



PERGAMON

Soil Biology & Biochemistry 34 (2002) 1235–1241

876
**Soil Biology &
Biochemistry**

www.elsevier.com/locate/soilbio

Soil carbon dioxide fluxes in northern semiarid grasslands[☆]

A.B. Frank^{*}, M.A. Liebig, J.D. Hanson

USDA—Agricultural Research Service, US Department of Agriculture, Agricultural Research Service, P.O. Box 459, Mandan, ND 58554, USA

Received 8 October 2001; received in revised form 5 March 2002; accepted 28 March 2002

Abstract

The high indigenous soil organic carbon content, root biomass, and microbial populations in prairie soils provide a source of carbon dioxide (CO₂) that is important in the carbon budget of grasslands. Soil chambers were used to measure soil CO₂ flux from a grazed mixed-grass prairie (GP), nongrazed mixed-grass prairie (NGP), and grazed western wheatgrass (WWG) [*Pascopyrum smithii* (Rybd) Löve] grasslands in the Northern Great Plains, USA. Objectives were to quantify soil CO₂ fluxes for each site and to determine the contribution of soil temperature, soil water content, and air temperature to soil CO₂ flux. Soil CO₂ fluxes were measured on each site about every 21 d at 13:00 h during the 25 April–27 October growing period from 1996 to 2000 for NGP and GP and from 1996 to 1998 for WWG. Dormant period fluxes were measured on the GP from 28 October to 26 April from 1999 to 2001. In addition, five sequential daytime measurements were made on each site for 3 days each year. Fluxes were low in the spring and autumn and peaked concurrent with biomass in late June to mid-July. Maximum fluxes for these dissimilar managed grasslands averaged 5.8 g CO₂-C m⁻² d⁻¹ for NGP, 6.9 g CO₂-C m⁻² d⁻¹ for GP, and 6.1 g CO₂-C m⁻² d⁻¹ for WWG. Soil fluxes measured during the dormant period decreased to near zero during the months of December, January, and February and then increased rapidly in March as soil temperatures increased. Daily soil flux during the growing period averaged 3.5 g CO₂-C m⁻² d⁻¹ for NGP, 4.3 g CO₂-C m⁻² d⁻¹ for GP, and 4.0 g CO₂-C m⁻² d⁻¹ for WWG. Dormant period fluxes for the GP averaged 0.5 g CO₂-C m⁻² d⁻¹. Regression analysis indicated that soil temperature accounted for 65%, soil water content 5%, and air temperature 3% of flux variability. Growing period soil CO₂ flux over years averaged 728 g CO₂-C m⁻² and dormant period CO₂ flux averaged 86 g CO₂-C m⁻². A predictive relationship describing the response of soil CO₂ flux to changes in soil temperature was developed using the minimum, maximum, and optimum soil temperatures for soil CO₂ flux. The model provides an estimate of the important dormant period soil flux component in annual ecosystem carbon budgets. © 2002 Elsevier Science Ltd. All rights reserved.

Keywords: Soil respiration; Soil CO₂ flux; Prairie grasslands; Carbon cycling

1. Introduction

Grassland soils are high in soil organic carbon and contain an extensive fibrous root system that creates an environment ideal for soil microbial activity (Conant et al., 2001). Measurements of CO₂ flux from grassland soils support their importance in the global carbon budget (Bremer et al., 1998; Dugas et al., 1999; Mielnick and Dugas, 2000; Norman et al., 1992). Grassland vegetation has been shown to sequester atmospheric CO₂ that is stored in the soil (Dugas et al., 1999; Frank et al., 2000; Frank and

Dugas, 2001; Kim et al., 1992). These same soils can be a source of CO₂ in the Northern Great Plains where grassland vegetation photosynthesizes for only about half the year. During the remainder of the year most of the vegetation is dormant and the opportunity to capture soil CO₂ through photosynthesis is lost.

The energy-rich grassland soils characteristic of the Northern Great Plains evolve large amounts of CO₂ during the night period when soil temperatures favor high root and microbial respiration and even during periods of low soil temperatures when plants are dormant and soil flux rates are much lower (Bremer et al., 1998; Mariko et al., 2000). Soil flux rates for a warm-season species dominated grasslands have varied from 1.25 g CO₂-C m⁻² d⁻¹ during a short time period in August for a tallgrass prairie in Nebraska (Norman et al., 1992), 4.36 kg CO₂-C m⁻² yr⁻¹ over a series of grazing simulated clipping treatments in a tallgrass prairie in northeast Kansas (Bremer et al., 1998), 1.45 kg CO₂-C m⁻² yr⁻¹ over a 6 year period for a tallgrass prairie in

[☆] US Department of Agriculture, Agricultural Research Service, Northern Plains Area, is an equal opportunity/affirmative action employer and all agency services are available without discrimination. The mention of commercial products in this paper is solely to provide specific information for the reader. It does not constitute endorsement by the USDA Agricultural Research Service over other products.

^{*} Corresponding author. Tel.: +1-701-667-3007; fax: +1-701-667-3054.

