

# Precipitation frequency controls interannual variation of soil respiration by affecting soil moisture in a subtropical forest plantation

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**Abstract:** Despite the significance of interannual variation of soil respiration ( $R_S$ ) for understanding long-term soil carbon dynamics, factors that control the interannual variation of  $R_S$  have not been sufficiently investigated. Interannual variation of  $R_S$  was studied using a 6-year data set collected in a subtropical plantation dominated by an exotic species, slash pine (*Pinus elliottii* Engelm.), in China. The results showed that seasonal variation of  $R_S$  was significantly affected by soil temperature and soil water content (SWC).  $R_S$  in the dry season (July–October) was constrained by seasonal drought. Mean annual  $R_S$  was estimated to be  $736 \pm 30$  g C·m<sup>-2</sup>·year<sup>-1</sup>, with a range of 706–790 g C·m<sup>-2</sup>·year<sup>-1</sup>. Although this forest was characterized by a humid climate with high precipitation (1469 mm·year<sup>-1</sup>), the interannual variation of  $R_S$  was attributed to the changes of annual mean SWC ( $R^2 = 0.66$ ,  $P = 0.03$ ), which was affected by annual rainfall frequency ( $R^2 = 0.80$ ,  $P < 0.01$ ) and not rainfall amount ( $P = 0.84$ ). Consequently, precipitation pattern indirectly controlled the interannual variation of  $R_S$  by affecting soil moisture in this subtropical forest. In the context of climate change, interannual variation of  $R_S$  in subtropical ecosystems is expected to increase because of the predicted changes of precipitation regime.

**Résumé :** Malgré l'importance de la variation interannuelle de la respiration du sol ( $R_S$ ) pour comprendre la dynamique du carbone à long terme, les facteurs qui régissent la variation interannuelle de  $R_S$  n'ont pas été suffisamment étudiés. La variation interannuelle de  $R_S$  a été étudiée à l'aide d'un jeu de données s'étalant sur six ans et collectées dans une plantation subtropicale dominée par une espèce exotique, le pin d'Elliott (*Pinus elliottii* Engelm.), en Chine. Les résultats ont montré que la variation saisonnière de  $R_S$  était significativement influencée par la température du sol et la teneur en eau du sol (TES). Durant la saison sèche (juillet à octobre),  $R_S$  était limitée par la sécheresse saisonnière. La moyenne annuelle de  $R_S$  a été estimée à  $736 \pm 30$  g C·m<sup>-2</sup>·an<sup>-1</sup> avec une étendue de 706–790 g C·m<sup>-2</sup>·an<sup>-1</sup>. Bien que cette forêt soit caractérisée par un climat humide avec de fortes précipitations (1469 mm·an<sup>-1</sup>), la variation interannuelle de  $R_S$  a été attribuée aux variations de la moyenne annuelle de la TES ( $R^2 = 0,66$ ,  $P < 0,01$ ) qui était influencée par la fréquence annuelle des précipitations ( $R^2 = 0,80$ ,  $P < 0,01$ ) et non par la quantité de précipitation ( $P = 0,84$ ). Par conséquent, le patron des précipitations a indirectement contrôlé la variation interannuelle de  $R_S$  en influençant l'humidité du sol dans cette forêt subtropicale. Dans le contexte des changements climatiques, la variation interannuelle de  $R_S$  dans les écosystèmes tropicaux devrait augmenter à cause des changements prévus dans le régime des précipitations.

[Traduit par la Rédaction]

## Introduction

Soils are the largest carbon reservoirs in terrestrial ecosystems (Batjes 1996). Small changes in the soil carbon pool may have considerable impacts on the atmospheric CO<sub>2</sub> budget. To gain insight into the long-term relationship between soil carbon pool dynamics and environment changes, it is important to understand the seasonal and interannual pattern of soil respiration ( $R_S$ ), as well as the controlling factors.

The seasonal patterns of  $R_S$  have been well documented in many ecosystems and are generally associated with changes of soil temperature ( $T_S$ ), soil water content (SWC), precipita-

tion amount and regime (Borken et al. 1999; Curiel Yuste et al. 2003; Harper et al. 2005), plant phenology (Curiel Yuste et al. 2004), root growth and litter production (Irvine et al. 2008; Ruehr and Buchmann 2010), or their combination (Luo and Zhou 2006). In general,  $T_S$  is the most important factor controlling the seasonal variation of  $R_S$ , but the dependence of  $R_S$  on  $T_S$  is largely mediated by SWC (Borken et al. 2006; Jassal et al. 2008).

In contrast, interannual variability in  $R_S$  is poorly understood. It has been investigated in some forests, including in semi-arid (Irvine and Law 2002), subhumid (Asensio et al. 2007), and humid regions (e.g., Savage and Davidson 2001;

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Epron et al. 2004; Concilio et al. 2009), as well as on a global scale (Raich et al. 2002). The interannual variation of  $R_S$  is attributed to changes of biotic (Irvine et al. 2007, 2008) and abiotic (Irvine and Law 2002; Epron et al. 2004) variables that usually exhibit year-to-year variation. First,  $R_S$  comprises root and microbial respiration. The underground root and microbial respiration are greatly promoted by above-ground photosynthesis (Carbone and Trumbore 2007; Kuzyakov and Gavrichkova 2010). Changes in aboveground processes (e.g., growth, disturbance, and death) can affect annual  $R_S$  by affecting substrate supply to the roots and microbial community (King et al. 2004; Irvine et al. 2008). Second, changes of abiotic variables (e.g., temperature, moisture, and precipitation) may also cause variation of annual  $R_S$  (Martin and Bolstad 2005). At a global scale, interannual variability of  $R_S$  was found to be affected by temperature (Raich et al. 2002) and precipitation (Chen et al. 2010), whereas at an ecosystem scale, the variation of annual  $R_S$  has generally been ascribed to changes in  $T_S$  (Falk et al. 2005; Phillips et al. 2010), water availability (Savage and Davidson 2001; Borken et al. 2002; Martin and Bolstad 2005), annual and seasonal rainfall amount (Asensio et al. 2007; Concilio et al. 2009), and precipitation regime (Harper et al. 2005) in dry regions. Under humid conditions, however, interannual variation of  $R_S$  was reported to be low in a cool-temperate forest (Mo et al. 2005) and a boreal mixed forest (Savage and Davidson 2001), and the effect of precipitation variation was usually negligible.

The region of southern China is characterized by a humid monsoon climate and has the largest subtropical evergreen vegetation cover in the world. Although this region has a high annual mean air temperature ( $T_A$ ) and abundant precipitation,  $T_A$  and rainfall vary greatly and follow different patterns. Seasonal droughts (July–October) are usually caused by an uneven distribution of rainfall over the year. Climatic factors such as  $T_A$  and precipitation have been predicted to become more variable; however, it is still not clear how these variables affect the interannual variability of  $R_S$  in this region.

The primary zonal forests (evergreen broad-leaved) were heavily destroyed by the end of 1970s. To prevent environmental degradation, reforestation campaigns were launched to complete ecological restoration in the 1980s (Wang et al. 2009). These plantations, which accounted for 41% of the total subtropical forest area, were largely coniferous plantations because of their fast growth. Slash pine (*Pinus elliottii* Engelm.) is an important exotic species among the conifers. Thus, it is important to understand the carbon cycle in the slash pine plantations. For this purpose, a series of studies on the carbon cycle have been conducted in this region (Wen et al. 2006, 2010; Yu et al. 2008; Wang et al. 2009). These studies suggested that the high temperature and abundant rainfall promote high gross ecosystem productivity (GEP) ( $1779 \text{ g C}\cdot\text{m}^{-2}\cdot\text{year}^{-1}$ ) and net ecosystem production (NEP) ( $395 \text{ g C}\cdot\text{m}^{-2}\cdot\text{year}^{-1}$ ). However, a seasonal drought, resulting from the uneven distribution of rainfall, depressed seasonal ecosystem respiration (Wen et al. 2006) and  $R_S$  (Wang et al. 2009). A recent study showed that large interannual variation in NEP (CV = 13%) was primarily explained by variation in  $T_A$  and the ratio of precipitation to evapotranspiration (Wen et al. 2010). Despite the significance of

$R_S$  to ecosystem carbon exchange (Valentini et al. 2000; Phillips et al. 2010), it remains unclear how these environmental variables affect annual  $R_S$  in this subtropical ecosystem.

The objectives of this study were to (i) investigate the variations of  $R_S$  at seasonal and interannual scales, (ii) clarify their relationships to environmental drivers and other carbon fluxes, and (iii) identify the effect of seasonal drought on seasonal and interannual variations of  $R_S$  in the humid subtropical forest in south China.

