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DETERMINANTS OF SOIL CO₂ FLUX FROM A SUB-HUMID GRASSLAND: EFFECT OF FIRE AND FIRE HISTORY

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Abstract. Soil CO₂ flux (Jₜ CO₂) was measured at midday over a 2-yr period in undisturbed tallgrass prairie (Konza Prairie, Kansas, USA) to quantify seasonal and annual budgets, to evaluate temperature and moisture as determinants of soil CO₂ flux, and to assess the effect of a common land management tool, spring fire, and fire history on soil respiration. We hypothesized that: (1) maximum rates and annual estimates of soil Jₜ CO₂ would be greater in more productive burned sites than in unburned sites, (2) soil Jₜ CO₂ would be greater in newly burned sites with a history of fire exclusion than in annually burned sites (consistent with differences in aboveground production), and (3) soil temperature and water availability would be primary abiotic determinants of soil Jₜ CO₂ in tallgrass prairie. A preliminary assessment of the effects of large herbivores on soil Jₜ CO₂ was included to evaluate the hypothesis that removal of aboveground biomass would reduce soil Jₜ CO₂. Results indicated that spring fire increased maximum monthly soil Jₜ CO₂ by 20–55% relative to unburned tallgrass prairie, with greatest monthly differences measured in April (fourfold higher in burned sites). In burned sites that differed in fire history, maximum monthly Jₜ CO₂ in annually burned prairie was 33% greater than in burned sites with a history of fire exclusion. Soil Jₜ CO₂ in these latter sites was still significantly higher than in unburned sites. Soil Jₜ CO₂ in sites grazed by bison was reduced by as much as 30% relative to adjacent ungrazed areas. Reduced root biomass and activity in grazed areas, unburned sites, and sites with a history of fire exclusion suggest that plants play a major role in determining soil Jₜ CO₂ in this grassland. Soil temperature at 5 cm was related strongly to midday Jₜ CO₂ in both annually burned sites (r² = 0.58) and unburned sites (r² = 0.71). In contrast, differences in soil moisture among sites, enhanced by comparing irrigated grassland to control areas, increased maximum monthly Jₜ CO₂ by only 8%. Thus, soil temperature was the primary abiotic determinant of soil Jₜ CO₂ during this study.

Maximum monthly estimates of soil Jₜ CO₂ in tallgrass prairie ranged from 10.3 µmol CO₂·m⁻²·s⁻¹ in unburned sites to 15.1 µmol·m⁻²·s⁻¹ in annually burned irrigated sites, whereas annual estimates varied from 4.7 to 7.8 kg CO₂/m². Over the 2-yr period, spring fire increased estimated annual soil Jₜ CO₂ by 38–51% relative to unburned sites, while irrigation increased annual soil Jₜ CO₂ by 13%. These estimates for tallgrass prairie are much higher than those reported for most temperate ecosystems but are similar to estimates for tropical forests. Characteristics of undisturbed tallgrass prairie that may lead to high levels of soil Jₜ CO₂ include: high above- and belowground productivity; a relatively high proportion of C stored belowground; levels of soil microbial biomass and activity that are among the highest in native ecosystems in the United States; and the lack of a single dominant factor such as temperature, moisture, or nutrient availability, that consistently limits biotic processes during the growing season. The sensitivity of soil Jₜ CO₂ in tallgrass prairie to different land use practices (fire and grazing) suggests that it is critical to include these factors in the development of grassland C budgets, as well as in regional models that estimate biogeochemical responses to land use change.

Key words: fire; grassland; grazing; land management; soil CO₂ flux; soil respiration; tallgrass prairie.

INTRODUCTION

Organic matter in soils represents a major fraction of the total global C budget, comprising more than twice the C present in the atmosphere (Eswaran et al. 1993, Chadwick et al. 1994) and about twice that contained in terrestrial biomass (Anderson 1992). Soils derived from mesic grasslands and more arid steppes covered, at least historically, >50% of the global terrestrial land surface, and thus are an important component of this budget. These soils, particularly those beneath the more mesic grasslands, are noted for their relatively high organic matter content and proportionally greater storage of C belowground compared with forest soils (Jenny 1930, Seastedt and Knapp 1993). An assessment of the impacts that climatic changes and land management activities may have on grassland soil processes, especially those that affect soil organic mat-
Plate 1. Fire was a frequent natural event in tallgrass prairies of North America prior to European settlement. Today, spring prescribed fires are a common land management tool in the Flint Hills tallgrass prairies of eastern Kansas. Prescribed fires, at frequencies ranging from one in 20 years to annual fire, are an integral part of the watershed-level experimental plan of the Konza Prairie LTER site (pictured above).

