# Measurement and Modeling of Soil $CO_2$ Flux in a Temperate Grassland under Mowed and Burned Regimes

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**ABSTRACT**

Soil-surface $CO_2$ flux ($R_s$), which is a large component of the carbon (C) budgets in grasslands, usually is measured infrequently using static or dynamic chambers. Therefore, to quantify annual C budgets, estimates of $R_s$ are required during days when no direct measurements of $R_s$ are available. Other researchers have developed empirical models based on soil temperature, soil volumetric water content ($\theta_v$), and leaf area index (*LAI*) that have provided reasonable estimates of $R_s$ during the growing season in ungrazed tallgrass prairie. However, the effects of mowing and grazing, which are common in grasslands, on predictions of $R_s$ from those models are uncertain. Predictions of $R_s$ during dormancy (post-senescence to spring fire) also are uncertain. Data from a year-long mowing study, which simulated grazing, were used to refit these models. Output from the models then was compared to independent data collected from nearby prairie sites. Results showed that LAI must be included to accurately estimate $R_s$ in mowed prairie ecosystems. When *LAI* was not included in the model, predicted daily $R_s$ following mowing was nearly four times greater than measured $R_s$, and cumulative, annual $R_s$ was overestimated by 95-102%. When *LAI* was included in the model, predictions of $R_s$ were comparable to measured $R_s$ in the mowing study. Annual estimates of cumulative $R_s$ ranged from 3.93 to 4.92 kg $CO_2$ $m^{-2}$. When comparing the model with independent chamber data from nearby sites, cumulative $R_s$ during those studies was within ±9% of cumulative estimates calculated from measured $R_s$. The model overestimated daily $R_s$ during a dry period, suggesting a nonlinear response of $R_s$ to soil water content; matric potential may be more appropriate than $\theta_v$ for modeling $R_s$. Data suggest that $R_s$, in addition to being dependent on soil temperature and soil water content, is dependent on the photosynthetic capacity of the canopy and the subsequent translocation of C belowground.

Key words: Carbon; soil-surface $CO_2$ flux; soil respiration; Konza Prairie; carbon budgets; fire; prairie; grazed.

The effect of terrestrial ecosystems on global atmospheric $CO_2$ concentrations is uncertain. However, a number of ecosystems may have the potential to sequester or release substantial quantities of $CO_2$ in response to climate change, increasing atmospheric $CO_2$, and land management (Glenn et al., 1993; White et al., 1999; Post and Kwon, 2000; Schimel et al., 2000). In many grasslands, high levels of soil organic matter, microbial activity, and root biomass (Rice and Garcia, 1994) make the rhizosphere a potentially large source or sink for atmospheric $CO_2$ (Ojima et al., 1993; Van Ginkel et al., 1999). Furthermore, land management practices such as mowing, grazing by ungulates, and burning of dead biomass may alter carbon (C) fluxes (Bremer et al., 1998; Knapp et al., 1998; LeCain et al., 2000) and, thus, may affect the amount of C sequestered or released annually from grasslands.

Efforts to quantify the global C budget have led to the recent implementation of a worldwide network of towers to monitor long-term $CO_2$ flux, several of which are located in grasslands (Baldocchi et al., 1996; Wofsy and Hollinger, 1997; Ham and Knapp, 1998). These towers typically measure net ecosystem exchange (*NEE*) of C above the canopies using eddy covariance methods. However, tower-based measurements of *NEE* are often suspect at night, during periods of low windspeed, and during periods of extremely low fluxes. Thus, chamber measurements and models of soil respiration ($R_s$; root and microbial) and dark respiration ($R_d$) are required to replace the missing data. Furthermore, measurements of soil and aboveground respiration also are required in order to partition the C balance of the ecosystem and estimate canopy photosynthesis. In grasslands, the C budget can be calculated as

$$NEE = P_c - R_s - R_d \quad [1]$$

where $P_c$ is canopy photosynthesis. Soil respiration represents a significant component of the C balance in grasslands (Gale et al., 1990; Kim et al., 1992; Ham et al., 1995). Therefore, accurate estimates of $R_s$ are crucial when partitioning prairie C budgets.

Although automated soil respiration chambers are used in a few instances (Goulden and Crill, 1997), soil-surface $CO_2$ flux is usually measured only periodically, by static or dynamic chambers (Bremer et al., 1998; Ham and Knapp, 1998; Knapp et al., 1998). Therefore, for calculations of seasonal and annual C budgets, estimates of $R_s$ are required during days when no direct measurements are available. Norman et al. (1992), during the First International Satellite Land Surface Climatology Project (ISLSCP) Field Experiment (FIFE; Sellers et al., 1992), developed two simple models for estimating $R_s$ in tallgrass prairie. One of their models predicted $R_s$ as a function of soil temperature and volumetric soil water content ($\theta_v$), whereas their other model also included leaf area index (*LAI*). They found both models to be acceptable, although inclusion of *LAI* slightly improved accuracy. Similar models have been developed to estimate $R_s$ in other grasslands (Mielnick and Dugas, 2000) and in other ecosystems (Schlentner and Van Cleve, 1985; Oberbauer et al., 1992; Hanson et al. 1993).

Research after FIFE in the same study area indicated that land management practices such as mowing, grazing, and fire caused significant alterations in prairie $R_s$ (Bremer et al., 1998; Knapp et al., 1998). Bremer et al. (1998) reported that $R_s$ decreased substantially in response to mowing and grazing and attributed the reduction to a decrease in canopy photosynthesis and reduced translocation of C to the rhizosphere. Knapp et al. (1998) found that fire caused prairie $R_s$ to increase significantly, presumably because exposed soils were warmer which stimulated biological activity in burned prairie. Therefore, models of $R_s$ also may need to account for differences in fluxes introduced by mowing, grazing, and fire. The models of Norman et al.

(1992) were developed from unmowed, ungrazed, burned and unburned grasslands using a small dataset collected during the growing season (July 24 to August 11). The applicability of the models to predict annual $R_s$, especially under grazed or mowed conditions, is uncertain. Furthermore, a closer examination of the effect of fire on predictions of $R_s$ may be useful.

As part of a year-long mowing (i.e., simulated grazing) study by Bremer et al. (1998), $R_s$, soil temperature, $\theta_v$, and *LAI* were measured intensively. This provided the opportunity to test the accuracy of the models of Norman et al. (1992) under mowed conditions. Because they developed their models from measurements collected only during the growing season, the accuracy of predicted $R_s$ during dormancy (i.e., post-senescence to spring fire) is uncertain. Therefore, the results from the year-long mowing study were used to refit the coefficients of the Norman model to improve accuracy when predicting annual $R_s$. Furthermore, measurements of soil temperature, $\theta_v$, $R_s$, and *LAI* at nearby flux monitoring towers provided the opportunity to test the models against independent data sets.

## MATERIALS AND METHODS

Measurements of $R_s$, soil temperature, $\theta_v$, and *LAI* for this report were obtained from four study sites (Table 1). The initial testing and recalibration of the models of Norman et al. (1992) were conducted with data from Bremer et al. (1998), who investigated the effects of mowing on $R_s$. Additional data from the three separate sites, unrelated to the mowing study, were used to test the model after recalibration. Two of those independent sites were components in a nearby fire study (both unmowed and ungrazed) and were located on adjacent burned and unburned watersheds. The fourth independent site was on another nearby burned, unmowed, and ungrazed watershed.