## Materials and methods

### Site description

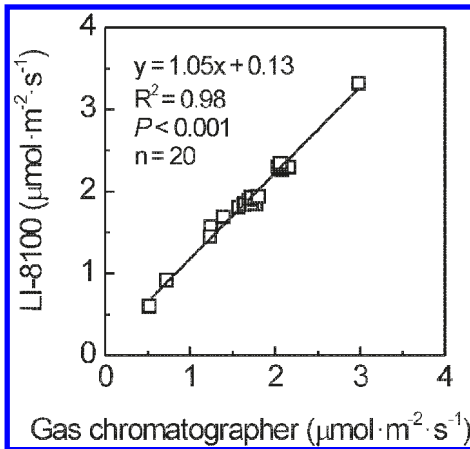
This study was conducted in a subtropical evergreen coniferous plantation at Qianyanzhou Ecological Station ( $26^{\circ}44'39''\text{N}$ ,  $115^{\circ}03'33''\text{E}$ , elevation 102 m) in southeast China. The slash pine plantation was established in 1985. A few Masson's pine (*Pinus massoniana* Lamb.) were also present. Average tree height, diameter at breast height, stand density, and maximum leaf area index were 15 m, 16.1 cm, 809 stems $\cdot\text{ha}^{-1}$ , and 5.6  $\text{m}^2\cdot\text{m}^{-2}$ , respectively (Wen et al. 2010). Soil parent material consisted of red sandstone and mud stone, and soils were mainly red earth with bulk density (0–20 cm) of  $1.50 \text{ g}\cdot\text{cm}^{-3}$ , soil organic carbon of  $8.8 \text{ g}\cdot\text{kg}^{-1}$ , pH of 4.90, and total N content of  $0.7 \text{ g}\cdot\text{kg}^{-1}$ . This region was characterized by a humid continental monsoon climate with large seasonal changes of  $T_A$  and an uneven distribution of rainfall. Mean annual  $T_A$ , precipitation, and solar radiation, from 1985 to 2008, were  $17.9^{\circ}\text{C}$ , 1469 mm, and  $4349 \text{ MJ}\cdot\text{m}^{-2}$ , respectively. The rainfall occurred mainly (approximately 60%) from March to June. Further detailed descriptions of the region has been made previously (Wen et al. 2006; Wang et al. 2009).

### Measurement of soil $\text{CO}_2$ efflux

Soil  $\text{CO}_2$  efflux was measured using a static closed chamber – gas chromatography system from January 2004 to July 2007. Subsequently, an automated soil  $\text{CO}_2$  flux system (LI-8100; LI-COR Biosciences Inc., Lincoln, Nebraska) equipped with a 10 cm survey chamber (8100-102; LI-COR Biosciences Inc.) was used to measure  $R_S$ .

For the static chamber – gas chromatography method, six sampling points were established in a  $15 \times 20 \text{ m}$  plot in June 2003. Six permanent square bases ( $50 \times 50 \text{ cm}$ ) with troughs were gently inserted into the soil to an approximate 3 cm depth. Static opaque chambers ( $50 \times 50 \times 50 \text{ cm}$ ) made of laminose steel were covered on the outside with cotton pads to reduce heat exchange between the inside of the chamber and the surrounding environment. The base troughs were sealed with water to prevent air exchange during the measurement. Two small electric fans were installed at opposite top corners of the chamber for air mixing. About 100 mL gas was sampled immediately after chamber closure using a gas-tight syringe with three joints through a tube (F46). Subsequently, another four samples for each chamber were collected, separated by a time interval of 10 min. The  $\text{CO}_2$  concentration was determined by a gas chromatographer (HP4890D; Agilent Technologies, Inc., Wilmington, Delaware) equipped with a flame ionization detector. Soil  $\text{CO}_2$  emission was then calculated from a linear regression of temporal changes of  $\text{CO}_2$  concentration according to eq. 1, and

**Fig. 1.** Comparisons of soil respiration measured by the static chamber – gas chromatography method and the LI-8100 method ( $n = 20$ ).



further calibrated with temperature and pressure variation based on eq. 2:

$$[1] \quad R_S = \frac{\Delta m}{A \cdot \Delta t} = \frac{V \cdot \Delta c}{A \cdot \Delta t}$$

$$[2] \quad R_S = \frac{V}{A} \cdot \frac{P}{P_0} \cdot \frac{T_0}{T} \cdot \frac{\Delta c}{\Delta t}$$

where  $R_S$  is soil respiration ( $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ ),  $\Delta m$  refers to an increase in  $\text{CO}_2$  in the chamber ( $\mu\text{mol}$ ),  $\Delta c$  and  $\Delta t$  are changes of  $\text{CO}_2$  concentration ( $\mu\text{mol}\cdot\text{m}^{-3}$ ) and elapsed time (s) from the closure of the chamber to gas sampling, respectively,  $V$  refers to volume of chamber ( $\text{m}^3$ ),  $A$  is ground area covered by the chamber ( $\text{m}^2$ ),  $T$  and  $P$  are the air temperature (K) in the chamber and pressure (kPa) at sampling time, respectively, and  $T_0$  (273 K) and  $P_0$  (101.3 kPa) are the temperature and pressure under standard conditions, respectively.

To continuously measure  $R_S$  with the LI-8100 instead of with the chamber – gas chromatography method, a subplot of  $10 \times 10$  m was established within the previous study plot in August 2007. Nine polyvinylchloride soil collars, with a diameter of 10 cm and a height of 6 cm, were placed on two diagonals of the subplot, separated by 2.4 m. These permanent soil collars were inserted into the soil to a depth of approximately 2 cm. Measurement started one week after insertion to reduce any disturbance-induced  $\text{CO}_2$  emission. Every soil collar was measured twice at an interval of 1 min with an observation time length of 2 min and a dead band of 30 s for each.

Soil respiration was measured between 9:00 and 11:00 am twice per week before July 2007 with the static chamber and biweekly afterwards with the LI-8100. There were 316 samples in total across the 6 years of study (2004–2009). Because two measurement methods for  $R_S$  were adopted, a comparison was necessary to unify the two data sets. For this purpose, a simultaneous measurement of  $R_S$  by the two methods was carried out from June to December in 2007. Figure 1 indicated that the two results were significantly correlated ( $P < 0.001$ ). Based on this result,  $R_S$  measured by gas

chromatography method was converted to LI-8100 method standard using the equation in Fig. 1.

### Measurement of environmental variables

For the chamber – gas chromatography method, air temperature inside the chamber was monitored by portable thermocouples (JM624; Jinming Instruments Co. Ltd., Tianjin, China). Air pressure was measured using an atmospheric pressure sensor (CS105; Vaisala Inc., Woburn, Massachusetts) near the study area. For both methods,  $T_S$  and SWC were measured simultaneously with  $R_S$ , at 5 cm depth near the sampling points, using a portable thermocouple (JM624) and a portable time domain reflectometer (TDR) (TSC-I; China Agricultural University, Beijing, China), respectively. Monitoring of  $T_S$ ,  $T_A$ , SWC (both measured at 5 cm depth), and precipitation were accomplished with half-hourly recording of a soil temperature sensor (105T; Campbell Scientific Inc., Logan, Utah), air temperature sensor (HMP45C; Campbell Scientific Inc.), TDR sensor (CS616-L; Campbell Scientific Inc.), and a rain gauge (TE525MM; Campbell Scientific Inc.) on data loggers (CR23XTD and CR10XTD; Campbell Scientific Inc.) near the study plot.

### Measurement of ecosystem carbon and water fluxes

Ecosystem carbon and water fluxes were measured by an eddy covariance system, which was described in detail by Wen et al. (2006, 2010). Gross ecosystem productivity (GEP), ecosystem respiration ( $R_E$ ), net ecosystem production (NEP), and evapotranspiration (ET) from 2004 to 2007 have been reported by Wen et al. (2010). The GEP,  $R_E$ , NEP, and ET in 2008 and 2009 were computed according to the same method used by Wen et al. (2010).

