Global Change Biology (2006) **12,** 2136–2145, doi: 10.1111/j.1365-2486.2006.01245.x

Temperature-independent diel variation in soil respiration observed from a temperate deciduous forest

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Abstract

The response of soil respiration (R_s) to temperature depends largely on the temporal and spatial scales of interest and how other environmental factors interact with this response. They are often represented by empirical exponential equations in many ecosystem analyses because of the difficulties in separating covarying environmental responses and in observing below ground processes. The objective of this study was to quantify a soil temperature-independent component in R_s by examining the diel variation of an R_s time series measured in a temperate deciduous forest located at Oak Ridge, TN, USA between March and December 2003. By fitting 2 hourly, continuous automatic chamber measurements of CO_2 efflux at the soil surface to a Q_{10} function to obtain the temperature-dependent respiration (R_t) and plotting the diel cycles of R_t, R_s, and their difference (R_i), we found that an obvious temperature-independent component exists in R_s during the growing season. The diel cycle of this component has a distinct day/night pattern and agrees well with diel variations in photosynthetically active radiation (PAR) and air temperature. Elevated canopy CO_2 concentration resulted in similar patterns in the diel cycle of the temperature-independent component but with different daily average rates in different stages of growing season. We speculate that photosynthesis of the stand is one of the main contributors to this temperature-independent respiration component although more experiments are needed to draw a firm conclusion. We also found that despite its relatively small magnitude compared with the temperature-dependent component, the diel variation in the temperature-independent component can lead to significantly different estimates of the temperature sensitivity of soil respiration in the study forest. As a result, the common practice of using fitted temperature-dependent function from night-time measurements to extrapolate soil respiration during the daytime may underestimate daytime soil respiration.

Keywords: Free air CO_2 enrichment (FACE), soil respiration, temperature response

Received 28 April 2005; revised version received 23 December 2005, 25 March 2006 and accepted 5 June 2006

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Oak Ridge National Laboratory, Oak Ridge, Tennesse 37831-6335, managed by UT-BATTELLE, LLC for the US Department of Energy, under contract DE-AC05-00OR22725.

Introduction

Soil respiration (R_s), defined as the total CO_2 efflux from the soil surface, is one of the largest CO_2 fluxes from land to atmosphere (Raich & Schlesinger, 1992; Schimel *et al*., 1994) and can result in a significant change to the global carbon cycle with slight modifications in its rate (Kirschbaum, 1995; Giardina & Ryan, 2000). R_s is commonly modeled using equations in which respiration rate is an exponential function of temperature. Parameters of the functions quantifying the temperature sensitivity of R_s are usually obtained using regression (Raich & Schlesinger, 1992; Lloyd & Taylor, 1994; Kirschbaum, 1995; Tjoelker *et al*., 2001). Temperature-

dependent models have provided a useful numerical tool for describing soil respiration and for predicting future climate change (Cox *et al*., 2000).

Despite the simplicity of temperature-dependent models, it is well known that R_s consists of CO_2 fluxes from several sources including soil microbial decomposition, root respiration, and rhizosphere microbial utilization of labile root exudates, and can be affected independently by other environment factors such as soil moisture, photosynthesis, precipitation, and substrate availability in addition to soil temperature (Davidson *et al*., 1998; Knohl *et al*., 2005; Misson *et al*., 2006). Their influences may be confounded with the soil temperature dependence of R_s, and obscure the apparent temperature sensitivities (Gu *et al*., 2004; Davidson *et al*., 2006). Attempts have been made to separate these different environmental responses and to introduce additional variables to R_s models. Models that include soil water content (e.g. Schlentner & Van Cleve, 1985) or air temperature and precipitation (e.g. Raich & Schlesinger, 1992) have been used to provide better description of seasonal to interannual variations of R_s in certain ecosystems.

With increasing availability of high frequency CO_2 flux measurements, long-term ecosystem carbon budgets can be computed from instantaneous fluxes. Approximation of the average daily flux rate using an R_s model depends largely on how well the model can capture the diel variations of R_s. Some environmental variables such as soil organic carbon storage, frequency of precipitation, or phenological stages of the stand may have strong seasonal or annual variations but may change little during the course of a day and are unlikely to contribute to changes in the R_s diel cycle. On the other hand, variables with strong diel cycles such as air temperature, soil water content, air humidity, soil substrate concentration are likely to have significant influences on the diel pattern of R_s. However, quantification of the effect of these variables on R_s individually is difficult because many of them and soil temperature tend to covary.

