

Net Carbon Fluxes Over Burned and Unburned Native Tallgrass Prairie

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Abstract

Prescribed burning of aboveground biomass in tallgrass prairie is common and may influence dynamics and magnitudes of carbon (C) movement between the surface and atmosphere. Carbon dioxide (CO₂) fluxes were measured for 2 yr using conditional sampling systems on two adjacent watersheds in an ungrazed tallgrass prairie near Manhattan, Kansas. One watershed was burned annually (BA) and the other biennially (BB). Leaf and soil CO₂ fluxes were measured in the source area. Net ecosystem exchange (NEE) of CO₂ reached a maximum daily gain of 26.4 g CO₂ · m⁻² · d⁻¹ (flux toward surface is positive) in July 1998 (year when both sites were burned and precipitation was above normal); gains were similar between sites in 1998. The maximum daily NEE loss of CO₂ was -21.8 g CO₂ · m⁻² · d⁻¹ from BA in September 1997 (year when only BA was burned and precipitation was below normal). When data were integrated over the two years, both sites were net sources of atmospheric CO₂; NEE was -389 g C · m⁻² · 2 yr⁻¹ on BA and -195 g C · m⁻² · 2 yr⁻¹ on BB. Burning increased canopy size and photosynthesis, but the greater photosynthesis was offset by corresponding increases in respiration (from canopy and soil). Carbon losses from fire represented 6–10% of annual CO₂ emissions (bulk came from soil and canopy respiration). Data suggest that annual burning promotes C loss compared to less-frequently burned tallgrass prairie where prairie is not grazed by ungulates. Greater precipitation in 1998 caused large increases in biomass and a more positive growing season NEE, indicating that C sequestration appears more likely when precipitation is high. Because C inputs (photosynthesis) and losses (canopy and soil respiration) were large, small measurement or modeling errors could confound attempts to determine if the ecosystems are long-term CO₂ sources or sinks.

Resumen

Las quemas prescritas en los pastizales altos son comunes y pueden influir en la dinámica y magnitud del movimiento de carbono (C) entre la superficie terrestre y la atmósfera. La fluctuación del dióxido de carbono (CO₂) se midió durante dos años mediante sistemas de muestreo condicional en dos cuencas hidrológicas contiguas en un pastizal sin pastoreo cerca de Manhattan, Kansas, Estados Unidos. Una de las cuencas fue quemada anualmente (BA) y la otra cada dos años (BB). Los cambios de CO₂ del suelo y de las hojas se midieron en el área de origen. El intercambio neto de CO₂ del ecosistema (NEE) alcanzó una máxima ganancia diaria de 26.4 g CO₂ · m⁻² · d⁻¹ (el cambio hacia la superficie es positivo) en julio de 1998 (año cuando ambos sitios se quemaron y la precipitación estuvo arriba de lo normal); las ganancias fueron similares entre sitios en 1998. La máxima pérdida diaria NEE de CO₂ fue -21.8 g CO₂ · m⁻² · d⁻¹ de BA en septiembre de 1997 (año cuando sólo BA fue quemado y la precipitación estuvo por abajo de lo normal). Cuando los datos se integraron en los dos años, ambos sitios fueron fuentes netas de CO₂ atmosférico; NEE fue -389 g C · m⁻² · 2 yr⁻¹ en BA y -195 g C · m⁻² · 2 yr⁻¹ en BB. Las quemas incrementan la cubierta aérea así como la fotosíntesis, pero la mayor fotosíntesis fue compensada por el aumento correspondiente en la respiración (de la cubierta vegetal y del suelo). Las pérdidas de carbono debido a el fuego representan del 6% al 10% de las emisiones anuales de CO₂ (el volumen proviene de la respiración del suelo y de la cubierta vegetal). Los datos indican que la quema anual promueve pérdida de C, en comparación con pastizales quemados menos frecuentemente, cuando un pastizal no es pastoreado por ungulados. Mayor precipitación en 1998 provocó grandes aumentos en la biomasa y una estación de crecimiento más positiva NEE, indicando que la retención de C parece más probable cuando la precipitación es alta. Porque los insumos (fotosíntesis) de C y las pérdidas (respiración de la cubierta y del suelo) fueron grandes, las mediciones pequeñas o errores de modelado podrían confundir los intentos al determinar si los ecosistemas a largo plazo son fuentes o depósitos de CO₂.

Key Words: conditional sampling, fire, grassland, Konza Prairie, land management, net ecosystem exchange

INTRODUCTION

Increasing concentrations of atmospheric CO₂ and the potential for climate change emphasize the need to quantify the global carbon (C) budget. A number of terrestrial ecosystems may have the potential to sequester or release substantial quantities of CO₂ in response to climate change, increasing atmospheric CO₂, and land management (Glenn et al. 1993; White et al. 1999; Post and Kwon 2000; Schimel et al. 2000). Grasslands cover 40.5% of the earth's surface (White et al. 2000) and may represent a significant source or sink for atmospheric C (Hall and Scurlock 1991; Thornley et al. 1991; Ojima et al. 1993; Seastedt et al.

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1994; Svejcar et al. 2008). Furthermore, land management practices such as the burning of biomass (living and dead) may alter C fluxes (Knapp 1985; Svejcar and Browning 1988; Knapp et al. 1998; Bremer and Ham 2002) and thus may affect the amount of C sequestered or released annually from grasslands. Controlled burning, which is an important land management tool in grasslands, also may be a substantial source of atmospheric C (Hao and Liu 1994) and may affect C storage and soil nitrogen levels (Hall and Scurlock 1991).

In an effort to quantify the global C budget, a worldwide network of measurement stations (e.g., Fluxnet, AmeriFlux, EUROFLUX) was implemented to monitor long-term CO₂ flux, and several are located in grasslands (Baldocchi et al. 1996; Wofsy and Hollinger 1997; Ham and Knapp 1998). At one AmeriFlux site in a native tallgrass prairie in Oklahoma, Suyker and Verma (2001) reported that the net annual C exchange in burned prairie was near zero when the C loss during the prescribed burn was incorporated into the budget; their study did not include the C budget of an unburned prairie. Owensby et al. (2006) reported that grazed and ungrazed tallgrass prairies in Kansas were C neutral over a 3-yr period. Ham and Knapp (1998), who investigated C fluxes during the autumnal transition from sink to source at the same tallgrass prairie site as the study reported here (also an AmeriFlux site), suggested that land management or climatic factors that affect the rate and timing of the sink-source transition could have a strong influence on the annual C budgets in tallgrass prairie.