### Measurement of litterfall carbon input

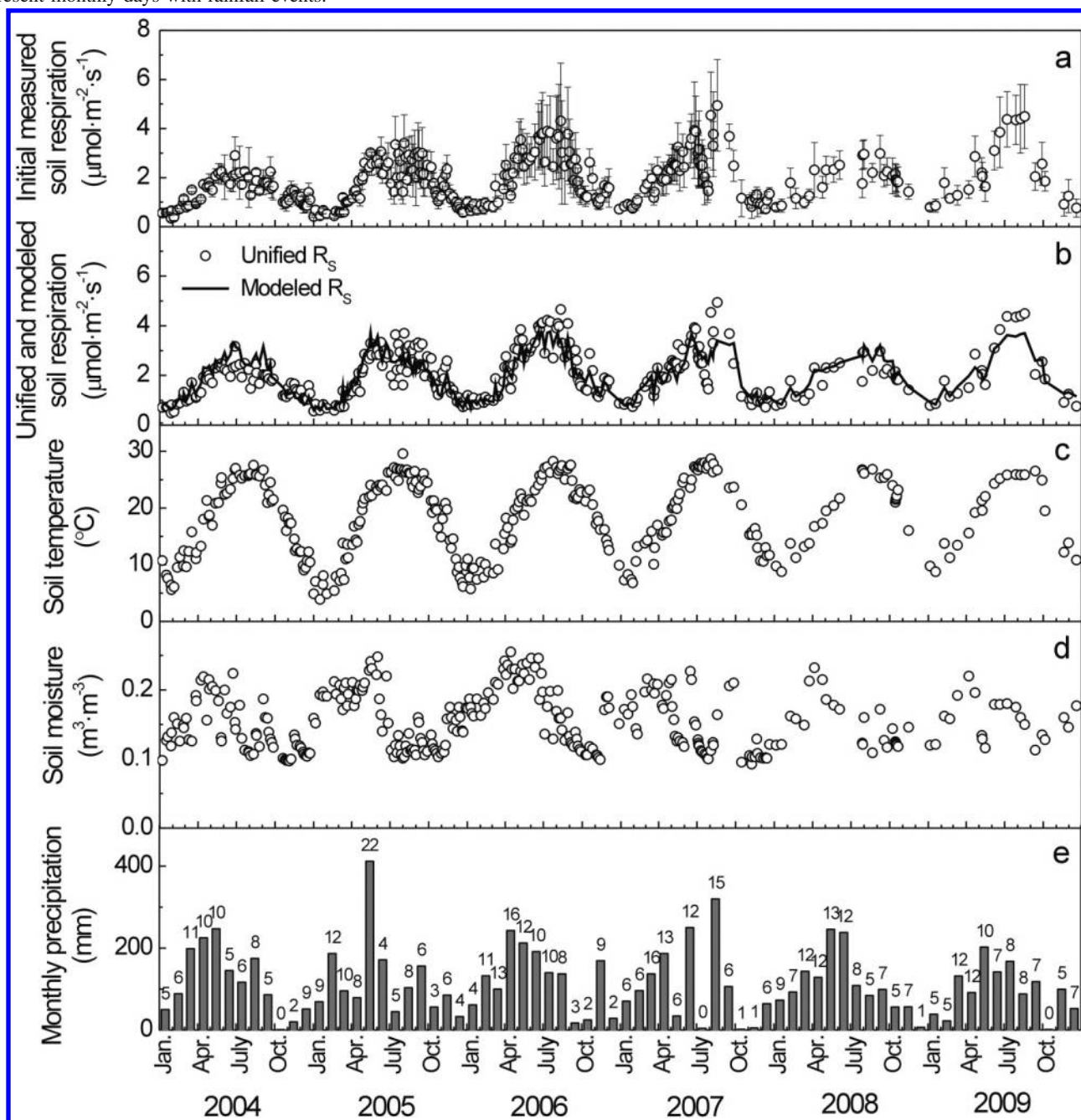
Litterfall was collected monthly by placing 14 litter traps (1  $\text{m}^2$  square) around the study area and then was separated into leaves, branches, flowers, and fruit. Each sample was oven-dried at 65 °C until constant mass was obtained. Litterfall carbon input was calculated according to the mass and carbon concentration as reported by Ma (2007).

### Soil respiration modeling and data analysis

An exponential eq. 3 derived from Van't Hoff (1898) was used to simulate the relationship between  $R_S$  and  $T_S$ . Measured soil respiration was normalized to  $R_S$  at 15 °C ( $R_{S,15}$ ) using eq. 4 (Falk et al. 2005). The relationship between  $R_{S,15}$  and SWC was developed by eq. 5. Considering the different activities of root dynamics and fresh litter decomposition between the growing season (April–November) and dormant season (December–March), eq. 6 was used to develop the response of  $R_S$  to  $T_S$  and SWC in both seasons. Annual  $R_S$  was estimated using fitted models, which were generated by eq. 6, and continuous  $T_S$  and SWC data sets. Linear and non-linear regressions (least squares) were performed with SPSS 13.0 (SPSS Inc., Chicago, Illinois), and figures were drawn using ORIGIN 8.0 (OriginLabs Corporation, Northampton, Massachusetts).

$$[3] \quad R_S = R_{S,15} e^{\beta(T_S - 15)}$$

**Fig. 2.** Soil respiration and environmental variables measured during the period 2004–2009: (a) initial measured soil respiration ( $n = 316$ ); (b) unified soil respiration according to  $y = 1.05x + 0.13$  in Fig. 1 and modeled soil respiration using eq. 7; (c) soil temperature at 5 cm depth; (d) volumetric soil moisture at 5 cm depth; and (e) monthly precipitation. In (a), (b), (c), and (d), the data were the averages of six measurements taken before July 2007 and nine samples taken afterwards, and bars denote  $\pm$  standard deviation. In (e), values above columns represent monthly days with rainfall events.



$$[4] \quad R_{S,15} = R_S / e^{\beta(T_S - 15)}$$

$$[5] \quad R_{S,15} = \gamma \text{SWC}^\delta$$

$$[6] \quad R_S = \alpha e^{\beta T_S} \text{SWC}^\delta$$

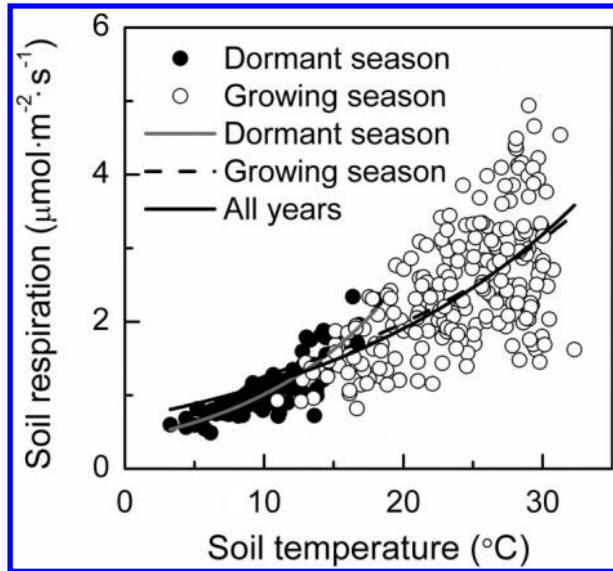
where  $R_S$  is soil respiration,  $R_{S,15}$  is normalized soil respiration at 15 °C,  $T_S$  is soil temperature, SWC is volumetric soil moisture, and  $\alpha$ ,  $\beta$ ,  $\gamma$ , and  $\delta$  are fitted parameters.

## Results

### Soil respiration and environmental conditions

Over the 6-year period, soil respiration greatly varied (Fig. 2a) and ranged from 0.49  $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  in January 2004 to 4.94  $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  in August 2007 (Fig. 2b). Soil respiration exhibited clear seasonal variations that followed the fluctuations of  $T_S$  (Figs. 2b and 2c). Although  $T_S$  followed a similar cycle each year, the interannual pattern of  $R_S$  was notably different within the study period (Figs. 2b and 2c). In

**Fig. 3.** Relationships between soil respiration and soil temperature using eq. 3 in the dormant season ( $R_S = 1.752e^{0.107(T_S-15)}$ ,  $R^2 = 0.74$ ,  $P < 0.001$ ; shaded solid line), growing season ( $R_S = 1.640e^{0.051(T_S-15)}$ ,  $R^2 = 0.37$ ,  $P < 0.001$ ; black broken line), and all years ( $R_S = 1.537e^{0.058(T_S-15)}$ ,  $R^2 = 0.61$ ,  $P < 0.001$ ; black solid line).



general, high  $R_S$  was observed only when both  $T_S$  and SWC were high (Figs. 2b, 2c, and 2d). This phenomenon indicated that SWC might contribute to  $R_S$  to some extent.

#### Seasonal variation of soil respiration and environmental conditions

To understand the effects of environmental variables on  $R_S$ , we correlated  $R_S$  with  $T_S$  using eq. 3.  $T_S$  could explain 61% of the variation of  $R_S$  during the 6 years ( $P < 0.001$ ) (Fig. 3). During the growing and dormant seasons,  $R_S$  was affected by  $T_S$  ( $R^2 = 0.37$  and  $0.74$ ,  $P < 0.001$ ) (Fig. 3).  $R_{S,15}$  was significantly correlated with SWC during all years, growing seasons, and dormant seasons (Fig. 4), suggesting that  $R_S$  was also affected by SWC.

