Biogeosciences Discuss., 8, 2875–2911, 2011
www.biogeosciences-discuss.net/8/2875/2011/
doi:10.5194/bgd-8-2875-2011

Biogeosciences
Discussions

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

C, with the potential to affect atmospheric [CO_2]. Therefore, a critical element in understanding the significance of increased net primary production (NPP) and R_S rates for C storage under elevated [CO_2] is identifying the origin of soil-respired carbon and its biotic and abiotic controls.

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 ∼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 [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 [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_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_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 ~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_2

During the 2003 and 2004 growing seasons, soil-respired CO_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

Gonzalez-Meler, 2005; Moore et al., 2009). The CO_2 concentration of each sample was measured at the time of sample collection. Eight gas samples from collars containing litter, and four samples from collars where the litter layer was excluded, were collected from each FACE plot at each sampling time. Gas samples were collected when the CO_2 concentration differed by at least 80 ppm from that of previous samples. Samples were collected from different collars to avoid alterations of convective patterns of CO_2 from soil to air and other recognized problems when collecting soil surface fluxes for building keeling plots (Phillips and Greg, 2001; Trueman and Gonzalez-Meler, 2005; Bowling et al., 2008; Kayler et al., 2010). Samples were shipped to the University of Illinois at Chicago for stable isotope analysis. In the laboratory, soil-respired CO_2 samples were purified by cryogenic extraction before they were analyzed for their stable C isotope composition with a Finnegan Delta Plus XL (Bremen, Germany) isotope ratio mass spectrometer. The $\delta^{13}C$ of soil-respired CO_2, in the absence of atmospheric air, was determined using Keeling Plot analyses (Pataki et al., 2003). The range in $[CO_2]$ of samples used to construct Keeling Plots was at least 320 ppm. Keeling Plot regressions with an r^2 value of <0.90 were excluded from further analysis.

2.5 Incubations for end-member determination

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 CO_2 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 CO_2-free air by pumping dry ambient air through the soda lime column. The IRGA, placed after the flask, was used to monitor the $[CO_2]$ 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 CO_2 from each sample, the incubation system was once again flushed with CO_2-free air, bypassing the closed incubation chamber, to ensure the lines and flask were free of H_2O and CO_2. CO_2-free air was then allowed to pass through the incubation chamber and the respired CO_2 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 CO_2 from roots and litter that are independent from the addition of the post treatment isotope label in these pools. The $\delta^{13}C$ value of respired CO_2 from roots, litter, and root-free soil from each plot (Table 1) was used in the partitioning of soil-respired CO_2 (see below).

2.6 Mixing models and end-member determination

Soil-respired CO_2 was first partitioned into C that was photosynthetically fixed since the beginning of CO_2 fumigation (referred to as “post-treatment” C) and C assimilated under ambient $[CO_2]$ before fumigation started in 1996 (referred to as “pre-treatment” C), according to the following two end-member mixing equation:

$$\delta^{13}C_{\mathrm{Rs\,CO2}} = f \cdot \delta^{13}C_{\mathrm{pre-tr}} + (1-f) \cdot \delta^{13}C_{\mathrm{post-tr}} \quad (1)$$

where $\delta^{13}C_{Rs\,CO2}$ 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 $\delta^{13}C_{Rs\,CO2}$ 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:

$$f = (\delta^{13}C_{Rs\,CO2} - \delta^{13}C_{post-tr})/E \qquad (2)$$

where E was found to be $12 \pm 0.1‰$.

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:

$$\delta^{13}\mathrm{C}_{\mathrm{Rs\,CO2}} = a \cdot \delta^{13}\mathrm{C}_{\mathrm{root\,CO2}} + b \cdot \delta^{13}\mathrm{C}_{\mathrm{SOM\,CO2}} + (1-(a+b)) \cdot \delta^{13}\mathrm{C}_{\mathrm{litter\,CO2}}, \tag{3}$$