The objectives of this study were to explore the possibility of quantifying a soil temperature-independent component in R_s in forests from frequently measured data and to explore its potential environmental drivers by relating its diel cycle with commonly measured environmental variables. We used data collected in a temperate deciduous forest located in Oak Ridge, TN, USA. Recent development of automated soil chamber technology provides the opportunity to make frequent (hourly, for example) measurements of soil CO_2 efflux, for long periods of time. Such *in situ* soil respiration data streams along with associated environmental and biological measurements should allow extracting a soil temperature-independent component from R_s by excluding the computed temperature-dependent component through statistical approaches. Based on this principle, we examined the fine temporal resolution R_s time series measured from the site to determine the characteristics of the temperature-independent component. Because part of the study site was equipped with free-air CO_2 enrichment (FACE) instruments (Hendrey *et al*., 1999), the effect of CO_2 enrichment treatment on the component was also investigated.

Methods

Site description

The research site is a planted sweetgum (*Liquidambar styraciflua*) forest, located in the Oak Ridge National Environmental Research Park (35°54′N; 84°20′W) in the southeastern United States. This closed-canopy, 15 m tall stand with evenly distributed spacing of 2.3 m × 1.2 m was planted as seedlings in 1988. The height and basal area of the trees are very uniform across the site. The soil is an Aquic Hapludult with silty clay loam texture, pH approximately 5.5–6.0, and is moderately drained. The climate is typical for the humid southern Appalachian region with mean annual temperature (1962–1993) of 13.9 °C. Precipitation is generally evenly distributed throughout the year with annual mean of 1371 mm (Norby *et al*., 2001).

The FACE apparatus consists of four 25 m diameter rings with rings 1 and 2 exposed to elevated CO_2 concentration (549 ppm in 2003) during growing season (April and November) since 1998 and rings 4 and 5 under ambient CO_2 concentration. Detailed site and operating information are documented at http://www.esd.ornl.gov/facilities/ORNL-FACE. We refer the CO_2-enrichment rings as 'high-CO_2' rings and the ambient rings as 'control' rings in this article.

Measurements

This study used measurements taken in 2003, excluding the first 104 days due to missing data resulting from equipment failure. R_s was measured using automated soil chamber system designed by Edwards & Riggs (2003). Chambers operate by closing over the soil in response to a control signal and remain closed for a 14-min period before opening again. An automated switching system was programmed to sequentially open and close chambers. Measurements on closed chambers were made using an infrared gas analysis system (IRGA, LiCor 6252, LiCor Inc, Lincoln, NE, USA). Air was pumped through all chambers and airlines continuously during both chamber-open and

chamber-closed positions. The flow rates were maintained at about 0.5 L min^{-1} when chambers were open with air bypassing the IRGA and at 0.9 L min^{-1} during the sample period while chambers were in the closed position. Twelve minutes was required to reach equilibrium in CO_2 values after chamber closure. Therefore, each chamber was signaled to close 12 min before data logging began. During operation the next chamber was closed while the previous chamber was still being measured. Each chamber was measured for a 7-min period with only the last 2 min recorded. The difference in CO_2 concentration ΔCO_2 ($\mu L\,L^{-1}$) is determined using a reference line outside the chamber simultaneously with air from a line from inside the chamber when closed. The ΔCO_2 is adjusted to standard pressure and temperature by the following:

$$\Delta CO_2(\text{std}) = \frac{98.5}{101.3} \times \frac{273}{273 + T_{\text{air}}} \times \frac{\Delta CO_2}{22.4}\ (\mu\text{mol}\,\text{L}^{-1}), \quad (1)$$

where 98.5 (kPa) is the average local air pressure for the study site, 101.3 is standard air pressure (kPa), T_{air} is air temperature (°C), 22.4 (L mol^{-1}) is the volume of a gas at standard pressure and temperature, and 273 is standard temperature (K). A second equation is used to correct for the flow rate F through the line to the measurement instrument. A calibration with a bubble gilibrator was performed to determine that a flow of 1063 mL min^{-1} was equal to the target rate of 900 mL min^{-1} at standard temperature and pressure. Using the following a flow rate at standard temperature and pressure is

$$F(\text{std}) = [(900 + (F - 1063))/1000]/60\ (\text{L}\,\text{s}^{-1}). \quad (2)$$

We then determine the CO_2 flux rate as

$$R_s = \Delta CO_2(\text{std}) \times F(\text{std})/A \quad (\mu\text{mol}\,\text{m}^{-2}\text{s}^{-1}), \quad (3)$$

where A is the ground surface area of the chamber in square meters. A measurement cycle using seven chambers for the control rings, and eight for the high-CO_2 rings took 110 min to complete before returning to a chamber for the next measurement.

Soil temperature was measured at 8 cm below the surface in each chamber using a thermocouple inserted through chamber ports and recorded when each respiration measurement was taken. The top 15 cm contains 80% of the soil organic matter. There is 2800 g C m^{-2} in the soil from surface to 15 cm with 1250 g C m^{-2} in the top 5 cm (Jastrow *et al*., 2005). 40% of fine roots are found in the top 15 cm of soil and 60% in the top 60 cm (Norby *et al*., 2004). There are no temperature measurements available at other soil depths at this site except at 10 cm from locations between the treatment plots. These 10 cm temperature measurements are nearly identical to the temperature measurements at 8 cm used in our analysis. There is a brief period after leaf fall in October with a very sparse insulating surface litter, which nearly completely disappears by early winter as the result of earthworm activity. Volumetric soil water content for 0–20 cm depth increment was measured biweekly in six randomly located permanent locations in each ring using a Time Domain Reflectometry (TDR) system. Half-hourly weather data and daily leaf area index (LAI) are from FACE data archive available from the web link given earlier.