The tallgrass prairies of North America once extended across parts of 13 states in the Midwest and Canada, with an estimated area of >680,000 km² (Samson and Knopf 1994). In most states, >99% of the original grassland has been converted to row crop agriculture, with concomitant reductions in soil organic matter (Burke et al. 1991). Only in eastern Kansas and Oklahoma do extensive tracts with intact soils remain. Common land management activities in this region include frequent prescribed fire (Plate 1) to increase aboveground primary production (Briggs and Knapp 1995) and grazing by domestic livestock (cattle). Both of these activities likely act as surrogates for naturally occurring grassland features: pre-European settlement wildfires and grazing by native herbivores (bison; Axelrod 1985), although the management of cattle precludes the migratory patterns of bison. Additionally, modeling studies of the relative effects of climate, burning, and grazing on ecosystem processes have suggested that management practices employing fire and grazing can significantly alter soil C storage in these grasslands (Seastedt et al. 1994).

Uncertainties regarding abiotic, biotic, and management controls of soil CO₂ flux from grassland soils led us to three specific research objectives. These were: (1) to quantify seasonal and annual soil CO₂ flux from undisturbed tallgrass prairie, the major sub-humid grassland type of central North America; (2) to evaluate temperature and moisture as determinants of soil CO₂ flux; and (3) to assess the effect of a common land management tool, spring fire, and fire history on soil J_CO₂. The latter objective builds on previous research in tallgrass prairie that has shown not only that the presence of fire is important in this system, but that sites that differ in fire history (time since the last fire) also vary significantly in response to fire (Seastedt and Knapp 1993, Briggs et al. 1994, Blair 1997). These objectives allowed us to test several hypotheses including: (1) that maximum rates and annual estimates of soil J_CO₂ would be greater in burned than unburned sites due to higher soil temperatures and greater belowground allocation of plant biomass in burned sites (Knapp 1984, Seastedt and Ramundo 1990); (2) that soil J_CO₂ would be greater in newly burned sites with a history of fire exclusion than in annually burned sites (consistent with increased aboveground production responses in sites with infrequent fire; Seastedt et al. 1991, Briggs et al. 1994); and (3) that soil temperature...
and water availability would be the primary controls of rates of soil $J_{CO_2}$ in tallgrass prairie. Finally, a preliminary assessment of how grazing by large herbivores may impact soil $J_{CO_2}$ was included to evaluate the hypothesis that removal of aboveground biomass would reduce soil $J_{CO_2}$. This prediction was based on several studies that have documented a post-herbivory reduction in C allocation belowground (Coughenour et al. 1985, Simones and Baruch 1991, Vinton and Hartnett 1992).

**METHODS**

**Study site**

Research was conducted at the Konza Prairie Research Natural Area (39°05’ N, 96°35’ W), a 3487-ha native (unplowed) tallgrass prairie site representative of the 50000-km² Flint Hills region of eastern Kansas. Alternating layers of Permian limestone and shale lie beneath soils that vary from deep (>1 m) silty clay loams in lowlands to rocky shallow soils on ridges. Konza Prairie has a typical Midwestern continental climate, with warm, wet summers and cold, dry winters. Mean annual air temperature (30-yr average) is 12.8°C, with an average annual precipitation of 835 mm, but interannual climatic variability is high (Borchert 1950). The flora of Konza Prairie is dominated by warm-season (C₄) grasses, including *Andropogon gerardii* and *Sorghastrum nutans*.

Since 1980, a watershed-level fire-frequency experimental design has been implemented at Konza Prairie (Knapp et al. 1998). This design includes replicated watersheds subjected to spring fires (April) at annual, 2-, 4-, 10-, and 20-yr intervals. Sites targeted for 20-yr intervals between fire are considered unburned when compared with other fire-frequency treatments. Grazing by large native ungulates (bison) also occurs on the site, but these herbivores have been reintroduced only relatively recently (full stocking since 1994).