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:

$$\delta^{13}\mathrm{C}_{\mathrm{nl\,CO2}} = (a/(a+b)) \cdot \delta^{13}\mathrm{C}_{\mathrm{root\,CO2}} + (b/(a+b)) \cdot \delta^{13}\mathrm{C}_{\mathrm{SOM\,CO2}}, \tag{4}$$

where a represents the fraction of root-respired CO_2 in R_S, b is the fraction of SOM decomposition in R_S, $\delta^{13}\mathrm{C}_{\mathrm{nl\,CO2}}$ is the $\delta^{13}CO_2$ from collars with no litter as determined from Keeling Plot analyses, $\delta^{13}\mathrm{C}_{\mathrm{root}}$ is the δ^{13}C of root-respired CO_2 determined from root incubations, and $\delta^{13}\mathrm{C}_{\mathrm{SOM}}$ is the δ^{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 $\mathrm{C}_{\mathrm{pre-tr}}$ and $\mathrm{C}_{\mathrm{post-tr}}$ 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 ±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 [CO_2]. Daytime R_S rates were 9% higher in 2003 and 17% higher in 2004 under elevated [CO_2] relative to ambient [CO_2] (Fig. 1). Nighttime rates of R_S were 2% and 12% greater under elevated [CO_2] in 2003 and 2004, respectively (Fig. 1).

3.3 Soil respiration components under elevated [CO_2]

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 CO_2 m^{-2} s^{-1} during the day and 3.04 ± 0.66 µmol CO_2 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 ± 5.3% during the day, ranging from 14.1 ± 4.4% in September to 36.8 ± 4.1% in June (Table 2). At night, the average contribution of R_R to total R_S was 33.7 ± 5.9%, ranging from 26.6 ± 4.5% in September to 51.4 ± 3.5% in August (Table 2).

3.3.3 Litter decomposition (R_L)

In 2004, R_L had a seasonal average of 2.56 ± 0.99 µmol CO_2 m^{-2} s^{-1} during the day and 1.16 ± 0.57 µmol 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 ± 10.5% during the day, ranging from 0% in June to 51.4 ± 6.7 in September (Table 2). At night, the average contribution of R_L to total R_S was 12.6 ± 6.2%, ranging from 0% in June to 24.3 ± 6.2% in July (Table 2).

3.3.4 SOM decomposition (R_{SOM})

In 2004, R_{SOM} had a seasonal average of 4.11 ± 0.44 µmol CO_2 m^{-2} s^{-1} during the day and 4.69 ± 0.21 µmol 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, 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 ± 1.9% during the day, ranging from 9.7 ± 4.7% in July to 18.5 ± 5.1% in September (Table 2). At night, the average contribution of pre-treatment SOM decomposition to total R_S was 20.0 ± 2.2%, ranging from 14.9 ± 6.3% in June to 24.8 ± 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-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_2conditions 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 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 ($R_{\text{pre-tr}}$), 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 $C_{\text{pre-tr}}$ and $C_{\text{post-tr}}$ 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.

References

Andrews, J. A., Harrison, K. G., Matamala, R., and Schlesinger, W. H.: Separation of root respiration from total soil respiration using Carbon-13 labeling during FACE, Soil Sci. Soc. America Journal, 63, 1429–1435, 1999.

Balesdent, J. and Mariotti, A.: Measurement of soil organic matter turnover using ^{13}C natural abundance Marcel Dekker, Inc., New York, NY, 1996.

Bernhardt, E. S., Barber, J. J., Pippen, J. S., Taneva, L., Andrews, J. A., and Schlesinger, W. H.: Long-term effects of free air CO2 enrichment (FACE) on soil respiration, Biogeochemistry, 77, 91–116, 2006.

Bond-Lamberty, B., Wang, C., and Gower, S. T.: A global relationship between the heterotrophic and autotrophic components of soil respiration?, Global Change Biology, 10, 1756–1766, 2004.

Bowling, D. R., McDowell, N. G., Bond, B. J., Law, B. E., and Ehleringer, J. R.: 13C content of ecosystem respiration is linked to precipitation and vapor pressure deficit, Oecologia, 131, 113–124, 2002.

Bowling, D. R., Pataki, D. E., and Randerson, J. T.: Carbon isotopes in terrestrial ecosystem pools and CO2 fluxes, New Phytologist, 178, 24–40, 2008.

Carbone, M. S., Czimczik, C. I., McDuffee, K. E., and Trumbore, S. E.: Allocation and residence time of photosynthetic products in a boreal forest using a low-level C-14 pulse-chase labeling technique, Global Change Biology, 14, 466–477, 2007.