*Study area*

The research for this report was conducted in the Flint Hills Prairie region near Manhattan, Kansas, USA. Three of the four sites, including the mowing study site and the two sites in the fire study, were located on Konza Prairie Biological Station (Konza Prairie [39$^{o}$ 06' N. 96$^{o}$ 33' W, ~340 m above mean sea level]). The fourth site was on the adjacent Rannells Flint Hills Prairie Preserve (referred to as Rannells Prairie; Agronomy Department, Kansas State University).

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. The Flint Hills region has a typical Midwestern continental climate, with warm, wet summers and cold, dry winters. Mean annual air temperature is 12.9$^{o}$C, and average precipitation is 844 mm (100 year averages). Interannual climatic variability is high (Borchert, 1950), with average maximum and minimum air temperatures of 19.6$^{o}$C (standard deviation=11.9$^{o}$C) and 6.3$^{o}$C (standard deviation=11.1$^{o}$C), respectively, and the standard deviation of annual precipitation is 207 mm.

Vegetation was tallgrass prairie dominated by warm-season ($C_4$) grasses, including *Andropogon gerardii* and *Sorghastrum nutans*. Growth is characterized by a rapid increase in canopy size following spring fire (Fig. 1), with peak aboveground biomass ranging from 178 g $m^{-2}$ on burned uplands to 755 g $m^{-2}$ on burned lowlands; most of the variability in aboveground biomass and is caused by precipitation (Briggs and Knapp, 1995). Growth is typically slower and peak aboveground biomass lower on unburned sites than on burned sites (Knapp and Seastedt, 1986; Briggs and Knapp, 1995). Senescence typically begins in late July, resulting in a decline in green aboveground biomass that is nearly complete by late October. During this study, peak aboveground biomasses were 365 g m$^{-2}$ on the mowed site (unmowed plots), 285 g m$^{-2}$ and 217 g m$^{-2}$ on the adjacent burned and unburned sites (in the fire study), respectively, and 637 g m$^{-2}$ on the fourth independent site (i.e., Rannells Prairie). Belowground biomass (0-90 cm), which was not measured in this study, may be two to four times greater than aboveground biomass, with values ranging from 700-2100 g m$^{-2}$ (Rice et al., 1998).

Baseline properties of the soils in the 0-15 cm profile were similar among sites, and exhibited the following average values: 6.1 (pH), 1.20 g m$^{-2}$ (bulk density), 25% (sand), 47% (silt), 28% (clay), 2.8% (soil organic carbon), and 0.22% (total nitrogen). Soil bulk densities were determined from volumetric samples (4.8 x 5.0 cm). All other analyses of baseline soil properties were conducted by the Soil Testing Laboratory, Kansas State University.

*Mowing study*

The mowing study by Bremer et al. (1998) was conducted on a lowland site on Konza Prairie from June 1996 to June 1997. Soils were deep (>1m), silty clay loams (Benfield series: fine, mixed, mesic, Udic Argiustolls). Twenty-seven plots (2 x 3 m, separated by 4-m-wide unclipped aisles) were established for the mowing study. Three treatments were applied to the plots: early-season clipping (EC); full-season clipping (FC); and no clipping (NC). Treatments simulated two cattle-grazing strategies and a control, where EC represented intensive-early stocking rate; FC represented the traditional, full-season stocking rate; and NC represented ungrazed prairie. Traditional, full-season stocking (1.62 ha steer$^{-1}$) in Kansas typically occurs between May 1 and October 1, and intensive-early stocking is practiced between May 1 and July 15, at 2x the traditional stocking rate (0.81 ha steer$^{-1}$; Smith and Owensby 1978). Vegetation in EC and FC plots was clipped to 5 cm and removed three times during the season. Clipping dates were June 7, June 25, and July 19 (DOY 159, 177, and 201), 1996 in EC and June 7, July 19, and September 20 (DOY 159, 201, and 264), 1996 in FC. On April 25, 1997, the dead aboveground biomass was burned from all plots and the surrounding area.

Soil $CO_2$ flux was measured weekly to monthly using a portable photosynthesis system (LI-6200, Li-Cor, Inc., Lincoln, NE) equipped with a 0.70-L chamber that covered a surface area of 4.13 x $10^{-3}$ $m^2$ (Norman et al., 1992). Data were collected from two locations in each plot; the exact locations varied from one measurement date to the next. 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.

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

Soil temperature and $\theta_v$ at 10 cm were measured concurrently with $R_s$ using dual-probe heat-capacity sensors (Tarara and Ham, 1997; Song et al., 1998; Basinger, 1999). The 10-cm sampling depth was chosen because previous studies had indicated that soil temperature and $\theta_v$ at 10 cm were correlated strongly with soil-surface $CO_2$ flux (Norman et al., 1992). Aboveground biomass was measured on clipping dates from 1 $m^2$ in the center of EC and FC plots. Leaf area was measured from a 0.25-$m^2$ subsample of this area. Clipped samples were transported to the laboratory, where leaf area was measured using an area meter (LI-3100, Li-Cor Inc.); samples were dried for 72 hours at 60$^{o}$C and weighed.

*Independent test sites*

Data from the following three independent test sites were used to validate the model of $R_s$ after it had been tested and recalibrated using data from the mowing study.

*Fire study*

Two of the independent test sites were components of a fire study that was conducted on Konza Prairie within 1 km of the mowing study from April to November, 1997. One site was on a burned watershed (B), and the other on an adjacent, unburned watershed (UB); both were expansive upland sites. For 16 years, the B watershed had been burned annually, and the UB watershed had been burned biennially. Neither site had been grazed during that time. In the year of this study, vegetation was removed by fire on the B site on April 17, and the UB site remained unburned. Further details of these sites are included in Bremer and Ham (1999).

Concurrent measurements of soil respiration, $\theta_v$, and soil temperature were collected weekly to monthly using the same instrumentation and methods as described for the mowing study. Dual-probe sensors were installed at 2.5- and 10-cm depths at four locations along 36 m transects. Three measurements of $R_s$ were collected from within 1.5 m of each dual-probe location; thus, 12 measurements of $R_s$ were collected from each site on each measurement day.

Green *LAI* and aboveground biomass were measured at 2-week intervals from May 6 to August 13, 1997. On each measurement date and at each site (i.e., burned and unburned), six 0.1

$m^2$ areas were harvested within 20 m of the dual-probe transects. Green *LAI* also was measured on the B site from May 26 to August 12, 1998 and was used in developing a simple model of green *LAI* described later in this section.

*Third independent site*

Measurements of $R_s$, soil temperature, $\theta_v$, and *LAI* also were collected from May to October, 1999 on the Rannells Prairie, which lies adjacent to Konza Prairie. This study site (B1) was an expansive upland watershed that had been burned annually for several decades. In the year of the study, B1 was burned on April 19. The site had been ungrazed since 1997; further details on the site can be found in Bremer et al. (2001).