**SOIL CO₂ flux**

Soil $J_{CO_2}$ was measured with a dynamic-chamber method adapted from Norman et al. (1992). A recent comparison of this technique with static chambers indicated that this method was less biased at all rates of CO₂ efflux (Nay et al. 1994). The system was designed for grasslands, and utilized a cylindrical chamber with an 850-cm³ volume and a 40.7-cm² circular area exposed to the soil surface. The chamber was coupled to a closed-flow gas exchange system (LI-COR 6200, LI-COR Inc., Lincoln, Nebraska, USA) that recirculated air from the infrared gas analyzer to the chamber; CO₂ evolved from the soil increased the concentration within the system. Pressure equilibrium between the air and the chamber was maintained by a 0.2-cm inside diameter tube (10.5 cm long) that vented the chamber to the atmosphere (Norman et al. 1992). The bottom edge of the chamber was sharpened so it could be pressed lightly into the soil to seal the chamber. At any placement of the chamber, two measurements were made sequentially by setting the operating software of the system to calculate CO₂ flux for the period of time required to increase the chamber CO₂ concentration by 5–10 µL/L. Time required varied from 10 s to 1 min/measurement, depending on soil $J_{CO_2}$. Measurements were made at ambient or slightly below ambient CO₂ concentrations (chamber CO₂ was decreased between measurements by routing a portion of the flow through soda lime). In burned sites, measurements were made by placing the chamber between plants so that no green biomass was included. In unburned sites, standing detritus and soil surface litter can be significant (Knapp and Seastedt 1996). In these sites, all standing dead biomass and intact leaves and stems on the surface were pulled away, and the chamber was placed between plants. Partially decomposed surface litter was left undisturbed. In both burned and unburned sites, preliminary measurements were made with various degrees of soil-surface disturbance to determine how sensitive the system was to the measurement protocol used. Significant soil-surface disturbance and forceful chamber insertion into the soil resulted in artificially high, transient levels of $J_{CO_2}$; thus these disturbances were avoided.

**Experimental design**

*Effect of fire.*—From May 1994 through May 1996, soil $J_{CO_2}$ was measured in two annually burned and two unburned (no fire in the last 16 yr) sites on Konza Prairie. Soils at these sites (as well as those described later) were moderately deep silty clay loams (Mollisols; Jantz et al. 1975). Measurements were made at 7–14 d intervals, depending on weather conditions, from April through October, and at 15–30 d intervals during the dormant season. Measurements were not made during periods of rain or when snow covered the surface. There were no periods of continuous snowcover >5 d during this study. For each date, sequential measurements were made at five locations per site, and soil temperature at 5 cm was measured concurrently with a thermocouple thermometer (Wescor TH-65). Measurements were made between 1000 and 1500, because diurnal measurements indicated that soil $J_{CO_2}$ was relatively constant during these hours.

*Effect of fire history.*—To determine the effects of fire history on $J_{CO_2}$, replicate 10 × 10 m plots were established in 1994 on upland and lowland sites (n = 3 plots per fire treatment per topographic treatment) in adjacent watersheds that were either annually burned (spring fires for >17 consecutive years) or unburned (burned only twice in the past 18 years). At each topographic position, a third fire treatment (burned once) was established by burning a replicate set of three plots on the unburned watershed on 4 May 1994 and 6–14 April 1995. The treatments unburned and burned once were assigned randomly to plots located within the un-
burned watersheds, and these plots were located on the same soil types and topographic positions as the annually burned plots (Blair 1997). Midday soil \( J_{\text{CO}_2} \), and temperature were measured as described above at five sampling locations within each plot.

**Effect of soil moisture.**—As part of the Long-Term Ecological Research (LTER) program at Konza Prairie, soil moisture was monitored every two weeks to monthly in burned and unburned sites, using both time-domain reflectometry (TDR) and neutron-probe techniques. The TDR system integrates soil moisture over 15-cm depths, and the neutron-probe system measures soil moisture at 25-cm increments. A preliminary analysis indicated that estimates of \( J_{\text{CO}_2} \) were much more dynamic than these integrated soil-moisture values. Thus, we could establish no relationship between variability in soil moisture and \( J_{\text{CO}_2} \). As an alternative means to assess the effect of soil moisture on \( J_{\text{CO}_2} \), we used an ongoing irrigation experiment. This long-term, transect-level experiment was established in 1991 in an annually burned site (Knapp et al. 1994), where soil moisture is most likely to limit productivity (Knapp 1985, Briggs and Knapp 1995). In this experiment, replicate \((n = 2)\) 100-m transects that span upland and lowland topographic positions are irrigated throughout the growing season to minimize plant water stress in the dominant species, *A. gerardii*. Irrigation was scheduled according to a model that used established Penman equations and data from an adjacent weather station. During the driest portions of the growing season, irrigation occurred weekly, or occasionally twice a week, with each event usually adding 20 mm of water to the site. Further details on this experiment can be found in Knapp et al. (1994). Soil \( J_{\text{CO}_2} \), and temperature were measured at upland and lowland sites \((n = 2)\) along both irrigated and control transects from June 1994 through May 1996.