Cisneros-Dozal, L. M., Trumbore, S. E., and Hanson, P. J.: Partitioning sources of soil-respired CO2 and their seasonal variation using a unique radiocarbon tracer, Global Change Biology, 12, 194–204, 2006.

Davidson, E. A. and Janssens, I. A.: Temperature sensitivity of soil carbon decomposition and feedbacks to climate change, Nature, 440, 165–173, 2006.

Davidson, E. A., Richardson, A. D., Savage, K. E., and Hollinger, D. Y.: A distinct seasonal pattern of the ratio of soil respiration to total ecosystem respiration in a spruce-dominated forest, Global Change Biology, 12, 230–239, 2006.

DeLucia, E. H., Drake, J. E., Thomas, R. B., and Gonzalez-Meler, M. A.: Forest Carbon Use Efficiency: Is Respiration a Constant Fraction of Gross Primary Production?, Global Change Biology, 13, 1157–1167, 2007.

Edwards, N. T. and Norby, R. J.: Below-ground respiratory responses of sugar maple and red maple saplings to atmospheric CO2 enrichment and elevated air temperature, Plant and Soil, 206, 85–97, 1999.

Ekblad, A. and Hogberg, P.: Natural abundance of 13C in CO2 respired from forest soils reveals speed of link between tree photosynthesis and root respiration, Oecologia, 127, 305–308, 2001.

Ellsworth, D. S.: CO2 enrichment in a maturing pine forest: are CO2 exchange and water status in the canopy affected?, Plant, Cell and Environment, 22, 461–472, 1999.

Gonzalez-Meler, M. A. and Taneva, L.: Integrated Effects of Atmospheric CO_2 Concentration on Plant and Ecosystem Respiration, in: Plant Respiration, edited by: Lambers, H. and Ribas-Carbo, M., Kluwer-Academic Publishers, Dordrecht, 211–259, 2005.

Gonzalez-Meler, M. A., Taneva, L., and Trueman, R. J.: Plant Respiration and Elevated Atmospheric CO2 Concentration: Cellular Responses and Global Significance, Annals of Botany, 94, 647–656, 2004.

Goulden, M. L., Miller, S. D., da Rocha, H. R., Menton, M. C., de Freitas, H. C., de Silva Figueira, A. M., and de Sousa, C. A. D.: Diel and seasonal patterns of tropical forest CO_2 exchange, Ecological Applications, 14, S42–S54, 2004.

Hamilton, J. G., DeLucia, E. H., George, K., Naidu, S. L., Finzi, A. C., and Schlesinger, W. H.: Forest carbon balance under elevated CO2, Oecologia, 131, 250–260, 2002.

Hanson, P. J., Edwards, N. T., Garten, C. T., and Andrews, J. A.: Separating root and soil microbial contributions to soil respiration: A review of methods and observations, Biogeochemistry, 48, 115–146, 2000.

Hanson, P. J., O'Neill, E. G., Chambers, M. L. S., Riggs, J. S., Joslin, J. D., and Wolfe, M. H.: Soil respiration and litter decomposition, Springer, New York, NY, 2003.

Heath, J., Ayres, E., Possell, M., Bardgett, R. D., Black, H. I. J., Grant, H., Ineson, P., and Kerstiens, G.: Rising Atmospheric CO2 Reduces Sequestration of Root-Derived Soil Carbon, Science, 309, 1711–1713, 2005.

Hendrey, G. R., Ellsworth, D. S., Lewin, K. F., and Nagy, J.: A free-air enrichment system for exposing tall forest vegetation to elevated atmospheric CO2, Global Change Biology, 5, 293–309, 1999.

Hogberg, P., Nordgren, A., Buchmann, N., Taylor, A. F. S., Ekblad, A., Hogberg, M. N., Nyberg, G., Ottosson-Lofvenius, M., and Read, D. J.: Large-scale forest girdling shows that current photosynthesis drives soil respiration, Nature, 411, 789–792, 2001.

Hoosbeek, M. R., Lukac, M., van Dam, D., Godbold, D. L., Velthorst, E. J., Biondi, F. A., Peressotti, A., Cotrufo, M. F., De Angelis, P., and Scarascia-Mugnozza, G.: More new carbon in the mineral soil of a poplar plantation under Free Air Carbon Enrichment (POPFACE): Cause of increased priming effect?, Global Biogeochemical Cycles, 18, GB1040, doi:1010.1029/2003GB002127, 2004.

