Responses of Soil Respiration to Clipping and Grazing in a Tallgrass Prairie

Dale J. Bremer,* Jay M. Ham, Clenton E. Owensby, and Alan K. Knapp

ABSTRACT
Soil-surface CO₂ flux (F) is an important component in prairie C budgets. Although grazing is common in grasslands, its effects on F, have not been well documented. Three clipping treatments: (i) early-season clipping (EC); (ii) full-season clipping (FC); and (iii) no clipping (NC); which represented two grazing strategies and a control, were applied to plots in a tallgrass prairie in northeastern Kansas, USA. Measurements of F were made with a portable gas-exchange system at weekly to monthly intervals for 1 yr. Concurrent measurements of soil temperature and volumetric soil water content at 0.1 m were obtained with dual-probe heat-capacity sensors. Measurements of F, also were obtained in grazed pastures. F ranged annually from 8.8 × 10⁻³ mg m⁻² s⁻¹ during the winter to 0.51 mg m⁻² s⁻¹ during the summer, following the patterns of soil temperature and canopy growth and phenology. Clipping typically reduced F, 21 to 49% by the second day after clipping despite higher soil temperatures in clipped plots. Cumulative annual F, were 4.94, 4.04, and 4.11 kg C m⁻² yr⁻¹ in NC, EC, and FC treatments, respectively; thus, clipping reduced annual F, by 17.5%. Differences in F between EC and FC were minimal, suggesting that different grazing strategies had little additional impact on annual F. Daily F, in grazed pastures was 20 to 37% less than F, in ungrazed pastures. Results suggest that grazing moderates F, during the growing season by reducing canopy photosynthesis and slowing translocation of carbon to the rhizosphere.

The rapid increase in atmospheric CO₂, combined with evidence of a terrestrial sink of CO₂ in the northern hemisphere (Claeys et al., 1995; Denning et al., 1995), emphasize the need for measuring the C balances of major ecosystems. Because grasslands cover large areas of the earth's surface, they might represent a significant sink or source of C (Hall and Scurlock, 1991; Thornley et al., 1991; Glenn et al., 1993). Soil-surface CO₂ flux (F) is a large component of the C balance in grasslands (Gale et al., 1990; Kim et al., 1992; Ham et al., 1995). Therefore, a complete global C budget should include an analysis of the processes that determine F, as well as an assessment of how land management affects prairie F.

Carbon dioxide in the soil is produced primarily by microbial and root respiration (Johansson, 1992; Cheng et al., 1993). Previous research has indicated that the rate of CO₂ production in the soil is largely a function of soil temperature and soil water content (Kucera and Kirkham, 1971; Grahammer et al., 1991; Norman et al., 1992; Hansen et al., 1993; Lloyd and Taylor, 1994). Soil respiration also is affected by the supply of C substrate, which is dependent on canopy photosynthesis, translocation, biogeochemical cycling in the rhizosphere, and surface litter (Davidson and Milthorpe, 1966; Hattrick and Bowling, 1973; Bingham and Stevenson, 1993; Fitter et al., 1998). Norman et al. (1992) found that predictions of prairie F, from soil temperature and soil water content were improved by including leaf area index (LAI) in the model.

Land management undoubtedly alters F, (Burke et al., 1991; Ojima et al., 1993; Seastedt and Coxwell, 1994). Grazing by cattle (Boos taurus), for example, typically removes 40 to 60% of the annual aboveground biomass from a prairie ecosystem (Launghbaugh and Owensby, 1978), which could dramatically affect F, (Knapp et al., 1998). Including grazing as a factor in prairie F, analysis is critical because grazing by domestic or native herbivores is common in grasslands.

There are several mechanisms by which grazing, via removal of leaf area, affects F, (Fig. 1). Reduced leaf area increases soil-surface irradiance, thereby raising soil temperatures and improving the environment for root and microbial respiration. Higher radiation at the soil surface also increases evaporation. However, defoliation reduces transpiration, which tends to conserve soil water deeper in the soil. Owensby et al. (1970) found that soil water was conserved in clipped plots, suggesting that reduced transpiration was the dominant factor. Thus, although increased evaporation may promote drying near the soil surface, grazing probably conserves soil water lower in the profile. The latter would improve the environment for soil respiration at greater depths.