Soil respiration was measured weekly to biweekly using the same portable chamber method as in the mowing and fire studies. On each measurement day, 10 measurements of $R_s$ were collected at 5-m intervals along two 20-m transects. Soil temperature and $\theta_v$ were measured at 5- and 10-cm depths with automated dual-probes that were placed along a 6-m transect within 20 m of $R_s$ measurements. The dual-probes at this site operated continuously in contrast to those at the other three study sites, where dual-probes had been read manually and concurrently with $R_s$ measurements. At the Rannells Prairie site, dual-probe measurements of soil temperature were logged every 60 s, then averaged and recorded every 30 min, and $\theta_v$ was estimated one to four times daily. The soil temperatures used in the $R_s$ model were only those recorded concurrently with measurements of $R_s$. Green *LAI* and aboveground biomass were determined at 2-week intervals from May 18 to September 30, 1999, using the same methods as in the other studies.

*Models of soil $CO_2$ flux*

This section introduces the models of $R_s$ developed by Norman et al. (1992). The accuracy of the models was tested under mowed conditions, and the coefficients then were adjusted using the intensive data set from the mowing study. Following that recalibration, the models were tested using additional data from the three independent study sites.

The first model of Norman et al. (1992) was:

$$R_s = (a + bLAI)\theta_{10} e^{[c(T_{s,10} - T_{s,ref})]} \quad [2]$$

where $\theta_{10}$ is the 0- to 10-cm volumetric water content in percent, $T_{s,10}$ is the soil temperature at 10-cm (degrees Celsius), $T_{s,ref}$ is the reference temperature appropriate to the (a + b *LAI*) $\theta_{10}$ value (i.e., the average soil temperature during the period of $R_s$ measurements used to obtain a and b), *a* is the minimum soil $CO_2$ flux at a given $\theta_{10}$, *b* defines the sensitivity of soil $CO_2$ flux to *LAI* and $\theta_{10}$, and *c* is a temperature coefficient so $Q_{10}$ = exp(10c); $R_s$ is in umol $m^{-2}$ $s^{-1}$. The second model of Norman et al. (1992) was:

$$R_s = a\left[\frac{(\theta_{20} - 12)}{(40 - 12)}\right] e^{[c(T_{s,10} - T_{s,ref})]} \quad [3]$$

where *a* is a maximum soil $CO_2$ flux at field capacity (maximum soil water holding capacity after drainage) and $T_{s,\,ref}$, *c* is the temperature coefficient, $\theta_{20}$ is the 0- to 20- cm volumetric percent soil water content (40% is near the soil field capacity, and 12% is the soil water content when soil $CO_2$ fluxes approach zero). This model placed a greater emphasis on available soil water than the model that included *LAI*. Our measurements of $\theta_v$ were sometimes above 40%, which artificially inflated predicted fluxes. Therefore, $\theta_v$ greater than 40% were adjusted downward to 40%.

*Estimating daily green leaf area index*

Green *LAI*, $\theta_{10}$, and $T_{s,10}$, were required by Eq. [2] to predict $R_s$. However, *LAI* seldom was measured on the same day as $\theta_{10}$ and $T_{s,10}$. Thus, LAI was modeled from available measurements of LAI at each site. In EC and FC plots in the mowing study, estimates of green *LAI* were interpolated from measurements of *LAI* on mowing dates. For NC plots, a simple model was devised to estimate daily green *LAI* for Eq. [2]. This model was derived from measurements of green *LAI* in the fire study (i.e., B site) and site B1 on Rannells Prairie (Fig. 1); from other studies on Konza Prairie (Kim and Verma, 1991); and from another tallgrass prairie in Oklahoma (Svejcar and Browning, 1988). Our model assumed a linear increase in green *LAI* from zero on the burn date to a peak on DOY 185, and then a linear decrease to zero again by DOY 300, the approximate end of senescence. In NC plots, the only measurement of *LAI* (2.23) was assumed to be the peak value. On the independent sites B, UB, and B1, LAI was interpolated from measurements of LAI at each respective site.

*Methods of analysis*

Data ($R_s$ as dependent; $\theta_v$, $T_{s,10}$, and *LAI* as independent) from the mowing study were fit by the least squares method to obtain the two modified parameters (a and b) in Eq. [2]. To optimize those parameters, various values for $Q_{10}$ and $T_{s,ref}$ were used. Norman et al. (1992) assumed a $Q_{10}$ of 2 for $R_s$ across a wide range of $\theta_v$, based on calculations from their site and from a literature review of $Q_{10}$ values on Konza Prairie (Grahammer, 1989). The $Q_{10}$ is also 2 for the microbial population on Konza Prairie and does not change appreciably during the year (C.W. Rice, personal communication). In the current study, regressions performed with $Q_{10}$

values greater than or less than 2 showed no improvement in predicting $R_s$. Therefore, $Q_{10}$ also was assumed to be 2 in our final analyses, resulting in $c$ = 0.069.

Norman et al. (1992) fixed $T_{s,ref}$ at 25°C in Eqs. [2] and [3], presumably because soil temperatures at 10 cm were between 20° and 30°C from July 24 to August 11, 1989 when they measured $R_s$, so 25°C represented an approximate average. Because our mowing study included annual measurements of $R_s$, the average annual soil temperature at 10 cm likely would be more appropriate for $T_{s,ref}$. Fluker (1958), during a 5-year study, reported that mean annual soil temperature averaged about 3.3°C warmer than mean annual air temperature at all depths to 3 m. Thus, $T_{s,ref}$ can be estimated from mean annual air temperature; mean annual air temperature was 12.9°C on Konza Prairie (100-yr average). Consequently, $T_{s,ref}$ was fixed at 16°C before the data from the mowing study were refit to Eq. [2] to obtain new values for coefficients $a$ and $b$.

To compare modeled $R_s$ with measured $R_s$, we used the single plot bias and the single plot root mean square error (RMSE):

$$bias = \frac{\sum_{i=1}^{N}\left(\hat{R}_s - R_s\right)}{N} \qquad [4]$$

$$RMSE = \sqrt{\frac{\sum_{i=1}^{N}\left(\hat{R}_s - R_s\right)^2}{N}} \qquad [5]$$

where $\hat{R}_s$ denotes modeled $R_s$, and N is the number of observations. These statistics, combined with their respective goodness of fit ($r^2$) and mean predicted $R_s$ values in each analysis, gave an indication of how well the models performed compared to measured quantities.

# RESULTS

In the following sections, measurements of $T_{s,10}$ and $\theta_{10}$ and estimates of *LAI* from the mowing study were used first in Eqs. [2] and [3] with the original coefficients of Norman et al. (1992) to compare predicted to measured $R_s$. Secondly, data from the mowing study were used to refit the coefficients in Eq. [2]. Finally, the model with the revised coefficients was tested using data from the three independent prairie sites.

*Test of original models of Norman et al.*

In mowed plots, the model without *LAI* (Eq. [3]) severely overestimated daily fluxes of $R_s$ by up to 3.8 times during the growing season (Figs. 2a and 2b). Overestimates were greatest following mowing, when actual $R_s$ decreased but higher soil temperatures (Bremer et al., 1998) caused predicted $R_s$ to increase. For example, between DOY 165 and 219 (first mowing of plots was on DOY 159), cumulative predicted $R_s$ overestimated measured $R_s$ by 83 and 120% in FC and EC plots, respectively. In comparison, cumulative $R_s$ in NC plots (Fig. 2c) during the same period was overestimated by only 10%. During dormancy, however, Eq. [3] overestimated daily $R_s$ in *all* plots by up to 10.5 times. Cumulative $R_s$ was overestimated in all treatments by 50 to 102% on an annual basis compared with cumulative values calculated from measured $R_s$ (Table 2).