Hungate, B. A., Holland, E. A., Jackson, R. B., Chapin III, F. S., Mooney, H. A., and Field, C. B.: The fate of carbon in grasslands under carbon dioxide enrichment, Nature, 388, 576–579, 1997.

Kayler, Z. E., Ganio, L., Hauck, M., Pypker, T. G., Sulzman, E. W., Mix, A. C., and Bond, B. J.: Bias and uncertainty of delta(CO2)-C-13 isotopic mixing models, Oecologia, 163, 227–234, 2010.

King, J. S., Hanson, P. J., Bernhardt, E. S., De Angelis, P., Norby, R. J., and Pregitzer, K. S.: A multiyear synthesis of soil respiration responses to elevated atmospheric CO2 from four forest FACE experiments, Global Change Biology, 10, 1027–1042, 2004.

Kuzyakov, Y.: Review: Factors affecting rhizosphere priming effect, J. Plant Nutr. Soil Sci., 165, 382–396, 2002.

Kuzyakov, Y. and Cheng, W.: Photosynthesis controls of rhizosphere respiration and organic matter decomposition, Soil Biol. Biochemistry, 33, 1915–1925, 2001.

Kuzyakov, Y. and Gavrichkova, O.: REVIEW: Time lag between photosynthesis and carbon dioxide efflux from soil: a review of mechanisms and controls, Global Change Biology, 16, 3386–3406, 2010.

Lee, X., Wu, H.-J., Sigler, J., Oishi, C., and Siccama, T.: Rapid and transient response of soil respiration to rain, Global Change Biology, 10, 1017–1026, 2004.

Liu, Q., Edwards, N. T., Post, W. M., Gu, L., Ledford, J., and Lenhart, S.: Temperature-independent diel variation in soil respiration observed from a temperate deciduous forest, Global Change Biol., 12, 2136–2145, 2006.

Lloyd, J. and Taylor, J. A.: On the temperature dependence of soil respiration, Functional Ecology, 8, 315–323, 1994.

Luo, Y.: Terrestrial Carbon-Cycle Feedback to Climate Warming, Annu. Rev. Ecol. Evol. Syst., 38, 683–712, 2007.

Makiranta, P., Minkkinen, K., Hytonen, J., and Laine, J.: Factors causing temporal and spatial variation in heterotrophic and rhizospheric components of soil respiration in afforested organic soil croplands in Finland, Soil Biol. Biochem., 40, 1592–1600, 2008.

Malcom, G. M., Lopez-Gutierrez, J. C., and Koide, R. T.: Little evidence for respiratory acclimation by microbial communities to short-term shifts in temperature in red pine (Pinus resinosa) litter, Global Change Biology, 15, 2485–2492, 2009.

Matamala, R. and Schlesinger, W. H.: Effects of elevated atmospheric CO2 on fine root production and activity in an intact temperate forest ecosystem, Global Change Biology, 6, 967–979, 2000.

Matamala, R., Gonzalez-Meler, M. A., Jastrow, J. D., Norby, R., and Schlesinger, W. D.: Slow root C turnover in forests: implications for carbon sequestration, Science, 302, 1385–1387, 2003.

Mencuccini, M. and Holtta, T.: The significance of phloem transport for the speed with which canopy photosynthesis and belowground respiration are linked, New Phytologist, 185, 189–203, 2010.

Moore, D. J. P., Gonzalez-Meler, M. A., Taneva, L., Pippen, J. S., Kim, H.-S., and DeLucia, E. H.: The effect of CO_2 enrichment on apparent stem respiration from *Pinus taeda* L. is confounded by high levels of soil CO_2, Oecologia, 158, 1–10, 2008.

Norby, R. J., Hanson, P. J., O'Neill, E. G., Tschaplinski, T. J., Weltzin, J. F., Hansen, R. A., Cheng, W. X., Wullschleger, S. D., Gunderson, C. A., Edwards, N. T., and Johnson, D. W.: Net primary productivity of a CO2-enriched deciduous forest and the implications for carbon storage, Ecological Applications, 12, 1261–1266, 2002.