E-mail address: franka@mandan.ars.usda.gov (A.B. Frank).

southeast Texas (Mielnick and Dugas, 2000), and an estimated $0.4\text{--}0.5\text{ kg CO}_2\text{-C m}^{-2}\text{ yr}^{-1}$ as the global average for grasslands (Raich and Schlesinger, 1992). In contrast, Hanson et al. (1993) estimated a mature forest soil flux to be $1.2\text{ kg CO}_2\text{-C m}^{-2}\text{ yr}^{-1}$.

Measurements of soil CO_2 flux from grassland ecosystems is strongly related to soil temperature. Equations for predicting soil CO_2 flux are generally enhanced when soil water (Mielnick and Dugas, 2000), LAI (Norman et al., 1992), and air temperature and precipitation (Raich and Potter, 1995) are added as model variables. Most soil flux studies are short term, often over only a portion of the year, but Mielnick and Dugas (2000) developed a 6 year database on soil fluxes for a tallgrass prairie. The main components of soil respiration are from root respiration and soil microbial activity. Dugas et al. (1999) estimated that 90% of total soil flux was due to root respiration, Norman et al. (1992) estimated 15–70%, Hanson et al. (1993) estimated 50%, and Kucera and Kirkham (1971) estimated 40%.

Our study includes soil CO_2 flux measurements over a 5 year period for the entire growing season with 2 years of over winter measurements for a Northern Great Plains semiarid mixed-grass prairie. Our guiding hypothesis is that soil CO_2 flux is a significant contributing factor to the annual carbon budget of northern semiarid grasslands. The objectives were to quantify soil CO_2 fluxes for grazed mixed-grass prairie (GP), nongrazed mixed-grass prairie (NGP), and grazed western wheatgrass [*Pascopyrum smithii* (Rybd) Löve] (WWG) sites, and to evaluate the relationship between soil temperature, air temperature, soil water content, and soil CO_2 flux for purposes of developing a predictive model.

2. Materials and methods

2.1. Site description

The sites in this study are located at the USDA, Agricultural Research Service, Northern Great Plains Research Laboratory, Mandan, ND, USA (latitude $46^{\circ}46'N$, longitude $100^{\circ}55'W$; elevation 518 m; mean annual precipitation 404 mm; mean daily air temperature $5^{\circ}C$). The sites and treatments were a grazed mixed-grass prairie (GP), nongrazed mixed-grass prairie (NGP), and grazed western wheatgrass (WWG) [*P. smithii* (Rybd) Löve]. Vegetation composition was characterized using point frame procedures (25 frames, 50 hits/frame) in 1995 and 1997. The two prairie sites are typical of a Northern Great Plains mixed-grass prairie ecosystem dominated by blue grama [*Bouteloua gracilis* (H.B.K.) Lag. ex Griffiths], needle-and-thread (*Stipa comata* Trin. and Rupr.), Carex (*Carex* spp.), Kentucky bluegrass (*Poa pratensis* L.), little bluestem [*Schizachyrium scoparium* (Michx.) Nash], side-oats grama [*Bouteloua curtipendula* (Michx.) Torr.], and western wheatgrass. The WWG site is 76% western

wheatgrass with minor components of Kentucky bluegrass, crested wheatgrass [*Agropyron desertorum* (Fisch. Ex. Link) Schult.], and broadleaf forbs.

Soil at these upland sites belonged to the Werner–Sen–Chama complex (loamy, mixed, superactive, frigid shallow Entic Haplustoll; fine-silty, mixed, superactive, frigid Typic Haplustoll; fine-silty, mixed, superactive, frigid Typic Calcicustoll). Soil texture for the sites ranged from a loam to a silt loam (particle size distribution averaged 25% clay, 54% silt, and 21% sand), soil pH for 0–30 cm depth averaged 6.6, and no water table was present. The GP and NGP never had fertilizer or herbicides applied. The GP was grazed at 2.6 ha per steer from about mid-May to October each year since 1916. The WWG was seeded in 1986, never had fertilizer or herbicides applied since seeding, and was grazed since 1987 at 2 ha per steer.

2.2. Soil CO_2 flux

Soil CO_2 flux was measured at about 20–30 d intervals between 1300 and 1500 h from 25 April to 27 October, hereafter referred as the growing period, in 1996 (10 d), 1997 (10 d), 1998 (10 d), 1999 (8 d) and 2000 (12 d). Measurements, hereafter referred to as the dormant period, were made about every 20–30 d intervals between 1300 and 1500 h from November 1999 to April 2000 (9 d) and from November 2000 to March 2001 (9 d). Soil flux measurements were also measured at 07:00, 10:00, 13:00, 16:00, and 19:00 h on 3 d (June, July, September) each year at each site. These sequential flux measurements were summarized for each year, but only 1998 data will be reported.