**Preliminary assessment of bison grazing.**—From June through October 1995, measurements of soil \( J_{\text{CO}_2} \) were made in a burned watershed grazed by bison (*Bos bison*) and in an adjacent burned, ungrazed watershed on Konza Prairie. Bison graze in distinct patches throughout the growing season (Fahnestock and Knapp 1993), and replicate \((5)\) measurements of \( J_{\text{CO}_2} \) were made in three well-defined grazing patches and in an equal number of adjacent ungrazed areas \((n = 3)\) within the grazed watershed. These were compared with measurements made in the ungrazed watershed. Soil temperatures were measured concurrently. More details on the grazing history and the management of bison on Konza Prairie can be found in Hartnett et al. (1996).

**Statistical analyses**

Analysis of variance \((P < 0.05)\) was used to compare the effects of treatment (fire, fire history, irrigation, or grazing), topographic position, date, and year. Differences among years were not statistically significant, thus data presented are combined for the 2-yr study period (year as a factor in analyses was eliminated). Similarly, the effect of topographic position in the fire history and irrigation study was not significant overall, and only for a few specific dates did topography have an effect. Thus for ease of presentation, data from uplands and lowlands are combined by eliminating topography as a factor. For comparisons by date, measurements were pooled by month for both years. Replicate watersheds were not used in the single growing season grazing assessment; thus treatment effects could not be separated from potential site effects. Regression analysis of \( J_{\text{CO}_2} \) vs. soil temperature was improved significantly by log transformation of the data. Because sampling intensity varied from the growing to the non-
growing season, monthly means compiled from the entire data set were used to estimate annual $J_{\text{CO}_2}$.

RESULTS

Effect of fire and fire history.—Maximum monthly values of midday soil $J_{\text{CO}_2}$ were $\sim\text{20\%}$ greater in annually burned compared with unburned sites (Fig. 1a), and from March through August, $J_{\text{CO}_2}$ was always significantly higher in annually burned plots. Greatest monthly differences were measured in April (fourfold higher in burned sites), after fire had occurred and when soil temperatures averaged $\sim\text{6\degree C}$ greater in burned sites (Fig. 1b). There was substantial hysteresis in the relationship between $J_{\text{CO}_2}$ and soil temperature in both burned and unburned sites (Fig. 1b). For any given temperature, $J_{\text{CO}_2}$ was higher in the spring and early summer months than in the late summer and fall. Moreover at the same temperature, $J_{\text{CO}_2}$ was greater in burned than unburned sites in the spring and early summer, but not later in the year (Fig. 1b).

The relationship between soil temperature and midday $J_{\text{CO}_2}$ was statistically significant in both unburned and burned sites (Fig. 2), but a much larger amount of the variance in $J_{\text{CO}_2}$ could be explained by soil temperature in unburned than burned sites. This reflects the greater seasonal hysteresis in burned sites. Nonetheless, the slopes of the relationships between $J_{\text{CO}_2}$ and soil temperature were not significantly different for burned and unburned treatments.

In the fire history study, soil temperatures were very similar in the two burned sites that differed in fire history, and both were significantly higher than in the unburned plots (data not shown, Blair 1997). Monthly rates of $J_{\text{CO}_2}$ were significantly affected by fire treatment from April to September. The monthly maximum $J_{\text{CO}_2}$ was $\text{33\%}$ greater in the annually burned sites compared with the sites burned for the first time in several years (infrequently burned; Fig. 3). This increase in midday $J_{\text{CO}_2}$ in the annually burned plots occurred in June, July, and August. In both fire treatments, $J_{\text{CO}_2}$ was greater than in the unburned plots for much of the growing season, particularly in the spring and early summer months. Relative to the unburned plots, the maximum monthly estimate of $J_{\text{CO}_2}$ was increased by 17 and 55%
in the infrequently and annually burned sites, respectively.

Effect of irrigation.—Over the 2-yr period of study, irrigation of annually burned prairie to maintain soil moisture at levels nonlimiting to plant growth affected midday \( J_{\text{CO}_2} \) only from July through September (Fig. 4). This contrasts with the effects of fire and fire history, in which treatment effects were manifest in the spring and early summer. The maximum monthly estimate of \( J_{\text{CO}_2} \) was increased \( \sim 8\% \) by irrigation, and the greatest increase in \( J_{\text{CO}_2} \) between irrigated and non-irrigated sites was 25\% in August. This typically is the driest month of the growing season.

Effect of grazing.—In June, July, and August, midday soil \( J_{\text{CO}_2} \) measured in bison grazing patches was significantly lower than in ungrazed sites (Fig. 5). There was no difference between grazed and ungrazed sites in the fall (October) when plants had senesced. The greatest decrease in \( J_{\text{CO}_2} \) in grazed patches (30\%) was measured in July. In contrast to \( J_{\text{CO}_2} \), soil temperatures were consistently higher in the grazed patches by 2–4°C (Fig. 5). Minor differences between sites in the ungrazed watershed and ungrazed sites within grazed watersheds (bison ungrazed in Fig. 5) are probably due to differences in grazing history between sites.