Considering the important influence of  $T_S$  and SWC on  $R_S$ , both  $T_S$  and SWC were applied to correlate with measured  $R_S$  using eq. 6 to generate empirical models for both the growing season (April–November) and dormant season (December–March). The empirical models for the growing and dormant seasons are shown by eq. 7 and eq. 8, respectively, and were used to estimate  $R_S$  as shown in Fig. 2b.

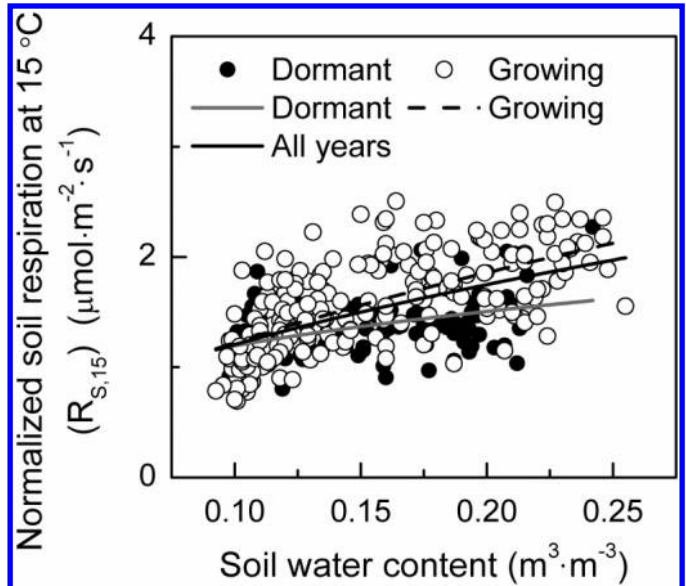
$$[7] \quad R_S = 1.996e^{0.067T_S} \text{SWC}^{0.695} \quad (R^2 = 0.65, P < 0.001)$$

$$[8] \quad R_S = 0.693e^{0.100T_S} \text{SWC}^{0.330} \quad (R^2 = 0.80, P < 0.001)$$

#### Interannual variation of soil respiration and environmental factors

Annual  $R_S$  was estimated using eqs. 7 and 8 with the annual half-hourly continuous data set of  $T_S$  and SWC at 5 cm depth. Annual  $R_{SS}$  from 2004 to 2009 were 706, 718, 790, 725, 746, and 733 g C·m<sup>-2</sup>·year<sup>-1</sup>, respectively. The largest

**Fig. 4.** Relationships between normalized soil respiration at 15 °C ( $R_{S,15}$ ) and soil moisture using eq. 5 in the dormant season ( $R_{S,15} = 2.574 \text{SWC}^{0.333}$ ,  $R^2 = 0.12$ ,  $P < 0.001$ ; shaded solid line), growing season ( $R_{S,15} = 4.910 \text{SWC}^{0.604}$ ,  $R^2 = 0.43$ ,  $P < 0.001$ ; black broken line), and all years ( $R_{S,15} = 4.146 \text{SWC}^{0.536}$ ,  $R^2 = 0.31$ ,  $P < 0.001$ ; black solid line).



difference of annual  $R_S$  was 84 g C·m<sup>-2</sup>·year<sup>-1</sup>. Mean annual  $R_S$  was 736 g C·m<sup>-2</sup>·year<sup>-1</sup>, with a coefficient of variation (CV) of 4%. There was little variation in annual mean  $T_A$  (CV = 2%) and annual mean  $T_S$  (CV = 0.7%); however, there was some variation in annual mean SWC (CV = 6.9%) and annual precipitation (CV = 8.6%). Across the 6-year period, annual  $R_S$  was not significantly correlated with annual mean  $T_A$ , annual mean  $T_S$ , or annual precipitation (Figs. 5a, 5b, and 5c), but it was positively correlated with annual mean SWC at a 5% significance level (Fig. 5d).

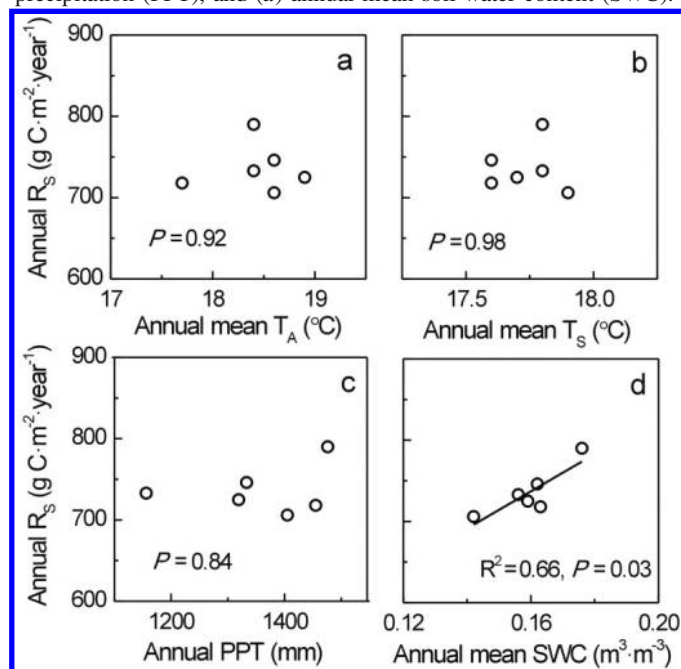
#### Precipitation, evapotranspiration, and soil water content

Interannual variation of SWC was not affected by precipitation, ET, or precipitation minus ET (Figs. 6a, 6b, and 6c). Because of canopy interception, not all rainfall events would affect SWC. According to our observations, there was no change in SWC when rainfall was less than 1.5 mm in this forest. Thus, rainfall events less than 1.5 mm were excluded as these were not effective rainfall events. After this data exclusion, the annual mean SWC was positively correlated with the number of annual days with effective rainfall events ( $R^2 = 0.80$ ,  $P < 0.01$ ) (Fig. 6d). These results suggested that the interannual variation of  $R_S$  was directly controlled by SWC, which was directly related to effective rainfall frequency. Therefore, the  $R_S$  was indirectly affected by effective rainfall frequency.

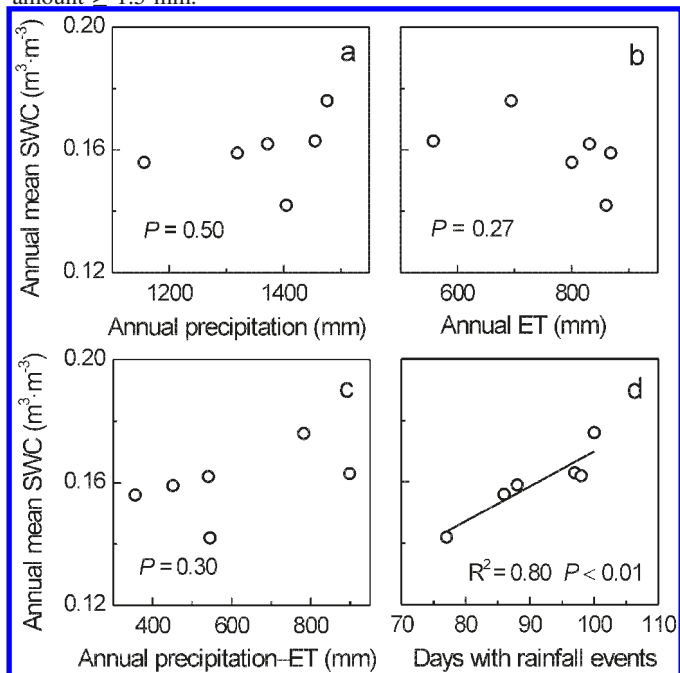
#### Annual soil respiration and ecosystem carbon fluxes and litterfall input

Interannual variation of  $R_S$  was not correlated with annual gross ecosystem productivity, ecosystem respiration, or net ecosystem productivity (Figs. 7a, 7b, and 7c). Moreover, the interannual pattern of  $R_S$  was not well correlated with annual litterfall input (Fig. 7d).

**Fig. 5.** Relationships between annual soil respiration ( $R_S$ ) and environmental factors measured during 2004–2009: (a) annual mean air temperature ( $T_A$ ), (b) annual mean soil temperature ( $T_S$ ), (c) annual precipitation (PPT), and (d) annual mean soil water content (SWC).