Inclusion of *LAI* in the model (Eq. 2) improved estimates of $R_s$, both during the growing season and during dormancy when *LAI*=0 (Figs. 2a-2c). The greatest improvements in predicted $R_s$ were in EC and FC plots during the growing season, because allowance was made for defoliation (i.e., mowing). Annual estimates of cumulative $R_s$ also were improved by Eq. [2], with overestimates of only 4 to 19% among treatments (Table 2); the majority of overestimation occurred when the canopy was dormant.

*Refitting coefficients of model to data from clipping study*

Least squares analyses initially were performed separately on growing-season data from EC, FC, and NC treatments and then on data pooled from all three treatments during the growing season (i.e., when *LAI* > 0) (Table 3). Compared with Eq. [2], predictions of mean $R_s$ were improved in all treatments by these analyses, as was bias, RMSE, and $r^2$. However, the best fit overall occurred when all data from the mowing study were pooled, including data collected during dormancy. The modified coefficients from this regression were substituted into Eq. [2]:

$$F_s = (0.052 + 0.047LAI)\theta_{10}\, e^{[0.069(T_{s,10} - 16)]} \quad [6]$$

The mean annual $R_s$ predicted by Eq. [6] was 4.44 compared with the measured 4.53 μmol $m^{-2}$ $s^{-1}$ (Table 3). Equation [6] generally overestimated $R_s$ when measured fluxes were below 1.5 μmol $m^{-2}$ $s^{-1}$ (Fig. 3). When measured $R_s$ was above 1.5 μmol $m^{-2}$ $s^{-1}$, predictions of $R_s$ were more accurate, but scatter about the 1:1 line was noticeably greater. This scatter was caused by high spatial variation in $R_s$ measurements (Fig. 4), which is typical during the growing season. For example, nine individual measurements of $R_s$ on DOY 187 ranged from 3.46 to 9.08 μmol $m^{-2}$ $s^{-1}$ in NC plots; spatial variation also was high in EC and FC plots. This variation likely was caused by great spatial heterogeneity in soil water content and in soil physical properties, which may impact rates of $CO_2$ evolution in the soil and the pathways for diffusion of $CO_2$ to the surface.

Equation [6] was applied to the individual treatments in the clipping study (Fig. 5a-5c). Predicted $R_s$ from Eq. [6] was more accurate than that from Eq. [2], particularly in mowed treatments during the growing season and in all treatments during dormancy. Cumulative, annual $R_s$ from Eq. [6] was within ±1% of measured $R_s$ (Table 2). Therefore, Eq. [6] appears suitable to use in mowed and unmowed tallgrass prairies for estimates of seasonal and annual $R_s$.

*Testing refitted model with independent data*

On the B and UB sites in the Konza Prairie fire study (Table 1), predictions of daily $R_s$ were within ± 1 umol $m^{-2}$ $s^{-1}$ of measured values on 10 of the 15 days when measurements were collected (Figs. 6a and 6b). Furthermore, cumulative $R_s$ during the study estimated from Eq. [6] was within ± 9% of cumulative $R_s$ estimated from measured $R_s$ on both the B and UB sites (Table 4). Therefore, Eq. [6] generally resulted in reasonable predictions of $R_s$ on both burned and unburned prairies.

One notable exception to the accuracy of the model occurred during a dry spell on the B site and to a lesser degree on the UB site between DOY 171 and 199 (Figs. 6a and 6b). Daily $R_s$ was overestimated by up to 2.6x, and cumulative $R_s$ was overestimated by 71% on the B site; this overestimate caused the higher RMSE on the B site compared with the other independent sites (Table 4). Further investigation revealed that the trend in measured $R_s$ during the dry period was related closely to $\theta_v$ above 10 cm (i.e., in the 0-10 cm profile)(Figs. 6a and 6b). In order to determine the impact of $\theta_v$ in the surface layer on predictions of $R_s$, $\theta_v$ values from 2.5 and 10 cm were pooled and used in Eq. [6]. Pooling of $\theta_v$ resulted in improved predictions of $R_s$, although predicted daily $R_s$ continued to overestimate measured $R_s$ by up to 2.2x, and cumulative $R_s$ remained overestimated by 50% during the dry period.

On site B1, the third independent test site, predictions of daily $R_s$ from Eq. [6] were within ± 1 umol $m^{-2}$ $s^{-1}$ on 9 of 16 days when measurements of $R_s$ were collected (Fig. 7).

Estimates of cumulative $R_s$ from predicted $R_s$ (Eq. [6]) during the growing season were within 2% of values calculated from measured $R_s$ (Table 4). When pooled $\theta_v$ from 5 and 10 cm were used in Eq. 6, the change in cumulative $R_s$ on site B1 was negligible (not shown).

## DISCUSSION

Equation [3], which did not include *LAI*, grossly overestimated $R_s$ in EC and FC plots during the growing season (Fig. 2). This illustrates the effect of neglecting the contribution of canopy photosynthesis and translocation to $R_s$ when predicting fluxes in mowed or grazed grasslands. After EC and FC plots were mowed, soil temperatures at 10 cm typically increased by 2 to 3$^{o}$C (Bremer et al., 1998). Therefore, the overestimation was caused by the combination of higher soil temperatures after mowing and not including the effects of defoliation on root metabolism, root exudation, and, consequently, on microbial activity in the rhizosphere. The dramatic improvement in predictions of $R_s$ by Eq. [2] in EC and FC plots confirms the importance of including some measure of canopy photosynthesis potential (e.g., *LAI*) in models of $R_s$. During dormancy, model sensitivity to $\theta_v$ (Bremer et al., 1998) probably contributed to the overestimation of $R_s$ by both Eqs. [2] and [3]. The mechanism by which $\theta_v$ affects $R_s$ also is different during the dormant season, when its impact on photosynthesis (plant water status) is not applicable.

Although predictions of $R_s$ improved when *LAI* was included in the model (Eq. [2]), estimates of cumulative, annual $R_s$ in mowed plots remained 16-19% higher than estimates calculated from measured $R_s$ (Table 2). This overestimation may have occurred because the coefficients for Eq. [2] published by Norman et al. (1992) were developed from data collected only from unmowed prairie during the growing season. The refitting of the model to data from mowed and unmowed plots and to data collected during dormancy improved predictions of daily $R_s$ (Figs. 5a-5c) and of cumulative, annual $R_s$ (Table 2). Therefore, Eq. [6] is appropriate for predicting cumulative $R_s$ in mowed and unmowed tallgrass prairie on an annual basis.

Although Eq. [6] consistently overestimated $R_s$ during dormancy when fluxes were low, the overestimation was slight (Figs. 5a-5c). For example, when measured $R_s$ was below 1 μmol $m^{-2} s^{-1}$, fluxes were overestimated by an average of 0.47 μmol $m^{-2} s^{-1}$ (Fig. 3). Because $\theta_v$ was consistently high during the winter of 1996-97 when measurements of $R_s$ were collected, the impact of dry soils on $R_s$ during dormancy is uncertain. Further research may be needed to clarify the effect of dry soils on fluxes during dormancy.

