

Diurnal and Seasonal Patterns in Ecosystem CO₂ Fluxes and Their Controls in a Temperate Grassland

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Abstract

There is considerable interest in understanding processes of carbon dioxide (CO₂) uptake and release in grasslands and the factors that control them. Many studies have investigated how CO₂ fluxes vary over time (monthly, seasonally, annually). However, with the exception of net ecosystem CO₂ exchange (NEE) and ecosystem respiration (R_{eco}), little information is available on diurnal flux patterns, despite their importance in determining total ecosystem CO₂ gains and losses. To better understand these variations, we measured CO₂ fluxes (NEE, R_{eco}, soil respiration [R_{soil}], canopy respiration [R_{canopy}], plant assimilation [assimilation]) with a climate-controlled closed-chamber system over 24 h once a month from May to September during the 2005 growing season in a mesic grassland in Yellowstone National Park. We also assessed how environmental factors (photosynthetic active radiation [PAR], air temperature, soil temperature, soil moisture) were associated with these diurnal and seasonal flux patterns to identify the main drivers of the fluctuations in CO₂. Measurements were conducted simultaneously on two plots: one irrigated, the other unirrigated. Absolute values of all fluxes were greatest in midsummer (June–July), and lowest in spring and fall (May, September) at both plots. Variation in soil moisture as a result of irrigation did not lead to pronounced differences in seasonal CO₂ fluxes and did not influence the diurnal patterns of CO₂ uptake and release. Instead, the diurnal and seasonal variations of our ecosystem fluxes were related to PAR and temperature (air/soil) and soil moisture and temperature (air/soil), respectively, at both plots. Thus, continued anthropogenic increases in greenhouse gas emissions that are expected to change the intensity of radiation, temperature, and precipitation may strongly affect the diurnal and seasonal patterns in CO₂ uptake and release. Such chamber-based information combined with the measurement of environmental variables could be important for modeling CO₂ budgets when no continuous measurements are available or affordable.

Resumen

Existe un gran interés de entender los procesos de absorción del dióxido de carbono (CO₂) así como la liberación del mismo en los pastizales y los factores que lo controlan. Muchos estudios han investigado que el flujo de CO₂ varía con el tiempo (mensual/estacional/anual). Sin embargo, con excepción de intercambio de CO₂ del ecosistema neto (NEE) y la respiración de ecosistema (Reco), hay poca información disponible sobre patrones de flujo diurno, a pesar de su importancia en la determinación del CO₂ total del ecosistema y sus ganancias y pérdidas. Para obtener una mejor comprensión de estas variaciones, hemos medido flujos de CO₂, (NEE, R_{eco}, respiración del suelo [R_{soil}], respiración de la cubierta [R_{canopy}], aprovechamiento por las plantas [asimilación]) con un sistema de cámara de clima controlado por un periodo de más de 24 horas, una vez por mes, de mayo a septiembre durante la temporada de crecimiento de 2005 en los pastizales del Parque nacional de Yellowstone. También medimos cómo los factores ambientales [radiación fotosintéticamente activa (PAR), temperatura del aire, la temperatura del suelo, y la humedad del suelo] se asociaron con estos patrones de flujo diurno y estacional para identificar los principales factores de las fluctuaciones de CO₂. Las mediciones se llevaron a cabo simultáneamente en dos parcelas, unas regadas, y otras sin riego. Los valores absolutos de los flujos fueron mayores a la mitad del verano (junio/julio) y los más bajos durante primavera y otoño (mayo/septiembre) en ambas parcelas. La variación en la humedad del suelo como resultado de riego no condujo a las evidentes diferencias en flujos estacionales de CO₂ y no influyó en los patrones diurnos de absorción de CO₂ y liberación. En su lugar, las variaciones estacionales y diurnas de los flujos de nuestros ecosistemas estuvieron relacionadas con PAR y la temperatura de (aire/suelo) y la humedad del suelo y la temperatura (aire/suelo), respectivamente, en ambas parcelas. Por lo tanto, incrementos continuos de las emisiones de gases de efecto invernadero que se esperan que cambien la intensidad de radiación, la temperatura y precipitación como resultado de la actividades humanas firmemente pueden afectar a los patrones diurnos y estacionales de absorción de CO₂ y a su liberación. Dicha información basada en mediciones de la cámara, junto con la medición del ambiente, podría ser importante para el modelaje de los recursos de CO₂ cuando no se tengan disponibles las mediciones continuas.

Key Words: closed-chamber technique, ecosystem respiration, net ecosystem exchange, plant assimilation, temporal scales

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INTRODUCTION

Grasslands are spatio-temporally heterogeneous landscapes where topographic gradients are associated with gradients of soil texture, water, carbon (C), and nutrients and plant biomass production and species composition (e.g., Schimel et al. 1985; Knapp et al. 1993; Frank et al. 1994; Turner et al. 1997; Risch and Frank 2006). The temporal variability found in grassland ecosystem is, in contrast, a function of seasonal patterns in soil moisture and temperature. Alterations in climate due to increasing levels of greenhouse gases in the atmosphere (Oreskes 2004) likely will affect plant and soil processes such as ecosystem productivity and carbon dioxide (CO₂) fluxes, which are influenced by temperature and precipitation (Lauenroth and Sala 1992; Knapp et al. 2002). Because grassland ecosystems cover approximately one-third of the earth's terrestrial surface area (Lieth 1978), and store 10–30% of the world's soil C (Anderson 1991; Eswaran et al. 1993), small changes in C pools and fluxes within these systems could have a considerable impact on the global C cycle.

