Distinct patterns in the diurnal and seasonal variability in four components of soil respiration in a temperate forest under free-air CO$_2$ enrichment

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Received: 1 March 2011 – Accepted: 14 March 2011 – Published: 18 March 2011

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Published by Copernicus Publications on behalf of the European Geosciences Union.
Abstract

Soil respiration ($R_S$) is a major flux in the global carbon (C) cycle and its responses to changing environmental conditions may exert a strong control on the residence time of C in terrestrial ecosystems and in turn influence the atmospheric concentration of greenhouse gases. Soil respiration consists of several components returning C of different nature and age to the atmosphere, with root/rhizosphere respiration often assumed to be the dominant and variable one. Rates of $R_S$ vary greatly in time and space and the mechanisms underlying this temporal variability, or the $R_S$ components responsible for it, are poorly understood. It is often assumed the $R_S$ and its components are under abiotic control at almost all time scales. In this study, we used the ecosystem $^{13}$C tracer at the Duke Forest Free Air CO$_2$ Enrichment site to separate forest $R_S$ into four components: root/rhizosphere respiration ($R_R$), litter decomposition ($R_L$), and decomposition of soil organic matter (SOM) of two age classes – up to 8 years old and SOM older than 8 years. We then examined and found that diurnal and seasonal variability in the components of $R_S$ occurred at different magnitudes and directions than total $R_S$. Soil respiration was generally dominated by $R_{SOM}$ during the growing season (44% of daytime $R_S$), especially at night. The contribution of heterotrophic respiration ($R_{SOM}$ and $R_L$) to $R_S$ was not constant during the growing season, indicating that the seasonal variability seen in $R_R$ alone cannot explain the seasonal variability in $R_S$. Although there was no diurnal variability in $R_S$, there were significant compensatory differences in the contribution of individual $R_S$ components to daytime and nighttime rates. The average contribution of $R_{SOM}$ to $R_S$ was greater at night (54%) than during the day (44%) whereas the average contribution of $R_R$ to total $R_S$ was ~30% during the day and ~34% during the night. In contrast, $R_L$ constituted 26% of $R_S$ during the day and only 12% at night. Interestingly, the decomposition of C older than 8 years ($R_{pre-tr}$), which could contain the most recalcitrant C-pools in this forest, showed more pronounced and consistent diurnal variability than any other $R_S$ component, with nighttime rates on average 29% higher than daytime rates. In contrast, the decomposition
of more recent, post-treatment C \((R_{\text{pre-tr}})\) did not vary diurnally. None of this diurnal variation in components of \(R_s\) could be explained by temperature and moisture variations and were likely due to biological controlling mechanisms. On growing season time scales some components of \(R_s\) varied with temperature moisture variations that also affect plant photosynthetic activity. Our results indicate that the variation observed in this forest on the components of \(R_s\) is the result of complex interaction between dominant biotic controls (plant activity, mineralization constants, competition for substrates) over abiotic controls (temperature, moisture) in diurnal and seasonal time scales. Because \(R_s\) integrates biological activity of several types of organisms, utilizing C of different chemistry, accessibility and ages, considering the controls and interaction among soil pools that result in the overall soil CO\(_2\) efflux is important in elucidating the controls on \(R_s\) on ecosystem and atmospheric C-pools at different time scales.

1 Introduction

Terrestrial ecosystems exchange large amounts of C with the atmosphere through the processes of photosynthesis and ecosystem respiration \((R_E)\). Annually, the difference between these large fluxes determines the extent of C storage in the terrestrial biosphere and small imbalances between these fluxes can lead to significant variation in atmospheric CO\(_2\) concentration. The role of ecosystems as a long-term sink or source for atmospheric C thus depends on the effects and feedbacks of changing environmental conditions on photosynthesis and the components of \(R_E\). The potential responses of \(R_E\) to environmental change are less clear than those of photosynthesis (Gonzalez-Meler et al. 2004; DeLucia et al., 2007), but are of fundamental importance in determining the residence time of C in terrestrial ecosystems. Improved understanding of the biotic and abiotic mechanisms controlling C release from terrestrial ecosystems, and the time scales at which these mechanisms operate, is necessary before the future role of the terrestrial biosphere in the global C cycle can be predicted.
Ecosystem respiration, which returns C to the atmosphere, is often dominated by soil respiration ($R_S$), which can constitute 50–80% of the total C emitted from ecosystems to the atmosphere annually (Raich et al., 2002; Davidson and Janssens, 2006; Davidson et al., 2006). Soil respiration results from a complex network of oxidation processes, carried out by different organisms at different temporal and spatial scales, and involving different substrates within the soil system (Taneva et al., 2006) and includes respiration by live roots, root-associated microorganisms, and microbial decomposition of root exudates (collectively referred to as root/rhizosphere respiration, $R_R$), as well as from heterotrophic respiration ($R_H$) associated with the decomposition of root and leaf litter, and other soil organic matter (SOM) pools of different ages. Ecosystem exposure to elevated [CO$_2$] has been shown to lead to enhanced $R_S$ rates initially (Zak et al., 2000; King et al., 2004; Bernhardt et al., 2006; Taneva et al., 2006). However, it remains unclear whether these changes are the result of increased $R_R$, $R_H$, or a combination of both (Gonzalez-Meler and Taneva, 2005; Subke et al., 2006).

Because individual components of $R_S$ return soil carbon of different age back to the atmosphere, a shift in their relative contributions to total $R_S$ with environmental changes, will impact the residence time of soil C and, therefore, atmospheric CO$_2$ levels, by affecting the C sink strength of soils. For instance, atmospheric CO$_2$ enrichment may cause increases in belowground plant biomass production (Hungate et al., 1997; Edwards and Norby, 1999; Matamala and Schlesinger, 2000; Pregitzer et al., 2000; Norby et al., 2002) and thus can lead to increased total $R_R$ rates. Greater soil C inputs under elevated [CO$_2$] may also increase substrate availability to soil microorganisms and lead to higher $R_H$ rates (Hamilton et al., 2002; Pendall et al., 2003; Makiranta et al., 2008; Wei et al., 2010). Increases in $R_S$ rates caused solely by a photosynthesis-driven direct enhancement of $R_R$ may have little consequence to SOM pool changes and atmospheric CO$_2$ concentration. Heterotrophic respiration, on the other hand, returns older soil C to the atmosphere and changes in both the sources and rates of $R_H$ with environmental conditions (e.g. elevated [CO$_2$], plant activity, altered soil moisture and/or temperature) could substantially affect the C sink capacity and turnover of soil.
Partitioning $R_S$ into its components is inherently difficult and a variety of methods have been applied to the separation of $R_R$ from $R_H$ (Hanson et al., 2000; Subke et al., 2006). The average contribution of $R_R$ to total $R_S$ in temperate forests has been estimated to be $\sim$45%, with a range of 10 to 90% (Hanson et al., 2000; Bond-Lamberty et al., 2004). The proportion of $R_R$ has been shown to be related to annual $R_S$ rates and may not be constant across temporal or spatial scales (Bond-Lamberty et al., 2004; Subke et al., 2006; Kuzyakov and Gavrichkova, 2010), challenging the use of a single annual value for $R_R/R_S$ in terrestrial C cycle models. An emerging pattern from $R_E$ partitioning studies is that photosynthesis exerts a strong influence on $R_S$ on diel and seasonal time scales (Hogberg et al., 2001; Bowling et al., 2002; Tang et al., 2005; Kuzyakov and Gavrichkova, 2010). Trueman and Gonzalez-Meler (2005) showed that both autotrophic and the heterotrophic oxidation of soil C pools older than 4 years were both influenced by changes in plant activity. These observations suggest that there are complex interactive effects between $R_S$ components that may operate at different time scales, involving several soil C pools that may differ in chemical composition and soil residence time (Heath et al., 2005). The interactive effects of biotic and abiotic variables on $R_S$ are unclear.