Grazing also reduces canopy photosynthesis (Fig. 1). Several grass species have adapted to grazing by rapidly replacing photosynthetic tissue following defoliation (McNaughton, 1983; Coughenour, 1985; Briske et al., 1996). Assimilate is reallocated to regrowing shoots at the expense of roots, so less C is translocated to the roots (Davidson and Milthorpe, 1966; Ryle and Powell, 1975; Danckwerts and Gordon, 1987). Crider (1955) found that removal of half or more of the foliage from seven grass species caused root growth to stop for up to 6 wk. Root respiration (R_r) also is related closely to the rate of C transported from the shoot (Osman, 1971; Hattrick and Bowling, 1973; Aguirrezañabal et al., 1994; Anthor, 1989, p. 52–54). Leaf area removal caused R_r to decline in several studies (Davidson and Milthorpe, 1966; Farrar and Jones, 1986; Bingham and Stevenson, 1993), although no response (Detling et al., 1979) and even increased R_r was measured after defoliation in other studies (Chapin and Slack, 1979; Holland et al., 1996). Root exudates in a tallgrass prairie may decline

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D.J. Bremer, J.M. Ham, and C.E. Owensby, Dep. of Agronomy, 400 Throckmorton Hall, Kansas State Univ., Manhattan, KS 66506; and A.K. Knapp, Div. of Biology, 251 Ackert Hall, Kansas State Univ., Manhattan, KS 66506, Contribution no. 98-234-J from the Kansas Agric. Exp. Station. Received 30 Jan. 1998. *Corresponding author (bremer@ksu.edu).


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*Abbreviations: LAI, leaf area index; EC, early-season clipping; FC, full-season clipping; NC, no clipping; IPAR, intercepted photosynthetically active radiation; F, soil-surface CO₂ flux; R_r, root respiration; W, volumetric water content.*
under clipping or grazing (Garcia, 1992), thereby hindering microbial activity and negatively affecting \( R_e \) by decreasing the mineralization of organic matter. Indeed, Garcia and Rice (1994) reported that clipping reduced microbial biomass in a tallgrass prairie. Reduced C translocation to the root also might lead to root death, which could enhance microbial activity but decrease net root metabolism and respiration. Kosonen (1969) found F, to be correlated positively to the amount of standing live crop in a meadow, emphasizing the role of canopy photosynthesis in F.

Therefore, in grazed pastures, rates of CO₂ evolution in the soil are affected by the complex interaction of several factors. Reduced canopy photosynthesis under grazing might cause root and microbial respirations to decline, but that decline could be offset by warmer and presumably wetter soils. The resulting concentration of CO₂ in the soil determines the soil-to-atmosphere CO₂ gradient that ultimately drives F, (Fig. 1).

Our objectives were to determine the effects of clipping and grazing on rates of soil CO₂ flux. Two grazing strategies that represent different stocking rates were simulated in a clipping study. Soil temperature, volumetric soil water content, and photosynthetically active radiation intercepted by the canopy were measured at weekly to monthly intervals to evaluate their effects on \( F_e \). Measurements of \( F_e \), gravimetric soil water content, and aboveground biomass also were collected in pastures grazed by cattle and bison, and were compared to results from the clipping study.

**MATERIALS AND METHODS**

**Study Site**

This study was conducted from June 1996 to June 1997 in the Konza Prairie Research Natural Area (Konza Prairie [39° 06’ N, 96° 33’ W, ~340 m above mean sea level]), 10 km south of Manhattan, KS. Vegetation at the site, which was burned annually, was tallgrass prairie dominated by the C₄ grasses big bluestem (Andropogon gerardii Vitman), little bluestem (A. scoparius Michx.), Indian grass (Sorghastrum nutans (L.) Nash), and switchgrass (Panicum virgatum L.) (Gitson and Hubert, 1987). The site was an expansive lowland with a 5% slope and a 315° aspect. The soil at the site was a silty clay loam (Benfield series: fine, mixed, mesic Udic Argiustolls). Soil in the 0 to 15 cm layer, which was sampled on 6 December (DOY 341), 1996, contained 4.5 ppm NH₄-N, 1.3 ppm NO₃-N, 4 ppm P, 318 ppm K, and 5.5% organic matter content (analyses conducted by the Soil Testing Laboratory, Kansas State Univ.). Soil N and P were determined calorimetrically with 1 N KCl and Bray 1 extract solutions, respectively. During the study, precipitation at Konza Prairie was 803 mm, which was 56 mm less than the 30-yr mean for the same period. However, soil water content was near field capacity at the beginning of the study, and precipitation was normal (489 mm) from June to October (DOY 152 to 304), 1996.