To reduce measurement noises, individual chamber data for control rings were averaged and high-CO_2 rings were averaged over each measurement cycle. The averaged values of soil respiration, soil temperature and soil volumetric water content during the observation period are shown in Fig. 1.

Calculating R_t *and* R_i

In order to quantify the temperature-independent component (R_i) in R_s, we assumed R_s being the combination of the temperature-dependent term (R_t) and R_i, i.e.,

$$R_s = R_t + R_i. \quad (4)$$

R_t can be described as a simple exponential function of soil temperature (Lloyd & Taylor, 1994; Bryla *et al*., 2001) unless soil moisture is below a fairly low threshold (−100 kPa, Skopp *et al*., 1990; Kirschbaum, 1995). Because the measured soil water content at the site was significantly above this threshold (−100 kPa at this site occurs at 25% of potential soil volumetric water content) throughout the studying period (Fig. 1), soil moisture regulation on the soil temperature response was omitted here. The following equation was used to model R_t,

$$R_t = AQ_{10}^{\frac{T_s - 10}{10}}, \quad (5)$$

where T_s is soil temperature measured at 8 cm depth, A a base flux rate at 10 °C T_s and Q_{10} the temperature sensitivity parameter. A and Q_{10} were obtained using ordinary nonlinear least squares with the ODRPACK software (Boggs *et al*., 1992). Both parameters can vary with changes in organic matter content of soil (Gu *et al*., 2004). To reduce such an influence, we partitioned the 8.5-month length into four phenological periods using the development stage of the observed LAI as the partitioning criterion (Fig. 2). They are early-growing period (from days 105 to 168, 2003); mid-growing (days 169–270), late-growing (days 271–318) and dormant periods (days 319–365), respectively.

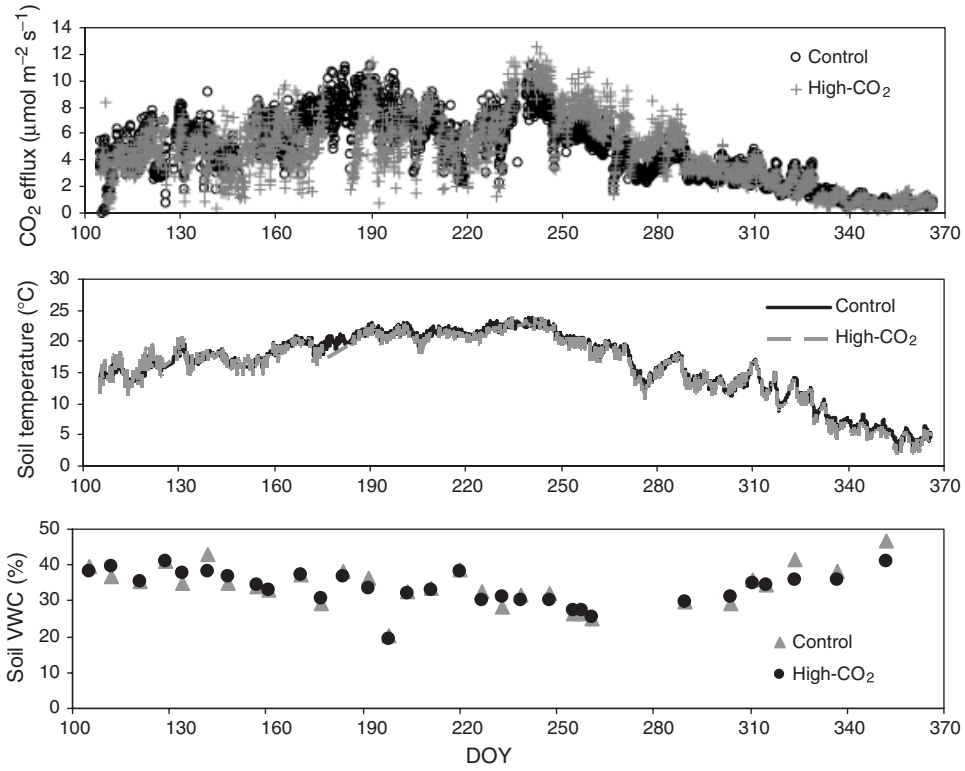

Fig. 1 Measurements of soil respiration (top), soil temperature at 8 cm (middle) and soil volumetric water content (bottom) averaged over ambient rings ('control') and over rings with elevated atmospheric CO_2 treatment ('high CO_2').