A closed gas flow system consisting of a 1259 cm^3 cylindrical chamber with a 95 mm diameter opening, a LI-COR model 6262 infrared gas analyzer, and a LI-COR model LI-670 gas flow control unit was used to measure CO_2 evolving from the soil (LI-COR, Lincoln, NE). Six rings (polyvinyl chloride 104 mm diameter by 50 mm depth) were placed for the duration of the study at 25 mm in the soil in a circular pattern of about 40 m in each direction from weather towers located in the center of each site. The initial ring placement was in live vegetation, but thereafter the soil surface within the collars was kept free of any live vegetation and residue. During the snow season the rings were only partly covered to prevent accumulation of packed snow within the rings but allow free air flow. Occasionally snow was deposited within the rings which was removed prior to making measurements. Measurements of fluxes before and after snow removal from the rings showed that light accumulation of snow did not affect fluxes. Soil temperature was measured using a temperature probe placed at 38 mm depth at the time of soil flux measurements. When the soil was frozen, soil temperatures were measured with copper–constantan thermocouples installed at 38 mm depth near the weather towers. Volumetric soil water was measured with model CS615 water content reflectometers installed at 80 mm soil depth

(Campbell Scientific Inc., Logan, UT). Air temperature was measured at 2 m above the soil surface using a model HMP35 temperature and humidity probe (Campbell Scientific, Inc.).

2.3. Biomass

Aboveground green biomass was measured at each site by clipping four representative 0.25 m² quadrats about 21 d before and after peak biomass, and at peak biomass which occurred about mid-July each year. The quadrats were located at about 40 m distance from the weather towers. Green plant material was separated from the dead material, oven dried (70 °C) and weighed to obtain total green biomass. Root biomass was sampled on dates of aboveground biomass sampling near the clipped area, and within several days of making the soil CO₂ flux measurements by taking four soil cores (66 mm diameter) to 0.3 m depth. No root samples were taken when soils were frozen. Root mass was obtained by elution with water, oven dried (70 °C), and weighed. No attempt was made to separate live and dead roots.

2.4. Soil carbon

Soil organic carbon and nitrogen contents were measured by taking three 32 mm diameter cores, about 0.15 m apart, 0.3 m depth, and within 4–6 m of the rings used for soil flux measurements during mid-July each year. Soil from the three cores was composited and processed by removing all visible root material. Subsamples were removed for determining bulk density and soil water content. Samples were dried at 31 °C for 72 h, crushed to pass a 2 mm sieve, ground to 200 µm, and stored in glass bottles. Total carbon and nitrogen contents were determined by dry combustion using a Carlo Erba model NA1500 automatic carbon–nitrogen analyzer (Hake Buckler Instruments, Inc., Saddle Brook, NJ), as described by Schepers et al. (1989). A separate subsample was acidified to determine inorganic carbon content (Loeppert and Suarez, 1996), which was subtracted from the total carbon content to obtain total organic carbon.

2.5. Statistical procedures

Standard error of the mean (SEM) was calculated to provide a measure of the variance for canopy biomass, root biomass, and soil CO₂ flux measurements. The Tukey's Studentized Range Test was used to compare soil fluxes between GP, NGP, and WWG sites. Stepwise regression was used to evaluate the contribution of soil temperature, air temperature, and soil water to soil CO₂ fluxes (SAS Institute, 1989).

A predictive relationship describing the response of soil CO₂ flux to changes in soil temperature was developed using an approach by Hanson (2000). Equation parameters

included: $A_1 = (T_{\max} - T)/(T_{\max} - T_{\text{opt}})$, $A_2 = (T - T_{\min})/(T_{\text{opt}} - T_{\min})$, and $A_3 = (T_{\text{opt}} - T_{\min})/(T_{\max} - T_{\text{opt}})$, where T is the measured soil temperature and T_{\max} the maximum soil temperature, T_{\min} the minimum soil temperature, and T_{opt} is the optimum soil temperature for soil CO₂ flux rates. The effect of soil temperature on soil CO₂ flux (g CO₂-C m⁻² d⁻¹) is then described as:

$$\text{Soil flux} = ((A_1 A_2^{A_3})^z) \text{maximum flux} \quad (1)$$

where for model optimization, the model shape parameter z was set at 1.5. Detling et al. (1978) used a value of z as 1.328 in describing a photosynthetic response in *B. gracilis*. The maximum measured soil flux 8.4 g CO₂-C m⁻² d⁻¹ was used to scale the predicted (P) for comparing with the observed (O) fluxes. The model goodness-of-fit was evaluated by calculating the percentage difference (%D) between the observed (O) and predicted (P) soil fluxes averaged for all observations (n):

$$\%D = \sum_{i=1}^n \left(\frac{P_i - O_i}{O_i} \right) 100/n \quad (2)$$

3. Results

3.1. Biomass

Aboveground biomass production was correlated to annual precipitation which totaled 487 mm in 1996, 345 mm in 1997, 517 mm in 1998, 565 mm in 1999, and 478 mm in 2000 compared to the long term average of 404 mm. Aboveground green biomass averaged over three clipping dates at time of peak production was greater for the WWG compared to the NGP and GP sites. Aboveground biomass and standard error of the mean (SEM) averaged 1063 (95) kg ha⁻¹ for NGP, 1322 (138) kg ha⁻¹ for GP, and 1425 (114) kg ha⁻¹ for WWG. The grazing intensity imposed on the GP site was not sufficient to reduce biomass compared to the NGP. These aboveground biomass data compare favorably with that of Schuman et al. (1999) who reported 1224 kg ha⁻¹ live biomass for a lightly grazed mixed-grass prairie. Root biomass was higher for the two prairie sites, averaging 12,486 (SEM of 4500) kg ha⁻¹ for NGP and 12,029 (4500) kg ha⁻¹ for the GP compared to only 6114 kg ha⁻¹ (2722) for the WWG site. Less root biomass in WWG than GNP and GP may have been due to root distribution as only 69% of root biomass in the WWG site was in the surface 30 cm soil depth compared to 80% for the NGP and GP sites (Frank and Dugas, 2001). Differences in root distribution with depth probably reflects the greater species diversity in the NGP and GP vs. the WWG site. Schuman et al. (1999) reported even greater root biomass totals (28,666 kg ha⁻¹) for a mixed-grass prairie.