In the test of Eq. [6] with independent data from the B and UB sites (1997), the overestimation of $R_s$ during the dry period was caused partially by soil temperature, which increased as the soil dried (not shown). However, exclusion of $\theta_v$ at 2.5 cm also contributed to the overestimation (Fig. 6). The sensitivity of $R_s$ to $\theta_v$ above 10 cm probably is related closely to a high percentage of root and microbial biomasses in the 0-10 cm profile of tallgrass prairie. For example, Rice et al. (1998) reported that on Konza Prairie, 44% of total root mass was in the 0-10 cm profile compared with only 25% at 10-20 cm. Also, microbial C biomass was up to 1.6x higher in the 0-5 cm compared with the 5-15 cm profile in a nearby tallgrass prairie (Rice et al. 1994; Bremer 1998; Williams et al. 2000). Thus, changes in $\theta_v$ above 10 cm, which are typically more severe than those deeper in the profile, likely would have significant effects on total microbial and root respirations and ultimately on $R_s$.

When $\theta_v$ from 2.5 and 10 cm were pooled and substituted into Eq. [6], predictions of $R_s$ were improved on the B site. However, predicted daily $R_s$ continued to respond poorly to extremes in observed $R_s$ during the dry period, suggesting a possible nonlinear relationship between $R_s$ and $\theta_v$. Davidson et al. (2000), in a discussion of the effects of soil water content on $R_s$, suggested that matric potential may be more appropriate than $\theta_v$ for modeling soil respiration. Further research may be necessary to determine the appropriate relationship between soil water content and $R_s$ in tallgrass prairie during drought.

*Summary*

In general, Eq. [6] predicted instantaneous $R_s$ to within ±1 μmol $m^{-2}$ $s^{-1}$ of measured $R_s$ although variances were sometimes greater than ±1 μmol $m^{-2}$ $s^{-1}$ between predicted and measured values, such as during drought. Nevertheless, cumulative fluxes on an annual or growing season basis were within ±9% on all four study sites (Tables 1, 2, and 4). When LAI was not included in the model (Eq. [3]), predictions of $R_s$ in mowed plots were overestimated grossly (Table 2; Figs. 2a and 2b) because no allowance was made for the reduced contribution by canopy photosynthesis to root respiration. Fluxes were substantially overestimated during a dry period on the B site (Fig. 6), but the pooling of $\theta_v$ from 2.5 and 10 cm improved predictions of $R_s$, presumably because a high degree of $R_s$ originates above 10 cm where a high percentage of roots and microbial populations reside. More importantly, the relationship between $R_s$ and soil water content may be nonlinear, and, therefore, Eq. [6] should be used with caution when soils are extremely dry; matric potential may be more appropriate than $\theta_v$ for modeling $R_s$.

Because Eq. [6] provided reasonable estimates of cumulative annual and growing season $R_s$, it appears well suited for use at long-term tower sites where frequent estimates of $R_s$ are required for calculating annual C budgets. Furthermore, new technologies are being developed that may improve the feasibility of application of Eq. [6]. For example, automated dual-probe heat-capacity sensors such as those used in this study and automated heat dissipation matric water potential sensors (Model 229, Campbell Scientific, Logan, UT) both can measure soil water content at shallow depths. Remote sensing techniques are being developed that estimate *LAI* (Knyazikhin et al., 1998) and soil water content in the surface layer (Passive microwave; Schmugge et al., 1992).

Equation [6] provided accurate predictions of $R_s$ for a tallgrass prairie in northeastern Kansas, USA, and should be accurate for other tallgrass prairies in the Midwestern US with similar climates and soils. The functional form of the equation is likely viable for grasslands worldwide although it should be reparameterized for grasslands with different climates, soils, and vegetative characteristics (e.g., $C_3$ prairies, short- or mixed-grass prairies). Furthermore, because the model does not include all of the mechanisms (e.g., soil texture, plant lignin content, nitrogen input) that affect $R_s$, periodic field measurements of $R_s$ are recommended to validate the accuracy of the model. Nevertheless, results show that $R_s$ in tallgrass prairie probably can be modeled to within ± 10% using the relatively simple empirical model (Eq. [6]).

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Table 1. Description of four study sites from which data were obtained for model calibration and validation.

| Location[*] | Date | Treatment | Use in Model | Number of $R_s$[†] Measurements |
|---|---|---|---|---|
| KPBS Mowing Study | 1996-97 | Mowed[‡] | Calibration | 776 |
| KPBS Fire Study | 1997 | Burned[§] | Validation | 180 |
| KPBS Fire Study | 1997 | Not Burned[§] | Validation | 180 |
| Rannells Prairie | 1999 | Burned[§] | Validation | 160 |

[*] The three sites on Konza Prairie Biological Station (KPBS) were located on separate watersheds.
[†] Soil-surface $CO_2$ flux ($R_s$).
[‡] Experiment included mowed and unmowed plots; all were annually burned.
[§] Unmowed and ungrazed.

Table 2. Estimates of cumulative soil-surface $CO_2$ flux on an annual basis calculated from measured and modeled fluxes.

| | Cumulative Fluxes | | | | | | |
|---|---|---|---|---|---|---|---|
| Treatment* | Measured | Modeled | | | % Error | | |
| | | Eq. 2† | Eq. 3‡ | Eq. 6§ | Eq. 2†† | Eq. 3‡‡ | Eq. 6§§ |
| | ..............kg $m^{-2}$.............. | | | | .......... % .......... | | |
| EC | 3.93 | 4.66 | 7.94 | 3.90 | 19 | 102 | -1 |
| FC | 4.08 | 4.74 | 7.95 | 4.04 | 16 | 95 | -1 |
| NC | 4.92 | 5.14 | 7.36 | 4.96 | 4 | 50 | 1 |

* Early-season clipping (EC), full-season clipping (FC), and no clipping (NC).
† From Norman et al. (1992); included leaf area index.
‡ From Norman et al. (1992); did not include leaf area index.
§ Our recalibrated version of Eq. 2; also included leaf area index.

Table 3. Data from no clipping (NC), full-season clipping (FC), and early-season clipping (EC) treatments in the mowing study were used to refit coefficients *a* and *b* in Eq. [2] (Norman et al., 1992). Coefficients *a* and *b* from each analysis are presented, as well as predicted soil $CO_2$ flux ($R_s$), single plot bias (Bias), root mean square error (RMSE), and goodness of fit ($r^2$). The same values are provided from Eq.[2] for comparison.

| Model | a | b | Measured *R*s | Predicted *R*s | Bias | RMSE | $r^2$ | n[*] |
|---|---|---|---|---|---|---|---|---|
| | | | ------------ umol $m^{-2}$ $s^{-1}$ | ------------ | | | | |
| 1. NC (LAI>0)[†] | 0.163 | 0.040 | 6.84 | 6.90 | +0.060 | 1.65 | 0.637 | 193 |
| Eq. [2] | 0.135 | 0.054 | | 6.63 | -0.215 | 1.70 | 0.635 | |
| 2. FC (LAI>0)[†††] | 0.100 | 0.098 | 5.61 | 5.61 | -0.004 | 1.60 | 0.568 | 187 |
| Eq. [2] | 0.135 | 0.054 | | 5.92 | +0.306 | 1.66 | 0.550 | |
| 3. EC (LAI>0)[†††] | 0.093 | 0.119 | 5.23 | 5.36 | +0.129 | 1.59 | 0.520 | 183 |
| Eq. [2] | 0.135 | 0.054 | | 5.75 | +0.515 | 1.92 | 0.371 | |
| 4. Pooled[‡] | 0.121 | 0.069 | 5.91 | 6.04 | +0.129 | 1.73 | 0.574 | 563 |
| (LAI>0)[†††] | 0.135 | 0.054 | | 6.11 | +0.195 | 1.76 | 0.546 | |
| Eq. [2] | | | | | | | | |
| 5. Pooled[‡‡‡] (annual)[*] | 0.052 | 0.047 | 4.53 | 4.44 | -0.090 | 1.53 | 0.770 | 776 |
| Eq. [2] | 0.135 | 0.054 | | 4.84 | +0.308 | 1.55 | 0.765 | |

[*] Number of observations in each respective data set.