A number of studies have used micrometeorological methods to generate continuous data on net ecosystem exchange (NEE; the difference between CO₂ assimilated and respired by plants and the decomposer food web) and nighttime ecosystem respiration (R_{eco}) for a variety of grasslands. Some authors also have examined how environmental factors, e.g., radiation, air temperature, soil temperature, soil moisture, and plant biomass, are associated with those fluxes (e.g., Suyker and Verma 2001; Flanagan et al. 2002; Hunt et al. 2002; Li et al. 2003; Flanagan and Johnson 2005; Zhao et al. 2006; Gilmanov et al. 2007; Aires et al. 2008; Li et al. 2008; Mercado et al. 2009). As a consequence, considerable information is available on how NEE and R_{eco} vary during diurnal, monthly, seasonal, and annual time scales and when environmental conditions are altered. In contrast, much less is known about diurnal variation in other key CO₂ fluxes such as soil respiration (R_{soil}), canopy (R_{canopy}) respiration, and plant assimilation (assimilation; Flanagan et al. 2002; Cao et al. 2004; Flanagan and Johnson 2005; Tang et al. 2005; Zhang et al. 2005; Riveros-Iregui et al. 2007). However, information on these diurnal CO₂ fluctuations and the factors that control them is important to mechanistically understand how ecosystem CO₂ budgets are determined, and to predict how they might change in the future. If the fluxes are correlated with environmental variables that vary diurnally, then these correlations might be useful to extrapolate a C budget and understand controls on the source–sink C dynamics for a particular ecosystem. Such approaches are needed when no continuous micrometeorological measurements are available, affordable, or applicable. In such cases other methods (e.g., a chamber technique) that measure plot-level CO₂ fluxes and only provide “snapshots” of fluxes in time have to be applied.

In this study we used the chamber technique to simultaneously measure NEE, assimilation, R_{eco}, R_{soil}, and R_{canopy} over single days at monthly intervals (May through September) during the 2005 growing season in a mesic grassland in Yellowstone National Park. In contrast to earlier studies that we conducted in Yellowstone and where we showed large spatio-temporal differences in ecosystem CO₂ fluxes (Risch and Frank 2006, 2007), the main goal of this study was to increase our understanding of how the fluxes vary over 24 h and how

these 24-h patterns change throughout the growing season. Further, we explored whether different environmental factors (photosynthetic active radiation [PAR], air temperature, soil temperature, soil moisture) control the fluxes at the two different time scales (diurnal and seasonal). We conducted all our measurements on two different plots: one was subject to ambient conditions, and the other one was irrigated throughout the entire season to learn more about how changes in soil moisture—one of the important variables determining seasonal variations in grassland CO₂ fluxes—affect fluxes over 24 h. In addition, we assessed whether it would be possible to develop regression models for each of the fluxes based on environmental variables, which would allow extrapolations of small-scale (plot-level) CO₂ measurements to larger scales if continuous flux measurements are not available, affordable, or applicable.

METHODS

Study Area and Sampling Design

The study was conducted on the northern winter range of Yellowstone National Park, located in the northwestern corner of Wyoming, United States (lat 44°55'N to lat 45°10'N and long 110°10'W to long 110°50'W), and home to large migratory herds of elk (*Cervus elaphus* L.), bison (*Bison bison* L.), and pronghorn (*Antilocarpa americana* [Ord.]). The northern winter range (~100 000 ha) primarily comprises grassland and shrub-grassland. It was inhabited by approximately 8 300 elk, 1 400 bison, and 225 pronghorn when this study was conducted in 2005 (winter counts 2003/2004; Northern Yellowstone Cooperative Wildlife Working Group 2005; P. J. White, personal communication, July 2005; R. Wallen, personal communication, July 2005). Elevations range from 1 600 m to 2 200 m and the climate is cool and dry, with mean annual temperatures and precipitation of 4.6°C and 379 mm, respectively (National Oceanic and Atmospheric Administration 2005). Soils of the northern winter range are mostly derived from glacial till of andesitic and sedimentary origin laid down during the Pleistocene (Keefer 1987).

We chose a grazed 25 × 25 m homogeneous grassland near Mammoth Hot Springs, Wyoming (1 920 m, lat 44°6'N, long 110°4'W) that was representative for mesic grasslands of Yellowstone's northern winter range. The vegetation was dominated by the two grasses *Poa pratensis* L. and *Phleum pratense* L. (Risch and Frank 2007). Shoot biomass averaged 240 g·m⁻² during the 2005 growing season, the soil was classified as a clay loam with a pH of 7.4 and a fine fraction (<2 mm) soil bulk density of 0.89 g·cm⁻³. The top 20 cm of the mineral soil contained 0.3% nitrogen and 3.5% C (Risch and Frank 2007). The location was chosen for logistic reasons (access to power plugs for recharging batteries during the measurements). In the center of the grassland we randomly selected two 2 × 1 m plots. We irrigated one of the plots every other week from April 2005 to September 2005 with 25% of the average monthly precipitation amount (30-yr) 1 d prior to our measurements. The two plots had comparable vegetation and biomass prior to starting the irrigation treatment.

Ecosystem CO₂ Exchange Measurements

On a clear day once a month we measured NEE and R_{eco} on a 50 × 50 cm area in the center of one half of each of the two

2 × 1 m plots and R_{soil} in the center of the other half of the plots. We always measured NEE first, and then R_{eco} , when conducting our measurements. The measurements were made simultaneously on both plots with two separate, temperature-controlled 50 × 50 × 50 cm closed-chamber systems. Walls of the chambers were non-CO₂ absorbing, transparent polycarbonate. Chamber temperatures were maintained within 2°C of ambient by pumping ice water through car transmission coolers mounted to the inside of the chambers and mixing the air inside the chambers with two fans. For specific chamber design used, see Risch and Frank (2006, 2007). Chamber CO₂ concentrations were measured with portable infrared gas analyzers (IRGA; LICOR 6262; LICOR Biosciences, Lincoln, NE) on a 0.5 L · min⁻¹ to 1 L · min⁻¹ air stream circulated from the chambers. IRGA temperatures and CO₂ and water concentrations were recorded every 5 s onto HOBO weather station data loggers (15-channel H21 HOBO weather station data logger; Onset Computer, Bourne, MA) with 12-bit 0-5 volt input adapters (HOBO weather station 12-bit voltage input adapter; Onset Computer). Measurements were conducted every 2 h starting at 0800 hours and ending at 0600 hours the following morning. Flux measurements were repeated twice for both NEE and R_{eco} at each time of sampling. Changes in chamber CO₂ concentrations were measured for 180 s after placing the chambers onto foam pads (to seal the base) mounted on aluminum frames. The frames were driven 3 cm deep into the soil at least 1 h before the first measurement. The chambers were vented for approximately 120 s after each 180-s measurement. The two NEE measurements were then averaged to obtain the flux for a specific time of the day for each plot. The same was done for the two R_{eco} measurements conducted at a specific hour. During NEE measurements, the chambers were exposed to full light. Complete darkness was simulated for the R_{eco} measurements by covering the chambers with black cloths.