3.2. Soil carbon

Soil organic carbon content did not increase in the 0–30 cm soil depth for the NGP, GP, or WWG during the years of study. Soil organic carbon content ranged from 6.3 kg C m⁻² in 1996 to 7.7 kg C m⁻² in 1998 for NGP, from 6.4 kg C m⁻² in 2000 to 6.9 kg C m⁻² in 1996 for GP; and from 7.2 kg C m⁻² in 1997 to 7.6 kg C m⁻² in 1998 for WWG. Soil organic carbon for each site was not different and averaged 6.8 kg C m⁻² for NGP, 6.7 kg C m⁻² for GP, and 7.4 kg C m⁻² for WWG.

3.3. Twelve hour soil fluxes

Flux measurements on 23 June, 20 July, and 10 September in 1998 are presented as representative of soil fluxes from 07:00 to 19:00 h during the growing period for all years (Fig. 1). The greatest variation in fluxes occurred on 23 June when SEM for the six flux measurements each hour ranged from 0.19 for NGP to 0.24 g CO₂-C m⁻² d⁻¹ for WWG. Variation in fluxes were less on 20 July (maximum SEM = 0.17) and 10 September (maximum SEM = 0.14) compared to 23 June. The differences between days was probably due to the combination of higher soil water content and lower soil temperature for 23 June compared to higher soil temperature and lower soil

water content for 20 July and 10 September (data not shown). Differences between the 1300 h measurements and the maximum flux during the 07:00–19:00 h measurement period were small ranging from a minimum difference of 0.08 g CO₂-C m⁻² d⁻¹ for GP on 20 July to a maximum difference of 1.12 g CO₂-C m⁻² d⁻¹ for NGP on 20 July. When averaged over sites and years the 1300 h fluxes were 4.2 g CO₂-C m⁻² d⁻¹ or only 9% more than the 07:00–19:00 h sequential measurements which averaged 3.8 g CO₂-C m⁻² d⁻¹. The period of minimum flux occurred at 07:00 h sampling period when fluxes averaged 3.3 g CO₂-C m⁻² d⁻¹ or 13% less than the five sequential flux measurements. Since daily flux measurements made at midday (1300–1500 h) were similar to the daily maximum flux rate for the sequential measurements (Fig. 1), the 13:00 h measurements are taken to be representative of daily fluxes. The sequential flux patterns for the three dates coincided with soil temperature which suggests high correlations between soil temperature and soil CO₂ flux similar to those reported by others (Kucera and Kirkham, 1971; Norman et al., 1992; Lloyd and Taylor, 1994; Bajracharya et al., 2000; Mielnick and Dugas, 2000).

3.4. Midday soil fluxes

Soil flux measurements at 13:00 h from 25 April to 27 October exhibited similar seasonal patterns across sites (Fig. 2). Overall, fluxes were low in the spring and autumn with maximum fluxes occurring during peak biomass production in late June and early July. Rochette et al. (1991) also reported that maximum soil respiration coincided with maximum periods of growth in wheat and maize. Maximum daily fluxes averaged across years were 5.7 g CO₂-C m⁻² d⁻¹ for NGP, 6.9 g CO₂-C m⁻² d⁻¹ for GP, and 6.1 g CO₂-C m⁻² d⁻¹ for WWG. Soil fluxes measured during the dormant period decreased to near zero during the months of December, January, and February and then increased rapidly in March as soil temperatures increased (Fig. 2). Total soil flux during the growing period followed the same trend as the maximum daily flux. The GP and WWG site had the greater daily fluxes than NGP (Table 1). The greater soil CO₂ flux for the GP and WWG may have been in part due to the additional nutrients returned to the soil through livestock excrements. Dormant period fluxes for the GP averaged 0.5 g CO₂-C m⁻² d⁻¹.