[†] Derived from data collected only during the growing season, when green leaf area index (LAI) was >0.

[‡] Pooled refers to the combined data sets of NC, FC, and EC.

[*] Derived from pooled, annual data that included the dormant period (when green LAI=0); this model represents Eq. [6].

Table 4. Estimates of cumulative soil $CO_2$ flux during the growing season from independent test sites unrelated to mowing study and the percent error, single plot bias, and root mean square error (RMSE) of predicted compared with measured soil $CO_2$ flux.

| Site | Measured | Eq. 6 | Single Plot Bias | RMSE | % Error[*] |
|---|---|---|---|---|---|
| | ............................. kg $CO_2$ $m^{-2}$ ............................. | | | | |
| B[†] | 4.48 | 4.87 | +0.51 | 2.19 | +9 |
| UB[‡] | 3.83 | 3.50 | -0.49 | 1.33 | -9 |
| B1[§] | 4.52 | 4.43 | -0.15 | 1.12 | -2 |

[*] % Error = 100*(Modeled-Measured)/Measured.
[†] Site B was a burned watershed on Konza Prairie Biological Station (DOY 107-324, 1997).
[‡] Site UB was an unburned watershed on Konza Prairie Biological Station (DOY 107-324, 1997).
[§] Site B1 was a burned watershed on the adjacent Rannells Prairie (DOY 142-300, 1999).

Fig. 1. Green leaf area index (LAI) from various years in the burned (B) and unburned (UB) sites of the fire study and in the adjacent Rannells prairie (B1). All three sites were ungrazed and unmowed (Table 1).

Fig. 2. Comparison of modeled and measured soil $CO_2$ fluxes in early-season clipping (EC), full-season clipping (FC), and no clipping (NC) treatments. Predicted fluxes were calculated using models of Norman et al. (1992); Eq. (2) included green leaf area index (LAI) and Eq. (3) did not.

Fig. 3. Comparison of modeled and measured values of instantaneous soil $CO_2$ fluxes. All soil $CO_2$ flux data collected from all treatments during the mowing study are shown (n=776).

Fig. 4. Daily measurements of soil-surface $CO_2$ flux ($F_s$) during course of one year from each of 9 unclipped (NC) plots. Range of $F_s$ on each respective day illustrates the high spatial variability that is typical in $F_s$ measurements in tallgrass prairie.

Fig. 5. Comparison of modeled and measured soil $CO_2$ fluxes in early-season clipping (EC), full-season clipping (FC), and no clipping (NC) treatments. Modeled fluxes were calculated using the original model of Norman et al. (1992) that included LAI (Eq. 2) and the model refitted to data from the mowing study (Eq. 6).

Fig. 6. Comparison of measured and predicted soil $CO_2$ fluxes ($R_s$) from Eq. (6) and volumetric soil water content (average between 2.5 and 10 cm) on burned (a) and unburned (b) tallgrass prairie. This represents a test of Eq. (6) to an independent set of $R_s$ measurements from nearby prairie sites.

Fig. 7. Comparison of modeled (Eq. 6) and measured soil $CO_2$ fluxes during the growing season on site B1.

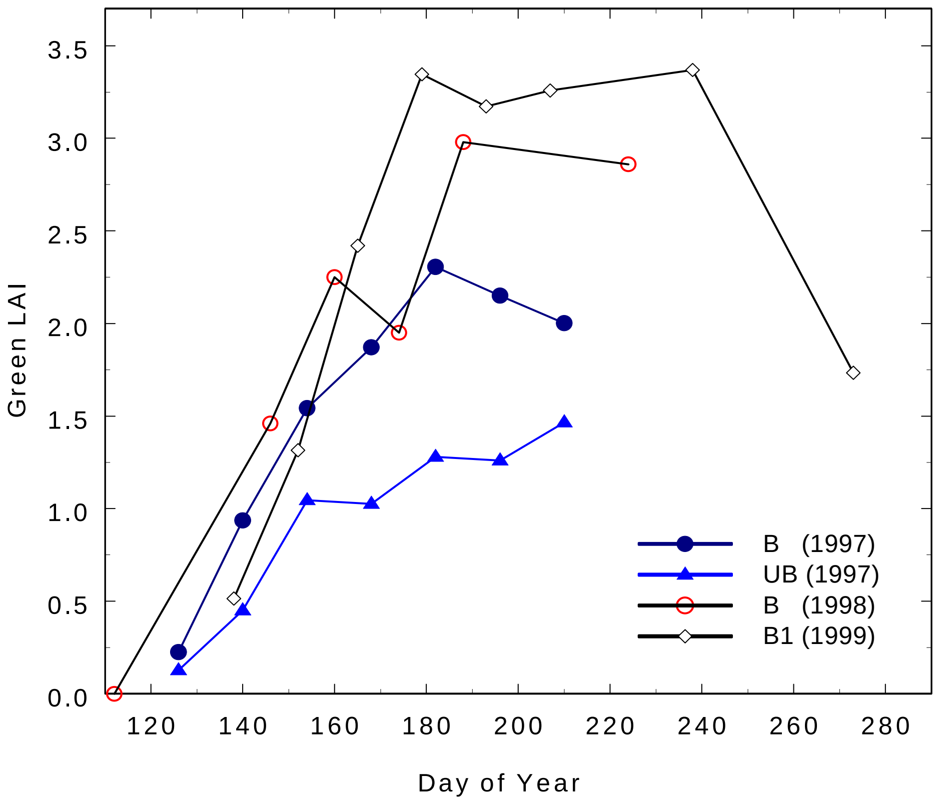
Green LAI
Day of Year
3.5
3.0
2.5
2.0
1.5
1.0
0.5
0.0
120
140
160
180
200
220
240
260
280
B (1997)
UB (1997)
B (1998)
B1 (1999)