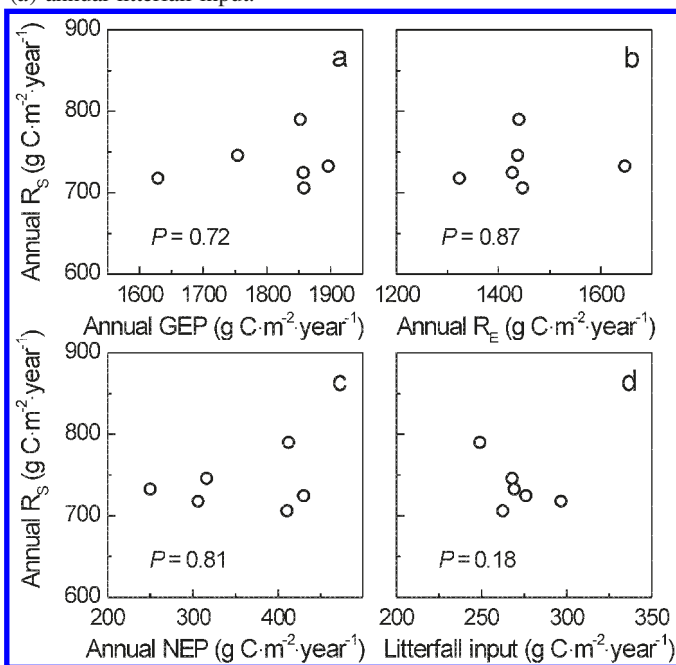
**Fig. 6.** Relationships between annual mean soil water content (SWC) and (a) annual precipitation, (b) annual evapotranspiration (ET), (c) annual precipitation minus ET, and (d) annual days with effective rainfall events. Effective rainfall events refer to rainfall amount  $> 1.5$  mm.



#### Interannual pattern of soil respiration in humid and dry seasons

Although annual precipitation was high, a humid season (March–June) and a dry season (July–October) (Fig. 2d) could be separated by differences in rainfall amount (Fig. 2e).

**Fig. 7.** Relationships between annual soil respiration ( $R_S$ ) and (a) annual gross ecosystem productivity (GEP), (b) annual ecosystem respiration ( $R_E$ ), (c) annual net ecosystem productivity (NEP), and (d) annual litterfall input.



Seasonal  $R_S$ , estimated by eqs. 7 and 8 with  $T_S$  and SWC data, and environmental variables in the humid and dry seasons are presented in Table 1. In the humid season, the interannual variation of  $R_S$  was linearly associated with SWC ( $R^2 = 0.86$ ,  $P = 0.005$ ) (Fig. 8a) but was not affected by  $T_S$  or rainfall. In the dry season, the interannual variation of  $R_S$  was also linearly associated with SWC ( $R^2 = 0.82$ ,  $P = 0.008$ ) (Fig. 8b) and not affected by  $T_S$  or rainfall.

In the humid and dry seasons, mean  $R_S$ s were 289 and 316  $\text{g C}\cdot\text{m}^{-2}\cdot\text{year}^{-1}$ , respectively, with maximum differences of 46 and 42  $\text{g C}\cdot\text{m}^{-2}\cdot\text{year}^{-1}$ , respectively. In the dry season, annual mean  $T_S$  was 24.1 °C, which was 5.6 °C higher than in the humid season. Based on a temperature sensitivity of 1.79 ( $Q_{10} = e^{10 \times 0.058}$ , computed from the result in Fig. 3),  $R_S$  in the dry season was predicted to be 38% higher than in the humid season. However,  $R_S$  in the dry season was only 9.3% higher than in the humid season. This relative depression of  $R_S$  might be due to the drought in the dry season.

## Discussion

### Seasonal variation of soil respiration and environmental conditions

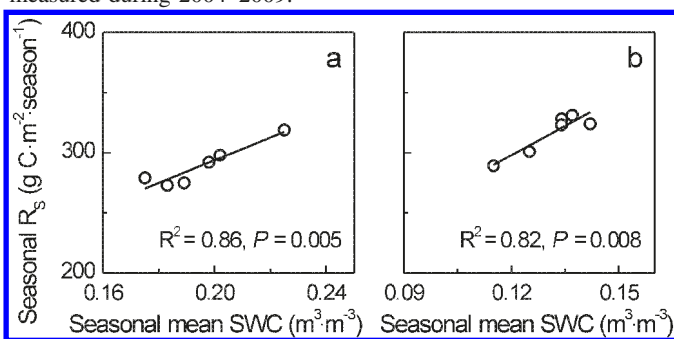
Soil temperature and moisture are usually the most important environmental factors controlling  $R_S$  (Epron et al. 2004; Martin and Bolstad 2005). In general,  $R_S$  is mainly determined by  $T_S$ , particularly under humid conditions (Wang et al. 2009; Ruehr et al. 2010). In the humid subtropical forest, we also found that  $R_S$  was greatly affected by  $T_S$  (Fig. 3). However, under dry environment conditions,  $R_S$  has been found to be dependent on SWC (Asensio et al. 2007). At our study site, although the precipitation was as much as 1469  $\text{mm}\cdot\text{year}^{-1}$ , the seasonal patterns of precipitation and  $T_S$  were usually asynchronous (Figs. 2c and 2e), which fre-

**Table 1.** The soil respiration and environmental variables in the humid and dry seasons.

	Humid season (March–June)				Dry season (July–October)			
	$R_S$ (g C·m <sup>-2</sup> )	Mean $T_S$ (°C)	Mean SWC (m <sup>3</sup> ·m <sup>-3</sup> )	Rainfall (mm)	$R_S$ (g C·m <sup>-2</sup> )	Mean $T_S$ (°C)	Mean SWC (m <sup>3</sup> ·m <sup>-3</sup> )	Rainfall (mm)
2004	279	18.8	0.175	816	301	23.5	0.125	378
2005	298	18.3	0.202	758	289	24.1	0.115	360
2006	319	18.3	0.225	753	331	23.9	0.137	320
2007	273	18.7	0.183	620	324	24.3	0.142	466
2008	292	18.6	0.198	756	328	24.4	0.134	348
2009	275	18.1	0.189	568	323	24.2	0.134	375
Mean	289	18.5	0.195	712	316	24.1	0.131	375

Note:  $R_S$ , soil respiration;  $T_S$ , soil temperature; SWC, volumetric soil moisture.

**Fig. 8.** Relationships between seasonal soil respiration ( $R_S$ ) and soil water content (SWC) in (a) the humid season and (b) the dry season measured during 2004–2009.



quently resulted in a dry season (July–October) (Fig. 2d). We found that  $R_S$  was also obviously affected by SWC (Fig. 4). Seasonal  $R_S$  in the dry season was largely depressed by drought (Table 1) caused by the uneven rainfall distribution (Fig. 2e). This result suggested that although under a humid climate,  $R_S$  in the subtropical forest was strongly constrained by seasonal drought, during which it represented similarly as semi-arid ecosystems. This result was consistent with that of our previous studies, which reported that the seasonal drought had a profound impact on GEP, ecosystem respiration, NEP (Wen et al. 2006, 2010), and  $R_S$  (Wang et al. 2009). Therefore, although the rainfall amount was high in this humid subtropical forest, the precipitation regime controlled the seasonal variation of ecosystem carbon cycle components such as soil respiration by affecting SWC and causing seasonal drought.

### Interannual variation of soil respiration and its controlling factors

Large interannual variation of  $R_S$  has been observed in some temperate ecosystems. For instance, interannual variation of  $R_S$  at Harvard Forest over 5 years was 15% (CV), with a maximum difference up to 230 g C·m<sup>-2</sup>·year<sup>-1</sup>, which largely comprised the variation of  $R_E$  and even exceeded the variation of NEP (Savage and Davidson 2001). In a mature ponderosa pine forest in Oregon, interannual variation of  $R_S$  across 6 years reached up to 427 g C·m<sup>-2</sup>·year<sup>-1</sup>, with a CV of 17% (Irvine et al. 2008). The two large variations of annual  $R_S$  were both ascribed to changes in SWC. Large interannual variations of  $R_S$  were also observed in a beech forest (Epron et al. 2004), broadleaf forests (Martin and Bolstad

2005), and a Mediterranean forest (Asensio et al. 2007; Concilio et al. 2009).  $R_S$  in a humid year was twice as high as in a dry year in a Mediterranean holm oak forest (Asensio et al. 2007). However, under humid environment conditions, the variation of annual  $R_S$  was low in a cool-temperate forest in Japan (Mo et al. 2005) and a forest in Maine (Savage and Davidson 2001). In the subtropical forest of the present study, the interannual variation of  $R_S$  was similar to that of the two humid regions in Japan and Maine, with a small CV of 4%. It seems reasonable because of the abundant precipitation and humid climate in subtropical China, though the seasonal drought frequently occurs. However, when considering the seasonal drought in this region, the result should be more similar to that of Irvine et al. (2008). By comparison, we found that our analysis method was little different than those of previous studies (Savage and Davidson 2001; Irvine et al. 2008).