We calculated NEE and R_{eco} using

$$\text{CO}_2 \text{ flux} = d\text{CO}_2/dt \cdot P/[R \cdot (273.15 + T)] \cdot V/A \quad [1]$$

where $d\text{CO}_2/dt$ (umol · mol⁻¹ · s⁻¹) = CO₂ accumulation inside the chamber during t seconds, P = atmospheric pressure (kPa), R = gas constant (8.314 kPa · m⁻³ · K⁻¹ · mol⁻¹), T = chamber temperature (°C), V = chamber volume (m³), and A = chamber bottom area (m²). CO₂ accumulation rates were corrected for water vapor (Hooper et al. 2002); air pressure corrections were conducted automatically by the LICOR 6262. Pressure changes within the chambers were assumed to be minimal because of the large volume of the chambers and the short measurement intervals (Healy et al. 1996).

Soil respiration was simultaneously measured at both plots with two 20 (high) × 10 cm (diameter) closed-chamber systems (for more detail see Risch and Frank 2006) immediately after completing the NEE and R_{eco} measurements. The chambers were slid onto polyvinyl chloride collars (10-cm diameter) that were driven 5 cm into the mineral soil after clipping and removing all the aboveground vegetation ≥ 2 h before the first measurement. Soil respiration was then calculated as the mean of two 180-s measurements (chambers vented for 120 s between measurements) using Equation 1. The chambers were calibrated against the LICOR 6400-09 soil respiration system (LICOR Biosciences) across a wide variety of soils in Yellowstone National Park to explore potential effects of pressure

disequilibrium inside the chambers on respiration measurements (e.g., Davidson et al. 2002). We found a significant linear relationship between the two methods:

$$y = 1.061x \quad [2]$$

($r^2 = 0.72$, $P < 0.001$, $n = 30$, where y is the LICOR 6400-09 soil respiration system and x is our own chamber). More pertinent to the aims of this calibration was that the x intercept was zero and there was no significant difference between the slope of the regression line and 1.0, indicating that the rates measured with our system were unbiased measures of R_{soil} . To adjust for potential measurement differences between the different-sized soil and NEE chambers, we also calibrated these chambers against each other across a wide variety of soils to accurately calculate R_{canopy} by subtracting R_{soil} from R_{eco} :

$$y = 0.4833x + 2.5128 \quad [3]$$

($r^2 = 0.74$, $P < 0.001$, $n = 33$, where y is the NEE chamber and x is our soil chamber). Soil respiration measurements were then corrected using Equation 3. CO₂ assimilation = photosynthesis (assimilation) was calculated by summing NEE and R_{eco} . Negative CO₂ flux values were CO₂ sources (CO₂ leaving the ecosystem), and positive values were CO₂ sinks (CO₂ absorbed by the vegetation).

Photosynthetic photon flux density was determined using PAR sensors (HOBO weather station photosynthetic light [PAR] smart sensor, Onset Computer) attached to the inside surface of the top of each chamber. Air temperature was recorded every 5 s with air temperature sensors (HOBO weather station 8-bit temperature/RH smart sensor, Onset Computer) attached to the top of each NEE chamber. Soil temperature (HOBO weather station 8-bit temperature smart sensor, Onset Computer) was also recorded every 5 s for the 0-cm to 20-cm mineral soil. Volumetric soil moisture content (%) was measured manually with a time domain reflectometer (TDR 100 soil moisture probe, Spectrum Technologies, Plainfield, IL). To obtain an accurate measure, we inserted the probe at six randomly selected locations to 12-cm depth immediately before the first CO₂ measurement. Average soil moisture for each plot was then derived by averaging the six values. Both soil temperature and soil moisture were measured within the 2 × 1 m plots, 15 cm from the edge, but outside the area used for CO₂ measurements.

Statistical Analyses

To analyze how CO₂ exchange variables, PAR, air temperature, soil temperature, and soil moisture differed over the course of 24 h (diurnal patterns), we normalized the data to remove the seasonal effects using

$$y_{\text{norm},i} = \frac{y_i}{\sqrt{\sum_{i=1}^n y_i^2}} \quad [4]$$

where y_i represent the nonnormalized (raw) data and $y_{\text{norm},i}$ the normalized data (Quinn and Keough 2002). We then averaged the normalized data and used nonlinear regression analyses to assess the diurnal patterns (proportions of fluxes at different