Estimates of annual amounts of soil \( J_{\text{CO}_2} \).—An annual estimate of total CO\(_2\) evolved from tallgrass prairie was calculated by scaling monthly midday averages to annual totals. The major assumptions in these estimates were that midday measurements were representative of other times of day, that the frequency of measurements (1–2-wk intervals in the growing season) was sufficient to capture seasonal dynamics, and that unusual outgassing events not sampled did not result in an underestimate of total CO\(_2\) respired. The first assumption was based on 2 d of diurnal measurements of \( J_{\text{CO}_2} \) (early and late in the growing season) at hourly intervals in both burned and unburned sites (data not shown). In all cases, either midday estimates of \( J_{\text{CO}_2} \) were intermediate between daily low and high \( J_{\text{CO}_2} \), measured, or \( J_{\text{CO}_2} \) varied <10\% during the day. Similar results were reported by Grahamer et al. (1991), especially when soil-moisture levels were high. With regard to the second assumption, sampling intervals were judged to be appropriate, with the exception of the April–May time period (when fires occurred). Depending on the timing of data collection after fire, estimates of \( J_{\text{CO}_2} \) for this month could vary significantly (compare estimates of \( J_{\text{CO}_2} \) for burned sites in April and May in Figs. 1 and 3). Finally, inspection of the raw data in Fig. 2 suggests that some isolated high levels of \( J_{\text{CO}_2} \) were measured occasionally, but these typically occurred after a rainfall event and were very short-term in nature. The magnitude of these fluxes did not seem sufficient to bias annual estimates substantially. Moreover, in some cases saturated soils resulted in very low \( J_{\text{CO}_2} \) for short periods of time, and these would likely offset the high fluxes.

Given these assumptions and based on the 2 yr of measurements, \( J_{\text{CO}_2} \) in annually burned tallgrass prairie averaged \( \sim 7.2 \) kg CO\(_2\)/m\(^2\) and was 38–51\% higher than in unburned prairie, depending on topographic position and soil type (Table 1). When comparing sites burned for the first time in several years to unburned sites, annual \( J_{\text{CO}_2} \) was increased by 27\% in the first year after fire. Irrigation of annually burned tallgrass prairie in
increased annual $J_{\text{CO}_2}$ by 13%, to the highest annual total of CO$_2$ evolved from the soil; almost 7.9 kg CO$_2$/m$^2$ (Table 1).

**DISCUSSION**

Soil temperature and moisture are two environmental factors that have been shown to be correlated strongly with soil $J_{\text{CO}_2}$ in a variety of ecosystems (Kim et al. 1992, Lloyd and Taylor 1994, Raich and Potter 1995). Similarly, biotic factors such as microbial biomass, substrate (organic matter) quality, and the activity of roots have been documented as determinants of soil $J_{\text{CO}_2}$ (Hanson et al. 1993, Vose et al. 1995, Luo et al. 1996). Fire, an inherent feature of the tallgrass prairie (Axelrod 1985) that today is used as a land management tool, has the potential to alter all of these factors. For example, fire generally results in an increase in soil temperatures compared with unburned prairie during the first 30–60 d of the growing season, but soil moisture may be reduced late in the summer (Knapp 1985, Briggs and Knapp 1995). Under an annual fire regime, soil organic matter and N availability are predicted to decrease (Ojima et al. 1990, 1994), microbial biomass and activity may be altered (Rice et al. 1998), and belowground plant biomass and root activity may be enhanced relative to unburned sites (Hayes and Seastedt 1987, Benning 1993). These latter responses are consistent with the view that annually burned sites are more N and water limited than unburned sites (Knapp and Seastedt 1996, Turner et al. 1997). Individually, these postfire responses may serve either to increase or decrease soil $J_{\text{CO}_2}$. However, based on the overall increase in aboveground production that occurs after fire, particularly in lowland sites (Briggs and Knapp 1995), we hypothesized that soil $J_{\text{CO}_2}$ would increase in burned relative to unburned sites.