3.5. Soil temperature, air temperature, soil water

Seasonal soil CO₂ flux patterns were similar to that for soil temperature (Fig. 2). The greater daily maximum flux across years for the GP in 1996, 1999, and 2000 than for the NGP and WWG coincided with the greater soil temperatures, especially during 1999 and 2000. Soil temperature during the growing period typically ranged between 0 and 10 °C at the start of the flux measurements in April and again at the end of the measurements in late October. Soil

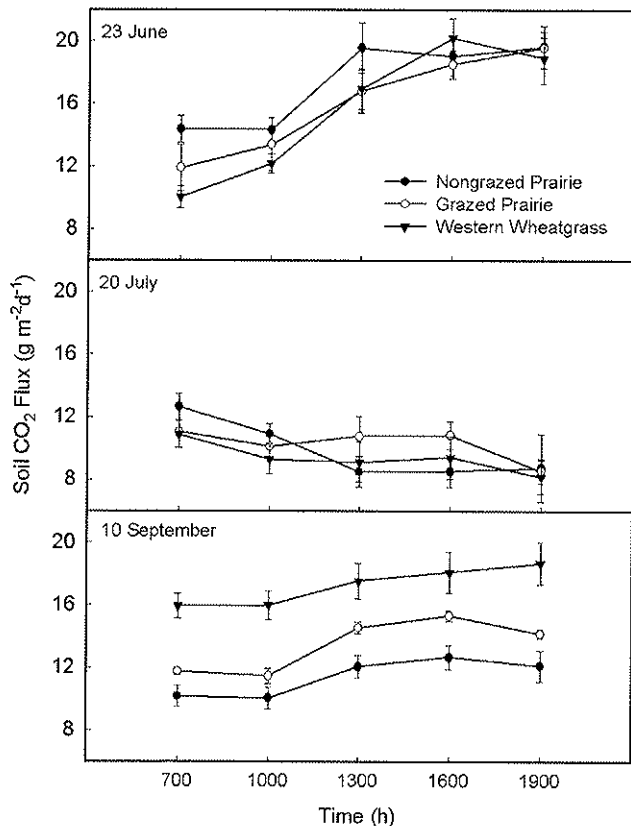


Fig. 1. Soil CO₂ fluxes at 07:00, 10:00, 13:00, 16:00, and 19:00 h for nongrazed prairie, grazed prairie, and western wheatgrass sites on 3 days in 1998. Vertical bars indicate the standard error of the treatment mean.

Table 1

Soil CO₂-C flux for nongrazed prairie, grazed prairie, and western wheatgrass sites. Soil CO₂ fluxes were measured from 1996 to 2000 for the nongrazed and grazed prairie and from 1996 to 1998 for the western wheatgrass site

Site	Growing period (25 April–23 October) (g CO ₂ -C m ⁻² d ⁻¹)	Dormant period (24 October–24 April) (g CO ₂ -C m ⁻² d ⁻¹)
Prairie	3.5 a ^a	ND
Grazed Prairie	4.3 b	0.5 (0.1) ^b
Western Wheatgrass	4.0 b	ND

^a Treatment means followed by different letters are significantly different at the 0.05 level by Tukey's studentized range test.

^b Number in parenthesis is the standard error of the treatment mean.

temperatures on dates of maximum soil fluxes averaged 20.2, 22.8, and 22.6 °C for NGP, GP, and WWG, respectively. Soil temperatures for the dormant period averaged 0.2 °C during the 1999–2000 dormant period and -3.4 °C during the 2000–2001 dormant period. Air temperature showed a similar response as soil flux and soil temperature across all years (Fig. 2). Air temperature on dates of maximum fluxes averaged 25.8 °C for NGP, 25.8 °C for GP, and 24.6 °C for WWG. Soil water content was near field capacity at the beginning and end of the growing season each year except in the autumn of 1999 when soil water recharge did not occur (Fig. 2). Soil water varied with precipitation and, except in 1999, decreased to levels less than 0.25 m³ m⁻³ during the period of greatest biomass accumulation.

3.6. Soil flux predictions

The stepwise regression equations (Table 2) and the contribution of soil temperature, air temperature, and soil water content to the model R^2 indicated soil fluxes were strongly affected by soil temperature (Table 3). Soil temperature was the dominant variable influencing soil fluxes and the only variable to meet the model significance level for entry (0.15) in 1999. Soil temperature produced model R^2 across sites that ranged from 0.44 for WWG to

Table 2

Equations from stepwise regression analysis using the model: Daily soil flux (g CO₂-C m⁻² d⁻¹) = soil temperature (Ta), air temperature (Ta), soil water content (SWC). Six dates in 2001 were included in year 2000 and in all site equations

Year/site	n	Equation
1996	30	Daily flux = -2.74 - (0.29Ts) + (7.62SWC)
1997	30	Daily flux = -5.51 + (0.33Ts) + (12.62SWC)
1998	30	Daily flux = 0.30 - (0.19Ta) + (0.48Ts)
1999	19	Daily flux = -0.54 + (0.33Ts)
2000	34	Daily flux = -0.20 - (0.19Ta) + (0.50Ts) + (2.93SWC)
Prairie	51	Daily flux = -4.20 + (0.33Ts) + (8.47SWC)
Grazed Prairie	68	Daily flux = -0.57 - (0.12Ta) + (0.36Ts) + (4.70SWC)
Western Wheatgrass	30	Daily flux = -2.45 + (0.26Ts) + (7.06SWC)
All Sites	149	Daily flux = -0.91 - (0.11Ta) + (0.36 + Ts) + (4.79SWC)