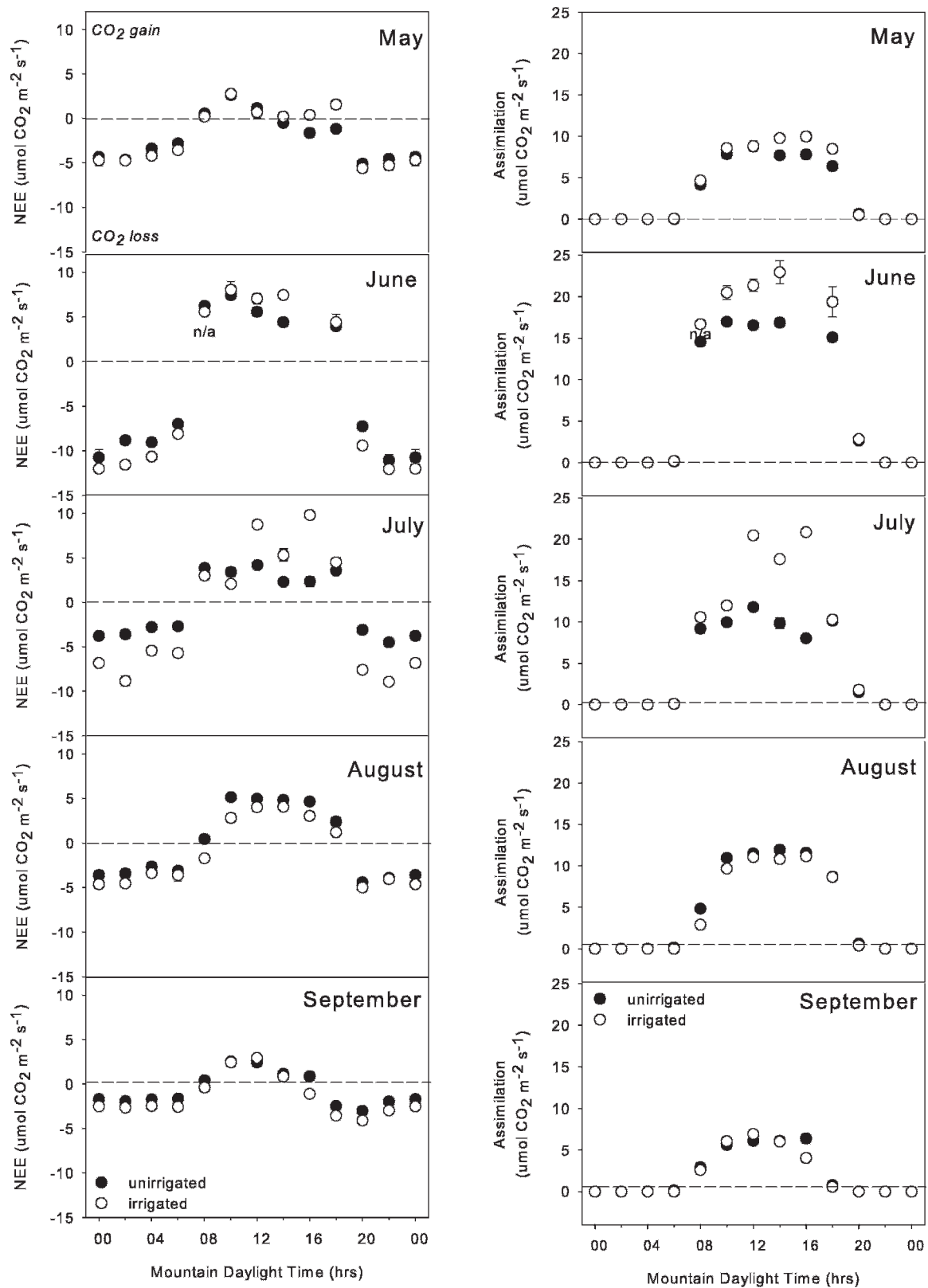


Figure 1. Diurnal and seasonal patterns in net ecosystem CO₂ exchange (NEE) and plant assimilation (assimilation) between May and September, $n = 2$. Error bars, standard errors representing the measurement errors made with our equipment; n/a, not available because of temporal occurrence of clouds.