Temperature- and moisture-dependent models are widely used for predicting the response of terrestrial ecosystems to changing environmental conditions (Lloyd and Taylor, 1994; Reichstein et al., 2003; Luo et al., 2007). Individual components of $R_S$, however, can often be independently affected by other abiotic or biotic variables, as well as by their interactions (Kuzyakov and Gavrichkova, 2010). A significant amount of photosynthetic carbon is returned to the atmosphere through $R_R$ within days of assimilation (Ekblad and Hogberg, 2001; Bowling et al., 2002; Trueman and Gonzalez-Meler, 2005; Taneva et al., 2006; Carbone et al., 2007; Mencuccini and Hölttä, 2010;
Kuzyakov and Gravrichkova, 2010), highlighting the importance of photosynthesis in influencing $R_S$ rates. Enhanced plant activity with elevated [CO$_2$] may also lead to changes in the decomposition rate of older SOM and, through “priming” and other indirect effects, can result in changes in the size of the SOM pool and, therefore, its turnover time (Kuzyakov, 2002; Subke et al., 2004). These biotic controls on components of $R_S$ can often be confounded with the temperature- and moisture-dependent functions observed to explain variations in $R_S$ at seasonal time scales, potentially leading to limitations in our mechanistic predictions of ecosystem C budgets (Liu et al., 2006).

In this study, we used the long-term $^{13}$C tracer at the Duke Forest Free Air CO$_2$ Enrichment (FACE) experiment (Chapel Hill, NC, USA) to partition growing season $R_S$ into the contributions of root/rhizosphere respiration, litter decomposition, and decomposition of two pools of root-free SOM in situ after 8 years of elevated CO$_2$ exposure. Stable isotope labeling techniques have been used successfully to partition $R_S$ into some of its components (e.g. Andrews et al., 1999; Matamala et al., 2003; Pendall et al., 2003; Taneva et al., 2006) and provide a non-disruptive alternative to disturbance or harvest methods of distinguishing the origin of soil-respired C. Our specific objectives were: (1) to determine the seasonal and diel variability of $R_S$ rates and components; and (2) to understand how $R_S$ components affect observed rates of $R_S$.

2 Materials and methods

2.1 Site description

The Forest Atmosphere Carbon Transfer and Storage 1 (FACTS-1) research site is located in the Blackwood Division of the Duke Forest, near Chapel Hill, North Carolina, USA (35°58′ N 79°05′ W). The Free Air CO$_2$ Enrichment (FACE) experiment at FACTS-1 is composed of six 30-m diameter plots in an intact loblolly pine (*Pinus taeda*) plantation. Three of the experimental plots are fumigated with CO$_2$ to maintain an
atmospheric $[^{12}C]CO_2$ that is approximately 200 µL L$^{-1}$ above ambient, or approximately 567 ± 4 µL L$^{-1}$ (averaged from 1996–2004; K. Lewin and R. Nettles, personal communication); the three control plots are fumigated with ambient air only (Hendrey et al., 1999). Continuous fumigation of all plots began on 27 August 1996, when the trees were 15 years old. CO$_2$ fumigation is switched off when temperatures are below 5 °C and when sustained wind speed exceeds 5 m s$^{-1}$. Starting 16 December 2002, fumigation was reduced to daytime only.

The loblolly pine plantation was established in 1983, with 3-year-old seedlings planted at 2 × 2.4 m spacing. Through natural regeneration, a number of hardwood species have become established in the understory, the most abundant of which are Acer rubrum, Liquidambar styraciflua, Liriodendron tulipifera, Ulmus alata, and Cercis canadensis. Soils at the site are clay-rich, low fertility Ultic Alfisols, derived from igneous rock, with a pH of ~5. Fine roots are found mostly in the upper 20 cm of the soil profile (Matamala and Schlesinger, 2000). Mean annual temperature is 15.5 °C and mean annual precipitation is 1140 mm.

2.2 Ecosystem $^{13}C$ tracer

The CO$_2$ used for fumigation at FACTS-1 is strongly depleted in $^{13}C$ vs. PDB ($\delta^{13}C \approx -43.1 \pm 0.6‰$ SE, where $\delta^{13}C = [(R_{\text{sample}} - R_{\text{reference}})/R_{\text{reference}}] \times 1000$ and $R =^{13}C/^{12}C$). By increasing atmospheric $[^{12}C]CO_2$ by 200 µL L$^{-1}$ in the treatment plots, the $\delta^{13}C$ of atmospheric CO$_2$ is changed from about −8 to −20 ± 0.4‰. Consequently, new needles and fine roots produced under FACE have a $\delta^{13}C$ of −41.8 ± 0.3‰ and −39.2 ± 0.8‰ compared to $\delta^{13}C$ of −29.9 ± 0.2‰ and −27.6 ± 0.2‰ at ambient conditions, respectively (Matamala et al., 2003; L. Taneva, unpublished data, 2003). The fumigated forest plots have been exposed to a continuous ecosystem $^{13}C$ label since the beginning of the CO$_2$ treatment in 1996 and, through its incorporation into plant biomass, the $^{13}C$ label has been incorporated into soil organic matter pools and is
detected in soil-respired CO\textsubscript{2} (Andrews et al., 1999; Schlesinger and Lichter, 2001; Taneva et al., 2006).