Twenty-seven plots (2 by 3 m, separated by 4 m, unclipped aisles) were established for the clipping study (Fig. 2). Three treatments, replicated nine times, were applied to the plots in a blocked, Latin square design. The treatments were early-season clipping (EC); full-season clipping (FC); and no clipping (NC). Treatments simulated two grazing strategies and a control, where EC represented intensive-early stocking rate; FC represented the traditional, full-season stocking rate; and
NC represented ungrazed prairie. Traditional, full-season stocking in Kansas typically occurs between 1 May and 1 October (DOY 121–274), and intensive-early stocking is practiced between 1 May and 15 July (DOY 121–197), at 2 × the traditional stocking rate (Lauchbaugh and Owensby, 1978). Vegetation in EC and FC plots was clipped to 5 cm and removed three times during the season. Clipping dates were 7 June, 25 June, and 19 July (DOY 159, 177, and 201), 1996 in EC and 7 June, 19 July, and 20 September (DOY 159, 201, and 264), 1996 in FC. On 25 April (DOY 115), 1997, the dead aboveground biomass was burned from all plots and the surrounding area. This is a common management practice in the tallgrass prairie, primarily because it improves the productivity of the grassland (Knapp and Seastedt, 1986).

Soil Surface Carbon Dioxide Flux

F; was measured weekly to monthly with the portable chamber method described and tested on the Konza Prairie by Norman et al. (1992). Data were collected from two locations in the center of each plot using a portable photosynthesis system (LI-6200, Li-Cor, Inc., Lincoln, NE) equipped with a 0.7 m² chamber that covered a surface area of 4.13 × 10⁻² m². Measurements were made between 1230 and 1630 h CST on each sampling day to minimize the effect of any diurnal fluctuations. The gas exchange system was calibrated in the field prior to F; measurements. While conducting measurements, the chamber was placed on bare soil between crowns of plants so that all vegetation was excluded from the chamber.

Norman et al. (1992) determined that when the sharpened edge of the soil chamber is pressed against water-saturated soil, a flush of air with high CO₂ concentration often is released, causing inaccurately high readings of F; in this study, trials when the soil surface was wet indicated that F; could be overestimated by 70%. Therefore, a foam gasket was constructed to prevent penetration of the chamber into wet soil and yet maintain an effective seal between the chamber and soil. This allowed measurements of F; to be collected regardless of soil water content.

Cumulative F; for each treatment was estimated by summing the products of weekly mean flux rates and the number of days between samples; it was corrected further for diurnal patterns in flux. Our measurements, collected during mid-afternoon, were assumed to represent daily maximums. Minimum daily flux was estimated as 80% of the maximum, based on diurnal data collected during the study (not shown) and on diurnal patterns observed by others working at this grassland (Grahammer et al., 1991; Norman et al., 1992; and Ham et al., 1995). Assuming that F; followed an ellipsoidal pattern over a 24-h period, the calculated average daily fluxes were 95.7% of the observed daily maximum. The corrected daily flux then was multiplied by the number of days between measurements to compute the cumulative flux over the period.

Soil Water Content and Soil Temperature

Soil temperature and volumetric water content (θ) were measured concurrently with F; using dual-probe heat-capacity sensors (Tarara and Ham, 1997). Dual-probe sensors were installed 10 cm below the surface in the north portion of each plot to prevent shading by the surrounding canopy. This sampling depth was chosen because previous studies had indicated that soil temperature and θ, at 10 cm were correlated strongly with soil-surface CO₂ flux (Norman et al., 1992). Data were collected and processed with a datalogger (21×, Campbell Scientific Inc., Logan, UT). Soil bulk density and organic matter content (5–15 cm depth) were measured in each block to provide parameter estimates for calculations of θ (Tarara and Ham, 1997). Bulk densities were determined from volumetric samples (4.8 cm diam. × 5.0 cm) and were 1.18, 1.16, and 1.24 g cm⁻³ in blocks 1, 2, and 3, respectively. Organic matter in the 5 to 15 cm layer was 5.4%.

Biomass, Leaf Area, and Canopy Measurements

Aboveground biomass was measured on clipping dates from 1 m² in the center of EC and FC plots. Leaf area was measured from a 0.25 m² subsample of this area. Biomass and leaf area were clipped to a height of 5 cm to maintain uniformity with the remainder of the plot. Clipped samples were transported to the laboratory where leaf area was measured using an area meter (LI-3100, Li-Cor Inc.); samples were dried for 72 h at 60°C and weighed. The LAI for each plot was estimated by multiplying the leaf area-to-biomass ratio of the (0.25 m²) subsample by the total biomass of the 1 m² sample. Total biomass for the growing season was calculated in EC and FC.
as the sum of biomass from all three clippings; biomass in NC plots was measured on 27 September (DOY 271), 1996. All biomass measurements included senesced tissue.