In tallgrass prairie, spring burning of aboveground biomass, including detritus from the previous year, is a common land-management practice that influences the ecophysiology and photosynthetic rates of plants (Wright 1974; Knapp 1985; Knapp and Seastedt 1986; Svejcar and Browning 1988) and soil respiration rates (Knapp et al. 1998) of the ecosystem. Furthermore, Bremer and Ham (1999) reported that spring burning had significant effects on surface-atmosphere fluxes of water and energy in tallgrass prairie, which suggests that surface-atmosphere fluxes of C also may be affected. In their study, which was conducted concurrently with this project and on the same sites, burning changed the microclimate of the surface and resulted in a larger canopy and greater latent heat fluxes than on unburned prairie.

The objectives of this study were to measure surface-atmosphere fluxes of CO₂ and to estimate cumulative C gains or losses from burned and biennially burned tallgrass prairie sites. Data were collected during a 2-yr period when burns were conducted annually on one site and biennially on the other site. Fluxes of CO₂ were measured at multiple scales including canopy (net ecosystem exchange [NEE]), leaf photosynthesis, and soil respiration to determine the various components of the C budget. Supporting measurements of green leaf area index (LAI) and green and dead aboveground biomass were collected to interpret the basic environmental and biophysical controlling factors and seasonal trends in the NEE of CO₂ of each site.

MATERIALS AND METHODS

Site Description

This study was conducted at an AmeriFlux site on Konza Prairie Biological Station (Konza Prairie: lat 39°04'56"N, long

96°33'37"W, ~439 m above mean sea level) near Manhattan, Kansas. Vegetation at the site was tallgrass prairie dominated by the C₄ grasses big bluestem (*Andropogon gerardii* Vitman), little bluestem (*A. scoparius* Michx.), and indiagrass (*Sorghastrum nutans* [L.] Nash). Soils were silty clay loams (Benfield series: fine, mixed, mesic Udic Argiustolls). Depth to shale and limestone fragments ranged from 0.2 m to 1.0 m. The upper 10 cm of the soil profile had a bulk density of 1.0 g·cm⁻³ to 1.2 g·cm⁻³ (determined from volumetric samples 4.8 cm diam. × 5.0 cm) and an organic matter content of 4–6% (Soil Testing Laboratory, Kansas State University). The 30-yr average annual precipitation at the site was 856 mm.

Data were collected from two adjacent, expansive upland watersheds approximately 60 ha each during a 2-yr period that began following the spring burn of 1997 and ended following the spring burn of 1999. For 16 yr one site had been burned annually (BA), and the other had been burned biennially (BB). In 1997 only BA was burned (17 April), and in 1998 both BA and BB were burned (22 April). Neither site had been grazed for 16 yr. One flux-measurement tower was established on each watershed; the tower on BA was approximately 500 m west of the tower on BB. Further information on the sites can be found in Bremer and Ham (1999).

Measurements of Net Ecosystem Carbon Exchange, Leaf Photosynthesis, and Soil Respiration

NEE of CO₂ for each site was measured using tower-based 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 (1998). Briefly, fluxes (F_c) of CO₂ were calculated every 30 min as

$$F_c = B\sigma_w\rho(\overline{c_{up}} - \overline{c_{dn}}), \quad [1]$$

where σ_w is the standard deviation of the vertical wind component; ρ is air density; $(\overline{c_{up}} - \overline{c_{dn}})$ 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 three-dimensional sonic anemometer (CSAT-3; Campbell Scientific, Logan, UT) mounted 2.5 m above the soil surface and operated in 10 Hz was used to measure ρ_w and control the gas-sampling system. Air for the determination of $(\overline{c_{up}} - \overline{c_{dn}})$ for CO₂ was continuously sampled at 0.5 L·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 the three-way solenoid valve (100 T; Bio-Chem Valve, Boonton, NJ). The valve was controlled using the output from the anemometer such 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 CO₂ 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). The IRGAs were calibrated automatically every 24 h using a standard gas with $\pm 1\%$ accuracy.

On the burned site in this study, Ham and Knap (1998) 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. No significant spatial variations in vegetation or topography were observed within 600 m of the towers.

Leaf-level net photosynthesis was measured in the field between 1100 and 1300 hours central standard time (CST) with a closed gas exchange system (LI-6200, Li-Cor) equipped with a 1-L cuvette. Data were collected from 7–10 leaves of big bluestem, the dominant species, on sites BA and BB each, in intervals of 2–3 wk between May and October of 1997 and 1998. Further description of this method can be found in Knapp (1993).

Soil CO₂ flux (R_s) was measured weekly to monthly from April to November 1997, using a portable photosynthesis system (LI-6200; Li-Cor) equipped with a 0.70-L chamber that covered a surface area of $4.13 \times 10^{-3} \text{ m}^2$ (Norman et al. 1992; Bremer et al. 1998). The bottom edge of the chamber was pushed about 1 cm into the soil between crowns of plants, so that all vegetation was excluded from the chamber. Twelve measurements of R_s were collected along single 36-m transects at each site (i.e., BA and BB); each transect was within 70 m of the micrometeorological towers in the predominantly upwind direction. Measurements were made between 1230 and 1630 hours CST on each sampling day to minimize the effect of any diurnal fluctuations.

Supporting Measurements and Data Acquisition

Wind speed and direction were measured with a wind monitor (R. M. Young, Traverse City, MI) positioned at 3 m. Air temperature and humidity were measured on the tower at 2.5 m using a Vaisala HMP35A probe (Vaisala, Helsinki, Finland). Global irradiance was measured with a pyranometer (8-48; Eppley Laboratories, Newport, RI), and photosynthetically active radiation (PAR) was measured with a quantum sensor (Li-190; Li-Cor). Precipitation was obtained from an existing network of gauges positioned throughout Konza Prairie Biological Station. All data acquisition and control at the tower were accomplished with two microloggers and accessories (CR10X, AM25T, AREL-12; Campbell Scientific). Averages and other statistics were computed and stored at 30-min intervals.

Green LAI and aboveground biomass were determined at 2-wk intervals from 6 May to 13 August 1997, and at 2- to 4-wk intervals from 26 May to 12 August 1998. On each measurement date and at each site (i.e., BA and BB), six 0.1-m² areas were harvested approximately 70 m south to southwest of the micrometeorological towers. In 1997 green biomass was sorted from dead biomass in samples from BB (unburned site); green leaf area from both BA and BB was measured with an area meter (LI-3100; Li-Cor). Total aboveground biomass was determined gravimetrically after samples had been dried for 72 h at 60°C.