Because R_s and T_s were measured simultaneously, it is possible to estimate R_t for every measured R_s. R_i was calculated as the difference between each R_s and R_t pair.

Results

Diel patterns in R_s, R_t, *and* R_i

Diel cycles of R_s, R_t, and R_i were constructed using 2-h averages. We first used all data in phenological periods 1–3 for obtaining the cycle shapes in growing season, and data in period 4 for dormant season. R_s and R_t both have similar growing-season diel variations in 'control' and in 'high CO_2' (Fig. 3). The daily minimum of the averaged R_s was between 04:00 and 06:00 hours, and maximum between 14:00 and 16:00 hours. The diel pattern of R_t showed much smaller fluctuations compared with that of R_s with its range only about half of variations of R_s. The diel pattern of R_i is different from those of R_t and R_s in both 'control' and 'high CO_2' with distinct day/night switches at around 08:00 and 20:00 hours, respectively. Correlating the variations in R_i during the growing season with that in air temperature, air humidity, and photosynthetically active radiation (PAR), we found that they could be best explained by the diel variation of PAR in 'high CO_2' and that of PAR shifted by 1 h in 'control' rings (Fig. 3a). We found no significant correlation between R_i and PAR in the dormant-season (Fig. 3b) for both 'control' and 'high CO_2' when the diel pattern of R_i does not show distinct day/night differences. Instead they appear as flat lines with only slight rise between 15:00–17:00 hours in both cases.

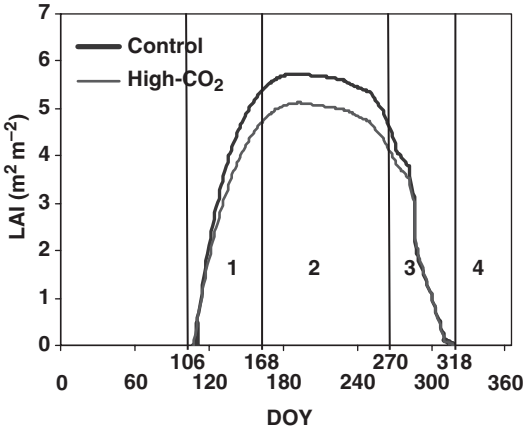

Fig. 2 Leaf area index (LAI) in 2003 and the phenological periods defined by photosynthetic activity for the ORNL free air CO_2 enrichment experiment. 1, 2 and 3 indicate early-growing, middle-growing and late-growing period, respectively. 4 defines the winter dormant period.