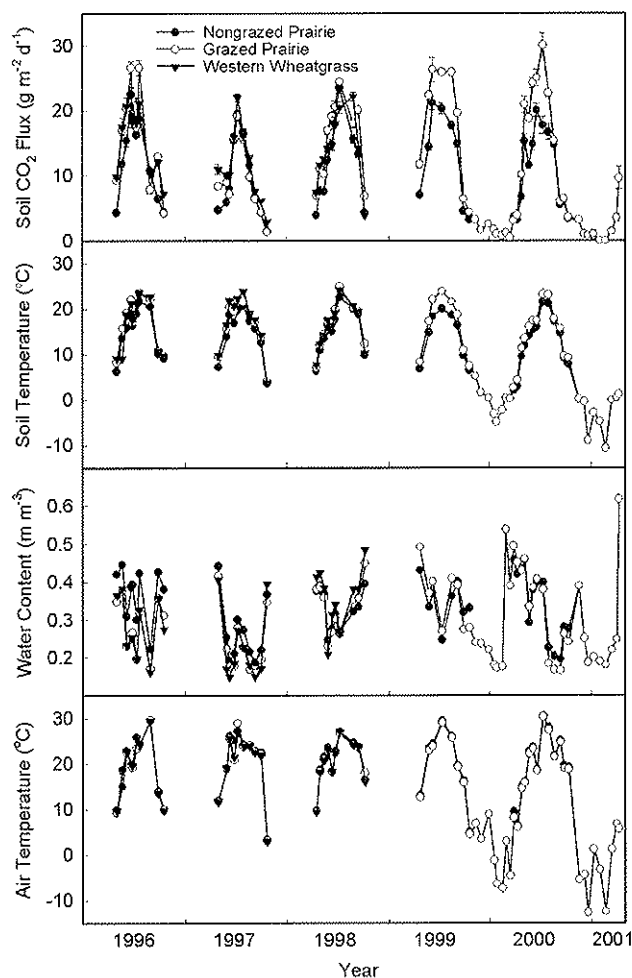


Fig. 2. Soil temperature, soil water content, air temperature, and soil CO₂ fluxes for nongrazed prairie, grazed prairie, and western wheatgrass measured about every 20–30 d from 1996 to 2001. Fluxes were measured for WWG only in 1996–1998. Dormant period fluxes were not measured in 1996–1998. Vertical bars indicate the standard error of the treatment mean for soil fluxes.

0.81 for NGP and across years from 0.47 in 1996 to 0.90 in 1999. Soil water content was the second variable to meet model entry requirements and increased model R^2 from as little as 0.04 for GP to 0.26 in 1997. The contribution of air temperature to model R^2 was generally quite small.

Table 3
Model R^2 from stepwise regression analysis based on the model: daily soil $\text{CO}_2\text{-C}$ flux = soil temperature, air temperature, soil water content

Variable	1996	1997	1998	1999	2000	All years	Prairie	Grazed Prairie	Western Wheatgrass
Soil temperature	0.47	0.56	0.84	0.90	0.71	0.65	0.68	0.71	0.44
Soil water content	0.55	0.82			0.82	0.70	0.81	0.75	0.56
Air temperature			0.89		0.80	0.73		0.77	

The strong relationship between soil temperature and soil CO_2 flux was the foundation for development of a predictive equation based only on soil temperature. Based on visual inspection of the relationship between the measured soil fluxes and soil temperatures, the parameters used in the model Eq. (1) were -12°C for T_{\min} , 29°C for T_{opt} , and 42°C for T_{\max} . The goodness-of-fit parameter, Eq. (2), was 1.5% when the z parameter was set at 1.5. Soil fluxes ranged from near zero at soil temperatures near -12°C to near $8\text{ g CO}_2\text{-C m}^{-2}\text{ d}^{-1}$ at 26°C . The relationship between soil flux and soil temperature was nearly linear between soil temperatures ranging from about 10 to 26°C (Fig. 3). Calculated Q_{10} values over soil temperatures of 10 – 25°C averaged 2.7, which compares favorably to the average Q_{10} of 2.4 reported by Raich and Schlesinger (1992), Lloyd and Taylor (1994) and Mielnick and Dugas (2000) for various vegetation systems. The Q_{10} does not account for factors other than soil temperature effects on CO_2 flux.

Others have developed exponential equations to describe the relationship between soil flux and soil temperature. When considering only a single variable, soil temperature has most often been the choice for predicting soil CO_2 fluxes