Models of CO₂ Flux and Calculations of Carbon Budgets

The components of NEE were defined as

$$NEE = P_g - R_c - R_s, \quad [2]$$

where P_g is gross canopy photosynthesis, R_c is above-ground respiration, and R_s is soil (root and microbial) respiration. During the growing season, NEE was estimated on a 30-min, daily, and seasonal basis by integrating the boundary layer CO₂ flux measurements obtained by relaxed eddy accumulation. Aboveground respiration was estimated using the model of Polley et al. (1992), which was developed from research conducted on Konza Prairie during the First International Satellite Land Surface Climatology Project Field Experiment. Soil respiration between the spring burn and November 1997 was estimated using surface chamber data collected at the sites (Bremer et al. 1998). Thereafter, soil respiration was estimated using a soil moisture- and temperature-based model developed from previous research on Konza Prairie (Norman et al. 1992; Bremer and Ham 2002).

Gross canopy photosynthesis was calculated as a residual using Equation 2. Because NEE during the dormant season is primarily a function of soil respiration (i.e., negligible photosynthesis and aboveground respiration), NEE during the dormant season was estimated using a soil moisture- and temperature-based model of Bremer and Ham (2002); the dormant season was approximately between late October and the spring burn in April of the following year.

Data were omitted when inadequate wind direction, abrupt changes in boundary-layer stability, or precipitation disrupted the measurement. Data also were lost because of maintenance, calibration, and repair of the sensors and supporting equipment. Missing sections of NEE data from each site were modeled from PAR according to the technique of Ham and Knapp (1998) and others (Baldocchi et al. 1997; Suyker and Verma 2001). At night, intermittent missing NEE was estimated by assuming that the magnitude of the flux was equal to the previous 30-min flux. If larger blocks of night data were missing, nightly respiration (sunset to sunrise) was assumed to be equal to that measured on previous or following nights.

Approximately 55–65% of the NEE data were either missing or rejected during the growing seasons of 1997 and 1998. This fraction of missing/rejected data is almost identical to that reported by Svejcar et al. (2008), who measured C fluxes from grasslands using the Bowen Ratio. When filling gaps using modeled NEE, careful attention was paid to days with precipitation because the relationship between NEE and PAR typically changed substantially following rain. In 1997 NEE data were unavailable between the burn (17 April) and 15 May. During this period NEE was modeled from PAR (Suyker and Verma 2001); the impact of PAR on NEE was assumed to increase linearly in correspondence with rapid growth of the canopy and hence with increasing photosynthetic rates. In 1998 NEE was unavailable between the burn (22 April) and 3 June. Replacement data were obtained during this period from a conditional sampling station also located on a burned and ungrazed tallgrass prairie site on the nearby Rannells Flint Hills Prairie Preserve (Owensby et al. 2006). Comparisons in NEE among the Konza and Rannells Prairie sites later in the season, when all three towers were operating, indicated average NEE to

within $\pm 6\%$ among sites. Because all three sites were burned in 1998, NEE was also assumed equal among the sites early in the growing season, when data from BA and BB were unavailable.

Annual, cumulative NEE was calculated between spring burns and represented the sum of growing and dormant season NEE. Cumulative R_c was the sum of all R_c between the burn and the end of senescence (i.e., when green LAI > 0); senescence was assumed complete by the end of October. Cumulative R_s was the sum of growing and dormant season R_s between spring burns. All C in the aboveground biomass was assumed lost to the atmosphere during spring fire on both sites. The dead biomass present at the time of spring fire included that from the previous growing season on BA and from the previous two seasons on BB. Aboveground biomass at the time of fire was determined from six 0.1-m² subsamples collected on sites BA and BB on 15 October 1997 (i.e., in the fall before both sites were burned) and from site BA on 5 May 1999 (only BA was burned in 1999, on 13 May). Laboratory analysis of biomass from the 1997 growing season indicated that the percentage of C in the biomass was 43% on BA and 41% on BB (BB not burned in 1997; all percentages by weight; analysis conducted by the Soil Testing Laboratory, Kansas State University).

A Note on Micrometeorological Measurement Systems

One limitation of nearly all studies using micrometeorological measurement systems (e.g., Wofsy et al. 1993; Santos et al. 2003; Suyker et al. 2003; Owensby et al. 2006; Svejcar et al. 2008) such as ours is the possibility that inherent variation among the tower sites confounds imposed treatment effects (e.g., fire) on the C fluxes. For example, variations in topography, soil depth, which affects water availability and C storage capacity, and species composition all may impact C fluxes (Risch and Frank 2006). After much evaluation, our two sites were chosen because they were adjacent, expansive, upland watersheds with deep soils and similar topography. Slight differences in species composition between treatments (e.g., more forbs on site BB) were the result of different burning frequencies (Towne and Owensby 1984) and, therefore, represented a normal factor when comparing C fluxes between prairies burned annually and less frequently. Because there was only one tower per watershed, it is not possible to assign a statistical uncertainty to the annual C balance data. However, the measurement uncertainty around the instruments used to make the flux measurements and errors around the gap-filling procedures can be approximated with a traditional error analysis. Errors can be both systematic and random and can range from 0 to $\pm 20\%$ (Goulden et al. 1996). When comparing the two burning treatments in this experiment, the impact of systematic errors is minimized because identical instrumentation and data processing were used for both sites. Thus, when evaluating differences in annual C balances between the two burning treatments, it is likely that the uncertainty in the comparison is on the order of ± 5 to $\pm 15\%$.

RESULTS AND DISCUSSION

Precipitation, Leaf Area Index, and Aboveground Biomass

In the first year of the study, precipitation during the growing season was 149 mm below the 30-yr average of 678 mm (April

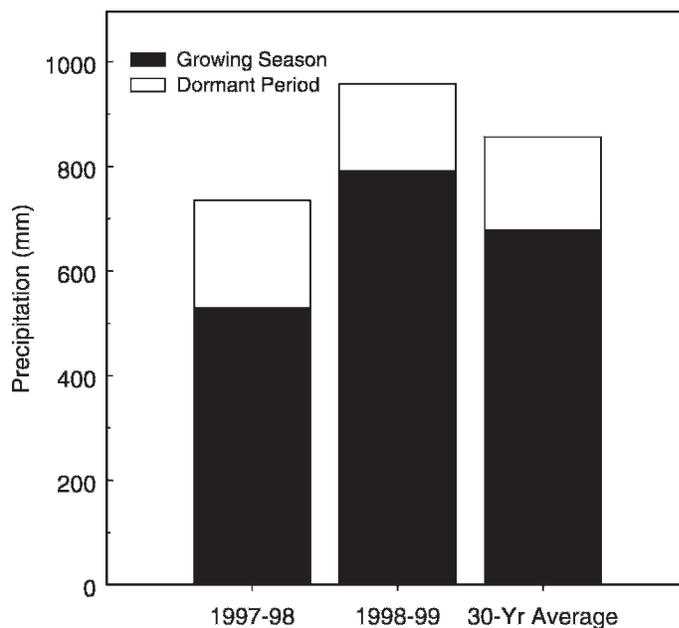


Figure 1. Precipitation between the springs (April to March) of 1997 and 1998 and between the springs of 1998 and 1999 (i.e., approximately between spring burns). Normal precipitation is the 30-yr average (1961–1990) during each respective period. Growing season refers to the period from April through October, and dormant season is from November through March of the following year.

through October) and in the second year was 113 mm above average (Fig. 1). Annual precipitation was 121 mm below the 30-yr average of 856 mm in the first year and 102 mm above average in the second year.