As we know, in eq. 6,  $\alpha$  denotes the reference  $R_S$  at  $T_S$  of 0 °C. It is mainly determined by the substrate availability, which is greatly affected by biological factors such as photosynthesis, root growth, microbial activity, and litterfall input (Rayment and Jarvis 2000; Luo and Zhou 2006; Carbone and Trumbore 2007). To exclude the possible effect of the periodicity in root growth and activity and availability of fresh litter for decomposition, we separated all  $R_S$  data into dormant and growing season and established empirical models eqs. 7 and 8. Annual  $R_S$  was estimated following the two models. If we follow the same method by Irvine et al. (2008) of creating empirical models with eq. 6 for each year and calculating annual  $R_S$  separately, the CV value of annual  $R_S$  will be enlarged to 10%. This CV value is comparable with that of the Harvard Forest and the ponderosa pine forest (Savage and Davidson 2001; Irvine et al. 2008) with obviously seasonal drought. Therefore, the different results may be ascribed to the different methods to some extent. This result suggested that Irvine et al. (2008) might overestimate the interannual difference of  $R_S$  to some extent because they did not consider the possible effect of seasonal variation of root and litter activity.

In general, interannual variation of  $R_S$  is attributed to changes in environmental factors, especially  $T_S$  and SWC (Irvine and Law 2002; Martin and Bolstad 2005; Phillips et al. 2010). However, it seems not to be the case for temperature in this study because the interannual variation of both  $T_A$  and  $T_S$  are very small (CV = 2% and 0.7%, respectively). On the other hand, Fig. 5d clearly showed that the changes in annual mean SWC accounted for the interannual variation of  $R_S$ .

This result was in agreement with that of a seasonally drought-stressed mature ponderosa pine forest (Irvine and Law 2002; Irvine et al. 2008) and beech, spruce, and pine stands in Germany (Borken et al. 2002). The reason might be that the seasonal drought affected greatly the soil microbe activity (Borken et al. 2006), as well as plant activity (López et al. 1998; Green et al. 2005).

The changes of annual mean SWC can be influenced by precipitation and ET. Variation in precipitation amount usually explains interannual variability in SWC, which subsequently influences annual  $R_S$  as in a temperate forest (Borken et al. 1999, 2006), within seasonally dry biomes (savannas, shrublands, and deserts) (Raich et al. 2002), in a Hesse forest (Epron et al. 2004), and a Mediterranean forest (Concilio et al. 2009). However, in this study, we found that SWC had no relation with precipitation amount but had a tight relation with rainfall frequency (Fig. 6d). It is reported that when rainfall is unevenly distributed across the year, rainfall frequency might be more important in controlling SWC than rainfall amount (Rambal and Debussche 1995). In contrast, we did not find strong correlation between rainfall frequency and SWC until small rainfall events (less than 1.5 mm) were excluded. This is reasonable because a small rainfall event was mainly intercepted by the forest canopy and could not reach the soil according to our observation. However, when a heavy rainfall occurs, a large proportion of the rainfall might be lost via surface runoff (Sharpley 1985). This suggests that both small and heavy rainfall events are of low efficiency for maintaining soil moisture. At our study site, the precipitation is unevenly distributed throughout the year, which results in frequent flood and drought in south China. Therefore it is reasonable that SWC showed a strong relationship with rainfall frequency instead of rainfall amount in this study.

A manipulated experiment indicated that decreased rainfall frequency obviously depressed  $R_S$  (Harper et al. 2005). We correlated  $R_S$  to rainfall frequency and found that their relationship was near but did not reach the distinguishing level in statistics ( $P = 0.1$ ). This result revealed that precipitation frequency controlled interannual variation of soil respiration by affecting soil moisture in the subtropical forest plantation.

That rainfall frequency drives interannual variation in  $R_S$  by affecting SWC might be explained as follows. First, higher rainfall frequency may greatly increase mean SWC as we discussed above. The SWC was positively correlated with  $R_S$  in this study. Increased SWC and rainfall availability may promote root growth and dynamics (López et al. 1998; Green et al. 2005), microbial communities and their activities (van Gestel et al. 1993; Wu and Brookes 2005; Xiang et al. 2008), and consequently  $R_S$ . Second, the increased rainfall frequency may also greatly increase the dry and humid alternation (Harper et al. 2005). An episodic rainfall may stimulate  $R_S$  (often called "Birch effect"), especially under dry soil conditions (Birch 1958). These pulses of  $R_S$  could explain 16%–21% of annual  $R_S$  (Lee et al. 2002), which might significantly influence the annual carbon budget (Xu et al. 2004).

Interannual variation of  $R_S$  has also been attributed to changes of biological processes such as litterfall and detritus input and root biomass growth (Ewel et al. 1987; Epron et al. 2004) and aboveground productivity (Irvine et al. 2007, 2008). However, our study showed that the interannual varia-

tion of  $R_S$  was not related to GEP,  $R_E$ , or NEP (Figs. 7a, 7b, and 7c). The interannual variation of net primary productivity (2003–2005) was similar to that of  $R_S$  at our study site, with a CV of 5.8% (Ma et al. 2008), because the ecosystem had a near-mature status. Although root respiration accounted for about 37% of  $R_S$  (unpublished data), a 6-year study duration might not induce great variation in root systems or root respiration for this near-mature forest stand. Furthermore, although litterfall reportedly greatly affected  $R_S$  (Ewel et al. 1987; Epron et al. 2004) and the fresh litterfall decomposition accounted for 19% of  $R_S$  in our previous study (Wang et al. 2009), litterfall input change did not affect the interannual variation of  $R_S$  (Fig. 7d).

## Conclusions

Seasonal and interannual patterns of soil respiration were studied using a 6-year data set collected in a subtropical coniferous plantation in China. Our results clearly indicated that seasonal soil respiration was affected by both soil temperature and moisture. Seasonal drought, which resulted from an uneven rainfall distribution across the year, strongly reduced soil respiration in the dry season (July–October). The mean annual soil respiration was estimated to be 736 g C·m<sup>-2</sup>·year<sup>-1</sup>, with a CV of 4%. Although this forest was characterized by a humid climate with abundant precipitation (1469 mm·year<sup>-1</sup>), the interannual variation of soil respiration was controlled by soil water content, which was determined by rainfall frequency, not rainfall amount. Consequently, precipitation frequency indirectly controlled the interannual variation of  $R_S$  by affecting soil moisture.

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## References

- Asensio, D., Peñuelas, J., Llusà, J., Ogaya, R., and Filella, I. 2007. Interannual and interseasonal soil CO<sub>2</sub> efflux and VOC exchange rates in a Mediterranean holm oak forest in response to experimental drought. *Soil Biol. Biochem.* **39**(10): 2471–2484. doi:10.1016/j.soilbio.2007.04.019.
- Batjes, N.H. 1996. Total carbon and nitrogen in the soils of the world. *Eur. J. Soil Sci.* **47**(2): 151–163. doi:10.1111/j.1365-2389.1996.tb01386.x.
- Birch, H.F. 1958. The effect of soil drying on humus decomposition and nitrogen availability. *Plant Soil*, **10**(1): 9–31. doi:10.1007/BF01343734.
- Borken, W., Xu, Y.-J., Brumme, R., and Lamersdorf, N. 1999. A climate change scenario for carbon dioxide and dissolved organic carbon fluxes from a temperate forest soil: drought and rewetting effects. *Soil Sci. Soc. Am. J.* **63**: 1848–1855. doi:10.2136/sssaj1999.6361848x.