Measurements of soil $J_{\text{CO}_2}$ in lowland burned and unburned sites over a 2-yr period supported this prediction (Fig. 1), with monthly soil $J_{\text{CO}_2}$ in burned sites as much as fourfold higher in the spring after fire. At this time of year, soils are typically wet, and soil temperatures in annually burned sites were 4–6°C higher than in the unburned sites. Overall, from April through June, soil $J_{\text{CO}_2}$ was 78% greater in the annually burned sites. These months are the wettest of the growing season, and this is also when the maximum rate of accumulation of aboveground biomass occurs in tallgrass prairie (Knapp et al. 1998). Fire effects on soil $J_{\text{CO}_2}$ diminished from July through September, when soil temperatures were more similar in burned and unburned sites. This is also the portion of the growing season when precipitation is lowest and soil moisture deficits are most likely to develop, particularly in burned prairie (Briggs and Knapp 1995). Indeed, only during July–September was soil $J_{\text{CO}_2}$ positively affected by irrigation (Fig. 4). No fire effect on soil $J_{\text{CO}_2}$ was detected during the nongrowing season (October–February).

Variation in soil $J_{\text{CO}_2}$ was strongly correlated with soil temperature in tallgrass prairie (Fig. 2), but a lesser proportion of the variation was explained by soil temperature in burned sites. This is consistent with the view that biotic processes in burned sites are limited by additional factors, such as soil moisture and N availability. The blanketing effect of the detrital layer coupled with reduced biomass and leaf area in unburned sites reduces evapotranspiration substantially relative to burned prairie. Thus, soil moisture limitations are less apparent in unburned sites in all but the driest years (Knapp and Seastedt 1996). However, the greater hysteresis in the relationship between soil temperature and soil $J_{\text{CO}_2}$ in annually burned sites (Fig. 1) cannot be attributed entirely to postfire differences between burned and unburned sites in soil moisture. This is because, at a given soil temperature, higher than expected soil $J_{\text{CO}_2}$ in burned sites occurred in the spring when intersite differences in soil moisture would be expected to be minimal (Briggs and Knapp 1995). Instead, increased early season soil $J_{\text{CO}_2}$ in burned sites
Table 1. Range of estimates of annual soil CO₂ flux (mean ± 1 se) from tallgrass prairie in northeast Kansas.

<table>
<thead>
<tr>
<th>Fire history</th>
<th>Topographic position</th>
<th>CO₂ flux (kg CO₂/m²)</th>
<th>Percentage increase</th>
</tr>
</thead>
<tbody>
<tr>
<td>Annual fire</td>
<td>lowland</td>
<td>7.31 ± 0.44</td>
<td>38</td>
</tr>
<tr>
<td>Unburned</td>
<td>lowland</td>
<td>5.29 ± 0.25</td>
<td>...</td>
</tr>
<tr>
<td>Annual fire</td>
<td>upland/lowlad</td>
<td>7.12 ± 0.32</td>
<td>51</td>
</tr>
<tr>
<td>Infrequent fire</td>
<td>upland/lowlad</td>
<td>5.99 ± 0.28</td>
<td>27</td>
</tr>
<tr>
<td>Unburned</td>
<td>upland/lowlad</td>
<td>4.70 ± 0.18</td>
<td>...</td>
</tr>
<tr>
<td>Annual fire + irrigation</td>
<td>upland/lowlad</td>
<td>7.87 ± 0.32</td>
<td>13</td>
</tr>
<tr>
<td>Annual fire (control)</td>
<td>upland/lowlad</td>
<td>6.94 ± 0.28</td>
<td>...</td>
</tr>
</tbody>
</table>

Notes: Values are from sites at varying topographic positions (upland, lowland, or combined data when no topographic effect was statistically detected) and subjected to different fire histories (annual fire, infrequent fire [burned in the year of measurement but previously protected from fire], and unburned). Data from sites irrigated to meet evapotranspirational demands and adjacent control sites are also included. Percentage increase is for burned treatments relative to unburned prairie, and for irrigated treatments relative to the controls.

at a given soil temperature, particularly in April, may be due to increased biotic activity (increased root growth) and earlier phenological development of the grasses (Knapp 1984).