Following fire in 1997, which removed essentially all vegetation from the surface, green LAI increased more rapidly on BA (burned), reaching $2.3 \text{ m}^2 \cdot \text{m}^{-2}$ by 1 July compared to $1.3 \text{ m}^2 \cdot \text{m}^{-2}$ on BB (unburned; Fig. 2A). Green LAI began to decline because of senescence after 1 July on the burned site and after 29 July on the unburned site. Nevertheless, LAI remained higher on BA than on BB during the entire growing season of 1997. In 1998 LAIs were generally higher than in 1997. For example, on BA, peak LAI in 1998 was 3.0 compared with 2.3 in 1997. Higher precipitation during the growing season was likely the cause of higher LAI in 1998 (Fig. 1). Although both BA and BB were burned in 1998, green LAI was substantially higher on BA than on BB early in the growing season (Fig. 2B). LAIs converged between sites during June and July, although LAIs generally remained higher on BA than on BB until mid-August, when it was essentially the same on both sites.

Green aboveground biomass in 1997 increased more rapidly on BA (burned site) than on BB (unburned site) and remained significantly higher throughout the period (Fig. 3A). Peak aboveground biomass was $285 \text{ g} \cdot \text{m}^{-2}$ on BA, which was 21% below the long-term average on Konza Prairie for burned uplands (Briggs and Knapp 1995). Although vegetation composition was not measured as a part of this study, records from Konza Prairie Biological Station revealed that fire on BA increased grass biomass by 24% and decreased forb biomass by 89% compared with BB (Konza Prairie Biological Station 2009). Fire on BA also likely favored production of C₄ grass

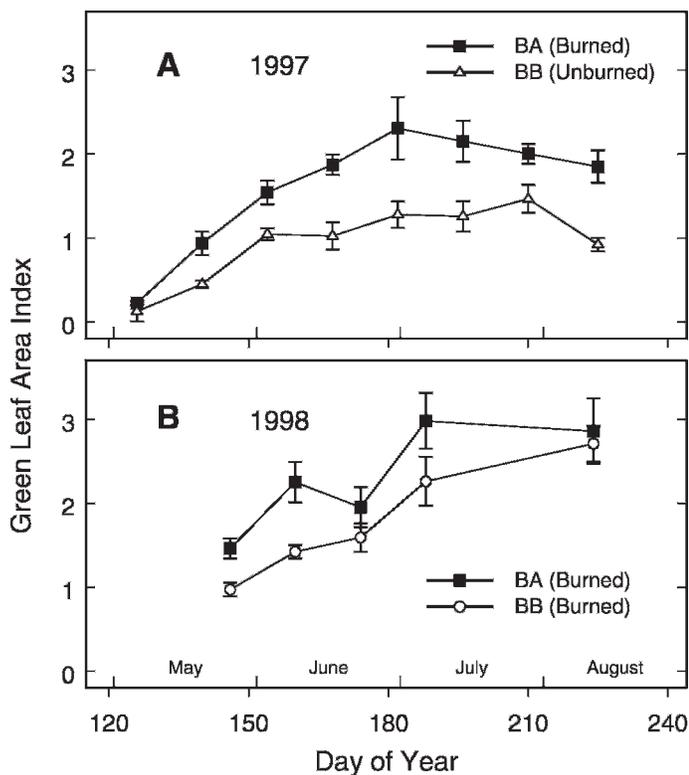


Figure 2. Seasonal patterns in green leaf area index from two adjacent tallgrass prairie sites during the growing seasons of (A) 1997 and (B) 1998. Site BA was burned in the spring of both years. Site BB was burned in the spring of 1998 but not in the spring of 1997. Vertical bars indicate ± 1 SE ($n = 6$).

species compared with BB, which may have had a greater biomass of C_3 grass species (Towne and Owensby 1984).

Peak biomass was $217 \text{ g} \cdot \text{m}^{-2}$ on BB, which was 39% below the long-term average for unburned uplands. The lower than average biomass likely was caused by low precipitation during May, June, and July. Dead biomass on BB averaged $268 \text{ g} \cdot \text{m}^{-2}$ during the summer. It likely contributed to the reductions in green LAI and aboveground biomass on BB by reducing irradiance at the surface, lowering soil temperature, and competing for light with the green vegetation (Knapp 1984; Knapp and Seastedt 1986; Svejcar and Browning 1988). On average, daytime soil temperature (0800 to 1800 hours CST) at 2.5 cm was 3.9°C lower in the unburned site early in the season (19 April–1 June; Bremer and Ham 1999), which probably delayed the emergence of shoots. Shading also may have caused physiological differences in plants on BB, such as reductions in photosynthesis, leaf conductance, leaf nitrogen content, nitrogen use efficiency, leaf thickness, and shoot biomass (Knapp 1985).

In 1998 aboveground biomass also was higher on BA than on BB early in the growing season (Fig. 3B), despite fire on both sites in that year. However, differences in biomass were negligible by August at peak biomass. Peak biomass in both plots was higher in 1998 than in 1997, reaching approximately $342 \text{ g} \cdot \text{m}^{-2}$ on both sites by 12 August; higher biomass in 1998 was probably a result of higher precipitation (Fig. 1). Peak biomass in 1998 was only 5% lower than the long-term