Orchard, V. A. and Cook, F. J.: Relationship between soil respiration and soil moisture, Soil Biol. Biochemistry, 15, 447–453, 1983.

Pataki, D. E., Ehleringer, J. R., Flanagan, L. B., Yakir, D., Bowling, D. R., Still, C. J., Buchmann, N., Kaplan, J. O., and Berry, J. A.: The application and interpretation of Keeling Plots in terrestrial carbon cycle research, Global Biogeochem. Cycles, 17, 1022–1036, doi:10.1029/2001GB001850, 2003.

Pendall, E., Del Grosso, S., King, J. Y., LeCain, D. R., Milchunas, D. G., Morgan, J. A., Mosier, A. R., Ojima, D. S., Parton, W. A., Tans, P. P., and White, J. W. C.: Elevated atmsopheric CO2 effects and soil water feedbacks on soil respiration components in a Colorado grassland, Global Biogeochem. Cycles, 17, 1046–1059, doi:10.1029/2001GB001821, 2003.

Phillips, D. L. and Gregg, J. W.: Uncertainty in source partitioning using stable isotopes, Oecologia, 127, 171–179, 2001.

Pregitzer, K. S., Zak, D. R., Maziasz, J., DeForest, J., Curtis, P. S., and Lussenhop, J.: Interactive effects of elevated CO2 and soil N availability on fine roots of Populus tremuloides, Ecological Applications, 10, 18–33, 2000.

Pregitzer, K. S., Loya, W. M., Kubiske, M. E., and Zak, D. R.: Soil respiration in northern forests exposed to elevated atmospheric carbon dioxide and ozone, Oecologia, 148, 503–516, 2006.

Raich, J. W., Potter, C. S., and Bhagawati, D.: Interannual variability in global soil respiration, 1980–94, Global Chnage Biology, 8, 800–812, 2002.

Reichstein, M., Rey, A., and Freibauer, A.: Modelling temporal and large-scale spatial variability of soil respiration from soil water availability, temperature and vegetation productivity indices, Global Biogeochemical Cycles, 17, 11–15, 2003.

Rochette, P., Flanagan, L. B., and Gregorich, E. G.: Separating soil respiration into plant and soil components using analyses of the natural abundance of Carbon-13, Soil Sci. Soc. America Journal, 63, 1207–1213, 1999.

Schlesinger, W. H. and Lichter, J.: Limited carbon storage in soil and litter of experimental forest plots under increased atmopsheric CO2, Nature, 411, 466–469, 2001.

Stoy, P. C., Palmroth, S., Oishi, A. C., Siqueira, M. B. S., Juang, J., Novick, K. A., Ward, E. J., Katul, G. G., and Oren, R. A. M.: Are ecosystem carbon inputs and outputs coupled at short time scales? A case study from adjacent pine and hardwood forests using impulse-response analysis, Plant, Cell Environ., 30, 700–710, 2007.

Subke, J.-A., Hahn, V., Battipaglia, G., Linder, S., Buchmann, N., and Cotrufo, M. F.: Feedback interactions between needle litter decomposition and rhizosphere activity, Oecologia, 139, 551–559, 2004.

Subke, J.-A., Inglima, I., and Cotrufo, M. F.: Trends and methodological impacts in soil CO2 efflux partitioning: A metaanalytical review, Global Change Biology, 12, 1–23, 2006.

Subke, J.-A., Voke, N. R., Leronni, V., Garnett, M. H., and Ineson, P.: Dynamics and pathways of autotrophic and heterotrophic soil CO2 efflux revealed by forest girdling, J. Ecol., 99, 186–193, 2011.

Sulzman, E. W., Brant, J. B., Bowden, R. D., and Lajtha, K.: Contribution of aboveground litter,belowground litter,and rhizosphere respiration to total soil CO2 effux in an old growth coniferous forest, Biogeochemistry, 73, 231–256, 2005.

Taneva, L. and Gonzalez-Meler, M. A.: Decomposition Kinetics of Soil Carbon of Different Age From a Forest Exposed to 8 Years of Elevated Atmospheric CO2 Concentration, Soil Biol. Biochem., 40, 2670–2677, 2008.