The response of soil \( J_{\text{CO}_2} \) to fire was dependent on fire history, but not as we predicted. Soil \( J_{\text{CO}_2} \), from plots burned for the first time following a period of fire exclusion was significantly greater than soil \( J_{\text{CO}_2} \), from comparable plots that remained unburned, but was less than soil \( J_{\text{CO}_2} \), from annually burned plots (Fig. 3). Growing season soil temperature and moisture were similar in plots that differed only in fire history, suggesting that biotic differences (plant, microbial, and faunal) may be key in explaining the higher levels of \( J_{\text{CO}_2} \) from annually burned sites compared to those burned infrequently. Annual spring burning generally increases new root production, and root and rhizome biomass (Hayes and Seastedt 1987, Seastedt and Ramundo 1990), and results in greater numbers and biomass of some soil invertebrate groups (James 1982, 1988, Seastedt 1984, Seastedt et al. 1986) relative to unburned prairie. Increased C inputs and warmer soil temperatures may result in greater microbial respiration in annually burned prairie, but this effect is dependent on adequate soil water content (Garcia 1992, Ojima et al. 1994). Fire in a site with a history of fire exclusion can lead to higher aboveground productivity in the growing season following a spring fire (a pulse in productivity) relative to annually burned or unburned prairie (Seastedt and Knapp 1993, Briggs et al. 1994, Blair 1997). However, it seems unlikely that changes in belowground productivity or biomass would occur as quickly. Indeed, Blair (1997) found that 2 yr of consecutive burning was required for significant increases in root biomass in previously unburned prairie. Moreover, N mineralization during the growing season following an infrequent fire was greater than on comparable annually burned sites (Blair 1997). This suggests that although abiotic factors (temperature and moisture) may be similar in annually burned and infrequently burned sites, the availability of other key resources, such as N, may differ. The relatively high N environment in infrequently burned sites may, in fact, contribute to a slower shift in biomass allocation belowground and thus, reduced soil \( J_{\text{CO}_2} \), relative to annually burned sites.

Responses of net N mineralization (a microbial process) and soil \( J_{\text{CO}_2} \), (a result of combined plant, microbial, and faunal activity) differed depending on fire frequency. In this study, \( J_{\text{CO}_2} \) was greatest in annually burned sites, lowest in unburned sites, and intermediate in sites burned for the first time. In contrast, net N mineralization (Blair 1997) was greatest in the unburned sites, lowest in the annually burned sites, and intermediate in the infrequently burned sites. This response appears to be due to both microclimatic changes and changes in the quantity and quality of root inputs with repeated burning (Ojima et al. 1994, Blair 1997). Thus, it appears that plants play a major role in determining both soil \( J_{\text{CO}_2} \), (via root respiration and allocation of C substrates belowground) and net N mineralization (via changes in quantity and quality of root inputs). Differences in root biomass have been reported to affect soil \( J_{\text{CO}_2} \), in other ecosystems (Vose et al. 1995, Luo et al. 1996). Kucera and Kirkham (1971) and Herman (1977) both estimated that 30–40% of the total soil \( J_{\text{CO}_2} \) in tallgrass prairie was due to root respiration. Thus, changes in root biomass in tallgrass prairie have the potential to alter substantially soil \( J_{\text{CO}_2} \).

Additional support for the role that belowground plant processes may play in determining soil \( J_{\text{CO}_2} \), comes from our preliminary assessment of the effects of grazing on soil \( J_{\text{CO}_2} \). In this comparison, the lowest levels of soil \( J_{\text{CO}_2} \), were measured consistently in bison-grazing patches where most of the aboveground biomass was removed (Fig. 5). Aboveground herbivory in grasslands can reduce productivity belowground and alter C allocation patterns such that aboveground tissues in grazed plants may receive a greater proportion of fixed and stored C than ungrazed plants (McNaughton 1985, but see Milchunas and Lauenroth 1993). These responses reduce plant and microbial activity below-
ground and provide the mechanism for reduced soil $J_{CO_2}$ in grazed sites. This occurred despite the increase in soil temperature and reduction in transpiring leaf area in these patches.

In summary, fire and fire history affect soil $J_{CO_2}$ in tallgrass prairie through their impacts on soil temperature, belowground biotic activity (root and microbial), and soil moisture. The importance of soil moisture on soil $J_{CO_2}$ depends on precipitation patterns and the presence of droughts. Droughts are not uncommon in tallgrass prairie (Borchert 1950), but during the 2 yr of this study, variations in soil moisture had little effect on soil $J_{CO_2}$, particularly in unburned sites where temperature explained 70% of the variance. Land management activities such as annual fire regimes are likely to result in the greatest loss of CO$_2$ from the soil through soil $J_{CO_2}$. This is consistent with simulation model predictions that organic matter will decline in tallgrass prairie if it is annually burned (Ojima et al. 1990). Grazing may reduce soil $J_{CO_2}$ in this grassland, but concurrent alterations in root productivity, species composition, and nutrient cycling make it difficult to project a net effect on soil organic matter.