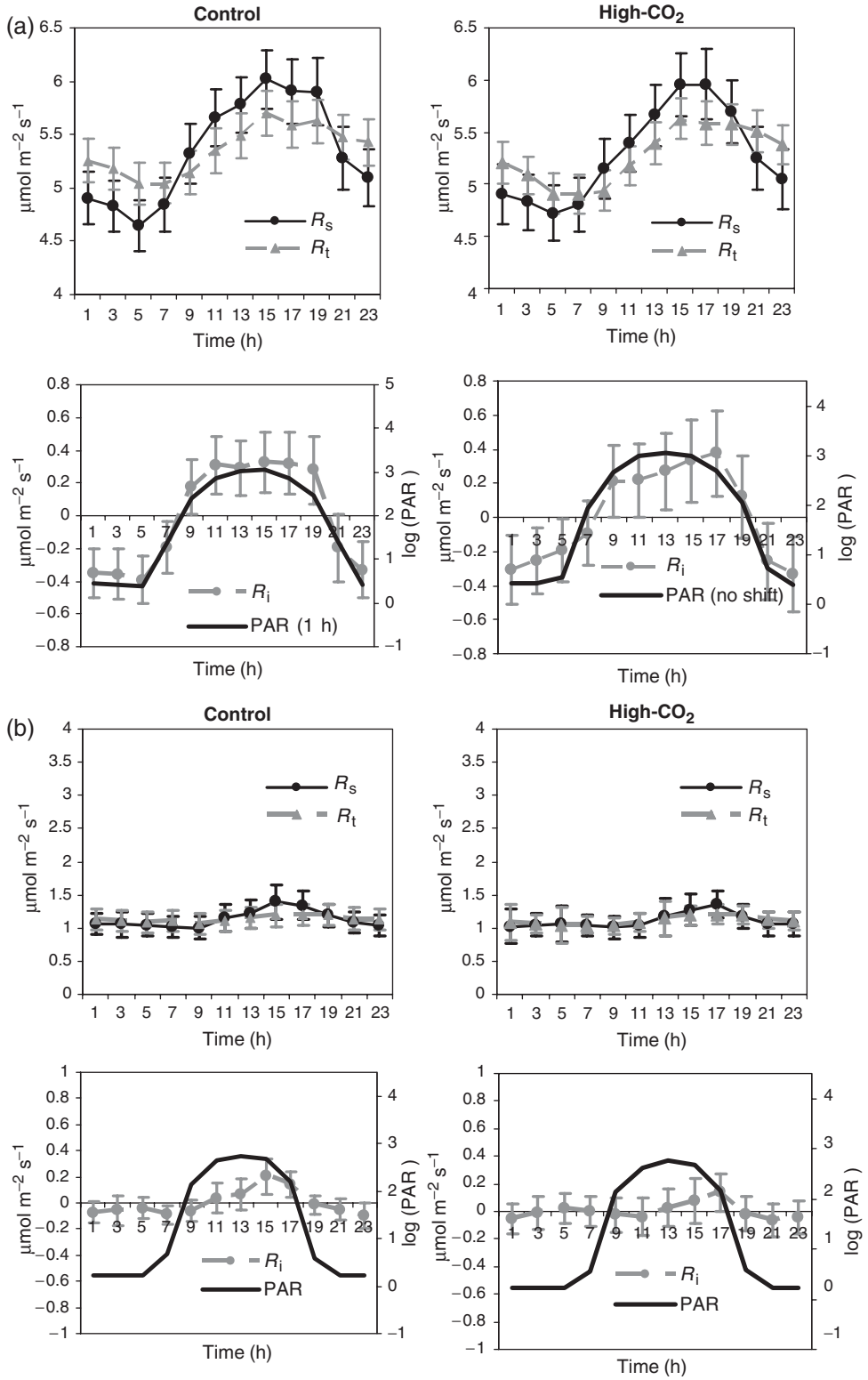

Fig. 3 (a) Comparison of the diel cycles of temperature-independent respiration component (R_i) and photosynthetically active radiation (lower panel) in 'control' (Left) and in 'high CO_2' (right) for growing season, i.e. phenological periods 1–3. R_i is calculated as the differences of observed soil respiration (R_s) and the fitted temperature-dependent component (R_t) (upper panel). Error bars indicate 95% confidence interval. (b) Same as (a) except for dormant season.

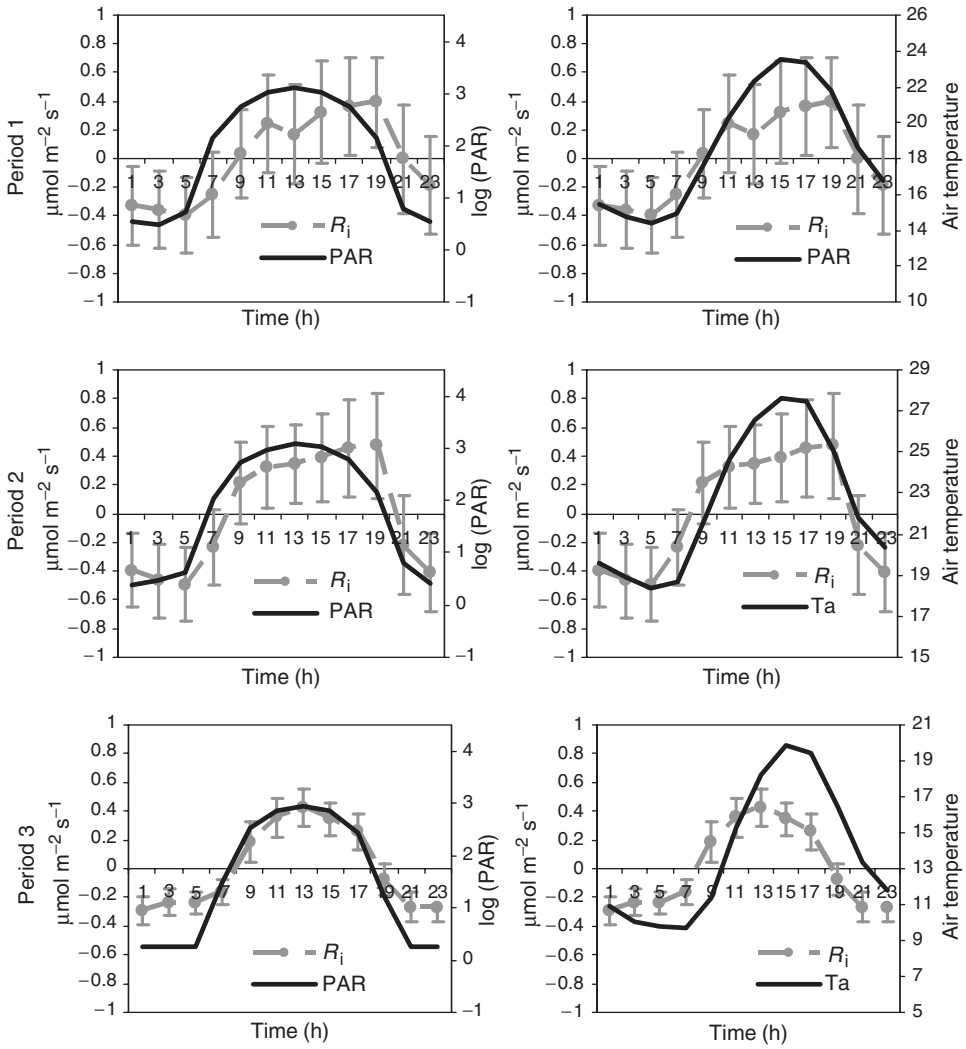

Fig. 4 Diel cycles of R_i in 'control' and its comparison with diel variation in photosynthetically active radiation (left) and diel variation in air temperature (right) in each phenological period of the growing season.