2.3 Growing season soil respiration

During the 2003 and 2004 growing seasons, soil respiration rates were measured with a field-portable infrared gas analyzer (IRGA; LiCor 6400-09, Lincoln, Nebraska, USA) at 12 PVC collars, randomly placed within each FACE plot. Soil collars were permanently inserted 3 cm into the mineral soil and were open to rainfall and litterfall, except during measurements. In May 2004, four additional soil collars were installed in each FACE plot, where the litter layer was completely removed down to the mineral soil and a thin layer of inert fiber glass was placed over the soil, in order to reproduce the CO\textsubscript{2} diffusivity and moisture content of the removed litter. Soil respiration rates were measured monthly during the growing season of the forest (May–October), both during the day (12:00–14:00 EST) and at night (22:00–00:00 EST). Measurements were made at the times previously determined to capture most of the variability in soil respiration rates (data not shown). The six FACE plots were grouped into three blocks, each including one treatment and one control plot. The measurement time in each plot was \(\sim 1\) h and, therefore, only one block was measured a day, in order to avoid temporal variability of soil respiration rates during time of measurement. Measurements in all three blocks were carried out on days with comparable environmental conditions and were usually completed within 5–6 days.

2.4 Sample collection and stable isotope analysis of soil-respired CO\textsubscript{2}

During the 2003 and 2004 growing seasons, soil-respired CO\textsubscript{2} samples were collected monthly from collars with and without litter layer, both during the day and at night, 24 h after soil respiration measurements were made (see above). Gas samples were collected from a LiCor 6400-09 soil chamber into evacuated 150-ml glass flasks, after being passed through a magnesium perchlorate water trap (see Trueman and
Temporal variability in soil respiration components

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Introduction

During the growing season of 2004 soil cores (0–10 cm) were collected from locations adjacent to collars after respiration and isotope measurements were done throughout the course of the experiment. Roots and leaf litter were removed from the soil immediately after soil collection. Live fine roots were rinsed in distilled water of all attached soil and soil was removed from the litter layer by hand. In order to determine the $\delta^{13}C$ of respired CO$_2$, the litter layer, live roots, and root-free soil collected from each FACE plot were incubated separately in the dark in custom-designed PVC chambers with screw caps (400-ml chambers for soil and litter incubations and 150-ml chambers for root incubation), using a method similar to that described in Taneva and Gonzalez-Meler (2008). The field incubation system consisted of a pump, a soda lime column placed before the incubation chamber, a desiccant column placed between the chamber and...
the glass flask, where the respired CO₂ was eventually collected, and an IRGA (LiCor 6262, Lincoln, Nebraska, USA). All components of the incubation system were connected to each other with Bev-A-Line® tubing (1/4” outer diameter). Before sample incubation, the chamber, the 150-ml glass flask, and the line were flushed with CO₂-free air by pumping dry ambient air through the soda lime column. The IRGA, placed after the flask, was used to monitor the [CO₂] of the air in the incubation system. The air-tight chamber remained close with three-way valves (Swagelok, Solon, OH, USA) for an incubation period of 20–30 min, depending on respiration rate. After the incubation and prior to collecting the respired CO₂ from each sample, the incubation system was once again flushed with CO₂-free air, bypassing the closed incubation chamber, to ensure the lines and flask were free of H₂O and CO₂. CO₂-free air was then allowed to pass through the incubation chamber and the respired CO₂ was transferred through the desiccant column into the glass flask, reaching a maximum value between 400 and 1200 ppm. Flask samples were shipped to the University of Illinois at Chicago for analysis. These incubation experiments were also done at the ambient rings to account for environmental variability in the isotopic composition of respired CO₂ from roots and litter that are independent from the addition of the post treatment isotope label in these pools. The δ¹³C value of respired CO₂ from roots, litter, and root-free soil from each plot (Table 1) was used in the partitioning of soil-respired CO₂ (see below).

2.6 Mixing models and end-member determination

Soil-respired CO₂ was first partitioned into C that was photosynthetically fixed since the beginning of CO₂ fumigation (referred to as “post-treatment” C) and C assimilated under ambient [CO₂] before fumigation started in 1996 (referred to as “pre-treatment” C), according to the following two end-member mixing equation:

\[
\delta^{13}C_{RsCO_2} = f \cdot \delta^{13}C_{pre-tr} + (1-f) \cdot \delta^{13}C_{post-tr}
\]

(1)
where $\delta^{13}C_{RsCO2}$ is the measured $\delta^{13}C$ of soil-respired CO$_2$ at time $t$, $\delta^{13}C_{post-tr}$ is the end-member for post-treatment C, $\delta^{13}C_{pre-tr}$ is the end-member for pre-treatment C at time $t$ and $f$ represents the fraction of pre-treatment C in soil CO$_2$ at time $t$ (Taneva et al., 2006).

The $\delta^{13}C_{pre-tr}$ is determined by directly measuring $\delta^{13}C_{RsCO2}$ in the control plots of the experiment at time $t$. This measured value incorporates respiration from both recalcitrant and labile soil C pools under ambient CO$_2$ conditions. Because the $\delta^{13}C$ of recalcitrant soil C pools has little or no seasonal variation (Balesdent and Mariotti 1996), any seasonal variability in $\delta^{13}C$ of soil-respired CO$_2$ in the control plots will be mainly due to differences in the signature of labile soil C pools (i.e. root/rhizosphere respiration), reflecting, for instance, seasonal fluctuations in photosynthetic discrimination. Because the $\delta^{13}C$ of the atmosphere in the CO$_2$-enriched plots was changed by a constant value ($E$) at the beginning of the experiment and because photosynthetic discrimination against $^{13}C$ is the same under ambient and elevated [CO$_2$] (due to lack of photosynthetic acclimation and conserved $C_i/C_a$ between ambient and elevated [CO$_2$] plots (Ellsworth, 1999), the difference in $\delta^{13}C$ of new photosynthate in the control and treatment plots also equals $E$. Therefore, the end-member for the $\delta^{13}C$ of soil-respired CO$_2$ in the enriched plots ($\delta^{13}C_{post-tr}$) can be derived by subtracting $E$ from the measured $\delta^{13}C_{pre-tr}$ and Eq. (1) can be rearranged as follows:

$$f = \left( \frac{\delta^{13}C_{RsCO2} - \delta^{13}C_{post-tr}}{E} \right) \quad (2)$$

where $E$ was found to be 12 ± 0.1‰.

### 2.7 Partitioning soil-respired CO$_2$ into its components

The litter exclusion experiments in 2004 enabled us to further partition soil-respired CO$_2$ into CO$_2$ originating from root/rhizosphere respiration ($R_R$), litter decomposition ($R_L$), and SOM decomposition ($R_{SOM}$).
The contribution of \( R_R \), \( R_{SOM} \), and \( R_L \) to total \( R_S \) can then be express as follows:

\[
\delta^{13}C_{RsCO_2} = a \cdot \delta^{13}C_{rootCO_2} + b \cdot \delta^{13}C_{SOMCO_2} + (1 - (a + b)) \cdot \delta^{13}C_{litterCO_2},
\]

where the fraction of root-respired \( CO_2 \) \((a)\) was determined from Eq. (4), \( b \) represents the fraction of soil-respired \( CO_2 \) produced in SOM decomposition, and the remaining \( CO_2 \) in \( R_S \), determined as \((1 - (a + b))\), represents \( CO_2 \) produced in litter decomposition.