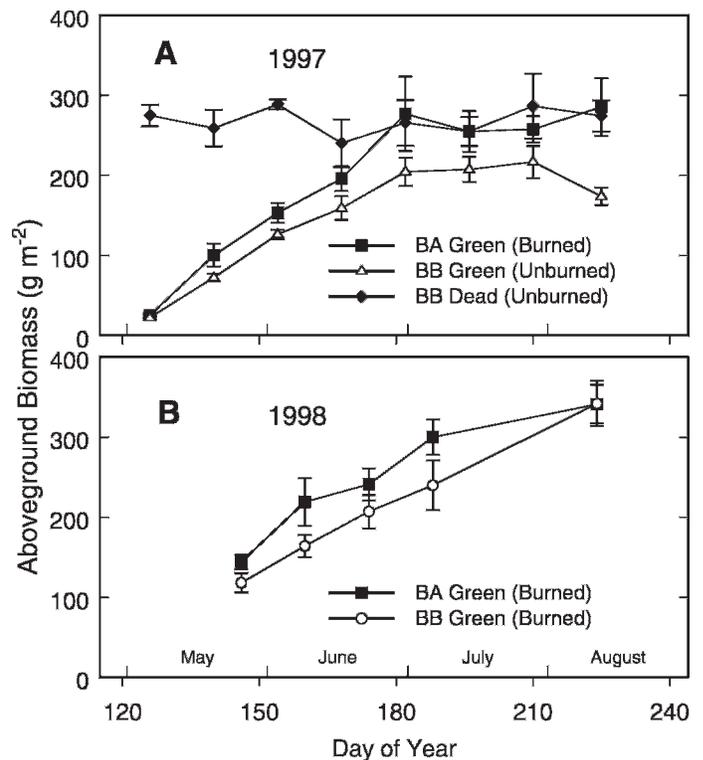


Figure 3. Seasonal patterns in aboveground biomass from two adjacent tallgrass prairie sites during the growing seasons of (A) 1997 and (B) 1998. Site BA was burned in the spring of both years. Site BB was burned in the spring of 1998, but not in the spring of 1997; hence the dead biomass on site BB in 1997. Vertical bars indicate ± 1 SE ($n = 6$).

average for burned uplands (Briggs and Knapp 1995). Abrams et al. (1986) reported the 10-yr average Konza Prairie biomass for unburned and burned uplands of $340 \text{ g} \cdot \text{m}^{-2}$ and $368 \text{ g} \cdot \text{m}^{-2}$, respectively.

Leaf-Level Photosynthesis and Soil CO_2 Fluxes

Leaf-level net photosynthesis (P_{leaf}) on big bluestem was higher on BA (burned) than on BB (unburned) site during May and early June 1997 (Fig. 4A). By late June, however, P_{leaf} became lower on BA and generally stayed lower during the remainder of the growing season. In 1998 P_{leaf} was also higher on BA than on BB during May and early June despite spring fire on both sites (Fig. 4B). However, by late June the differences had converged, and thereafter P_{leaf} was either similar between treatments or tended to be higher on BB.

Soil CO_2 flux averaged 15% lower on BB (unburned) than on BA (burned) during the growing season of 1997 (Fig. 5). Bremer et al. (1998) reported that soil respiration in this grassland was significantly reduced when the canopy was clipped or grazed by cattle or bison, presumably from reduced canopy photosynthesis and hence less translocation of C belowground. Therefore, lower soil respiration on BB was likely a result of its smaller canopy compared with BA (Fig. 2A). Differences in soil respiration became negligible between treatments during a dry period in late June and early July. However, the differences reemerged following rain, with

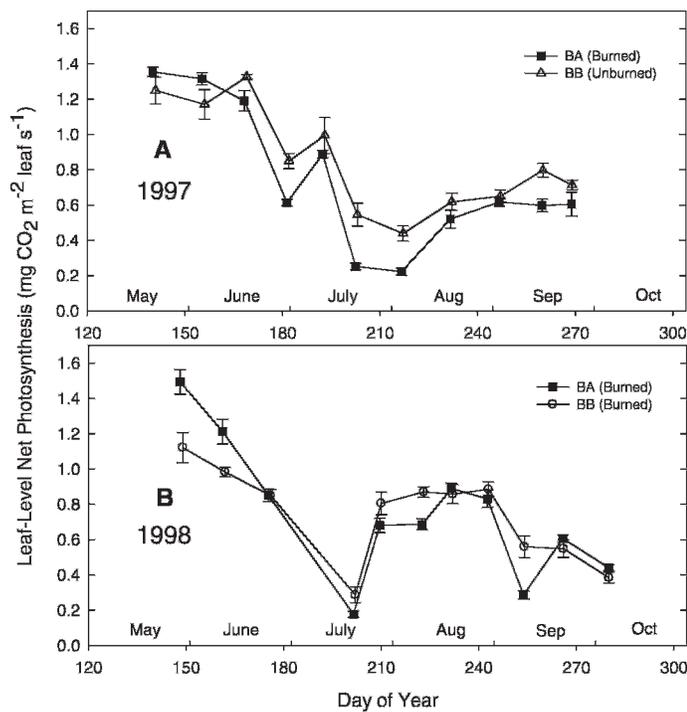


Figure 4. Leaf-level net photosynthesis of big bluestem (*Andropogon gerardii* Vitman) from two adjacent tallgrass prairie sites during the growing seasons of (A) 1997 and (B) 1998. Site BA was burned in the spring of both years. Site BB was burned in the spring of 1998, but not in the spring of 1997. Vertical bars indicate ± 1 SE ($n = 7$). In some cases, error bars are smaller than symbols.

soil respiration remaining lower on BB. By the end of the growing season, soil CO₂ flux became very low, and differences between treatments were negligible.

Net Ecosystem Exchange of CO₂

Seasonal NEE generally followed the growth of the canopy in the spring and senescence in the fall during both years of the study (Figs. 2A and 2B, 6A and 6B). The maximum magnitude of daytime NEE of CO₂ was 1.48 mg CO₂ · m⁻² · s⁻¹, which occurred in 1998 during peak growth (mid-July); higher precipitation in 1998 resulted in generally higher daytime NEE than in 1997. Nighttime losses ranged from -0.08 mg CO₂ · m⁻² · s⁻¹ to -0.63 mg CO₂ · m⁻² · s⁻¹ during both growing seasons and were generally higher following burning. In 1997 daily NEE of CO₂ increased from a net loss of -5.44 g CO₂ · m⁻² · d⁻¹ on BA on the day of the burn (17 April) to a maximum gain of 24.8 g CO₂ · m⁻² · d⁻¹ on 7 June (flux toward the surface is positive). Daily NEE also increased on the unburned site (BB), although maximum gains were lower than on BA; maximum daily gain on BB was 21.2 g CO₂ · m⁻² · d⁻¹ on 18 June. Maximum NEE losses of CO₂ for the year occurred during senescence on both sites, but losses were greater on BA. Maximum losses reached -21.8 g CO₂ · m⁻² · d⁻¹ on 23 September on BA and -14.5 g CO₂ · m⁻² · d⁻¹ on BB on 18 August. In 1998 magnitudes of daily NEE were similar between sites, varying from a maximum gain of 26.4 g CO₂ · m⁻² · d⁻¹ on 14 July to a maximum loss of -15.84 g CO₂ · m⁻² · d⁻¹ on 2 October. During the dormant season (November to March),