Intercepted photosynthetically active radiation (IPAR) was measured weekly to monthly, or as weather permitted, with a ceptometer lightbar (Sunfleck Ceptometer, Decagon Devices, Inc., Pullman, WA). Photosynthetically active radiation was measured sequentially above and below the canopy at the soil surface in the center of each plot. Data were collected between 1100 to 1400 h CST on days with clear skies. Solar elevation angles at the time of measurement ranged from 65° to 45° during the growing season and decreased to 25° during mid-winter.

**Measurements from Grazed Rangeland**

F measurements were collected from adjacent grazed and ungrazed pastures at three separate sites, chosen for their similarity to the clipping site in topography and soils. Two sites on the Konza Prairie were stocked at the traditional full-season rate (~5 animals per hectare). One site was stocked with cattle and the other with North American bison (*Bison bison*). Parallel, 100 m transects were marked on either side of a fence separating grazed and ungrazed areas. Transects were spaced a minimum of 20 m from the fence to avoid border effect but close enough to minimize differences in slope and soil properties. The third site was located approximately 2 km east of the Konza Prairie on the Rannels Flint Hills Prairie (Agronomy Department, Kansas State University, Manhattan), which was grazed by cattle under an intensive-early stocking rate (~10 cattle per hectare). At all sites, F was measured every 5 m along the transect. In addition, 10 measurements of gravimetric soil water content (10 cm depth) and four samples of aboveground biomass (0.1 m² areas) were collected along each transect. Data were collected on 1 d at each location except for the bison site, where data were collected on 2 d spaced 21 d apart. All measurements at the grazed sites were obtained during the growing season, late in the grazing cycle.

Tests of differences in F, soil temperature, soil water content, and biomass among treatments were conducted with the general linear model procedure of SAS (*P* < 0.05; SAS Institute Inc., Cary, NC). Orthogonal linear contrasts compared the responses of F among treatments immediately before and after clipping, and were determined with the mixed linear model of SAS.

**RESULTS AND DISCUSSION**

Data from unclipped plots are presented first, followed by comparisons with clipped plots. The mechanisms that affect F, including IPAR (i.e., canopy photosynthesis), soil temperature, and *, are presented before the discussion of F, because they are affected first by clipping (Fig. 1).

**Results from Unclipped, Ungrazed Tallgrass Prairie**

During the year, values of F, in unclipped plots ranged from $8.8 \times 10^{-3}$ to 0.45 mg m⁻² s⁻¹ (Fig. 3a), which were comparable to previous measurements of F in this grassland (Norman et al., 1992; Ham et al., 1995; Knapp et al., 1998). The annual cycle of F in the tallgrass prairie was correlated highly to soil temperature (*r² = 0.73*) (Fig. 3a, c), a relationship that has been observed by others (Kucera and Kirkham, 1971; Knapp et al., 1998). However, annual F also was related strongly to canopy growth and phenology. During the winter, when soil temperatures were below 8°C (DOY 323, 1996 to DOY 69, 1997) and canopy photosynthesis was negligible, F was below 0.04 mg m⁻² s⁻¹. The rise in F following the spring burn was caused by rapid warming of the soil and the corresponding growth of a new canopy. Flux was highest during summer, when both canopy photosynthesis and soil temperatures were at their peaks. F decreased during autumn, as the canopy senesced and the soil cooled.

During the summer months (DOY 180–240), changes
in F, in unclipped plots were related more to θ, (r = 0.45) than to soil temperature (r = −0.17). Figure 3a and 3b illustrate how the lowest F rates coincided exactly with the lowest θ, during three summer drying cycles. Previous research has indicated that when soil temperatures are above 14 to 20°C during the growing season, soil respiration is regulated mainly by θ, in a tallgrass prairie (Grahammer, 1990; Garcia, 1992). In general, annual patterns in F were governed by seasonal changes in soil temperature and canopy growth, while the temporal dynamics of growing season F, are governed by θ, (i.e., precipitation).

**Results from Clipped Plots**

**Radiation Regime**

Significant amounts of leaf area and biomass were removed from EC and FC plots on their respective clipping dates (Table 1). This had an immediate impact on intercepted radiation (Fig. 4), which affects canopy photosynthesis, translocation, and the surface energy balance. IPAR (Fig. 4) provided an estimate of potential canopy photosynthesis and the effect that clipping had on that potential (Russell et al., 1989). After clipping, IPAR immediately decreased to 0.03 to 0.18 (Fig. 4), reflecting lower LAI and indicating lower production of photosynthetic; IPAR then increased rapidly during regrowth. For example, the first clipping in FC initially reduced IPAR from 0.63 to 0.18, but it increased to 0.66 during the following 40 d. The regrowth rate did not appear different between the FC and EC treatments. After the second clipping in EC (DOY 177), three distinctly different canopy heights were present in EC, FC, and NC plots, with IPARs of 0.08, 0.44, and 0.75, respectively.