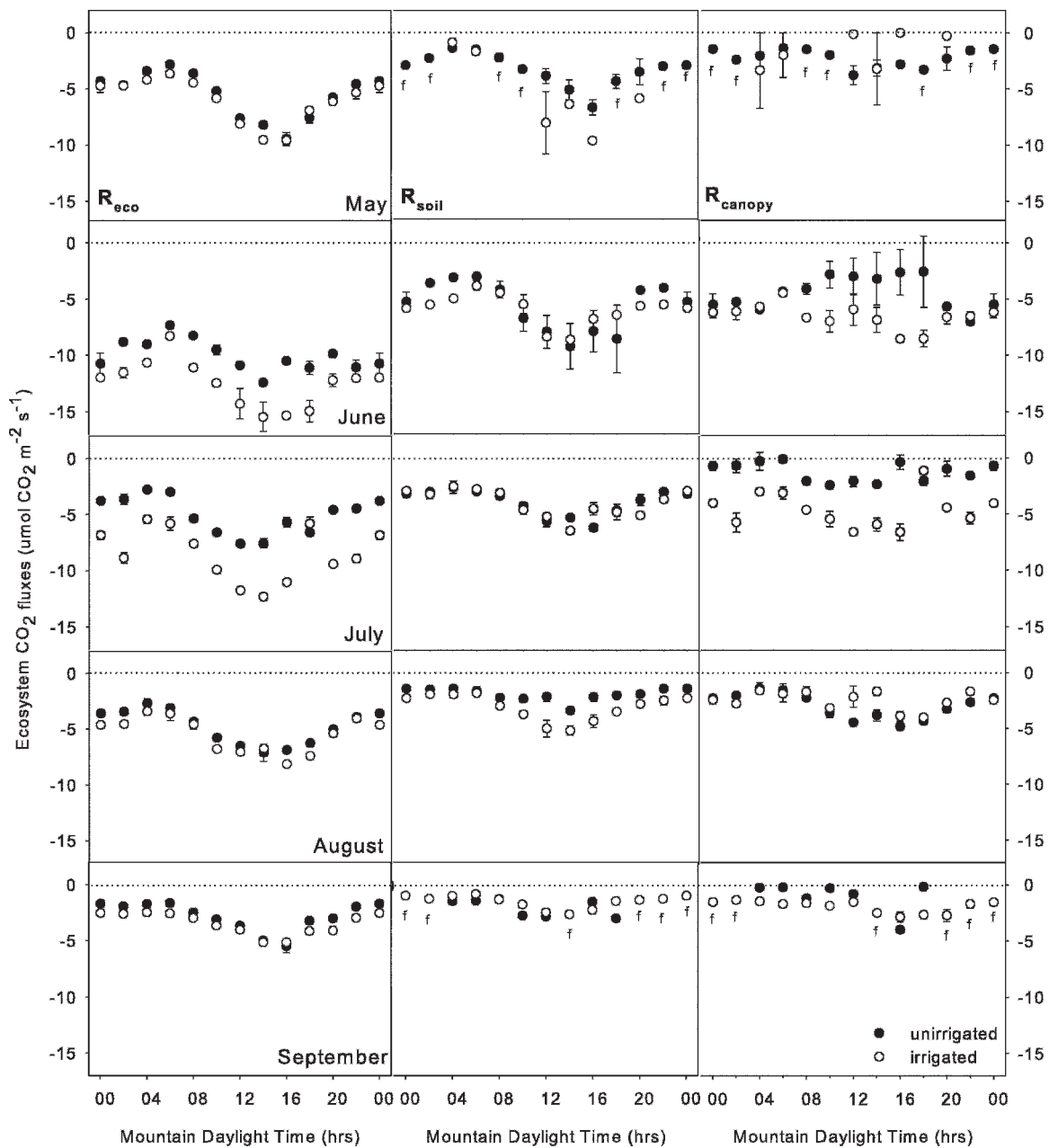


Figure 2. Diurnal and seasonal patterns in ecosystem respiration (R_{eco}), soil respiration (R_{soil}), and canopy respiration (R_{canopy}) between May and September, $n = 2$. Error bars, standard errors representing the measurement errors made with our equipment; f, equipment failure.

times during the day) in CO_2 fluxes: normalized CO_2 fluxes were the dependent variables and time of the day the independent variables. In addition, we used stepwise regression analyses (backward) to assess which variables best explained the diurnal CO_2 flux patterns. Normalized NEE, assimilation, R_{eco} , R_{soil} , and R_{canopy} were dependent and normalized PAR, air temperature, soil temperature, and soil moisture independent variables. To assess how the CO_2 fluxes changed during the growing season we calculated average daily CO_2 fluxes (removal of diurnal effects), and again used stepwise regression analyses to assess which variables best explained these seasonal changes. NEE, assimilation, R_{eco} , R_{soil} , and R_{canopy} were dependent and PAR, air temperature, soil temperature, and soil moisture independent variables.

One of the draw backs of the chamber method is that R_{soil} cannot be measured at the same time that NEE, R_{eco} , and assimilation are measured when only one gas analyzer is available or affordable; it requires a separate chamber setup and separate measurements. It therefore would be helpful if predicting R_{soil} were possible based on R_{eco} . We assessed this possibility by developing a regression model.

RESULTS AND DISCUSSION

Diurnal and Seasonal Patterns in Ecosystem CO_2 Fluxes

Absolute values in CO_2 fluxes were highest in midsummer (June–July), and lowest in spring (May) and fall (September;

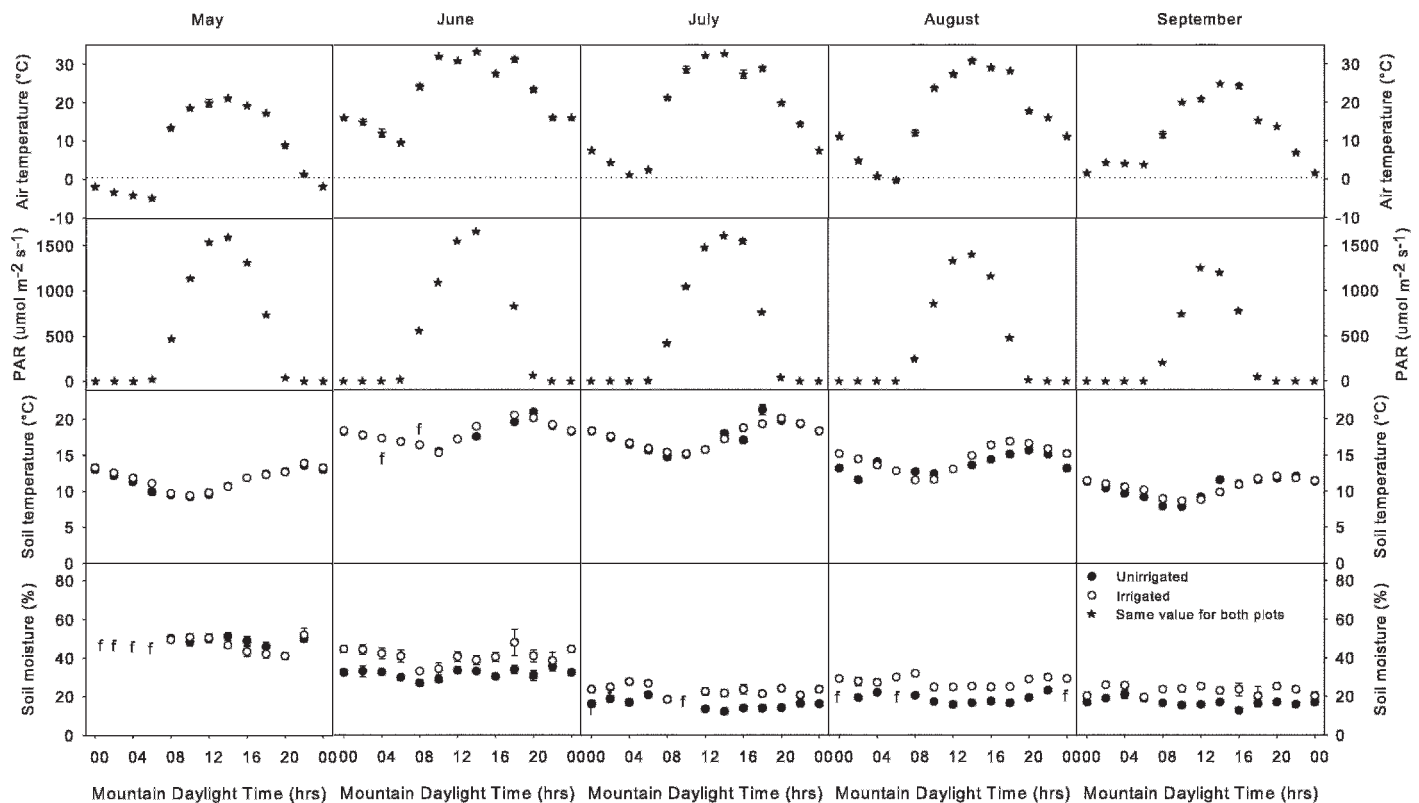


Figure 3. Diurnal and seasonal patterns in air temperature, photosynthetic active radiation (PAR), soil temperature, and soil moisture between May and September. Error bars, standard errors representing the measurement errors made with our equipment; f, equipment failure.