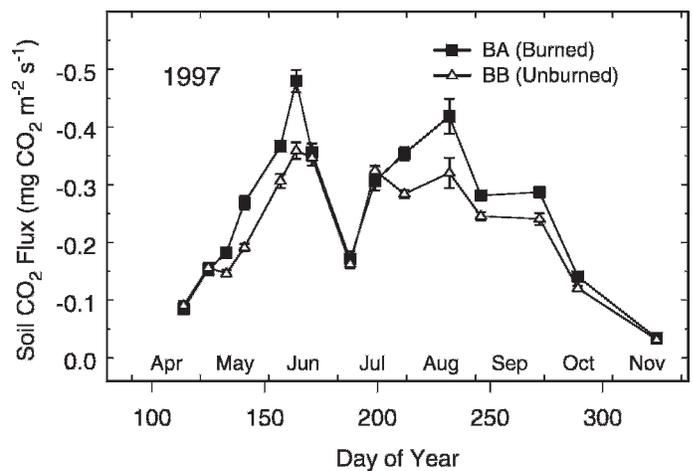


Figure 5. Soil-surface CO₂ fluxes from two adjacent tallgrass prairie sites during and after the growing season of 1997. Site BA was burned in the spring, and site BB was not burned. Vertical bars indicate ± 1 SE ($n = 12$).

NEE of CO₂ was similar between treatments in both years and averaged -3.6 g CO₂ · m⁻² · d⁻¹ in 1997–1998 and -3.9 g CO₂ · m⁻² · d⁻¹ in 1998–1999.

In 1997 NEE was 60% higher on BA (burned) compared with BB (unburned) early in the growing season (Fig. 6A). For example, daily NEE from 16 May to 15 June averaged 11.9 g CO₂ · m⁻² · d⁻¹ on BA and 7.5 g CO₂ · m⁻² · d⁻¹ on BB. Higher NEE on BA during this period was likely caused by a combination of higher P_{leaf} and higher green LAI compared with BB (Figs. 2A and 4A). During a dry period in late June through early July, differences in NEE between treatments diminished, and fluxes were similar until the end of July. However, by August, NEE became lower on BA and remained lower during the remainder of the growing season. Between early August and late October, daily NEE averaged nearly three times lower on BA (-6.33 g CO₂ · m⁻² · d⁻¹) compared with BB (-2.32 g CO₂ · m⁻² · d⁻¹). Night fluxes of CO₂ were considerably higher (more negative; data not shown) on BA during that period, indicating higher respiration from its larger canopy and higher soil respiration. Estimates of canopy respiration (R_c) from 1 August through the end of senescence (about 27 October) indicated that R_c was nearly double on BA (577 g CO₂ · m⁻²) compared with BB (294 g CO₂ · m⁻²). Soil respiration was approximately 44% higher on BA (1733 g CO₂ · m⁻²) than on BB (1206 g CO₂ · m⁻²) during that period (Fig. 5), which also probably contributed to lower NEE on BA. Although LAI was greater on BA than on BB during that period (Fig. 2A), the lower P_{leaf} on BA (Fig. 4A) may have reduced the contribution of P_g to NEE and thus offset the impact of higher LAI on NEE.

From 4 June through 21 October 1998, when simultaneous measurements of NEE were available from sites BA and BB (both burned), differences in NEE were negligible (Fig. 6B); NEE between sites was within $\pm 5\%$. The similarity in NEE between sites in the year when both were burned indicates that no inherent differences existed between sites. Bremer and Ham (1999), who investigated the surface energy balance on these two sites in the same year (i.e., 1998, when both sites were

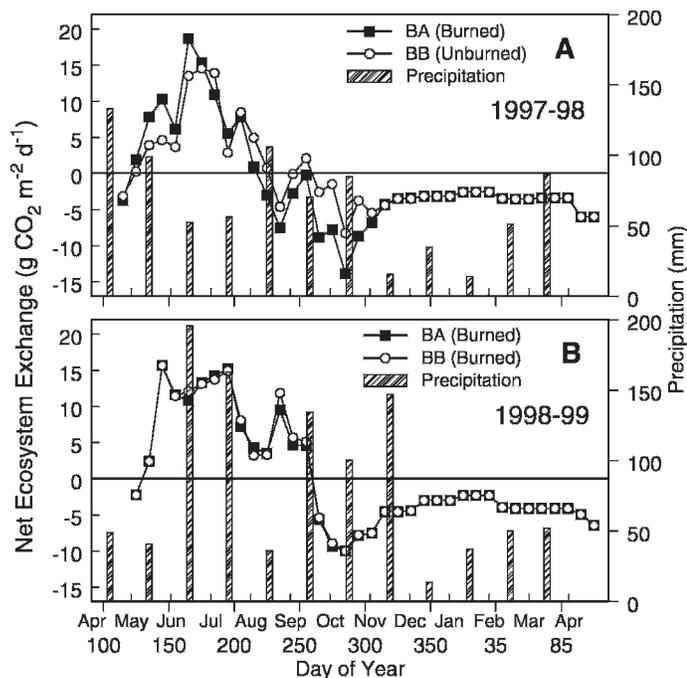


Figure 6. Average daily net ecosystem exchange of carbon dioxide from two adjacent tallgrass prairie sites between the spring burns of (A) 1997 and 1998 and (B) 1998 and 1999 and corresponding monthly precipitation. Site BA was burned annually. Site BB was burned in the spring of 1998, but not in the spring of 1997. Data are presented in 10-d averages to show seasonal trends. Net ecosystem exchange during dormancy was modeled.

burned), also reported similar energy fluxes between sites. In addition, no significant changes in vegetation were observed within 600 m of either tower; all vegetation was native tallgrass prairie within that area.

Interestingly, NEE in 1998 was similar between sites despite greater LAI and aboveground biomass in BA than in BB in early June and July (Figs. 2B and 3B). This similarity in NEE between sites despite differences in LAI and aboveground biomass contradicts patterns in NEE in the preceding year (1997), when only BA was burned. For example, in early June and July 1997, LAI, aboveground biomass, and NEE were all greater on BA than on BB (Figs. 2A, 3A, and 6A). Therefore, in 1998, given negligible differences in NEE between sites in early June and July despite differences in LAI and aboveground biomass, it is likely that if any differences in NEE existed between sites earlier in the season (i.e., from the burn through 4 June when NEE data were not available), they were also likely negligible or much smaller than in 1997.

The transition from sink to source was approximately 10 August in 1997, although both sites did reemerge again briefly as sinks in early September, following high rainfall during August. In 1998 the transition occurred nearly a month later, around 13 September. The latter was approximately the same date as reported for site BA in 1996 (Ham and Knapp 1998). Lower than normal precipitation early in the growing season of 1997 (Fig. 1), coupled with an extended cloudy period during August, may have caused the earlier transition from source to sink. Conversely, precipitation was above normal during the growing seasons of 1996 (703 mm) and 1998 (791 mm;

Fig. 1), which may have delayed the transition from sink to source.