During the winter months, IPAR did not indicate levels of potential canopy photosynthesis, because senescence had reduced canopy photosynthesis to trace levels by late October (DOY 290) (Ham and Knapp, 1998). The abrupt decline in IPAR in all treatments following the spring burn (DOY 115) resulted from the removal of the standing dead canopy that remained from the previous growing season; hence less shading of the soil. Therefore, the primary effect of the burn was a rapid increase in soil temperature caused by increased irradiance at the surface. This stimulated biological processes in the soil (i.e., root and microbial respirations), as well as rapid growth of a new canopy (Knapp and Seastedt, 1986; Garcia and Rice, 1994). The latter is illustrated in Fig. 4, which shows that IPAR increased following the 25 April burn from 0.02 to about 0.5 by 7 June (DOY 158).

**Soil Temperature**

The effect of higher irradiance at the soil surface following clipping was evident in soil temperature at the 10 cm depth. Before the first clipping date, soil temperatures were the same in all treatments (Fig. 5c; DOY 157). Soil temperatures in EC and FC increased after their first clipping (DOY 159), rising to about 3°C higher than soil temperature in NC. By 28 June (DOY 180), the soil temperature had risen further in EC, following its second clipping. On that day, soil temperature was highest in EC (31.4°C), intermediate in FC (30.4°C), and lowest in NC (28.6°C), reflecting the pattern of IPAR among treatments (Fig. 4). Although these differences are small, their impact on F can be significant. For example, previous research on Konza Prairie indicated that a 3°C rise in soil temperature would cause F to increase by 0.11 mg m⁻² s⁻¹ (Norman et al., 1992). Similar responses in soil temperature were observed in EC and FC following other clipping dates. In NC, shading by the canopy caused soil temperatures to be significantly lower than those of the clipped plots until late autumn.

By 18 November (DOY 322), shorter days and lower solar elevation angles limited incoming radiation, and differences in soil temperatures were minimal (Fig. 6c). However, the effect of shading in NC plots remained evident the following spring, as the soil began to warm. Soil temperature in NC was significantly lower than in EC and FC on 20 March (DOY 79), and FC on 17 April (DOY 107). Following the burn on 25 April (DOY 115), soil temperature increased rapidly in all treatments, but was consistently lower in FC than in EC and NC. This reflects the more patchy burn pattern in FC plots, because FC was clipped late in the previous growing sea-

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**Table 1. Biomass and leaf area index (LAI) from early-season clipping (EC) and full-season clipping (FC) on clipping dates: DOY 159, 177, 201, 264, and from EC and no clipping (NC) on DOY 271, 1996. Data missing intermittently because not all treatments were clipped on each date.**

<table>
<thead>
<tr>
<th>DOY</th>
<th>EC</th>
<th>FC</th>
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<th>EC</th>
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<td>g m⁻²</td>
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<td>m² m⁻¹</td>
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<tr>
<td>159</td>
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<td>125</td>
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<td>119</td>
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<td>0.57</td>
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<tr>
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<td>342</td>
<td>365</td>
<td>0.77</td>
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Fig. 5. Growing season dynamics of: (a) soil-surface CO$_2$ flux; (b) soil water content (10 cm); and (c) soil temperature (10 cm) in the following treatments: early-season clipping (EC); full-season clipping (FC); and no clipping (NC) (1996). Open arrows (V) at top indicate clipping dates of FC and closed arrows (k) near the bottom indicate clipping dates of EC. Vertical dashed lines highlight clipping dates. Symbols (X) along the abscissa of each graph indicate significant differences between at least two treatments on a given day ($P < 0.05$), and plus (+) indicates significant differences among all treatments on a given day.

Fig. 6. Autumn, winter, and spring dynamics of: (a) soil-surface CO$_2$ flux; (b) soil water content (10 cm); and (c) soil temperature (10 cm) in early-season clipping (EC), full-season clipping (FC), and no clipping (NC) treatments (1996–1997). Vertical dashed line highlights the date vegetation was burned on all plots (DOY 115, 1997). Symbols (X) along the abscissa of each graph indicate significant differences between at least two treatments on a given day ($P < 0.05$), and plus (+) indicates significant differences among all treatments on a given day.

In season, it had little regrowth and consequently less standing dead canopy (i.e., fuel for fire). This allowed more cool-season species to survive, and partial shading of the soil surface was prevalent in FC plots. Smith and Owsenby (1978) observed that intensive-early stocked pastures (EC) burned more uniformly than pastures stocked at the season-long rate (FC).