Figure 1

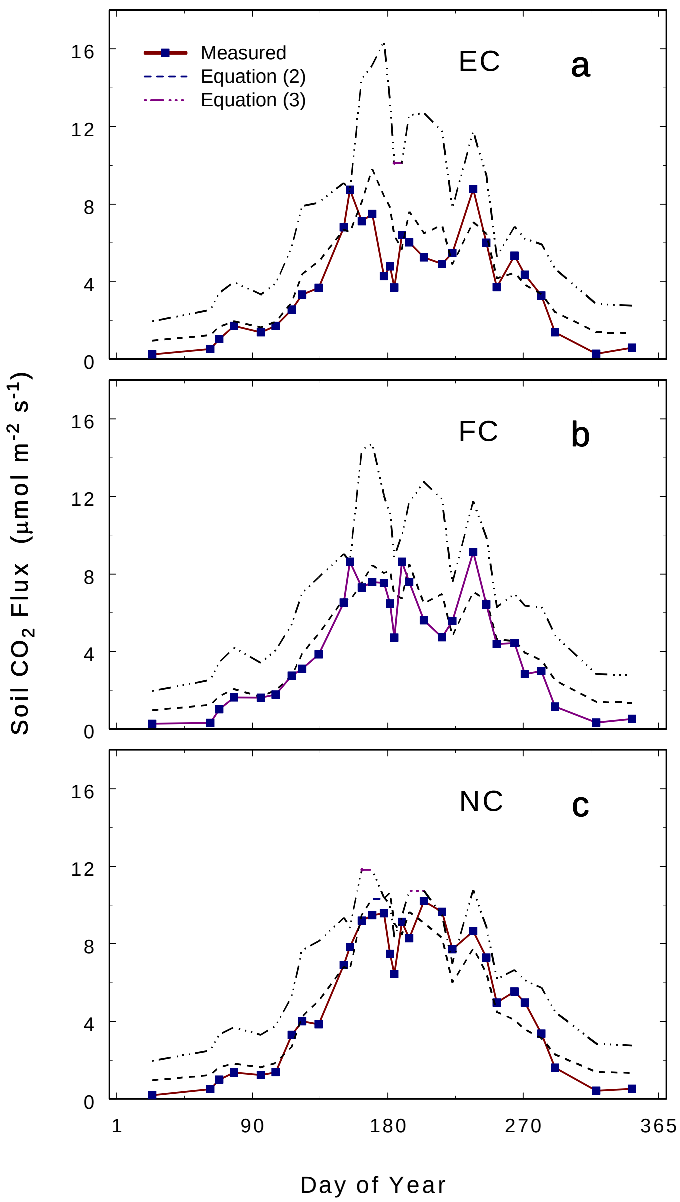
Measured
Equation (2)
Equation (3)
EC
a
FC
b
NC
c
Soil $CO_2$ Flux (µmol $m^{-2}$ $s^{-1}$)
0
4
8
12
16
1
90
180
270
365
Day of Year

Figure 2

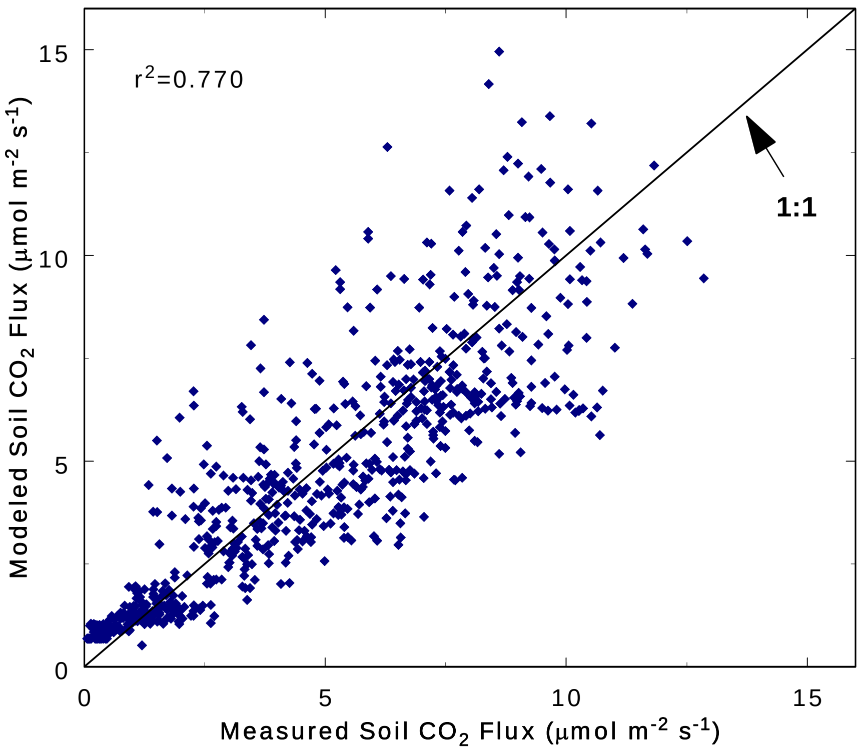
r2=0.770
1:1
Modeled Soil CO2 Flux (μmol m-2 s-1)
Measured Soil CO2 Flux (μmol m-2 s-1)
0
5
10
15
0
5
10
15

Figure 3

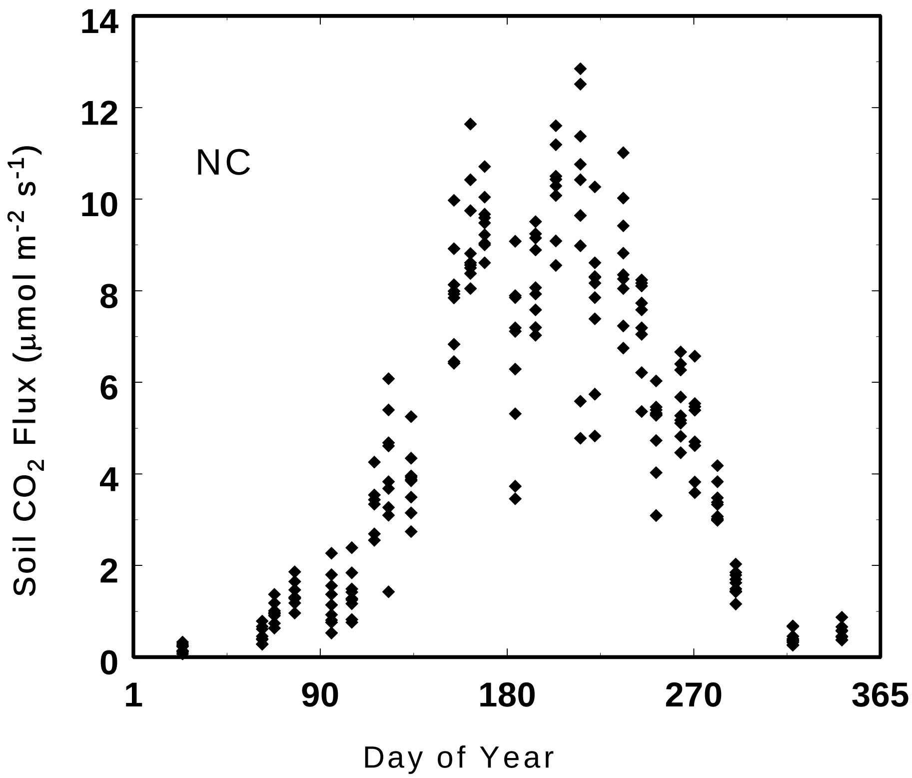
NC
Soil $CO_2$ Flux (μmol $m^{-2}$ $s^{-1}$)
Day of Year
0
2
4
6
8
10
12
14
1
90
180
270
365