Cumulative Seasonal and Annual C Fluxes

With any type of long-term flux measurements, errors can multiply and accumulate over time. This is especially true when attempting to integrate tower-based flux measurements over long periods (Goulden et al. 1996; Moncrieff et al. 1997). Our primary objective, however, was to measure flux differences between burned and biennially burned tallgrass prairie rather than quantify the yearly C budget with great accuracy. Because differences between the burned and unburned sites were large during the growing season, any slight bias in the flux data had a muted impact on the conclusions.

Comparisons of total C in peak biomass with NEE revealed that approximately 50–57% of the C gained by the ecosystem early in the growing season had been partitioned to aboveground biomass (Table 1). Interestingly, the percentage was nearly identical (~57%) on all sites following fire across years, and slightly less (~50%) on the unburned site (BB) in 1997.

In 1997 cumulative C gain during the growing season was 88% higher on the unburned (BB) than on the burned site (BA; Table 2), reflecting the higher respiratory losses observed on the burned site late in the growing season (Fig. 6A). Cumulative, annual NEE for the 1997–1998 burn-to-burn period, not including C lost during fire, were $-108 \text{ g C} \cdot \text{m}^{-2}$ on the burned site and $-48 \text{ g C} \cdot \text{m}^{-2}$ on the unburned site. Thus, both sites were sources for C in 1997, but the annual loss of C from the burned site (BA) was more than double that from the unburned site (BB). In 1998, following fire on both sites, NEE was substantially higher during the growing season than in the previous year (Table 2); higher precipitation (Fig. 1) likely contributed to higher NEE during that period. Suyker et al. (2003), in a 3-yr study from an annually burned native tallgrass prairie in Oklahoma, also reported that moisture stress was a dominating factor in the regulation of annual C exchange. In 1998 NEE was similar between sites during the growing season. Annual NEE during the 1998–1999 period showed gains of $15 \text{ g C} \cdot \text{m}^{-2}$ on site BA and $27 \text{ g C} \cdot \text{m}^{-2}$ on site BB.

Fluxes of CO_2 at multiple scales were used to estimate the individual components of NEE (Eq. 2). Annual estimates of NEE were combined with annual R_s and R_c to estimate P_g (Table 3) using Equation 2. In 1997, P_g was approximately 22% higher on the burned compared with the unburned site. Higher respiratory losses from the canopy and soil combined to give the burned site its lower annual NEE than on the unburned site. In 1998, P_g was higher on both sites compared with 1997, probably because of greater precipitation during the 1998 growing season. Gross canopy photosynthesis also was higher on site BA than on BB during 1998. As with 1997, higher R_c and R_s on BA caused its annual NEE to be slightly lower than on BB, although the differences between sites were not as great as in 1997. Interestingly, Bremer et al. (1998) reported annual R_s of $1350 \text{ g C} \cdot \text{m}^{-2}$ in 1996 from a nearby, annually burned prairie, which was nearly identical to annual R_s from BA in 1997 in this study; precipitation in 1996 was also below normal, similar to 1997.

When the amount of C lost during fire (i.e., combustion of previous years' dead biomass) was added into the C budget,

Table 1. Comparison of carbon (C) content determined from peak aboveground biomass and cumulative net ecosystem exchange (NEE). Cumulative NEE is reported for the period between the spring burn and the date when peak biomass was measured. Site BA was burned (B) both years, while site BB was not burned (NB) in 1997 and burned in 1998. Also presented are the ratios of C found in aboveground biomass to C accumulated by the ecosystem (i.e., NEE) during the period of growth.

Year	Site	C in peak aboveground biomass	NEE ¹	C in aboveground biomass/NEE
		----- g C · m ⁻² -----		
1997	BA (B)	123.3	214.8	0.574
	BB (NB)	88.5	177.7	0.498
1998	BA (B)	147.4	259.4	0.568
	BB (B)	147.8	258.1	0.573

¹Estimated by integrating flux data (i.e., tower data and flux models).

sites BA and BB both became significant sources for C (Table 4). For example, during the entire 2-yr period that included two burns on BA and one burn on BB, approximately $-389 \text{ g} \cdot \text{m}^{-2}$ of C were lost to the atmosphere from BA and $-195 \text{ g} \cdot \text{m}^{-2}$ were lost from BB. Thus, annual burning resulted in an approximate 2-fold increase in C losses compared with biennial burning. These data suggest that burning may, in some years, change the prairie from an annual sink of atmospheric CO₂ into an annual source, although climatic variation (e.g., precipitation) and other land management factors such as grazing also may significantly affect the sink or source status of the tallgrass prairie. Overall, C losses resulting from the fire itself represented about 6–10% of the total annual CO₂ emissions (the bulk of losses originating from soil and canopy respiration; Table 3).

Estimated annual C exchange from the annually burned (BA) site ($-231 \text{ g} \text{ C} \cdot \text{m}^{-2}$ in 1997 and $-158 \text{ g} \text{ C} \cdot \text{m}^{-2}$ in 1998; Table 4) was similar to estimates of annual C from other annually burned tallgrass prairies. For example, annual C exchange ranged from $-36 \text{ g} \text{ C} \cdot \text{m}^{-2}$ to $61 \text{ g} \text{ C} \cdot \text{m}^{-2}$ at a site near this study (Owensby et al. 2006) and from $-151 \text{ g} \text{ C} \cdot \text{m}^{-2}$ to $4 \text{ g} \text{ C} \cdot \text{m}^{-2}$ in a tallgrass prairie in Oklahoma (Suyker et al. 2003); both of the latter were 3-yr studies and indicated that tallgrass prairie may be either source or sink for atmospheric CO₂.

Our estimates of annual C exchange were also similar to estimates of $-147 \text{ g} \text{ C} \cdot \text{m}^{-2}$ to $439 \text{ g} \text{ C} \cdot \text{m}^{-2}$ in a tallgrass prairie in Texas that was burned only once at the beginning of a 6-yr study (Svejcar et al. 2008). In a savanna in Brazil, annual C exchange was $144 \text{ g} \text{ C} \cdot \text{m}^{-2}$ and $288 \text{ g} \text{ C} \cdot \text{m}^{-2}$, respectively, in burned and unburned sites (Santos et al. 2003). Thus, estimates of annual C exchange may vary as much interannually at one site as it does from one grassland site to another. Climatic variability caused significant year-to-year fluctuations in annual C exchange at one tallgrass prairie site (Suyker and Verma 2003). Other factors such as plant community and plant residues and characteristics of the soil such as texture and depth may cause differences among sites in their potential to sequester atmospheric C (Parton et al. 1987; Paul and Clark 1989), which may affect annual C exchange. In our study sites BA and BB were adjacent with similar soils, but as noted above, plant composition was altered by the different burning frequencies.