In order to gain more insights into the seasonal evolution of the diel variations in R_i, we examined the diurnal cycles for each phenological period of the growing season separately. Plotting the diel cycles of R_i and PAR in 'control' reveals that the time lag of R_i to PAR is most significant in the Spring early-growing period (period 1). The lag fades away in middle and late growing periods (i.e. summer and fall; Fig. 4a). The diel cycles of R_i were in phase with that of air temperature in spring but gradually shifted forward and became ahead of diel cycle of air temperature in summer and fall by about 2–3 h (Fig. 4b). Similar phase shift was found in 'high CO_2' (not shown).

Magnitude of R_i *in soil respiration*

The regression analyses as described above results in negative values for nocturnal R_i averages, indicating that night time R_t's based on temperature sensitivity from data throughout the day are overestimated. In order to account for R_i as a respiration term, we fitted nocturnal data between 22:00 and 04:00 hours only, when R_i is at its minimum. The fitted soil temperature response curve was then used to determine R_t at other measurement times. The calculated R_i based on R_t estimated using nocturnal data only ensured nonnegative average. The computed results are presented in Fig. 5. The shapes of the diel cycles in R_i do not change much from those obtained previously (see Fig. 4) by using the nocturnal data only. The daily averages of R_s and R_t increased from early-growing to mid-growing period and then decreased in late-growing and dormant periods in both 'control' and 'high CO_2' with maximum value of about 6.6 $\mu mol\, m^{-2}\, s^{-1}$ in mid-growing period and minimum value of 1.2 $\mu mol\, m^{-2}\, s^{-1}$ in dormant period. The daily average of R_i of the mid-growing

