$^{-1}$) (30-minute average) on grazed and ungrazed areas averaged over indicated 20-day periods for the 1999 growing season.

the relatively small portion of the total photosynthetic capacity affected by trampling had a minimal impact on NCE. Trampling usually affects soil physical properties negatively by reducing water infiltration rates, thereby reducing soil water availability. Because the area affected by trampling was minimal, the effects on NCE were likely small. Similarly, the fertilization effects of urine and fecal deposition likely had a minimal effect. Simpson and Stobbs (1981) indicated that under intensive grazing (stocking densities more than twice that in this study) only 2%–3% of the area was covered by fecal and urine patches. In addition, fecal and urine deposits are not uniformly distributed within a pasture. Loafing areas and water sources receive a much higher proportion of the urine and fecal deposits.

Grazing also modified water and energy fluxes from the prairie. Bremer et al. (2001), using data from the same towers as in this study, indicated that in 1999 grazing reduced evapotranspiration (ET) by 28% during midsummer (mean ETs were 3.60 mm•d^{-1} on grazed area and 4.99 mm•d^{-1} on the ungrazed). Less leaf area on the grazed area than on the ungrazed (78% lower) and below-normal precipitation kept the soil dry near the surface, which reduced transpiration and evaporation from soil. With lower ET, there was greater soil water in the 0–30 cm in profile on the grazed area. Summed over the growing season, cumulative ETs were estimated at 526 and 494 mm on the ungrazed and grazed areas, respectively. As the canopy senesced in the late season on the ungrazed area and

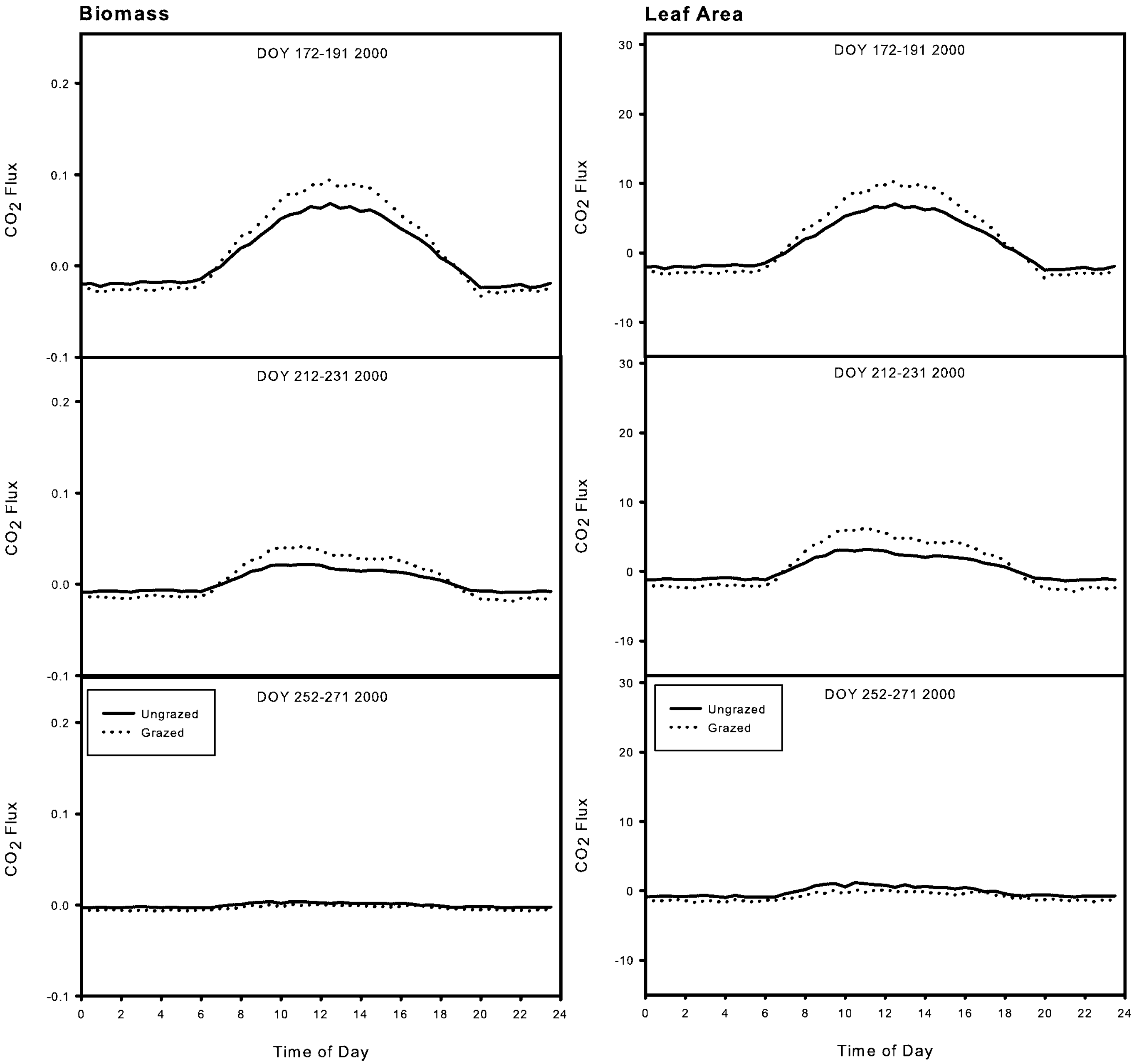

Figure 11. Net carbon dioxide capture efficiency reported as net carbon exchange per unit of aboveground biomass (ABM) (μmol$\cdot$m$^{-2}\cdot$s^{-1} [g ABM]$^{-1}$) or green leaf area index (μmol$\cdot$m$^{-2}\cdot$s^{-1} [Green LAI m$^2\cdot$m^{-2}]$^{-1}$) (30-minute average) on grazed and ungrazed areas averaged over indicated 20-day periods for the 2000 growing season.