Taneva, L., Pippen, J. S., Schlesinger, W. H., and Gonzalez-Meler, M. A.: The turnover of carbon pools contributing to soil CO2 and soil respiration in a temperate forest exposed to elevated CO2 concentration, Global Change Biology, 12, 983–994, 2006.

Tang, J., Baldocchi, D. D., and Xu, L.: Tree photosynthesis modulates soil respiration on a diurnal time scale, Global Change Biology, 11, 1298–1304, 2005.

Trueman, R. J. and Gonzalez-Meler, M. A.: Accelerated belowground C cycling in a managed agriforest ecosystem exposed to elevated carbon dioxide concentrations, Global Change Biology, 11, 1258–1271, 2005.

Trueman, R. J., Taneva, L., Gonzalez-Meler, M. A., Oechel, W. C., and BasiriRad, H.: Carbon losses in soils previously exposed to elevated atmospheric CO2 in a chaparral ecosystem: Potential implications for a sustained biospheric C sink, J. Geochem. Exploration, 102, 142–148, 2009.

Vargas, R., Carbone, M. S., Reichstein, M., and Baldocchi, D. D.: Frontiers and challenges in soil respiration research: from measurements to model-data integration, Biogeochem, 102, 1–13, 2011.

Wei, W., Weile, C., and Shaopeng, W.: Forest soil respiration and its heterotrophic and autotrophic components: Global patterns and responses to temperature and precipitation, Soil Biol Biochem., 42, 1236–1244, 2010.

Zak, D. R., Pregitzer, K. S., King, J. S., and Holmes, W. E.: Elevated atmospheric CO2, fine roots and the response of soil microorganisms: a review and hypothesis, New Phytologist, 147, 201–222, 2000.

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 ± 0.5	-40.4 ± 1.0
Root-free SOM	-26.5 ± 0.1	-34.5 ± 0.6
Aboveground Litter	-28.7 ± 0.4	-37.9 ± 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 $\mu mol\ CO_2\ m^{-2}\ s^{-1}$ and show average values ($n = 3$) ± standard error.

	R_{root}	% R_{root}	R_{SOM}	% R_{SOM}	R_{litter}	% R_{litter}	$R_{pre-tr\,C}$	% $R_{pre-tr\,C}$
Day								
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

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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)

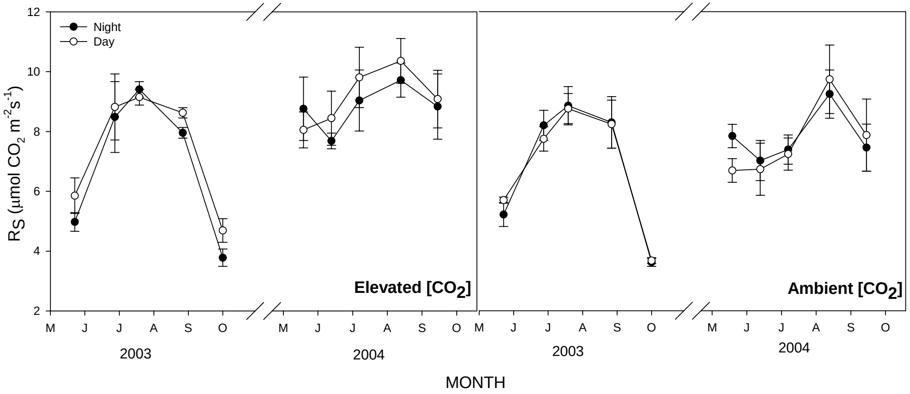

Fig. 1. Diel soil respiration rates at FACTS-1 under ambient and elevated [CO_2] during the growing seasons of 2003 and 2004. Values are means ± standard error ($n = 3$).