**Soil Water Content**

Precipitation was nearly normal from June through October (DOY 153–305), 1996. No significant differences occurred among treatments in $\theta$, at 10 cm throughout the growing season (Fig. 5b). However, Owensby et al. (1970) found higher soil water content in the 1.5 m soil profile of clipped plots. Thus, in the present study, significant differences in $\theta$, among treatments may have occurred at lower depths.

Following senescence, $\theta$, was consistently higher in NC compared with EC and FC plots (Fig. 6b). The NC plots were covered with a dense mat of dead biomass, which probably acted as a surface mulch. This slowed evaporation and conserved soil water. By 17 April (DOY 107), $\theta$, began to decline in all treatments, probably because of increasing potential ET and lack of pre-
cipation (precipitation was 18 mm below normal during April-May). The burn on 25 April (DOY 115) removed the surface mulch, which probably accelerated evaporation in all treatments. However, soils initially dried slower in FC plots than in EC and NC (DOY 118). This may have been an effect of the uneven burn pattern in FC plots, which caused more canopy shading and cooler soils compared with EC and NC plots. On 28 April (DOY 118), 3 d after the burn, G remained significantly higher in NC than in EC plots. However, this difference diminished following the next rain, and by 2 June (DOY 153), G was the same among treatments.

**Soil-Surface Carbon Dioxide Flux**

Clipping consistently caused large reductions in F, (Fig. 5a). Intensive measurements showed that F responded within 2 h of clipping and declined steadily over the next 2 d prior to reaching a new steady-state level (data not shown). Although F was similar among treatments at the start of the study, fluxes in FC and EC decreased 22% by 13 June (DOY 165), 6 d after their first clippings (Fig. 5a). In EC plots, F declined an additional 34% by 28 June (DOY 180), 3 d after EC’s second clipping. The only day during the growing season was 28 June when significant differences in F were observed among all treatments (P < 0.05). By that day, clipping frequency had created distinct differences in canopy height and PAR absorption (Fig. 4); F was highest in unclipped plots and lowest in the most recently clipped plots. On 25 July (DOY 207), 6 d after clipping, F in EC and FC dropped to 47% below that in NC. Orthogonal contrasts revealed strongly significant responses in F, (P < 0.0002) to the clippings on 7 and 25 June and 19 July (DOY 159, 177, and 201). The final clipping in FC occurred late in the season, when senescence and lower soil temperatures caused lower F in all treatments. Nevertheless, F decreased faster in FC and was significantly lower (P < 0.05) than that in EC and NC on 24 September (DOY 268) and 1 October (DOY 275), 4 and 11 d, respectively, after the clipping.

Soil CO₂ flux was lower in clipped plots, despite their higher soil temperatures. Higher soil temperature in an uncropped prairie typically causes F to increase (Kucera and Kirkham, 1971; Norman et al., 1992). However, F in FC and EC actually was correlated negatively with soil temperature (r = −0.46 to −0.54) during the peak growing season (DOY 157–240). This suggests a strong effect of removal of photosynthetic tissue on F (Fig. 1). The reduction of F in clipped plots apparently was linked more to canopy photosynthesis than to soil temperature during the growing season (Fig. 4, 5a, and 5c). Further evidence of this is the eventual recovery of F in EC and FC plots by DOY 234, which followed the same trend as canopy regrowth (i.e., IPAR) (Fig. 4 and 5a).

Although soil water was never severely limiting during the summer, F was sensitive to changes in G. Norman et al. (1992) observed large reductions in F, on Konza Prairie during a summer drought. Similarly, F, decreased in all treatments in the present study as the soil dried between 28 June and 5 July (DOY 180–187) (Fig. 5a, b). However, the ranking of differences in F, among treatments remained the same during the dry down. This indicates that clipping or grazing continues to influence F, and, hence, the C dynamics of grasslands even during summer droughts, which are common on the prairie (Borchert, 1950). Flux rates recovered by 10 July (DOY 192) after a rainfall.

Late in the year (DOY 240–323), F, declined steadily and was correlated strongly with soil temperature in all treatments (r² = 0.67–0.82) (Fig. 5a, c). However, senescence caused a rapid decline in photosynthesis, and the correlation between F, and photosynthesis might have been just as strong. Data from a nearby eddy flux station estimated that senescence caused a decline in ecosystem net CO₂ exchange from a maximum gain of 17.8 g CO₂ m⁻² d⁻¹ on 13 August (DOY 226) to a maximum loss of 10.3 g CO₂ m⁻² d⁻¹ on 16 October (DOY 290) (Ham and Knapp, 1988). The autumnal decline in F, likely was due to the combined effects of leaf senescence and decreasing soil temperature.