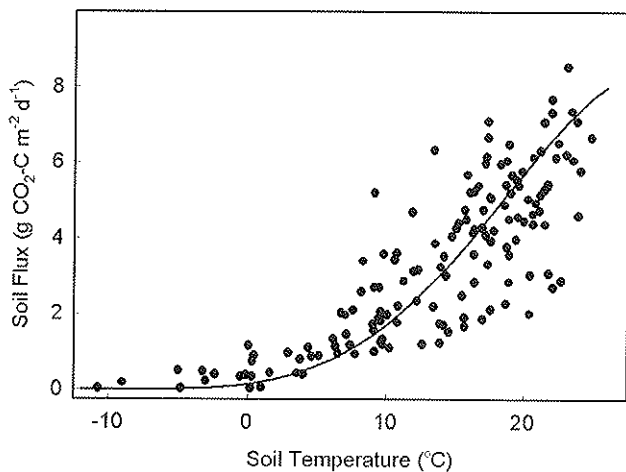


Fig. 3. Observed average daily soil CO_2 flux ($n = 148$) vs. soil temperature and predicted soil CO_2 fluxes as a function of soil temperature. The equation for the line is: Soil flux ($\text{g CO}_2\text{-C m}^{-2}\text{ d}^{-1}$) = $((A_1 A_2 A_3)^z)$ maximum flux. Equation parameters are: $A_1 = (T_{\max} - T)/(T_{\max} - T_{\text{opt}})$, $A_2 = (T - T_{\min})/(T_{\text{opt}} - T_{\min})$, and $A_3 = (T_{\text{opt}} - T_{\min})/(T_{\max} - T_{\text{opt}})$ where T is the measured soil temperature and T_{\max} the maximum soil temperature, T_{\min} the minimum soil temperature, and T_{opt} is the optimum soil temperature for soil CO_2 flux rates. For model optimization, the shape parameter, z , was set at 1.5 and maximum flux rate was $8.4\text{ g CO}_2\text{-C m}^{-2}\text{ d}^{-1}$.

(Rochette et al., 1991; Norman et al., 1992; Lloyd and Taylor, 1994; Bajracharya et al., 2000; Mariko et al., 2000; Mielnick and Dugas, 2000). Mielnick and Dugas (2000) reported soil temperature accounted for 46% of flux variability and when soil water content was included in the equation, it accounted for about a 6% increase in flux variation over soil temperature alone. Norman et al. (1992) increased equation prediction capability for soil CO_2 flux by including LAI with soil temperature.

4. Discussion

Daily quantity of CO_2 flux from soils at each of the three sites represents amounts of CO_2 that are substantial and must be considered when determining the potential of grasslands to sequester carbon. Monteith et al. (1964) suggested that only 50% of the respiratory CO_2 during the growing period is recaptured by green vegetation. However, dormant period CO_2 originating from the soil is not captured by vegetation, so for complete accountability these sources of CO_2 should be included in the annual carbon budget. Growing period (25 April–27 October) flux calculated as the average daily soil CO_2 flux over the 185 d growing period across NGP, GP, and WWG was $728\text{ g CO}_2\text{-C m}^{-2}$. Dormant period flux calculated over the 180 d period from 28 October to 24 April for the GP site totaled $86\text{ g CO}_2\text{-C m}^{-2}$. These data compare favorably with soil CO_2 fluxes for other vegetation types, even where soil temperatures seldom fall below 0°C . Mielnick and Dugas (2000) reported soil CO_2 fluxes of $1.45\text{ kg CO}_2\text{-C m}^{-2}\text{ yr}^{-1}$ for a tall grass prairie, Raich and Schlesinger (1992) estimated global fluxes from grasslands averaged 0.4 – $0.5\text{ kg CO}_2\text{-C m}^{-2}\text{ yr}^{-1}$, and Hanson et al. (1993) estimated fluxes from a forest floor of $1.2\text{ kg CO}_2\text{-C m}^{-2}\text{ yr}^{-1}$.

Carbon dioxide respiratory fluxes from grassland soils occur naturally as these soils are high in organic C, contain an extensive fibrous root system, microbial population, and generally have surface residues which add CO_2 through decomposition. Soil organic carbon in the upper 30 cm of soil in the NGP, GP, and WWG did not change during this study. This suggests the carbon budgets for these grasslands are at or near equilibrium but the short-term nature of this study may have preclude detecting soil carbon changes. The rate of CO_2 loss during the dormant period is mainly a function of soil temperature and soil water content. Bremer et al. (1998) reported winter soil CO_2 fluxes of 0.76 g

$\text{CO}_2\text{-C m}^{-2} \text{d}^{-1}$ for a tall grass prairie site in Kansas where soil temperatures were at or greater than 0°C . Dormant period fluxes from the GP averaged $0.5 \text{ g CO}_2\text{-C m}^{-2} \text{d}^{-1}$ over two dormant periods when soil temperatures were as low as -12°C . The period of maximum soil flux reported here coincides with periods of maximum canopy CO_2 uptake and biomass production (Frank and Dugas, 2001). Although annual root respiration contributed 15–70% of total soil respiration for grasslands in Nebraska (Norman et al., 1992), 40% for a tallgrass prairie in Kansas (Kucera and Kirkham, 1971), 90% for a tallgrass prairie in Texas (Dugas et al., 1999), and 50% for a mature forest in Tennessee (Hanson et al., 1993), CO_2 fluxes to the atmosphere would be minimized since maximum canopy CO_2 uptake occurs during the same period.

The magnitude of soil CO_2 fluxes measured from the three different grasslands in this study shows the importance of soil flux measurements in developing a carbon budget for Northern Great Plains grasslands, particularly dormant period soil fluxes. Since the three grasslands differed in vegetation and management the model equation developed from soil flux and soil temperature measurements should be useful for estimating soil CO_2 fluxes for similar semiarid grasslands. The model is especially useful in providing an estimate of the important dormant period soil flux component in annual ecosystem carbon budgets.