Because the ratio of \( R_R \) to \( R_{SOM} \) in the plots without litter is the same as that in plots with litter, the fractions of \( R_R \) and \( R_{SOM} \) in plots without litter (nl) can be expressed as follows:

\[
\delta^{13}C_{nlCO_2} = (a/(a + b)) \cdot \delta^{13}C_{rootCO_2} + (b/(a + b)) \cdot \delta^{13}C_{SOMCO_2},
\]

where \( a \) represents the fraction of root-respired \( CO_2 \) in \( R_S \), \( b \) is the fraction of SOM decomposition in \( R_S \), \( \delta^{13}C_{nlCO_2} \) is the \( \delta^{13}CO_2 \) from collars with no litter as determined from Keeling Plot analyses, \( \delta^{13}C_{root} \) is the \( \delta^{13}C \) of root-respired \( CO_2 \) determined from root incubations, and \( \delta^{13}C_{SOM} \) is the \( \delta^{13}C \) measured with litter- and root-free soil incubations (Table 1; incubations discussed above). To calculate the actual amount of \( C \) each of these components contribute to total \( R_S \), the fractional values of \( a \), \( b \), and \((1 - (a + b))\) calculated over the growing season were multiplied by the measured \( R_S \) rate at time \( t \).

Assuming that the fraction of soil-respired \( CO_2 \) (i.e. in total \( R_S \)) derived from pre-treatment \( C \) pools (i.e., \( C \) assimilated before 1996; Eq. 1) all originated from SOM decomposition, SOM decomposition was further partitioned into pre-treatment (oxidation of soil pools older than 8 years) and post-\( CO_2 \) treatment \( C \) decomposition. The contributions of \( C_{pre-tr} \) and \( C_{post-tr} \) were applied to the rate of SOM decomposition estimated from Eq. (3).

In addition, a sensitivity analyses was made to estimate the sensitivity of the calculated \( R_R \), \( R_{SOM} \) and \( R_L \) components of \( R_S \) to endmember determinations. For this sensitivity analyses we applied a \( \pm 1\% \) to the root, SOM and litter respired \( CO_2 \) determinations form the incubation chambers to account for potential errors in gas collections
and for potential rapid shift in substrates used for respiration in the isolated components. We performed this analysis for each month and time of day we calculated the root litter and SOM component partitioning of $R_S$.

### 2.8 Soil temperature and moisture

Continuous soil temperature measurements were taken at 10 cm depth in each FACE plot, using Siemens Type M 841/S1 thermistors (one per plot). Continuous soil moisture measurements were taken with a Campbell Scientific Model CS 615 probes (Logan, Utah, USA) consisting of two 30 cm long metal rods, over which each moisture measurement is integrated. Soil temperature and moisture measurements were taken every 5 or 30 s, averaged over 30 min intervals and automatically logged with Campbell 21X or 23X data loggers.

The rate of total $R_S$ and each $R_S$ component was plotted against soil temperature and soil moisture at each measurement date and time (regressions not shown). The relationship between soil temperature and $R_S$ and its components was determined by fitting a second-order exponential growth function to the data, according to the equation $f = ae^{bx}$ (Lloyd and Taylor, 1994). The relationship between $R_S$ and each $R_S$ component and soil moisture was determined by fitting linear functions to the data, according to the equation $f = y_0 + ax$ (Orchard and Cook, 1983).

### 2.9 Statistical analyses

Temporal variability in $R_S$ and $R_S$ components was examined with mixed-effects regression analysis (Proc Mixed, SAS v. 9.1, Cary, NC). Rates of $R_S$ in 2003 and 2004 were fitted to a regression model with CO$_2$ treatment, time of day, month, and year as covariates, and interactions of CO$_2$ treatment with time of day and year. Regression models with effects for month, time of day (day or night), month by time of day interaction, and a random effect for plot were fitted to $R_R$, $R_{SOM}$, $R_{pre-tr}$, $R_{post-tr}$, and $R_L$ rates.
3 Results

3.1 Seasonal and interannual variability of soil respiration ($R_S$)

Soil respiration rates were not significantly stimulated by ecosystem exposure to elevated [CO$_2$] during 2003 ($p > 0.5$), but there was a significant CO$_2$ treatment effect on $R_S$ in 2004 ($p < 0.03$), when overall $R_S$ rates were higher (Fig. 1). Rates of $R_S$ were on average 14% higher under elevated [CO$_2$] in 2004 relative to ambient CO$_2$ conditions. The magnitude of the CO$_2$ treatment effect on $R_S$ differed during the day and night and varied seasonally in the two years of measurement (Fig. 1). Daytime $R_S$ rates under elevated [CO$_2$] in 2003 were between 1% (in August, $p > 0.8$) and 20% (in September, $p > 0.1$) higher than daytime $R_S$ rates under ambient [CO$_2$]. Nighttime $R_S$ rates in 2003 were between −5% (in August, $p > 0.5$) and 10% (in September, $p > 0.5$) higher than nighttime rates under ambient [CO$_2$]. In 2004, the enhancement of daytime $R_S$ rates in the treatment plots was between 9% (in August, $p > 0.1$) and 21% (in July, $p < 0.002$). Nighttime $R_S$ rates under elevated [CO$_2$] in 2004 were between 5% (in August, $p > 0.4$) and 17% (in July, $p < 0.02$) higher than $R_S$ rates in the control plots.

Rates of $R_S$ differed significantly in the two years of study ($p < 0.0001$); $R_S$ rates in 2004 were on average 16% higher than $R_S$ rates in 2003 (Fig. 1). Rates of $R_S$ in both treatment and control plots showed seasonal variability in both years of study ($p < 0.0001$) with higher $R_S$ in the middle of the growing season (Fig. 1).

3.2 Differences in nighttime and daytime $R_S$

Daytime and nighttime $R_S$ rates were not significant different during the two years of measurements ($p > 0.2$) under either ambient or elevated [CO$_2$], with the exception of a significant CO$_2$ treatment x time interaction in 2003 ($p < 0.04$; Fig. 1). In 2003, daytime $R_S$ rates were on average 6% higher than nighttime rates under elevated [CO$_2$]; at ambient [CO$_2$], average daytime and nighttime $R_S$ rates differed by less than 1%. In 2004, daytime $R_S$ rates were 3% higher than nighttime rates under elevated [CO$_2$].
and 3% lower than nighttime rates under ambient [CO₂]. Daytime \( R_S \) rates were 9% higher in 2003 and 17% higher in 2004 under elevated [CO₂] relative to ambient [CO₂] (Fig. 1). Nighttime rates of \( R_S \) were 2% and 12% greater under elevated [CO₂] in 2003 and 2004, respectively (Fig. 1).