Figure 4

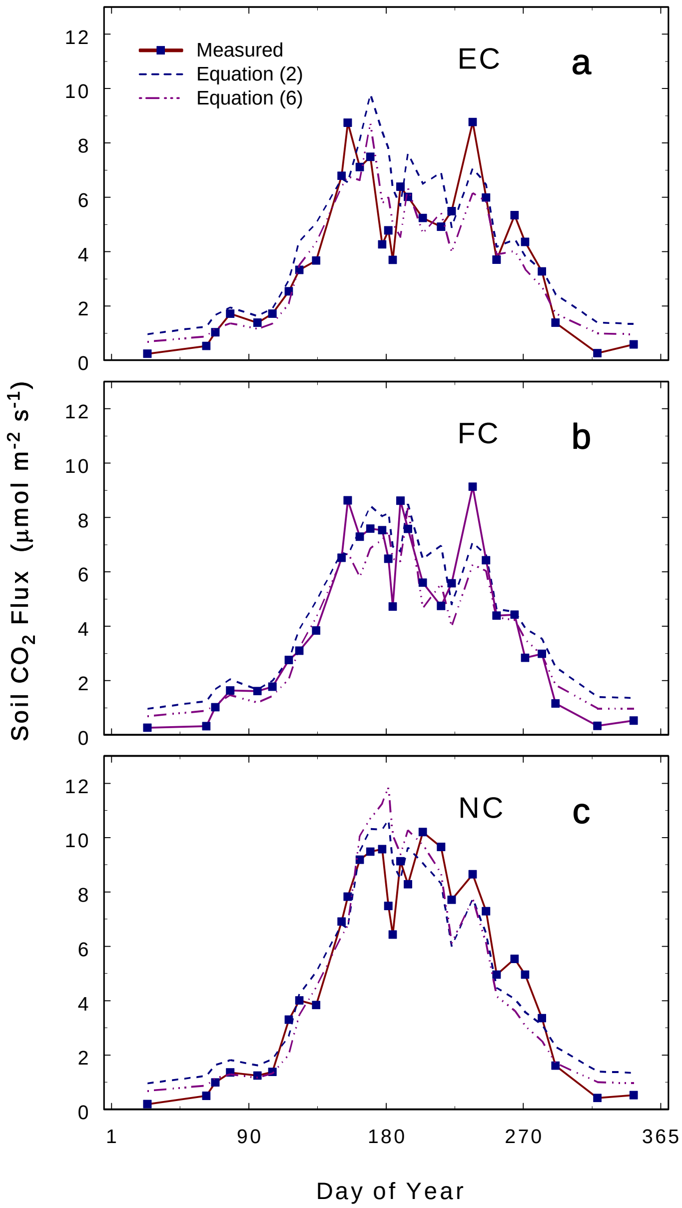
Measured
Equation (2)
Equation (6)
EC
a
FC
b
NC
c
Soil CO2 Flux (µmol m-2 s-1)
Day of Year
0
2
4
6
8
10
12
1
90
180
270
365

Figure 5

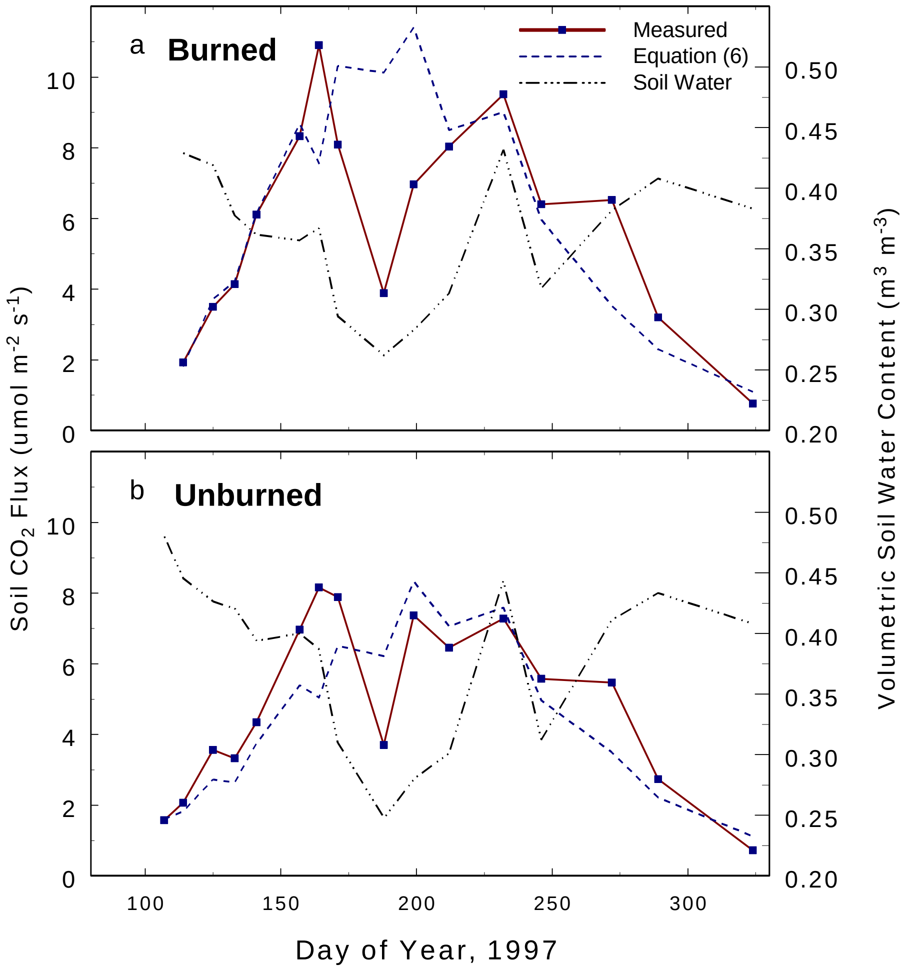
a
Burned
b
Unburned
Measured
Equation (6)
Soil Water
Soil CO2 Flux (umol m-2 s-1)
Volumetric Soil Water Content (m3 m-3)
Day of Year, 1997
0
2
4
6
8
10
0.20
0.25
0.30
0.35
0.40
0.45
0.50
100
150
200
250
300

Figure 6

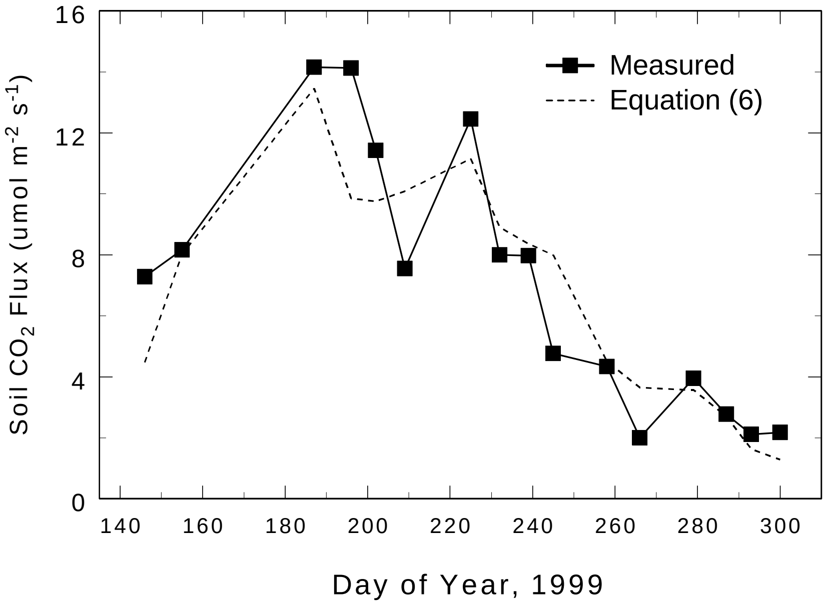
Measured
Equation (6)
Soil CO2 Flux (umol m-2 s-1)
Day of Year, 1999
0
4
8
12
16
140
160
180
200
220
240
260
280
300

Figure 7