References

- Bajracharya, R.M., Lal, R., Kimble, J.M., 2000. Diurnal and seasonal $\text{CO}_2\text{-C}$ flux from soil as related to erosion phases in central Ohio. *Soil Science Society America Journal* 64, 286–293.
- Bremer, D.J., Ham, J.M., Owensby, C.E., Knapp, A.K., 1998. Response of soil respiration to clipping and grazing in a tallgrass prairie. *Journal Environmental Quality* 27, 1539–1548.
- Conant, R.T., Paustian, K., Elliott, E.T., 2001. Grassland management and conversion into grassland: effects on soil carbon. *Ecology Applications* 11, 343–355.
- Detling, J.K., Parton, W.J., Hunt, H.W., 1978. A simulation of *Bouteloua gracilis* dynamics on the North American shortgrass prairie. *Oecologia* 38, 167–191.
- Dugas, W.A., Heuer, M.L., Mayeux, H.S., 1999. Carbon dioxide fluxes over bermudagrass, native prairie, and sorghum. *Agricultural and Forest Meteorology* 93, 121–139.
- Frank, A.B., Dugas, W.A., 2001. Carbon dioxide fluxes over a northern, semiarid, mixed-grass prairie. *Agricultural and Forest Meteorology* 108, 317–326.
- Frank, A.B., Sims, P.L., Bradford, J.A., Mielnick, P.C., Dugas, W.A., Mayeux, H.S., 2000. Carbon dioxide fluxes over three Great Plains grasslands. In: Follett, R.F., Kimble, J.M., Lal, R. (Eds.), *The potential of U.S. grazing lands to sequester carbon and mitigate the greenhouse effect*, Lewis Publishers, Boca Raton, FL, pp. 167–187.
- Hanson, J.D., 2000. Generic crop production. In: Ahuja, L.R., Rojas, K.W., Hanson, J.D., Shaffer, M.J., Ma, L. (Eds.), *Root zone water quality model: modeling management effects on water quality and crop production*, Water Resources Publications, LLC, Highlands Ranch, Colorado, pp. 81–118.
- Hanson, P.J., Wullschlegel, S.D., Bohlman, S.A., Todd, D.E., 1993. Seasonal and topographic patterns of forest floor CO_2 effects from an upland oak forest. *Tree Physiology* 13, 1–15.
- Kim, J.S., Verma, B., Clement, R.J., 1992. Carbon dioxide budget in a temperate grassland ecosystem. *Journal of Geophysical Research* 97, 6057–6063.
- Kucera, C.L., Kirkham, D.R., 1971. Soil respiration studies in tallgrass prairie in Missouri. *Ecology* 52, 912–915.
- Lloyd, J., Taylor, J.A., 1994. On temperature dependence of soil respiration. *Functional Ecology* 8, 315–323.
- Loeppert, R.H., Suarez, D.L., 1996. Carbonate and gypsum. In: Sparks, D.L., (Ed.), *Methods of Soil Analysis*, third ed, SSSA Book Series No. 5, ASA and SSSA, Madison, WI, pp. 437–474, Part 3.
- Mariko, S., Nishimura, N., Mo, W., Matsui, Y., Kibe, T., Koizumi, H., 2000. Winter CO_2 flux from soil and snow surfaces in a cool-temperate deciduous forest, Japan. *Ecological Research* 15, 363–372.
- Mielnick, P.C., Dugas, W.A., 2000. Soil CO_2 flux in a tallgrass prairie. *Soil Biology and Biochemistry* 32, 221–228.
- Monteith, J.L., Szeicz, G., Yabuki, K., 1964. Crop photosynthesis and the flux of carbon dioxide below the canopy. *Journal of Applied Ecology* 1, 321–337.
- Norman, J.M., Garica, R., Verma, S.B., 1992. Soil surface CO_2 fluxes and the carbon budget of a grassland. *Journal Geophysical Research* 97, 18845–18853.
- Raich, J.W., Potter, C.S., 1995. Global patterns of carbon dioxide emissions from soils. *Global Biogeochemical Cycles* 9, 23–26.
- Raich, J.W., Schlesinger, W.H., 1992. The global carbon dioxide flux in soil respiration and its relationship to vegetation and climate. *Tellus* 44B, 81–99.
- Rochette, P., Desjardins, R.L., Pattey, E., 1991. Spatial and temporal variability of soil respiration in agricultural fields. *Canadian Journal of Soil Science* 71, 189–196.
- SAS Institute Inc., 1989. *SAS/STAT® User's Guide*, Version 6, Fourth Edition. Vol. 2, Cary, NC: SAS Institute Inc., 846 pp.
- Schepers, J.S., Francis, D.D., Thompson, M.T., 1989. Simultaneous determination of total C, total N, and ^{15}N on soil and plant materials. *Communications in Soil Science and Plant Analysis* 20, 949–959.
- Schuman, G.E., Reeder, J.D., Manley, J.T., Hart, R.H., Manley, W.A., 1999. Impact of grazing management on the carbon and nitrogen balance of a mixed-grass rangeland. *Ecological Applications* 9, 65–71.