Estimates of maximum and annual soil $J_{CO_2}$ in comparison with other ecosystems.—Maximum monthly estimates of soil $J_{CO_2}$ in this study of tallgrass prairie ranged from 10.3 $\mu$mol-m$^{-2}$-s$^{-1}$ in unburned sites to 15.1 $\mu$mol-m$^{-2}$-s$^{-1}$ in annually burned irrigated sites. Using leaf area index (LAI) values from Schimel et al. (1991) and dark respiration estimates for the dominant C$_4$ grass A. gerardii from Knapp et al. (1993), aboveground plant canopy respiration (5.3–5.8 $\mu$mol CO$_2$-m$^{-2}$-s$^{-1}$) is substantially lower than soil $J_{CO_2}$. These estimates of soil $J_{CO_2}$ are comparable to previous measurements of maximum daily or monthly soil $J_{CO_2}$ for this grassland, which ranged from 11.8 to 14.5 $\mu$mol-m$^{-2}$-s$^{-1}$ (Norman et al. 1992, Ham et al. 1995), but are much higher than earlier tallgrass prairie estimates made using a static-chamber alkali-absorption technique (Kucera and Kirkham 1971, Buyanovsky et al. 1987). This technique has been reported to underestimate seriously soil $J_{CO_2}$ at high fluxes (Nay et al. 1994). Our estimates for tallgrass prairie also are much greater than the maximum values measured with similar techniques (alkali-absorption techniques excluded) in other, less productive grasslands (California annual grassland, 2.2–3.8 $\mu$mol-m$^{-2}$-s$^{-1}$ by Luo et al. [1996]), agricultural systems (cotton in Arizona, 2.8 $\mu$mol-m$^{-2}$-s$^{-1}$ by Nakayama et al. [1994]), tundra (3.0 $\mu$mol-m$^{-2}$-s$^{-1}$ by Oberbauer et al. [1992]), or forests (young ponderosa pine in California, 3.6 $\mu$mol-m$^{-2}$-s$^{-1}$ by Vose et al. [1995]; 29-yr-old slash pine in Florida, 3.9 $\mu$mol-m$^{-2}$-s$^{-1}$ by Ewel et al. [1987]; mature oak forest in Tennessee, 5.7 $\mu$mol-m$^{-2}$-s$^{-1}$ by Hanson et al. [1993]). Only in lowland tropical forests (14.0 $\mu$mol-m$^{-2}$-s$^{-1}$) have similar values been measured (Kursar 1989).

Annual estimates of soil $J_{CO_2}$ from tallgrass prairie varied from 4.7 to 7.8 kg CO$_2$/m$^2$ (Table 1). Losses of C from fire are estimated at 0.23 kg C/m$^2$ based on the long-term average of aboveground production from annually burned sites (Knapp et al. 1998), but this loss is an order of magnitude smaller than the annual C flux via soil $J_{CO_2}$ (2.13 kg C/m$^2$). There are fewer estimates of annual soil $J_{CO_2}$ from other ecosystems for comparison, but Hanson et al. (1993) reported that annual forest floor CO$_2$ efflux from oak-dominated forests in Tennessee and elsewhere in North America and Europe ranged from 0.6 to 3.9 kg CO$_2$/m$^2$. In their study, 3.0 kg CO$_2$/m$^2$ was a representative annual estimate across a range of topographic positions. Kursar (1989) estimated an annual flux of 5.3 kg CO$_2$/m$^2$ in Panamanian forests, which was within the range of other estimates for these tropical systems (1.5–8.0 kg CO$_2$/m$^2$). Finally, in agricultural fields (wheat–soybean rotation) in Argentina, Alvarez et al. (1995) estimated an annual soil $J_{CO_2}$ of 1.2 kg CO$_2$/m$^2$. Thus, annual soil $J_{CO_2}$ in tallgrass prairie can be as much as 55–160% greater than in temperate deciduous forests, four- to sixfold greater than in agricultural systems, and similar to estimates for tropical forests with much longer growing seasons.

Why is soil $J_{CO_2}$ so high in tallgrass prairie? Tallgrass prairie can be characterized as an ecosystem (1) with high net primary productivity (Briggs and Knapp 1995); (2) in which the dominant vegetation allocates >50% of this productivity belowground and, consequently, a relatively high proportion of all C is stored belowground, especially relative to forests (Seastedt and Knapp 1993); (3) in which soil microbial biomass and activity are among the highest in native ecosystems in the United States (Zak et al. 1994); (4) with a relatively long (6-mo) growing season; and (5) where no single factor such as temperature, moisture, or nutrient availability consistently limits biotic processes during the growing season (Seastedt and Knapp 1993). We contend that these characteristics are key in explaining the substantially higher levels of soil $J_{CO_2}$ measured in this ecosystem relative to others. In addition, because land management activities such as fire and grazing affect many of these attributes, the sensitivity of soil $J_{CO_2}$ in tallgrass prairie to different land use practices is not surprising (Table 1). As a result of this sensitivity, these factors must be accounted for in grassland C budgets and regional models that estimate biogeochemical responses to land use change (Burke et al. 1991).

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