### 3.3 Soil respiration components under elevated [CO₂]

#### 3.3.1 Pre-Treatment and Post-Treatment C in \( R_S \) in 2003 and 2004

In 2003, the contribution of post-treatment C (less than 8 years old) to daytime \( R_S \) ranged from 58.6 ± 8.3\% in May to 87.5 ± 5.1\% in July (Fig. 2). At night, the contribution of post-treatment C to \( R_S \) ranged from 56.2 ± 12.9\% in June to 84.0 ± 3.8\% in August.

In 2004, the daytime contribution of post-treatment C to \( R_S \) was higher than in 2003 and ranged from 82.5 ± 9.1\% in May to 89.9 ± 3.5\% in July (Fig. 2). The contribution of post-treatment C to nighttime \( R_S \) was less than during the day and ranged from 76.6 ± 9.1\% in August to 84.8 ± 6.3\% in May (Fig. 2).

#### 3.3.2 Root/rhizosphere respiration (\( R_R \))

In 2004, \( R_R \) had a seasonal average of 2.81 ± 0.50 µmol CO₂ m⁻² s⁻¹ during the day and 3.04 ± 0.66 µmol CO₂ m⁻² s⁻¹ at night (Fig. 3; Table 2). Overall daytime and nighttime \( R_R \) rates were not significantly different (\( p > 0.03 \)), despite significant differences in diel rates in August. Overall, \( R_R \) rates were 8% lower during the day than at night (Table 2). Significantly higher rates of \( R_R \) were observed in the middle of the season (July and August) relative to rates early or late in the season (June and September), both during the day (36\%; \( p < 0.001 \)) and at night (39\%; \( p < 0.0001 \)). These differences were mostly due to much lower daytime \( R_R \) rates in September and much higher nighttime rates in August, relative to the rest of the season (Table 2). Daytime and nighttime \( R_R \) rates in the middle of the season were also significantly different from those early or late in the season (\( p < 0.0001 \)).
The average contribution of $R_R$ to total $R_S$ was $29.7 \pm 5.3\%$ during the day, ranging from $14.1 \pm 4.4\%$ in September to $36.8 \pm 4.1\%$ in June (Table 2). At night, the average contribution of $R_R$ to total $R_S$ was $33.7 \pm 5.9\%$, ranging from $26.6 \pm 4.5\%$ in September to $51.4 \pm 3.5\%$ in August (Table 2).

3.3.3 Litter decomposition ($R_L$)

In 2004, $R_L$ had a seasonal average of $2.56 \pm 0.99 \mu mol\ CO_2\ m^{-2}\ s^{-1}$ during the day and $1.16 \pm 0.57 \mu mol\ CO_2\ m^{-2}\ s^{-1}$ at night (Fig. 3; Table 2). Overall, daytime $R_L$ rates were significantly different from nighttime rates ($p < 0.0001$), despite non-significant differences in diel rates in June and July (Fig. 3). On average, daytime $R_L$ rates were $55\%$ higher than nighttime $R_L$ rates. Neither daytime nor nighttime rates of $R_L$ showed seasonal variability ($p > 0.2$).

The average contribution of $R_L$ to total $R_S$ was $26.3 \pm 10.5\%$ during the day, ranging from $0\%$ in June to $51.4 \pm 6.7$ in September (Table 2). At night, the average contribution of $R_L$ to total $R_S$ was $12.6 \pm 6.2\%$, ranging from $0\%$ in June to $24.3 \pm 6.2\%$ in July (Table 2).

3.3.4 SOM decomposition ($R_{SOM}$)

In 2004, $R_{SOM}$ had a seasonal average of $4.11 \pm 0.44 \mu mol\ CO_2\ m^{-2}\ s^{-1}$ during the day and $4.69 \pm 0.21 \mu mol\ CO_2\ m^{-2}\ s^{-1}$ at night (Fig. 3; Table 2). There were significant differences in daytime and nighttime $R_{SOM}$ rates ($p < 0.02$), mostly because of significant differences between daytime and nighttime $R_{SOM}$ rates in September ($p < 0.01$; Fig. 3). Overall, daytime $R_{SOM}$ rates were $14\%$ lower than nighttime $R_{SOM}$ rates. Significantly higher rates of $R_{SOM}$ were observed early in the season (June and July) relative to later in the season (August and September) during the day ($23\%; p < 0.003$), mostly because of high $R_{SOM}$ rates in June (Fig. 3; Table 2); there were no significant differences between early- and late-season nighttime $R_{SOM}$ rates ($p > 0.2$).
The average relative contribution of $R_{SOM}$ to total $R_S$ was 44.1 ± 6.6% during the day, ranging from 34.5 ± 8.0% in September to 63.5 ± 8.4% in June (Table 2). At night, the average contribution of $R_{SOM}$ to total $R_S$ was 53.7 ± 5.8%, ranging from 44.7 ± 7.3% in August to 70.8 ± 9.7% in June (Table 2).

### 3.4 Post-treatment SOM decomposition

$R_{SOM}$ can be further distinguished between two age pools: pre-treatment C consisting of C fixed by the ecosystem prior to September 1996 (>8 years old), and post-treatment C, assimilated after fumigation began (<8 years old). In 2004, the seasonal average rate of post-treatment SOM decomposition was 2.83 ± 0.53 µmol CO$_2$ m$^{-2}$ s$^{-1}$ during the day and 2.89 ± 0.45 µmol CO$_2$ m$^{-2}$ s$^{-1}$ at night (Fig. 4). Overall rates of post-treatment SOM-C decomposition did not significantly differ between day and night ($p > 0.7$; Fig. 4). Post-treatment SOM decomposition showed seasonal variability, with higher rates earlier in the season (June and July), both during the day (40%, $p < 0.0001$) and at night (34%, $p < 0.001$). The average contribution of post-treatment SOM decomposition to total $R_S$ was 30.4 ± 6.8% during the day, ranging from 16.2 ± 5.4% in September to 48.6 ± 5.6% in June (Table 2). At night, the average contribution of post-treatment $R_{SOM}$ to total $R_S$ was 33.7 ± 7.5%, ranging from 22.5 ± 4.8% in August to 55.9 ± 6.5% in June (Table 2).