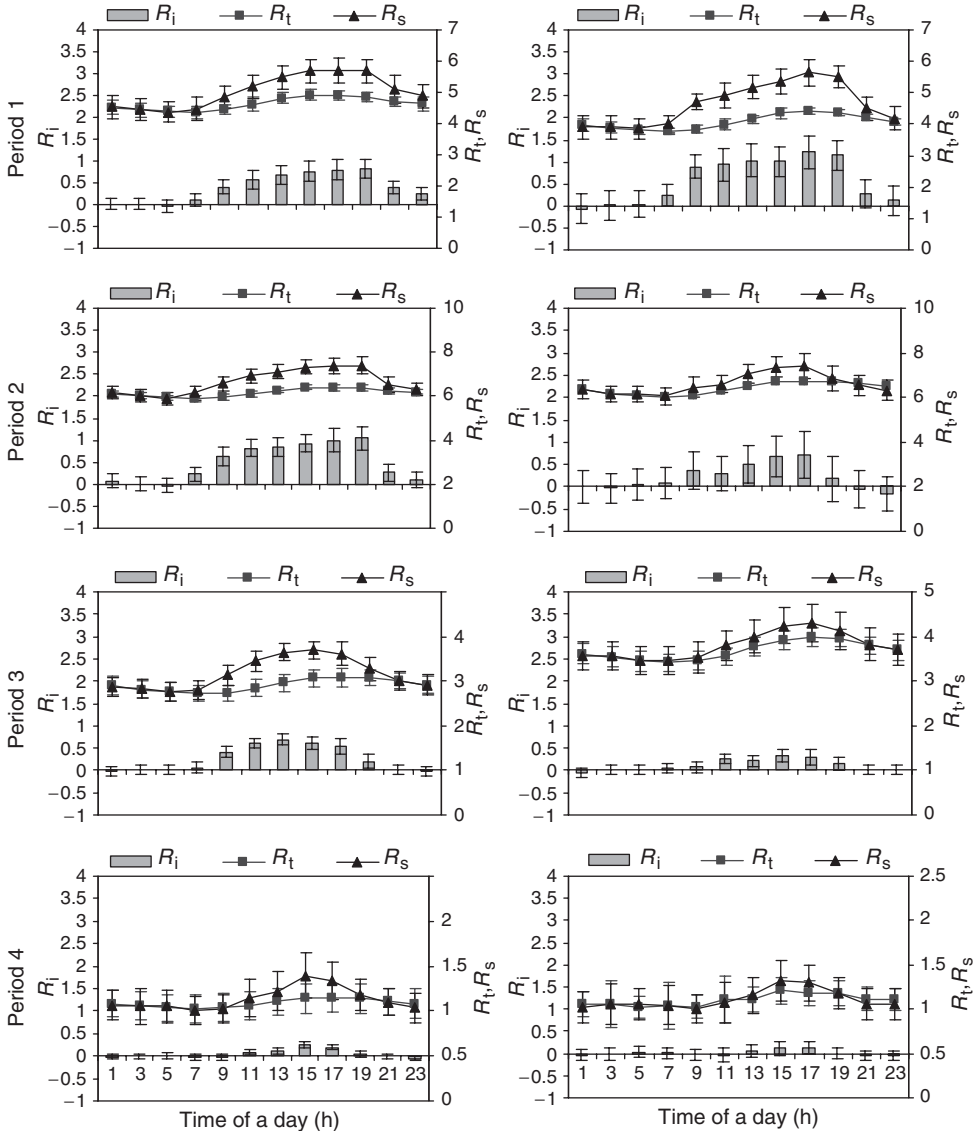

Fig. 5 Daily patterns of R_s, R_t, R_i for phenological periods 1 (top) to 4 (bottom) (see Fig. 1 for period definition) for 'control' (left) and 'high CO_2' (right). Error bars indicate 95% confidence interval.

period has highest value among the four phenological periods and accounts for about 14.5% of the diurnal (08:00–20:00 hours) average of R_s in the 'control' treatment. The highest value appears in the early-growing period with about 19.5% of the diurnal average of R_s in 'high-CO_2' treatment. The diel variations of R_i in the early-growing and middle-growing periods are much larger than those in the late-growing and dormant periods. R_i in 'high CO_2' has higher daily average than in 'control' in early-growing period and smaller daily averages in the remaining three phenological periods. The diel variations of R_i in the dormant period is insignificant in 'high CO_2' with error bars of all the 12 time periods crossing the zero line.

Influence of R_i on Q_{10} estimation

The temperature-dependent function of R_t, has been commonly used for obtaining an estimate of the temperature sensitivity of soil respiration, or Q_{10} in Eqn (5). However, R_i identified in this study may introduce a bias in the estimation of Q_{10}. In order to examine how R_i can affect the estimation of Q_{10}, we compared fitting results using nocturnal (here 22:00–04:00 hours) data vs. those using diurnal (10:00–16:00 hours) data. Because the two parameters A and Q_{10} in Eqn (5) are interdependent; a fixed value of A at 2.5 $\mu mol\, m^{-2}\, s^{-1}$ was assumed for this comparative purpose. The estimated Q_{10}'s and regression statistics are presented in Table 1.

Table 1 Estimated parameters for temperature response of soil CO_2 efflux for different phenological periods

	Q_{10}		R^2		RMSE		Sample Number	
Phenological periods (DOY in 2003)	CTL	HC	CTL	HC	CTL	HC	CTL	HC
1 (105–168)	2.43 (2.73)	2.03 (2.57)	0.23 (0.14)	0.12 (0.06)	1.12 (1.39)	1.36 (1.53)	178 (179)	192 (197)
2 (169–270)	2.28 (2.52)	2.39 (2.54)	0.12 (0.13)	0.14 (0.05)	1.31 (1.49)	1.79 (2.02)	298 (305)	280 (264)
3 (271–318)	1.63 (2.27)	2.63 (2.99)	0.80 (0.64)	0.40 (0.37)	0.34 (0.43)	0.89 (1.02)	150 (148)	153 (149)
4 (319–365)	4.69 (4.87)	4.78 (4.23)	0.69 (0.71)	0.57 (0.51)	0.90 (0.76)	0.82 (0.86)	148 (147)	146 (148)

Values outside of the parentheses are based on nocturnal (10:00–16:00 hours) observations, inside of the parentheses are based on diurnal (10:00–16:00 hours) observations. All regressions are statistically significant ($P<0.001$).
CTL, control; HC, high-CO_2.

Q_{10}'s estimated from diurnal data are constantly larger than those from nocturnal data in the three growing-season periods in both 'control' and 'high-CO_2' treatment. The increases in the estimated Q_{10} range from $\sim 6\%$ (period 2, 'high CO_2') to $\sim 40\%$ (period 3, 'control'). We also show that nocturnal data fit the temperature-dependent equation better than diurnal data with greater R^2 and smaller RMSE in all growing-season periods except in middle-growing period in the 'control' treatment. Estimation of Q_{10} does not show such consistency between 'control' and 'high CO_2' during the dormant period. Estimated Q_{10} using diurnal data is greater than that from nocturnal data in 'control', while slightly smaller in the 'high-CO_2' treatment during the dormant period.

Discussion

This study clearly showed that a distinct soil temperature-independent soil respiration component could be identified using high-frequency surface CO_2 efflux measurements at the Oak Ridge FACE site in spite of the strong correlation between soil temperature and soil respiration. This signal component could have been otherwise treated as noise if the fitting of measurements to the empirical temperature-dependent function was not analyzed. The lack of detectable variations of the component in dormant season indicates that the strong diurnal pattern of the component in the growing season is unlikely a result of instrument artifacts.