By 21 October (DOY 295) F, had decreased to below 0.09 mg m⁻² s⁻¹, yet significant differences remained among treatments (Fig. 6a). This suggests that beyond the growing season, both grazing and grazing strategy affect the C dynamics in a grassland. Residual effects from clipping were evident as late as 10 March (DOY 63), when F, was significantly lower in FC than in EC.

Following the spring burn, F, increased rapidly in all treatments along with soil temperatures and canopy growth. Although residual effects from clipping were evident in soil temperature and G, following the burn, no significant effect on F, was observed. By 2 June (DOY 153), F, in all treatments returned to levels similar to those of the previous summer.

**Measurements in Grazed Pastures**

Grazing also caused significant reductions in F, (Fig. 7). Flux rates declined by 20 to 37% under grazing, averaging 23% less in cattle-grazed pastures, and 27% less in bison-grazed pastures.
less in the bison-grazed pasture. The higher reduction of \( F \), under bison grazing probably was caused by different grazing behaviors, although it might have been specific to the site. Cattle select the most palatable plants and plant parts during grazing (Owensby, 1997), leaving behind patchy vegetation. Bison are also selective, preferring areas with high grass-to-forb cover ratios, but they tend to graze more uniformly within those areas (Vinton and Hartnett, 1992). In this study, \( F \) was measured in an area of the bison pasture that was evenly grazed; the remaining vegetation was not as patchy as in cattle pastures.

Spatial variability of \( F \) was high, which is typical in the tallgrass prairie (Grahammer et al., 1991; Norman et al., 1992). The coefficient of variation (CV) ranged from 14 to 38% among sites but tended to be higher in grazed areas. The mean CV in grazed pastures was 27% compared with 21% in ungrazed pastures. The higher variation in grazed areas probably was caused by the patchiness in vegetation or soil properties introduced by grazing.

Soil water content was not significantly different between adjacent grazed and ungrazed pairs (data not shown). Gravimetric water content at 10 cm was high (mean = 29%) on nearly all dates, except on 9 August (DOY 222), when soil water content was about 17% at the bison site. Dry soils probably caused the lower \( F \) observed on that day (Fig. 7).

On the day of \( F \), measurements, aboveground biomass was 56% lower in grazed pastures, averaging 191 g m\(^{-2}\) compared with 431 g m\(^{-2}\) in ungrazed areas. The smaller amount of aboveground biomass in grazed pastures represented a reduction in canopy photosynthesis and was likely the main cause of reduced \( F \), as was discussed previously. Therefore, these results from actual grazed pastures were consistent with the findings from the clipping study. This also emphasizes the need for models of \( F \), to include some measure of canopy photosynthesis (e.g., LAI and IPAR) in grazed grasslands.

**Annual Soil Carbon Dioxide Flux and Comparison to Other Ecosystems**

Estimated annual \( F \), from unclipped plots was 4.94 kg CO\(_2\) m\(^{-2}\) (Fig. 8), which is comparable to other estimates of annual \( F \) on Konza Prairie (Knapp et al., 1998). Annual \( F \), in EC and FC were approximately 4.04, and 4.11 kg m\(^{-2}\), respectively. Thus, clipping (i.e., simulated grazing) reduced annual \( F \) by 17 to 18%. The difference in annual \( F \), between EC and FC was insignificant, which indicates that any differences in \( F \), between EC and FC during the year were transient (Fig. 5a and 6a). This suggests that the intensive-early and traditional full-season grazing strategies ultimately have similar impacts on annual \( F \).

Our estimate of annual \( F \), in an unclipped tallgrass prairie (4.94 kg CO\(_2\) m\(^{-2}\)) was three to four times greater than estimates of 1.26 to 1.78 kg CO\(_2\) m\(^{-2}\) yr\(^{-1}\) from other less productive grasslands in California (Luo et al., 1996). Hanson et al. (1993) reported that annual \( F \), in a Tennessee oak forest and elsewhere in North America and Europe ranged from 0.6 to 3.9 kg CO\(_2\) m\(^{-2}\). Kursar (1989) estimated an annual \( F \), of 5.3 kg CO\(_2\) m\(^{-2}\) in a Panamanian forest, which was within the range of other estimates for these tropical systems (1.5–8.0 kg CO\(_2\) m\(^{-2}\)). Therefore, annual \( F \), in a tallgrass prairie was 1.3 to 8 times greater than that in temperate oak forests but similar to annual \( F \), in lowland tropical forests with much longer growing seasons.