soil water was depleted, there was greater ET on the grazed area than the ungrazed. Soil water in the 0–30-cm soil layer was higher during the middle and late growing season on the grazed area as a result of the reduced ET. Because late-season water deficit is common in the Flint Hills tallgrass prairie, late-season NCE was likely higher on the grazed area than on the ungrazed because of reduced water stress as well as the younger, more photosynthetically efficient leaves.

Soil CO_2 flux was affected by grazing and season. In general, soil CO_2 flux was greatest when carbon acquisition was the greatest. Schlesinger and Andrews (2000) stated that soil respiration was the primary path by which CO_2 fixed by plants returned to the atmosphere. In our study, during peak growth soil CO_2 flux rates were as high as 0.62 mg C$\cdot$m$^{-2}\cdot$s^{-1} during midday on the ungrazed area. During winter, they were still 0.07–0.14 mg C$\cdot$m$^{-2}\cdot$s^{-1}. When grazing reduced leaf area significantly, soil CO_2 flux rates were greatly reduced. In the 1999 growing season, with a greatly reduced leaf area on the grazed area, soil CO_2 flux rates in midseason were half that of the ungrazed. It appears that substrate availability for soil microbes has a large impact on soil CO_2 flux. Craine et al. (1999) showed that both shading and clipping reduced soil CO_2 flux by 40% and 19% respectively in a Minnesota grassland. Bremer et al. (1998) reported similar findings in Kansas tallgrass prairie. Knapp et al. (1998), in a study dealing with fire impacts in Kansas tallgrass prairie, determined that there was a link between aboveground NPP and soil CO_2 flux. We agree with Craine et al. (1999), who concluded that variations in factors that affect carbon availability to the belowground system are important determinants of soil CO_2 flux and should be included explicitly in studies that measure or model ecosystem carbon flow. Integrated over the entire 3 years, the average annual soil carbon fluxes were 1 900 $g\ C \cdot m^{-2} \cdot y^{-1}$ for the ungrazed and 1 588 $g\ C \cdot m^{-2} \cdot y^{-1}$ for the grazed. These values are similar to those of Bremer et al. (1998). Ham et al. (1995) reported that soil respiration was about 85% of the total respiration in tallgrass prairie. Using that value, total respiration (soil + canopy) would be 2 235 $g\ C \cdot m^{-2} \cdot y^{-1}$ and 1 869 $g\ C \cdot m^{-2} \cdot y^{-1}$ for the ungrazed and ungrazed, respectively. Assuming NCE is zero on an annual basis (based on the tower data), then NPP must equal these values. Thus, grazing likely caused a 17% reduction in NPP, but lower respiration in the grazed plot negated this impact on net carbon exchange.

Even though we determined a carbon balance for the grazed and ungrazed areas for each of the 3 years of the study, we cannot say with certainty that the grasslands under these 2 treatments are either sequestering carbon or losing carbon. The uncertainties associated with the measurements using eddy flux techniques and gap filling accuracy are certainly greater than the small net carbon balance numbers we derived from the measurements. One way of putting the carbon balance uncertainty in perspective would be to sum the carbon lost from the ecosystem through soil CO_2 flux. That loss is continuous and is the major pathway for carbon to return to the atmosphere. If we assume an arbitrary ± 5% error rate for the eddy flux measurements with carbon acquisition and carbon loss from soil CO_2 flux being 1 600–1 900 $g\ C \cdot m^{-2}$, then the resultant 80 to 95 $g\ C \cdot m^{-2}$ is greater than the carbon balance estimates we derived. Indeed, the ± 5% error is half to equal the NCE for the years in this study. Another source of error would be the estimates for loss during burning. Standard errors for the carbon loss from burning were ± 22 $g\ C \cdot m^{-2}$ on the ungrazed area and ± 16 $g\ C \cdot m^{-2}$ for the grazed, therefore better quantifying that loss would reduce the uncertainty in the carbon budget.

ENVIRONMENTAL IMPLICATIONS

Mitigation of greenhouse gasses through management strategies has been a focus of research in the global climate-change arena. Grasslands with their large carbon stores and the short-lived nature of grass root systems were thought to be a potential source of relatively long-term carbon storage. The implication of this research is that proper management of mesic grasslands may not increase carbon stores, but maintain them. Contrary to arable agriculture where tillage causes outgassing of CO_2, proper management of grasslands does not contribute to atmospheric greenhouse gases. The lack of increased carbon storage in ungrazed systems indicates that in natural grassland systems, eliminating grazing to increase carbon sequestration is likely not a viable option.

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