The seasonal evolution of the temperature-independent component indicates that this component is associated with the phenological stage of the stand. Photosynthesis has been identified as a strong influence on the autotrophic component of R_s in various forest ecosystems (Ekblad & Högberg, 2001; Högberg *et al*., 2001; Bowling *et al*., 2002; Steinmann *et al*., 2004; Irvine *et al*., 2005; Knohl *et al*., 2005; Tang *et al*., 2005). Given that the diel cycle of the temperature-independent component correlated well with that of PAR, we suggest that this component reflects influence of photosynthesis on root and rhizosphere respiration. However, we did not find obvious time lags between the diel cycles of this respiration term and that of PAR as observed in that of soil respiration to photosynthesis measured in a savanna environment (Tang *et al*., 2005). A plausible explanation is that although it usually takes hours to several days for photo-assimilated carbon atom to travel from leaf to soil surface flux (Farrar, 1985; Dilkes *et al*., 2004), the indirect effect of photosynthesis on root respiration through either ion uptake or production of labile root exudates may take place much faster. Mineral ion uptake results from the activity of the root transport system in coordination with the photosynthetic activity of the shoot (Forde, 2002). Uptake rates can fluctuate diurnally and respond to light intensity (Gastal & Saugier, 1989). Studies on the phloem transport of some grass species have shown that it works as wave transmission, the unloading of ions in shoots may trigger the immediate loading of ions into root tips (Salisbury & Ross, 1992; Thompson & Holbrook, 2004). If this is the case in the ecosystem studied here, then the photosynthesis signal can be transferred much faster than actual movement of carbon molecules and roots may respond to a photosynthetic signal in near real time even though the sugar available for immediate use in root and exudates respiration may be synthesized a few days ago and stored in root tissues. The fast transferred signal can thus result in the synchronized diel cycles of the temperature-independent soil respiration and PAR. However, until experiments on measuring photosynthate transport in similar ecosystems, this hypothesis remains speculative and cannot be favored over other possibilitiy that the temperature-independent respiration component can be the result of a combination of other environmental factors.

The temperature sensitivity of soil respiration is probably one of the most critical parameters in biogeochemical models. Despite that this temperature sensitivity is a result of the interaction of many direct and

indirect effects of soil temperature, water content and substrate supply (Davidson *et al.*, 2006), its estimation will rely on empirical regressions until mature mechanistic models become available. With the improvement of soil respiration data both on measurement accuracy and on temporal scale refinement, our study indicated that it is possible to evaluate the function used for the sensitivity estimation based on the measurements of soil respiration. As illustrated in Table 1, the distinct day/night diurnal patterns in the soil temperature-independent component can result in significant variability of estimated Q_{10} if the temperature-independent respiration component is not quantified. A common practice is to use fitted temperature response from night-time measured eddy-covariance CO_2 flux to estimate daytime soil respiration (Griffis *et al.*, 2004; Rambal *et al.*, 2004). A potential implication of this study is that this practice may severely underestimate daytime respiration, which can cause larger errors in seasonal or annual budgets.

The elevated CO_2 treatment introduced some additional interesting findings. Elevated CO_2 resulted in similar diurnal patterns of the temperature-independent respiration component but a different seasonal evolution. Elevated CO_2 enhanced the component in early period of growing season but suppressed it in middle to late periods of growing season. The mechanism of such phenomenon is unclear. We speculate that it is because the temperature-independent respiration is largely related to root growth and root exudation, which is an important determinant of nutrient availability to plants (Rovia and Davey 1974) and both are largely regulated by photosynthesis (Lejay *et al.*, 2003). It has been found that elevated CO_2 treatment stimulates carbon assimilation in forests (Long & Drake, 1992) and, at this site, increases carbon allocation to fine roots (Norby *et al.*, 2002).

In conclusion, although soil temperature response of soil respiration is important for modeling purposes, it might be inadequate to account for the diel variation of soil respiration in forest ecosystems. We analyzed high-frequency measurement at a deciduous forest in Southeastern US and found that a clear temperature-independent component can be identified. Given its strong correlation with the diel variation of PAR and association with phenological stages of the stand, we speculate that this component is an immediate response to canopy photosynthesis. The strong diel variation of the temperature-independent component indicates that it could alter the estimation of temperature sensitivity of soil respiration significantly and that the common practice of using night-time data and temperature response function to extrapolate daytime rates may underestimate soil respiration.

Acknowledgments

We thank Eric A. Davidson and two anonymous reviewers for their comments and suggestions on the paper. This study is a contribution to the AmeriFlux Data Assimilation System Project (3ERKP484), supported by the US Department of Energy, Office of Science, Biology and Environmental Research Program, Climate Change Research Division.

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