Figs. 1 and 2). The interval during a 24-h sampling period at which positive NEE occurred was shortest early and late and longest during the middle of the growing season for both plots (Fig. 1). For example, NEE was positive for 4 h (0800–1200 hours) in May, 10 h (0800–1800 hours) in June, July, and August, and 6 h in September (1000–1600 hours) at the unirrigated plot. Assimilation was highest in June and was positive between 0800 hours and 2000 hours during all measurements, except in September, when plants only assimilated CO_2 for 8 h, stopping after 1600 hours (Fig. 1). Ecosystem respiration peaked between 1200 hours and 1600 hours independent of month throughout the entire season (Fig. 2). Similar to R_{eco} , R_{soil} peaked between 1200 hours and 1600 hours from May to August, but varied little during the 24-h sampling period in September. Canopy respiration showed the least variation over 24 h during all months of measurement (Fig. 2). Air temperature peaked at 1400 hours during all measurements (Fig. 3) and was correlated with PAR. We observed a shift in peak soil temperature over the course of the season: in May, highest soil temperature occurred at 2200 hours, in June at 2000 hours, in July and August at 1800 hours, and in September at 2200 hours. Soil moisture did not vary much over 24 h during any of the measurements (Fig. 3). Regarding diurnal patterns without considering seasonal differences (normalized data), we found that NEE and assimilation peaked at noon, whereas highest R_{eco} , R_{soil} , and R_{canopy} were found later in the day at 1600 hours throughout the 2005 growing season (Fig. 4). The diurnal patterns in R_{eco} and R_{soil} were more pronounced than the ones in R_{canopy} .

We are not aware of any other study that provided data of diurnal patterns for NEE, assimilation, R_{eco} , R_{soil} , and R_{canopy} that were measured simultaneously within the same ecosystem over the course of the season. However, our diurnal patterns in NEE, with low fluxes and short periods of net CO_2 gains (positive NEE) in spring and fall and high fluxes and long periods of net CO_2 gain in midsummer, are similar to what has been reported from other grassland ecosystems (e.g., Ham and Knapp 1998; Hunt et al. 2002; Kato et al. 2004; Xu and Baldocchi 2004; Flanagan and Johnson 2005; Li et al. 2005; Zhao et al. 2006). The 1200 hours to 1600 hours peaks in R_{soil} found in Yellowstone National Park were similar to fluxes measured in alpine grasslands in China and an oak–grass savanna in California (Cao et al. 2004; Tang et al. 2005; Zhang et al. 2005). Our midsummer diurnal R_{eco} patterns were similar to empirically measured (Flanagan and Johnson 2005) and modeled (with NEE, soil temperature, and moisture data; Flanagan et al. 2002) rates in a mixed grassland in Alberta, Canada.

It has been shown that R_{soil} contributed up to 77% to R_{eco} at the seasonal scale for grasslands of Yellowstone National Park (Risch and Frank 2006) and on average 75% in a grass–clover sward in Ireland (Gilmanov et al. 2007). However, little is known about how these fluxes interact over the course of short time periods, i.e., 24 h. The only study we are aware of was conducted by Hu et al. (2008), and showed that R_{soil} contributed between 19% and 36% to R_{eco} in two alpine meadows on the Tibetan Plateau over 1 d in July. In our study we were able to examine the contribution of R_{soil} to R_{eco} at