Table 2. Cumulative net ecosystem exchange (NEE) of carbon (C) during growing and dormant seasons and annual NEE. Estimates of NEE were from two watersheds on Konza Prairie between the spring burns of 1997–1998 and 1998–1999; C lost during the fire is not included in these values. In 1997 site BA was burned (B) on 17 April, and site BB was not burned (NB). In 1998 both sites were burned on 22 April. Growing season NEE represents the period between the respective burn dates in 1997 and 1998 and 27 October; the latter date is the approximate end of senescence. The dormant period was assumed from 28 October to the following spring burn.

Period	Site	Growing season	Dormant period	Annual NEE
		NEE	NEE	
----- g C · m ⁻² -----				
1997–98	BA (B)	68	-176	-108
	BB (NB)	128	-176	-48
1998–99	BA (B)	207	-192	15
	BB (B)	219	-192	27

Responses of soil C storage to spring fire have also been mixed, which further indicates that grasslands can be either sources or sinks for atmospheric CO₂. For example, a number of studies have reported decreases in soil organic C following fire (Ajwa et al. 1999; Harris et al. 2008), particularly in dry years (Garcia and Rice 1994), which supports results from our study. Other researchers, however, have reported increases in soil organic C in response to fire (Ojima et al. 1994; Ansley et al. 2006; Dai et al. 2006), while others reported no change in soil organic content after fire (Fynn et al. 2003). Clearly the interactions of factors that cause a prairie to be sink or source for atmospheric CO₂ are not simple. Data from our and other studies, however, indicate that burning and burning frequencies have significant effects on the C balance of grasslands.

MANAGEMENT IMPLICATIONS

Mitigation of greenhouse gas emissions via land management strategies has been a focus of research in the global climate change scenario. Spring burning in grasslands has historically been used as a management strategy to increase green leaf area and biomass for improved grazing and to control juniper (*Juniperus virginiana*) encroachment. Greater aboveground biomass production in burned than unburned grasslands might maintain or even increase C storage in the ecosystem. The present research, however, indicates that annual burning may result in greater losses of C to the atmosphere than less frequent, periodic burning. Therefore, less frequent burning may be beneficial in terms of maintaining C stores in grasslands and mitigating climate change. Certainly the control of juniper encroachment is possible with less frequent burning (e.g., every 2 yr or more) as long as trees are burned before becoming too large. The implications of less frequent burning on grazing efficacy may be less certain and may require further investigation.

Seasonal NEE generally followed the growth of the canopy in the spring and senescence in the fall during both years of the study. In 1997 daily NEE of CO₂ following spring fire averaged about 60% greater on BA (burned) than on BB (unburned) early in the growing season. However, daily NEE became lower on BA than on BB during senescence due to higher respiratory

Table 3. Estimates of cumulative, annual fluxes of carbon (C). Values are reported for the period between spring burns of 1997–1998 and 1998–1999. Site BA was burned annually. Site BB was burned in 1998 and not burned in 1997.

Variable	1997–1998		1998–1999	
	Site BA	Site BB	Site BA	Site BB
	----- g C · m ⁻² -----			
P_g^1	1669	1368	2269	1997
R_s^2	1354	1185	1666	1495
R_c^3	423	231	588	475
NEE ⁴	-108	-48	15	27

¹Gross photosynthesis: calculated as residual in Equation 2.

²Soil respiration: measured until November 1997; thereafter estimated using model of Bremer and Ham (2002).

³Canopy photosynthesis: estimated using model of Polley et al. (1992).

⁴Net ecosystem exchange: measured with relaxed eddy accumulation. Does not include C lost during fire (combustion).

losses of CO₂ from the larger canopy on BA. In 1998, when both sites were burned, NEE was similar between sites. Magnitudes of daily NEE ranged from a maximum gain of 26.4 g CO₂ · m⁻² · d⁻¹ in 1998 to a maximum loss of -21.8 g CO₂ · m⁻² · d⁻¹ during senescence on the burned site (BA) in 1997. Over a 2-yr period, both study sites were net sources of atmospheric CO₂ when including CO₂ lost during dormancy and also to spring fire. The site burned on both years lost a total of -389 g C · m⁻² · 2 yr⁻¹, while the site burned every other year lost -195 g C · m⁻² · 2 yr⁻¹. Because there are many sources of uncertainty around the flux tower measurements, one cannot be certain that there is a statistically significant difference between 2-yr C balances shown in Table 4 (-389 g C · m⁻² · 2 yr⁻¹ vs. -195 g C · m⁻² · 2 yr⁻¹). However, it is consistent with biogeochemical principles that greater C losses are possible under increased fire frequency. In general, comparisons of burned and unburned prairie showed that burning 1) increased canopy LAI and biomass and 2) increased gross canopy photosynthesis, but that increase was offset by corresponding increases in ecosystem respiration (both canopy and soil respiration). C losses resulting from the fire itself represented only 6% to 10% of the total annual CO₂ emissions (the bulk coming from soil and canopy respiration). Comparisons between 1997 and 1998 showed that increased precipitation in 1998 caused a large increase in biomass, a later transition from sink to source for atmospheric CO₂, and a more positive growing season NEE. Therefore, C sequestration in tallgrass prairie appears more likely when precipitation is above average. Owensby et al. (2006) reported that annually burned grazed and ungrazed tallgrass prairie was C-storage neutral during a 3-yr study. Our data suggest that annual burning, in the absence of grazing by ungulates, promotes C loss compared to less-frequently burned tallgrass prairie. Because the inputs (P_g) and losses ($R_c + R_s$) of C are so large (Table 3), however, small measurement or modeling errors could easily confound attempts to determine if the ecosystems are long-term CO₂ sources or sinks.

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Table 4. Two-year carbon balances for tallgrass prairie sites burned annually (BA) and burned biannually (BB). Included are annual net ecosystem exchange excluding carbon (C) lost to fire (NEE); C lost annually during fire from aboveground biomass; and biennial net ecosystem exchange including C lost to fire (NEE* = sum of NEE and C lost to fire).

Parameter	Period	Site BA		Site BB	
		----- g C · m ⁻² -----			
NEE	1997–1998	-108		-48	
	1998–1999	15		27	
Fire	1997–1998	-123		-174 ¹	
	1998–1999	-173		0	
NEE*	1997–1998	-231		-222	
	1998–1999	-158		27	
Total NEE*	1997–1999	-389		-195	

¹The 1998 spring fire on BB included biomass from the prior two years of growth (1996–1997).

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