### 3.5 Pre-treatment SOM decomposition

In 2004, the seasonal average rate of pre-treatment SOM decomposition had a seasonal average of 1.28 ± 0.16 µmol CO$_2$ m$^{-2}$ s$^{-1}$ during the day and 1.81 ± 0.26 µmol CO$_2$ m$^{-2}$ s$^{-1}$ at night (Fig. 4). Unlike rates of post-treatment SOM decomposition, the rates of pre-treatment SOM decomposition differed significantly between day and night ($p < 0.0001$), despite non-significant differences in June ($p > 0.4$), with nighttime rates 29% higher than daytime rates (Table 2). Seasonal variability in the decomposition of pre-treatment SOM was also significant but, unlike rates of post-treatment SOM decomposition.
decomposition, rates of pre-treatment SOM decomposition earlier in the season (June and July) were lower than rates later in the season (August and September), both during the day (25%, \( p < 0.005 \)) and at night (36%, \( p < 0.0001 \)).

The average relative contribution of pre-treatment SOM decomposition to total \( R_S \) was \( 13.7 \pm 1.9\% \) during the day, ranging from \( 9.7 \pm 4.7\% \) in July to \( 18.5 \pm 5.1\% \) in September (Table 2). At night, the average contribution of pre-treatment SOM decomposition to total \( R_S \) was \( 20.0 \pm 2.2\% \), ranging from \( 14.9 \pm 6.3\% \) in June to \( 24.8 \pm 5.3\% \) in September (Table 2).

### 3.6 Sensitivity analyses of endmember determinations

It has been documented that the isotopic composition of respired CO\(_2\) can shift relatively rapid with changes in substrates, diffusion or other factors (see Vargas et al., 2011). To account for this potential variation, we performed a sensitivity analysis for each month and time of day for which the component partitioning of \( R_S \) was measured by calculating the effect of a 1‰ shift in the isotopic composition of respired CO\(_2\) of any given endmember on the component partitioning results of \( R_S \). We found that for every 1‰ change in the isotopic composition of end members respired-CO\(_2\), the \( R_R \) component of \( R_S \) varied up to 15% whereas the variation in the \( R_{SOM} \) or \( R_L \) contribution to \( R_S \) was less than 6% on average.

### 3.7 Soil temperature and moisture

There were no significant differences in daytime and nighttime soil temperature or moisture for the measurement periods in this study \( (t\text{-test}, \ p > 0.05) \). None of the relationships between total \( R_S \) or individual \( R_S \) components and soil temperature or moisture were significant (regressions not shown).
4 Discussion

In this study, we documented that variations in individual components of $R_S$ do not always lead to measurable variations in overall $R_S$ efflux rates. We also report that diel differences in rates of $R_S$ components are not easily explained by passive temperature and moisture controls, and that biotic controls of $R_H$ may be important in determining rates of SOM oxidation. While this is not the first study to separate $R_S$ into more than two components (Sulzman et al., 2005; Cisneros-Dozal et al., 2006; Subke et al., 2011), to our knowledge, this is among the first reports of the diel and seasonal changes in the contribution of several $R_S$ components to total growing season efflux rates under field conditions. Our results suggest that using $R_S$ as an integrator of fast and slow soil biological activity and their responses to environmental change may be too coarse; individual components contributing to soil CO$_2$ efflux could respond differently to the same variables. Understanding the sources of soil CO$_2$ efflux and its dependent biotic and abiotic controls are important in elucidating the environmental effects on $R_S$ rates at different time scales.

By combining the ecosystem $^{13}$C tracing of fumigation CO$_2$ (as in Taneva et al., 2006) with incubations of litter, roots, and root-free soil, we were able to partition $R_S$ further into rhizosphere-, litter-, and two pools of soil-derived C in situ during the day and at night throughout the growing season of a warm-temperature forest exposed to elevated atmospheric [CO$_2$] after 8 years of $^{13}$C application. Due to the lack of a $^{13}$C tracer in the control plots at the Duke Forest FACE site, we were only able to study $R_S$ components under ecosystem exposure to elevated [CO$_2$] and a comparison of the contributions of different $R_S$ components under ambient and elevated CO$_2$ conditions was not possible. Several studies have reported increased $R_S$ rates under elevated [CO$_2$] (Zak et al., 2000; King et al., 2004; Bernhardt et al., 2006; Taneva et al., 2006) and our results are in agreement with these reports (Fig. 1). Even though the stimulation of $R_S$ by elevated [CO$_2$] in this study was not always significant, we recognize that our results are constrained by enhanced $R_S$ rates in the treatment plots. By taking advantage of

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the ecosystem $^{13}$C tracer, however, we were able to examine if and how the temporal dynamics of $R_S$ components translate into temporal variability of total $R_S$.

### 4.1 Soil respiration and its components

We studied the daytime and nighttime differences and seasonal dynamics of four $R_S$ components in a temperate forest exposed to elevated [CO$_2$] and found that the presence of absence of temporal variability of total $R_S$ rate could not be attributed to variability in the rate of any single $R_S$ component. The seasonal contribution of $R_R$ to total $R_S$ in this study ranged from 14% to 37% during the day, in the lower end of the annual range of 20–84% reported for temperate coniferous forests (Subke et al., 2006). Our estimate of the contribution of $R_R$ to $R_S$ is also lower than the estimates of 55% for the beginning of the FACTS-1 experiment in September 1997 (Andrews et al., 1999) or that of 48% derived from a processed-based $Q_{10}$ approach (Hamilton et al., 2002), both calculated from midday rates of $R_S$. Furthermore, most of the studies reviewed by Subke et al. (2006), report the fraction of $R_R$ in $R_S$ on an annual basis, while our results are from the growing season only when rates of $R_S$ are at their maximum. Interestingly, Subke et al. (2006) report a relative increase in the fraction of $R_R$ with increasing $R_S$ rate, suggesting that $R_R$ may dominate $R_S$ during the growing season, whereas $R_H$ may be the relative dominant during the dormant season when total $R_S$ rates are low. The proportion of $R_R$ in $R_S$ found in this study is consistent with the relatively low levels of root productivity and turnover in this pine forest as compared to other temperate forests (Matamala and Schlesinger, 2000; Matamala et al., 2003).