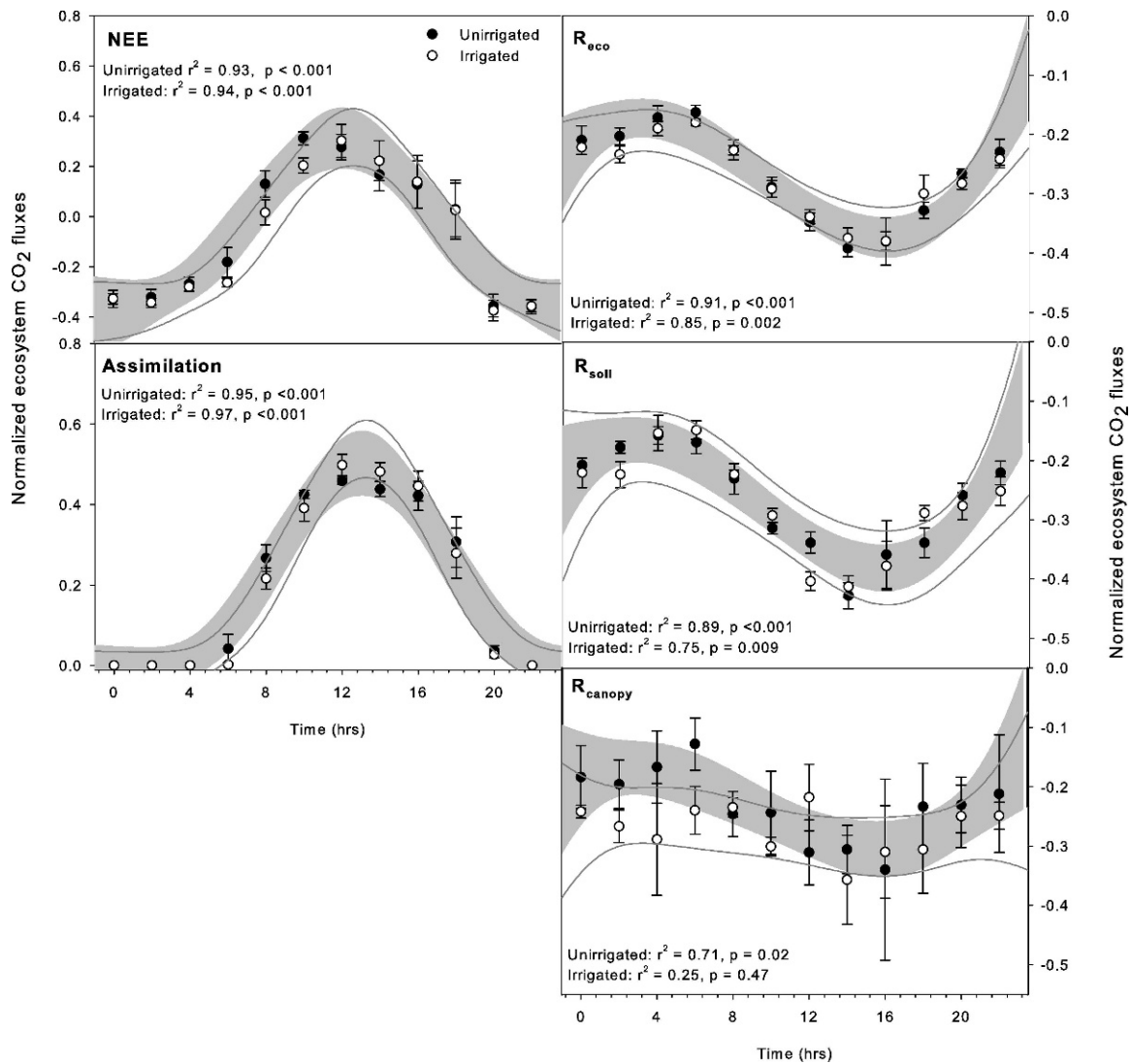


Figure 4. Diurnal patterns in net ecosystem CO₂ exchange (NEE), plant assimilation (assimilation), ecosystem respiration (R_{eco}), soil respiration (R_{soil}), and canopy respiration (R_{canopy} ; normalized seasonal averages from May to September; $n = 5$) for both plots. Error bars, standard error; the 95% confidence intervals (gray area, unirrigated; clear area between gray lines, irrigated) are based on Gaussian (NEE and assimilation) and on polynomial (cubic; R_{eco} , R_{soil} , and R_{canopy}) regressions. For simplicity reasons, the Gaussian model for assimilation was also fitted for the dark periods when photosynthetic active radiation = 0 and assimilation = 0.

different times of the day (Fig. 5 inset) averaged across diurnal periods sampled each month of the growing season. R_{soil} contributed between 42% and 64% to R_{eco} over the course of the day on the two plots; thus the values showed considerable diurnal variations and were somewhat lower than the ones measured by Risch and Frank (2006). The reason for these differences could be related to different soil types (sandy loams and loamy sands in Risch and Frank [2006]; clay loam in this study) or plant species composition between the two studies. In addition, we explored the relationship between R_{soil} and R_{eco} by combining all measurements made over 24 h throughout the 2005 growing season and assessed how well R_{eco} could be used to predict R_{soil} (Fig. 5). R_{soil} showed a strong linear and positive relationship to R_{eco} . Thus, it would be possible to predict R_{soil} at different times of the day when only R_{eco} values are available, given that enough calibration data was previously collected for a specific ecosystem.

Irrigation Effect

Huxman et al. (2004a) proposed a model of how rainfall pulse events affect ecosystem CO₂ fluxes in semiarid and arid ecosystems: they predicted that NEE would be lower after the precipitation pulse as R_{eco} increases, and were able to prove this in a study using experimental grassland plots sown with native and nonnative grass species on two different soil types in Arizona (Huxman et al. 2004b). They explained the increases in CO₂ release with the physical displacement of soil CO₂ by the penetrating water (degassing) as well as by increases in decomposition, N mineralization, and microbial activity (Huxman et al. 2004a, 2004b). Consequently, we expected the ecosystem CO₂ fluxes of our unirrigated plot to differ from the ones measured at the irrigated plot over the course of 24 h.

Soil moisture was between 6.5% and 9% higher on the irrigated plot compared to the unirrigated plot from June to September 2005 (Fig. 3). However, the amount of CO₂ uptake

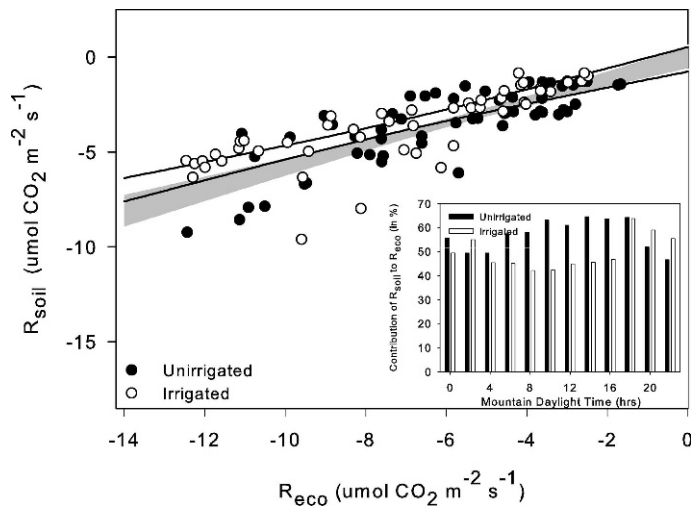


Figure 5. Linear relationship between ecosystem respiration (R_{eco}) and soil respiration (R_{soil}) using diurnal measurements made over the course of the season on both plots (unirrigated: $y = -0.015 + 0.58 \cdot x$; $r^2 = 0.67$, $P < 0.001$, $n = 60$; irrigated: $y = -0.13 + 0.49 \cdot x$; $r^2 = 0.72$, $P < 0.001$, $n = 58$). The 95% confidence intervals (gray area, unirrigated; clear area between black lines, irrigated) are based on linear regressions. The inset shows the contributions (season averages, %) of R_{soil} to R_{eco} over the course of the day for the unirrigated and irrigated plots.