- Borken, W., Xu, Y.J., Davidson, E.A., and Beese, F. 2002. Site and temporal variation of soil respiration in European beech, Norway spruce and Scots pine forests. *Glob. Change Biol.* **8**(12): 1205–1216. doi:10.1046/j.1365-2486.2002.00547.x.
- Borken, W., Savage, K., Davidson, E.A., and Trumbore, S.E. 2006. Effects of experimental drought on soil respiration and radiocarbon efflux from a temperate forest soil. *Glob. Change Biol.* **12**(2): 177–193. doi:10.1111/j.1365-2486.2005.001058.x.
- Carbone, M.S., and Trumbore, S.E. 2007. Contribution of new photosynthetic assimilates to respiration by perennial grasses and shrubs: residence times and allocation patterns. *New Phytol.* **176**(1): 124–135. doi:10.1111/j.1469-8137.2007.02153.x. PMID: 17803644.
- Chen, S., Huang, Y., Zou, J., Shen, Q., Hu, Z., Qin, Y., Chen, H., and Pan, G. 2010. Modeling interannual variability of global soil respiration from climate and soil properties. *Agric. For. Meteorol.* **150**(4): 590–605. doi:10.1016/j.agrformet.2010.02.004.
- Concilio, A., Chen, J., Ma, S., and North, M. 2009. Precipitation drives interannual variation in summer soil respiration in a Mediterranean-climate, mixed-conifer forest. *Clim. Change*, **92**(1–2): 109–122. doi:10.1007/s10584-008-9475-0.
- Curiel Yuste, J., Janssens, I.A., Carrara, A., Meiresonne, L., and Ceulemans, R. 2003. Interactive effects of temperature and precipitation on soil respiration in a temperate maritime pine forest. *Tree Physiol.* **23**(18): 1263–1270. PMID:14652226.
- Curiel Yuste, J., Janssens, I.A., Carrara, A., and Ceulemans, R. 2004. Annual  $Q_{10}$  of soil respiration reflects plant phenological patterns as well as temperature sensitivity. *Glob. Change Biol.* **10**(2): 161–169. doi:10.1111/j.1529-8817.2003.00727.x.
- Epron, D., Ngao, J., and Granier, A. 2004. Interannual variation of soil respiration in a beech forest ecosystem over a six-year study. *Ann. For. Sci.* **61**(6): 499–505. doi:10.1051/forest:2004044.
- Ewel, K.C., Cropper, W.P., Jr., and Gholz, H.L. 1987. Soil  $CO_2$  evolution in Florida slash pine plantations. I. Changes through time. *Can. J. For. Res.* **17**(4): 325–329. doi:10.1139/x87-054.
- Falk, M., Paw U, K.T., Wharton, S., and Schroeder, M. 2005. Is soil respiration a major contributor to the carbon budget within a Pacific Northwest old-growth forest? *Agric. For. Meteorol.* **135**(1–4): 269–283. doi:10.1016/j.agrformet.2005.12.005.
- Green, J.J., Dawson, L.A., Proctor, J., Duff, E.I., and Elston, D.A. 2005. Fine root dynamics in a tropical rain forest is influenced by rainfall. *Plant Soil*, **276**(1–2): 23–32. doi:10.1007/s11104-004-0331-3.
- Harper, C.W., Blair, J.M., Fay, P.A., Knapp, A.K., and Carlisle, J.D. 2005. Increased rainfall variability and reduced rainfall amount decreases soil  $CO_2$  flux in a grassland ecosystem. *Glob. Change Biol.* **11**(2): 322–334. doi:10.1111/j.1365-2486.2005.00899.x.
- Irvine, J., and Law, B.E. 2002. Contrasting soil respiration in young and old-growth ponderosa pine forests. *Glob. Change Biol.* **8**(12): 1183–1194. doi:10.1046/j.1365-2486.2002.00544.x.
- Irvine, J., Law, B.E., and Hibbard, K.A. 2007. Postfire carbon pools and fluxes in semiarid ponderosa pine in Central Oregon. *Glob. Change Biol.* **13**(8): 1748–1760. doi:10.1111/j.1365-2486.2007.01368.x.
- Irvine, J., Law, B.E., Martin, J.G., and Vickers, D. 2008. Interannual variation in soil  $CO_2$  efflux and the response of root respiration to climate and canopy gas exchange in mature ponderosa pine. *Glob. Change Biol.* **14**(12): 2848–2859. doi:10.1111/j.1365-2486.2008.01682.x.
- Jassal, R.S., Andrew, T., Black, T., Novak, M.D., Gaumont-Guay, D., and Nescic, Z. 2008. Effect of soil water stress on soil respiration and its temperature sensitivity in an 18-year-old temperate Douglas-fir stand. *Glob. Change Biol.* **14**(1): 1–14. doi:10.1111/j.1365-2486.2008.01573.x.
- King, J.S., Hanson, P.J., Bernhardt, E.Y., Deangelis, P., Norby, R.J., and Pregitzer, K.S. 2004. A multiyear synthesis of soil respiration responses to elevated atmospheric  $CO_2$  from four forest FACE experiments. *Glob. Change Biol.* **10**(6): 1027–1042. doi:10.1111/j.1529-8817.2003.00789.x.
- Kuzyakov, Y., and Gavrichkova, O. 2010. Time lag between photosynthesis and carbon dioxide efflux from soil: a review of mechanisms and controls. *Glob. Change Biol.* **16**(12): 3386–3406. doi:10.1111/j.1365-2486.2010.02179.x.
- Lee, M.S., Nakane, K., Nakatsubo, T., Mo, W., and Koizumi, H. 2002. Effects of rainfall events on soil  $CO_2$  flux in a cool temperate deciduous broad-leaved forest. *Ecol. Res.* **17**(3): 401–409. doi:10.1046/j.1440-1703.2002.00498.x.
- López, B., Sabaté, S., and Gracia, C. 1998. Fine roots dynamics in a Mediterranean forest: effects of drought and stem density. *Tree Physiol.* **18**(8–9): 601–606. PMID:12651348.
- Luo, Y., and Zhou, X. 2006. Soil respiration and the environment. Academic Press/Elsevier, San Diego, California. pp. 79–112.
- Ma, Z.Q. 2007. Carbon storage dynamics in the process of ecological restoration in red-soil hilly region. Master's thesis, Institute of Geographic Sciences and Natural Resources Research, Chinese Academy of Sciences. [In Chinese with English abstract.]
- Ma, Z., Liu, Q., Wang, H., Li, X., Zeng, H., and Xu, W. 2008. Observation and modeling of NPP for *Pinus elliottii* plantation in subtropical China. *Sci. China Ser. Earth Sci.* **51**(7): 955–965. doi:10.1007/s11430-008-0075-7.
- Martin, J.G., and Bolstad, P.V. 2005. Annual soil respiration in broadleaf forests of northern Wisconsin: influence of moisture and site biological, chemical, and physical characteristics. *Biogeochemistry*, **73**(1): 149–182. doi:10.1007/s10533-004-5166-8.
- Mo, W., Lee, M., Uchida, M., Inatomi, M., Saigusa, N., Mariko, S., and Koizumi, H. 2005. Seasonal and annual variations in soil respiration in a cool-temperate deciduous broad-leaved forest in Japan. *Agric. For. Meteorol.* **134**(1–4): 81–94. doi:10.1016/j.agrformet.2005.08.015.
- Phillips, S.C., Varner, R.K., Frolking, S., Munger, J.W., Bubier, J.L., Wofsy, S.C., and Crill, P.M. 2010. Interannual, seasonal, and diel variation in soil respiration relative to ecosystem respiration at a wetland to upland slope at Harvard Forest. *J. Geophys. Res.* **115**(G2): G02019. doi:10.1029/2008JG000858.
- Raich, J.W., Potter, C.S., and Bhagawati, D. 2002. Interannual variability in global soil respiration, 1980–1994. *Glob. Change Biol.* **8**(8): 800–812. doi:10.1046/j.1365-2486.2002.00511.x.
- Rambal, S., and Debussche, G. 1995. Water balance of Mediterranean ecosystem under a changing climate. In *Global change and Mediterranean-type ecosystems. Edited by J.M. Moreno and W.C. Oechel*. Springer, New York. pp. 386–407.
- Rayment, M.B., and Jarvis, P.G. 2000. Temporal and spatial variation of soil  $CO_2$  efflux in a Canadian boreal forest. *Soil Biol. Biochem.* **32**(1): 35–45. doi:10.1016/S0038-0717(99)00110-8.
- Ruehr, N.K., and Buchmann, N. 2010. Soil respiration fluxes in a temperate mixed forest: seasonality and temperature sensitivities differ among microbial and root-rhizosphere respiration. *Tree Physiol.* **30**(2): 165–176. doi:10.1093/treephys/tp106. PMID: 20008837.
- Ruehr, N.K., Knohl, A., and Buchmann, N. 2010. Environmental variables controlling soil respiration on diurnal, seasonal and annual time-scales in a mixed mountain forest in Switzerland. *Biogeochemistry*, **98**(1–3): 153–170. doi:10.1007/s10533-009-9383-z.
- Savage, K.E., and Davidson, E.A. 2001. Interannual variation of soil respiration in two New England forests. *Global Biogeochem. Cycles*, **15**(2): 337–350. doi:10.1029/1999GB001248.
- Sharpley, A.N. 1985. Depth of surface soil-runoff interaction as affected