Maximum daily \( F \), in an unclipped tallgrass prairie (0.51 mg m\(^{-2}\) s\(^{-1}\)) also was much higher than maximum values of \( F \), reported for several other ecosystems. In a California grassland, Luo et al. (1996) observed maximum \( F \), of 0.18 mg m\(^{-2}\) s\(^{-1}\), whereas flux rates were 0.09 to 0.35 mg m\(^{-2}\) s\(^{-1}\) in an Arizona cotton field (Nakayama et al., 1994) and 0.06 mg m\(^{-2}\) s\(^{-1}\) in the tundra (Oberbauer et al., 1986). In forests, measurements of maximum \( F \), ranged from 0.16 mg m\(^{-2}\) s\(^{-1}\) in a 3-yr-old ponderosa pine forest in California (Vose et al., 1995) to 0.23 mg m\(^{-2}\) s\(^{-1}\) in a 29-yr-old slash pine forest in Florida (Ewel et al., 1987) and 0.25 mg m\(^{-2}\) s\(^{-1}\) in a mature oak forest in Tennessee (Hanson et al., 1993). Maximum \( F \), in lowland tropical forests was 0.62 mg m\(^{-2}\) s\(^{-1}\) (Kursar, 1989), which is apparently the only recorded \( F \), similar to that from the tallgrass prairie.

The high fluxes in this tallgrass prairie were caused in part by the large amounts of C accumulated annually in the biomass, where more than 50% of the annual increment in production is belowground (i.e., in the roots; Kucera et al., 1967). In addition, those authors reported a rapid turnover rate of roots in the prairie; average replacement of underground biomass is 4 yr.

A high proportion of C is stored belowground and that C is recycled relatively quickly. Garcia and Rice (1994) reported that soil microbial populations are 10 to 50% higher in a tallgrass prairie than in agricultural ecosystems. They also noted that microbial activity is higher in the tallgrass prairie compared to other grasslands.

In a tallgrass prairie, a large portion of the C absorbed by the canopy during the growing season is respired. For example, an estimated 1.212 kg C m\(^{-2}\) was respired from the soil during the growing season (i.e., 1 May–31 October), based on \( F \), measurements from our unclipped plots. Dark respiration from the canopy during the same period was estimated as 0.346 kg C m\(^{-2}\), using the equation of Polley et al. (1992). Using our biomass data, we estimated the C accumulated in the shoots and
roots during the growing season to be 0.392 kg C m⁻². This assumes that aboveground biomass is 40% of the total (roots + shoots). Assuming no net change in soil C, the total C absorbed by the canopy during the growing season was 1.95 kg m⁻² (sum of all respiration and biomass accumulation). From these calculations, an equivalent of 62 and 18% of the C absorbed by the canopy is respired from the soil and the canopy, respectively, during the growing season. Therefore, respiration from the ecosystem is three to four times greater than the C accumulated in new biomass during the growing season. In a nearby study, Ham et al. (1995) showed that during the growing season, daily ecosystem respiration was equivalent to 85% of the C sequestered by the canopy. Consequently, the tallgrass prairie is characterized by large C gains offset by large, immediate respiratory losses from the rhizosphere.

CONCLUSIONS

Clipping in a tallgrass prairie reduced F, by 21 to 49% within 2 d after defoliation. Similarly, F, was 20 to 57% lower in grazed pastures than in adjacent ungrazed areas. Clipping reduced annual F, by 17 to 18%. This indicates that grazing has large impacts on the C dynamics of grasslands. Ham et al. (1995) found that CO₂ enrichment caused daily F, to increase by about 10% on this grassland. Thus, the effect of clipping or grazing can be about two to five times greater than the effect of doubled CO₂, underscoring the effect of land management on F, Annual F, was not substantially different between the two simulated grazing strategies, which suggests that the presence or absence of grazers is more important than grazing strategy when annual F, budgets are determined. Because these estimates of F, are based on data collected only during 1 yr, annual F, might change under different climatic conditions, such as during an extended drought. Furthermore, the clipping study did not consider the effects of animal compaction of the soil or animal excreta that are present under grazed conditions. Additional research might be needed to study the effect of those factors on biogeochemical cycling and F,.

Annual F, in an unclipped prairie was affected strongly by both soil temperature and canopy growth and phenology. However, during the summer, F, was also regulated by θ. In clipped plots, a decline of F, occurred despite a corresponding rise in soil temperature, which implied an important contribution to F, by canopy photosynthesis. Accurate models of F, for grazed pastures must include some estimate of canopy photosynthesis (e.g., LAI and IPAR), in addition to soil temperature and θ.

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