and release (Figs. 1 and 2) as well as the diurnal patterns in CO_2 fluxes did not seem to differ between the two plots as indicated by the overlapping 95% confidence intervals shown in Figure 4. These results would suggest that the diurnal patterns of CO_2 uptake and release were robust to the differences in soil moisture that we detected in the grassland under study in 2005. However, soil moisture was found to be nonlimiting in Yellowstone during the 2005 growing season (Risch and Frank 2007; April to September; 30-yr average: 233 mm, 2005: 255 mm), which may explain why the CO_2 flux patterns did not differ between irrigation treatments. Although several authors studied how manipulations of precipitation affect grassland CO_2 fluxes intra- and interannually (e.g., Huxmann et al. 2004a, 2004b; Chimner and Welker 2005; Harper et al. 2005), we are aware of only one study that presented data on how diurnal patterns in CO_2 fluxes differed under variable soil moisture conditions: Verma et al. (1992) found that the diurnal patterns in CO_2 fluxes were different in a Nebraska prairie when soil moisture was low enough to cause

plants to become stressed over the course of 24 h. Thus, diurnal patterns in CO_2 uptake and release might be sensitive to changes in soil moisture, but probably only when moisture conditions are limiting. However, the interpretation of our results is rather speculative because of the lack of replication in our experiment. More extensive studies will be required to understand potential threshold responses of diurnal patterns of CO_2 flows to variable soil moisture.

Environmental Control of Diurnal and Seasonal Patterns in Ecosystem CO_2 Fluxes

Because no significant differences were found in the diurnal patterns between the two irrigation treatments throughout the 2005 growing season, we combined the data for further analyses. PAR, together with air and soil temperature, was responsible for diurnal variations in NEE, assimilation, R_{eco} , and R_{soil} , whereas PAR and soil moisture controlled the diurnal variations in R_{canopy} (Table 1). The seasonal variability in assimilation, R_{eco} , R_{soil} , and R_{canopy} was controlled by soil moisture and air or soil temperature (Table 1). Soil moisture and temperature, together with PAR, explained the seasonal variation in NEE. Thus, overall, radiation and temperature were the major drivers of diurnal differences in CO_2 fluxes, whereas soil moisture and temperature were more important in controlling the seasonal differences in fluxes measured in this mesic Yellowstone grassland throughout the 2005 growing season.

No study, to our knowledge, has so thoroughly addressed these relationships among key ecosystem CO_2 fluxes at the same time. Many researchers have examined how environmental variables are linked to seasonal variation in NEE or R_{eco} (e.g., Flanagan et al. 2002; Hunt et al. 2002; Kato et al. 2004; Flanagan and Johnson 2005; Li et al. 2005; Zhao et al. 2006; Riveros-Iregui et al. 2007). For example, Flanagan et al. (2002) found highly variable NEE when they measured the fluxes during a “normal,” a wet, and a dry summer in a grassland system in Alberta, Canada. Chimner and Welker (2005) showed strong control of R_{eco} by seasonal patterns in soil moisture in a Wyoming grassland. Similarly, research has been conducted on how environmental variables control the diurnal variations in NEE and R_{eco} (e.g., Verma et al. 1989, 1992; Ham and Knapp 1998; Hunt et al. 2002; Kato et al. 2004; Flanagan and Johnson 2005; Li et al. 2005). In contrast, considerably less is known about how the diurnal patterns in assimilation, R_{soil} , and R_{canopy} are related to environmental variables. Riveros-Iregui et al. (2007) discussed the role of PAR and soil

Table 1. Parameters for linear regression models (stepwise regression) explaining diurnal (24-h differences) and seasonal (based on daily averages) patterns in CO_2 fluxes.¹

	Diurnal patterns			Seasonal patterns		
	Variables	r^2	P-value	Variables	r^2	P-value
NEE	PAR, air T, soil T	0.89	< 0.001	Soil M, soil T, PAR	0.72	0.001
Assimilation	PAR, air T	0.96	< 0.001	Soil M, air T	0.88	0.001
R_{eco}	PAR, air T, soil T	0.93	< 0.001	Soil M, air T	0.93	< 0.001
R_{soil}	PAR, air T, soil T	0.94	< 0.001	Soil M, soil T	0.78	0.003
R_{canopy}	PAR, soil M	0.51	0.001	Soil M, air T	0.76	0.007

¹NEE, net ecosystem CO_2 exchange; R_{eco} , ecosystem respiration; R_{soil} , soil respiration; R_{canopy} , canopy respiration; PAR, photosynthetic active radiation; air T, air temperature; soil T, soil temperature; and soil M, soil moisture.

temperature on diurnal patterns of R_{soil} in a montane conifer forest in the Rocky Mountains. They showed that changes in R_{soil} were directly linked to increases and decreases in soil temperature from roughly midnight to 0700 hours and from noon to 1800 hours, respectively, on 18 June 2006. In contrast, the changes in R_{soil} in the early morning and early evening were independent of changes in soil temperature, but coincided with changes in PAR.

IMPLICATIONS

Our study documents large diurnal and seasonal variation in NEE, assimilation, R_{eco} , R_{soil} , and R_{canopy} in a mesic grassland in Yellowstone National Park during the 2005 growing season. Our results also indicated that PAR and temperature controlled the diurnal responses of ecosystem CO_2 fluxes. Similarly, soil moisture and temperature were the drivers of the seasonal variations. Based on our results, we would expect that the increases in diffuse radiation (Mercado et al. 2009) and temperature as well as changes in precipitation regimes that are expected as a consequence of continued anthropogenic greenhouse gas emissions (Oreskes 2004) will alter ecosystem CO_2 fluxes at both the diurnal and seasonal scales. Understanding these short- and intermediate-term dynamics and their controls is important to derive meaningful CO_2 budgets and predict how future changes in radiation and climate might feed back on the C cycle. As a consequence, the interactions detected in our study could be useful to derive rough estimates of ecosystem CO_2 uptake and losses in grasslands if continuous measurements are not available, applicable, or affordable.

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