Heterotrophic respiration was the dominant component of growing season $R_S$ in this forest, constituting 63 to 86% of daytime $R_S$ rates (Table 2), within the reported range of 16–80% for the contribution of $R_H$ to $R_S$ in temperate coniferous forests (Subke et al., 2006). It is recognized that $R_H$ can result from a number of soil C pools of different composition and turnover time. Usually $R_H$ is treated as a single $R_S$ component, but it is recognized that $R_H$ can result from a number of soil C pools of different composition,
turnover time, and turnover controls. In this study, we partitioned \( R_H \) into litter decomposition and SOM decomposition and found that the contribution of \( R_{SOM} \) to daytime \( R_S \) rates ranged from 35 to 64% (Table 2). Litter decomposition in this study constituted from 0 to 51% of total \( R_S \). Cisneroz-Dozal et al. (2006) found the contribution of litter decomposition to total \( R_S \) to range from 1 to 42% of \( R_S \) during the growing season of a temperate deciduous forest and they attribute this variability to forest floor moisture content, in agreement with other studies (Hanson et al., 2003; Goulden et al., 2004; Lee et al., 2004). No significant relationships between soil moisture/temperature and \( R_L \) were found during the day or at night in this study, suggesting other possible controls on \( R_L \) in this forest (see Malcom et al., 2009). Although root litter decomposition was not directly accounted for in this study, its contribution to SOM decomposition is expected to be low due to low root productivity and slow root turnover rates in this forest.

4.2 Temporal variability in total \( R_S \) and \( R_S \) components

In this forest, \( R_S \) rates varied during the growing season, with higher \( R_S \) rates in the middle of the season (July and August; Fig. 1). While greater rates of \( R_R \) in July and August were correlated with increased \( R_S \), the contribution of \( R_H \) (\( R_{SOM} \) and \( R_L \)) to \( R_S \) was not constant during the growing season (Table 2), indicating that seasonal variability in \( R_R \) alone cannot explain the seasonal variability in \( R_S \). Notably, when \( R_S \) rates were at their highest, the rates of both \( R_R \) and \( R_{SOM} \) increased. These results indicate that increases in \( R_S \) rates are not always solely driven by higher root and rhizosphere activity, as seen in other studies (e.g. Hogberg et al., 2001). Different soil C pools may interact to produce observed rates of \( R_S \) and measurements of soil CO\(_2\) efflux alone cannot account for the variability of and interactions between \( R_S \) components (Trueman and Gonzalez-Meler, 2005).

Similarly, daytime rates of total \( R_S \) did not differ significantly from nighttime rates, but there were significant diel changes in individual \( R_S \) components (Figs. 1 and 3). All three components, \( R_R \), \( R_{SOM} \), and \( R_L \), had significantly different rates between day
and night, although the magnitude and direction of the difference in rates of each component varied throughout the growing season. The contribution of $R_R$ to total $R_S$ was greater at night later in the season than during the day (Table 2). The observed diel differences in $R_R$ are likely the result of the diurnal variability in the allocation of photosynthetic C to roots (Trueman and Gonzalez-Meler, 2005; Tang et al., 2005) and not necessarily to changes in soil temperature and moisture; daytime and nighttime values of soil temperature and moisture were not significantly different (Table 3). Because the diel differences in $R_R$ were not always significant in this study, the time lag between photosynthesis and $R_R$ may not be constant during the growing season of this forest (but see Stoy et al., 2007).

The average contribution of $R_{SOM}$ to $R_S$ was greater at night than during the day (Table 2). Since total $R_S$ rate did not differ between day and night, it is reasonable to expect that nighttime decreases in $R_R$ due to the absence of photosynthesis may be compensated for by increases in nighttime $R_{SOM}$. Root/rhizosphere respiration was not always lower at night, however, and lower $R_R$ did not always translate to higher $R_{SOM}$ (Fig. 3 and Table 2). Whether these variations were independent or the result of more complex interactions needs further study. Interestingly, the decomposition of C older than 8 years ($R_{pre-tr}$) showed more pronounced and consistent diel differences than any other $R_S$ component, with nighttime rates on average 29% higher than daytime rates. In contrast, the decomposition of more recent, post-treatment C ($R_{post-tr}$) did not differ between day and night, suggesting that the variability in $R_{SOM}$ appear to be due to changes in the decomposition of older C, rather than the decomposition of recently added SOM. Furthermore, the decomposition of older C was always higher at night and increased consistently during the growing season. These results indicate that oxidation of older decadal soil pools, or components within these C pools, may be able to respond to short-term biotic and/or abiotic changes. If decomposition of decadal SOM pools can rapidly respond to ecosystem exposure to environmental change, the implications for atmospheric $[CO_2]$ could be substantial.
The presence of unpredictable diel patterns in the rates of $R_S$ components, with no changes in soil temperature or moisture, suggests that primary and secondary responses of decomposers to changes in soil conditions exist. Because $R_S$ components may have different seasonal and diel patterns from total $R_S$, extrapolation of daytime measurements of $R_S$ to monthly or annual scales or application of growing season $Q_{10}$ values to annual $R_S$ may introduce a bias in long-term ecosystem C budgets. In our study, decomposition of SOM, particularly pre-fumigation SOM ($R_{pre-tr}$), was the only $R_S$ component that exhibited consistently higher contribution to $R_S$ at night, which increased towards the end of the growing season, despite no significant differences in intrinsic decomposition kinetics between $C_{pre-tr}$ and $C_{post-tr}$ at FACTS-1 (Taneva and Gonzalez-Meler 2005) and other studies (Trueman et al., 2009). These results suggest that the oxidation of decadal soil C pools may be affected by short-term environmental or biotic controls that may result from interactions between plant and decomposer activity.

Indirect evidence has shown that $R_R$ may be a possible driver of $R_S$ variability (Hogberg et al., 2001; Janssens et al., 2001; Bond-Lamberty et al., 2004; Subke et al., 2006). In this study, variability in $R_R$ alone was insufficient in explaining the seasonal and diel variability of $R_S$ because temporal changes in other $R_S$ components compensated for changes in $R_R$ and the decomposition of older soil C pools constituted a substantial fraction of total $R_S$ during the growing season of this forest (Table 2). Our results indicate that plant activity may exert a direct and/or indirect control over $R_S$ through cascading effects on other $R_S$ components beyond $R_R$. Plant activity has been previously linked to greater rates of SOM decomposition (Kuzyakov and Cheng, 2001; Kuzyakov, 2002; Subke et al., 2004; Trueman and Gonzalez-Meler, 2005) and an increasing number of studies have indicated that $R_S$ components are not independent of each other, but have interactive effects on $R_S$. These studies indicate that predicted increases in above- and belowground NPP with elevated $[CO_2]$ may not necessarily translate into greater soil C storage, as increases in plant activity may simultaneously increase the decomposition of recent and older C in forests (Hoosbeek et al., 2004;
Subke et al., 2004; Sulzman et al., 2005; Trueman and Gonzalez-Meler, 2005). Despite the importance of potential priming of SOM decomposition by enhanced plant activity with changing environmental conditions, mechanisms of priming remain poorly understood.