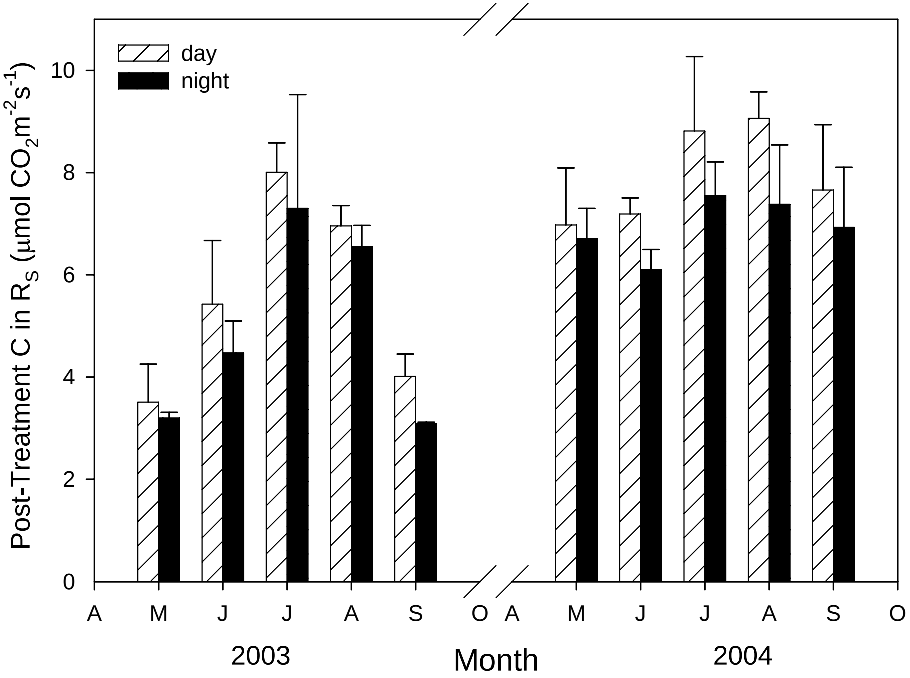

Fig. 2. The contribution of pre-treatment and post-treatment soil carbon to day and night soil respiration rate during the growing seasons of 2003 and 2004 at FACTS-1. Values are means ($n = 3$) ± standard error.

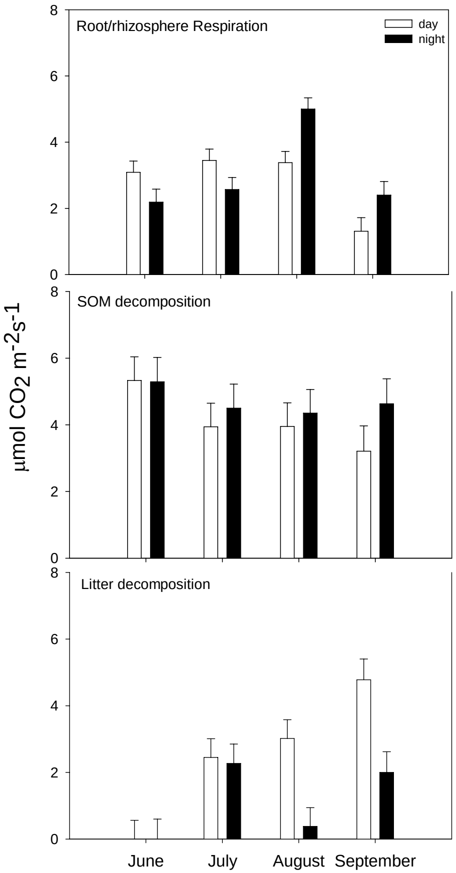

Fig. 3. Contribution of soil respiration components to total soil respiration during the day and at night in 2004 at FACTS-1. Values are means ($n = 3$) ± standard error.

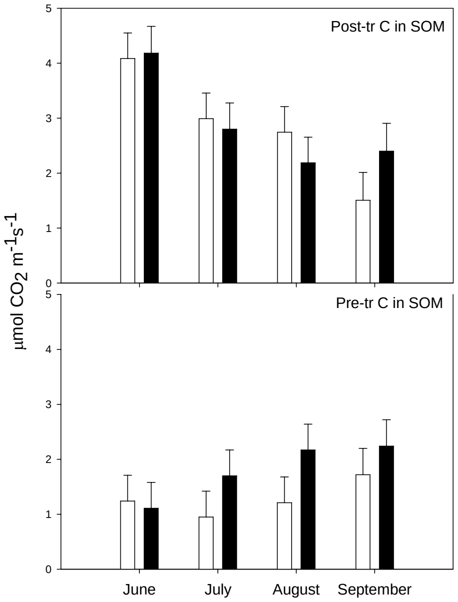

Fig. 4. The contribution of post- and pre-treatment soil organic carbon to daytime and nighttime soil respiration at FACTS-1. Values are means ($n = 3$) ± standard error.