In summary, the results from these experiments show that the lack of diel changes in total $R_S$ cannot be interpreted as a sign that source components within $R_S$ do not vary. Conversely, because the diel changes in the four components of $R_S$ we measured was not consistent, the seasonal variation seen in $R_S$ for this forest cannot be attributed to proportional variation within these components. Our results also suggest that there are interactions between components of $R_S$ at both diel and seasonal time scales. Although the nature of these interactions could not be elucidated here, caution should be employed when applying temperature- and moisture-dependent functions to $R_S$, as soil organisms and roots are likely to actively modulate their activity rather than passively respond to abiotic factors.

**Acknowledgements.** This research was funded by NSF and DOE; LT was supported by a University of Illinois at Chicago Graduate Fellowship. We gratefully acknowledge the staff of Brookhaven National Laboratory and the Duke Forest for maintenance and operation of the FACTS-1 experiment. We thank Alice Niederland, J. S. Pippen, and T. Sagimoto for help in the field and Leah Simoni, Sergey Oleynik, and Matt Lorz for assistance in the laboratory. We thank Jim Burns for his help with statistical analyses. Dave Moore and Adrian Rocha provided constructive and insightful comments on earlier versions of this manuscript. The FACTS-1 experiment is supported by the Office of Science (BER), US Department of Energy.

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Table 1. The $^{13}$C signature of respired CO$_2$ from roots, root-free soil organic matter, and aboveground litter from control and treatment plots at FACTS-1. The average values listed here were derived from incubations (see methods) and site- and time-specific measurements were used as end-member values in the partitioning of soil-respired CO$_2$ (Eqs. 3 and 4). Average values are expressed in per mil ± standard error ($n = 3$).

| End-member (from incubations) | Ambient [CO$_2$] $\delta^{13}$C (‰) ± SE$^b$ | Elevated [CO$_2$] $\delta^{13}$C (‰) ± SE |
|------------------------------|--------------------------------|--------------------------------|
| Roots                        | $-29.1 \pm 0.5$                | $-40.4 \pm 1.0$                |
| Root-free SOM                | $-26.5 \pm 0.1$                | $-34.5 \pm 0.6$                |
| Aboveground Litter           | $-28.7 \pm 0.4$                | $-37.9 \pm 0.6$                |
Table 2. Absolute and relative contribution of soil respiration components to total CO$_2$ efflux during the day and at night in treatment plots at FACTS-1. Respiration rates are expressed in µmol CO$_2$ m$^{-2}$ s$^{-1}$ and show average values ($n = 3$) ± standard error.

| Day     | $R_{\text{root}}$ | % $R_{\text{root}}$ | $R_{\text{SOM}}$ | % $R_{\text{SOM}}$ | $R_{\text{litter}}$ | % $R_{\text{litter}}$ | $R_{\text{pre-tr C}}$ | % $R_{\text{pre-tr C}}$ |
|---------|------------------|----------------------|------------------|---------------------|---------------------|-----------------------|------------------------|------------------------|
| June    | 3.09 ± 0.34      | 36.8 ± 4.1           | 5.33 ± 0.71      | 63.5 ± 8.4          | 0.00 ± 0.56         | 0.0 ± 6.7             | 1.24 ± 0.47            | 14.8 ± 5.6             |
| July    | 3.45 ± 0.34      | 35.1 ± 3.5           | 3.94 ± 0.71      | 40.1 ± 7.2          | 2.45 ± 0.56         | 24.8 ± 5.7            | 0.95 ± 0.47            | 9.7 ± 4.7              |
| August  | 3.38 ± 0.34      | 32.6 ± 3.3           | 3.95 ± 0.71      | 38.2 ± 6.8          | 3.02 ± 0.56         | 29.2 ± 5.4            | 1.21 ± 0.47            | 11.7 ± 4.5             |
| September | 1.31 ± 0.41    | 14.1 ± 4.4           | 3.21 ± 0.76      | 34.5 ± 8.0          | 4.78 ± 0.62         | 51.4 ± 6.7            | 1.72 ± 0.48            | 18.5 ± 5.1             |
| Night   |                  |                      |                  |                     |                     |                       |                        |                        |
| June    | 2.19 ± 0.39      | 29.3 ± 5.2           | 5.29 ± 0.73      | 70.8 ± 9.7          | 0.00 ± 0.60         | 0.0 ± 8.0             | 1.11 ± 0.47            | 14.9 ± 6.3             |
| July    | 2.57 ± 0.36      | 27.5 ± 3.9           | 4.50 ± 0.72      | 48.2 ± 7.7          | 2.27 ± 0.58         | 24.3 ± 6.2            | 1.70 ± 0.47            | 18.2 ± 5.0             |
| August  | 5.00 ± 0.34      | 51.4 ± 3.5           | 4.35 ± 0.71      | 44.7 ± 7.3          | 0.38 ± 0.56         | 3.9 ± 5.8             | 2.17 ± 0.47            | 22.2 ± 4.8             |
| September | 2.40 ± 0.41    | 26.6 ± 4.5           | 4.63 ± 0.75      | 51.2 ± 8.2          | 2.00 ± 0.62         | 22.1 ± 6.9            | 2.24 ± 0.48            | 24.8 ± 5.3             |
Table 3. Soil temperature (°C) and volumetric soil water content at 10 cm in the treatment plots at FACTS-1. Reported values are means and standard error (n = 3).

| Month    | Soil temperature (°C) |            | Soil moisture (% vol) |            |
|----------|------------------------|------------|-----------------------|------------|
|          | Day        | Night   | Day       | Night   |
| June     | 20.15 (0.31) | 20.26 (0.34) | 0.21 (0.01) | 0.21 (0.01) |
| July     | 21.30 (0.17) | 21.38 (0.17) | 0.20 (0.02) | 0.20 (0.02) |
| August   | 21.20 (0.12) | 21.34 (0.11) | 0.28 (0.03) | 0.27 (0.03) |
| September| 19.10 (0.57) | 19.17 (0.42) | 0.29 (0.00) | 0.29 (0.00) |
Fig. 1. Diel soil respiration rates at FACTS-1 under ambient and elevated [CO₂] during the growing seasons of 2003 and 2004. Values are means ± standard error ($n = 3$).
Fig. 2. The contribution of pre-treatment and post-treatment soil carbon to day and night soil respiration rate during the growing seasons of 2003 and 2004 at FACTS-1. Values are means \((n = 3) \pm \text{standard error.}\)
**Fig. 3.** Contribution of soil respiration components to total soil respiration during the day and at night in 2004 at FACTS-1. Values are means ($n = 3$) ± standard error.
Fig. 4. The contribution of post- and pre-treatment soil organic carbon to daytime and nighttime soil respiration at FACTS-1. Values are means \((n = 3) \pm \text{ standard error.} \)