- by rainfall, soil slope, and management. *Soil Sci. Soc. Am. J.* **49**(4): 1010–1015. doi:10.2136/sssaj1985.03615995004900040044x.
- Valentini, R., Matteucci, G., Dolman, A.J., Schulze, E.-D., Rebmann, C., Moors, E.J., Granier, A., Gross, P., Jensen, N.O., Pilegaard, K., Lindroth, A., Grelle, A., Bernhofer, C., Grünwald, T., Aubinet, M., Ceulemans, R., Kowalski, A.S., Vesala, T., Rannik, Ü., Berbigier, P., Loustau, D., Guðmundsson, J., Thorgeirsson, H., Ibrom, A., Morgenstern, K., Clement, R., Moncrieff, J., Montagnani, L., Minerbi, S., and Jarvis, P.G. 2000. Respiration as the main determinant of carbon balance in European forests. *Nature*, **404** (6780): 861–865. doi:10.1038/35009084. PMID:10786790.
- Van Gestel, M., Merckx, R., and Vlassak, K. 1993. Microbial biomass responses to soil drying and rewetting: the fate of fast- and slow-growing microorganisms in soils from different climates. *Soil Biol. Biochem.* **25**(1): 109–123. doi:10.1016/0038-0717(93)90249-B.
- Van't Hoff, J.H. 1898. Lectures on theoretical and physical chemistry. Part 1. Chemical dynamics. Edward Arnold, London. pp. 224–229.
- Wang, Y., Wang, H., Ma, Z., Wen, X., Li, Q., Liu, Y., Sun, X., and Yu, G. 2009. Contribution of aboveground litter decomposition to soil respiration in a subtropical coniferous plantation in southern China. *Asia-Pac. J. Atmos. Sci.* **45**(2): 137–147.
- Wen, X.-F., Yu, G.-R., Sun, X.-M., Li, Q.-K., Liu, Y.-F., Zhang, L.-M., Ren, C.-Y., Fu, Y.-L., and Li, Z.-Q. 2006. Soil moisture effect on the temperature dependence of ecosystem respiration in a subtropical *Pinus* plantation of southeastern China. *Agric. For. Meteorol.* **137**(3–4): 166–175. doi:10.1016/j.agrformet.2006.02.005.
- Wen, X.-F., Wang, H.-M., Wang, J.-L., Yu, G.-R., and Sun, X.-M. 2010. Ecosystem carbon exchange of a subtropical evergreen coniferous plantation subjected to seasonal drought, 2003–2007. *Biogeosciences*, **7**(1): 357–369. doi:10.5194/bg-7-357-2010.
- Wu, J., and Brookes, P.C. 2005. The proportional mineralisation of microbial biomass and organic matter caused by air-drying and rewetting of a grassland soil. *Soil Biol. Biochem.* **37**(3): 507–515. doi:10.1016/j.soilbio.2004.07.043.
- Xiang, S.R., Doyle, A., Holden, P.A., and Schimel, J.P. 2008. Drying and rewetting effects on C and N mineralization and microbial activity in surface and subsurface California grassland soils. *Soil Biol. Biochem.* **40**(9): 2281–2289. doi:10.1016/j.soilbio.2008.05.004.
- Xu, L., Baldocchl, D.D., and Tang, J. 2004. How soil moisture, rain pulses, and growth alter the response of ecosystem respiration to temperature. *Global Biogeochem. Cycles*, **18**(4): GB4002. doi:10.1029/2004GB002281.
- Yu, G.R., Zhang, L.M., Sun, X.M., Fu, Y.L., Wen, X.F., Wang, Q.F., Li, S.G., Ren, C.Y., Song, X., Liu, Y.F., Han, S.J., and Yan, J.H. 2008. Environmental controls over carbon exchange of three forest ecosystems in eastern China. *Glob. Change Biol.* **14**(11): 2555–2571. doi:10.1111/j.1365-2486.2008.01663.x.

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8. Yue Du, Hongyan Han, Yanfen Wang, Mingxing Zhong, Dafeng Hui, Shuli Niu, Shiqiang Wan. 2018. Plant functional groups regulate soil respiration responses to nitrogen addition and mowing over a decade. *Functional Ecology* **32**:4, 1117-1127. [[Crossref](#)]
9. Munemasa Teramoto, Naishen Liang, Jiye Zeng, Nobuko Saigusa, Yoshiyuki Takahashi. 2017. Long-term chamber measurements reveal strong impacts of soil temperature on seasonal and inter-annual variation in understory CO<sub>2</sub> fluxes in a Japanese larch (*Larix kaempferi* Sarg.) forest. *Agricultural and Forest Meteorology* **247**, 194-206. [[Crossref](#)]
10. María T. Domínguez, Andrew R. Smith, Sabine Reinsch, Bridget A. Emmett. 2017. Inter-annual Variability of Soil Respiration in Wet Shrublands: Do Plants Modulate Its Sensitivity to Climate?. *Ecosystems* **20**:4, 796-812. [[Crossref](#)]
11. Zhuo Wu, Quansheng Ge, Erfu Dai. 2017. Modeling the Relative Contributions of Land Use Change and Harvest to Forest Landscape Change in the Taihe County, China. *Sustainability* **9**:5, 708. [[Crossref](#)]
12. Mingjie Xu, Huimin Wang, Xuefa Wen, Tao Zhang, Yuebao Di, Yidong Wang, Jianlei Wang, Chuanpeng Cheng, Wenjiang Zhang. 2017. The full annual carbon balance of a subtropical coniferous plantation is highly sensitive to autumn precipitation. *Scientific Reports* **7**:1. . [[Crossref](#)]
13. Yakun Tang, Yunming Chen, Xuefa Wen, Xiaomin Sun, Xu Wu, Huimin Wang. 2016. Variation of carbon use efficiency over ten years in a subtropical coniferous plantation in southeast China. *Ecological Engineering* **97**, 196-206. [[Crossref](#)]
14. Wenjun Wei, Wenzhong You, Huidong Zhang, Tingwu Yan, Yixin Mao. 2016. Soil respiration during freeze-thaw cycles in a temperate Korean Larch (*Larix olgensis* herry.) plantation. *Scandinavian Journal of Forest Research* **31**:8, 742-749. [[Crossref](#)]
15. Erfu Dai, Zhuo Wu, Quansheng Ge, Weimin Xi, Xiaofan Wang. 2016. Predicting the responses of forest distribution and aboveground biomass to climate change under RCP scenarios in southern China. *Global Change Biology* **22**:11, 3642-3661. [[Crossref](#)]
16. Jianlei Wang, Huimin Wang, Xiaoli Fu, Mingjie Xu, Yidong Wang. 2016. Effects of site preparation treatments before afforestation on soil carbon release. *Forest Ecology and Management* **361**, 277-285. [[Crossref](#)]
17. Huihui Feng, Yuanbo Liu. 2015. Combined effects of precipitation and air temperature on soil moisture in different land covers in a humid basin. *Journal of Hydrology* **531**, 1129-1140. [[Crossref](#)]
18. Yongsheng Wang, Shulan Cheng, Huajun Fang, Guirui Yu, Xiaofeng Xu, Minjie Xu, Lei Wang, Xiaoyu Li, Gaoyue Si, Jing Geng, Shun He. 2015. Contrasting effects of ammonium and nitrate inputs on soil CO<sub>2</sub> emission in a subtropical coniferous plantation of southern China. *Biology and Fertility of Soils* **51**:7, 815-825. [[Crossref](#)]
19. Rui Wang, Shengli Guo, Jishao Jiang, Defeng Wu, Nana Li, Yanjun Zhang, Qingfang Liu, Rujian Li, Zhiqi Wang, Qiqi Sun, Lanlan Du, Man Zhao. 2015. Tree-scale spatial variation of soil respiration and its influence factors in apple orchard in Loess Plateau. *Nutrient Cycling in Agroecosystems* **102**:2, 285-297. [[Crossref](#)]
20. Yidong Wang, Huimin Wang, Mingjie Xu, Zeqing Ma, Zhong-Liang Wang. 2015. Soil organic carbon stocks and CO<sub>2</sub> effluxes of native and exotic pine plantations in subtropical China. *CATENA* **128**, 167-173. [[Crossref](#)]

21. Bin Yang, Xuefa Wen, Xiaomin Sun. 2015. Seasonal variations in depth of water uptake for a subtropical coniferous plantation subjected to drought in an East Asian monsoon region. *Agricultural and Forest Meteorology* **201**, 218-228. [[Crossref](#)]
22. Huihui Feng, Yuanbo Liu. 2014. Trajectory based detection of forest-change impacts on surface soil moisture at a basin scale [Poyang Lake Basin, China]. *Journal of Hydrology* **514**, 337-346. [[Crossref](#)]
23. Yakun Tang, Xuefa Wen, Xiaomin Sun, Huimin Wang. 2014. Interannual Variation of the Bowen Ratio in a Subtropical Coniferous Plantation in Southeast China, 2003-2012. *PLoS ONE* **9**:2, e88267. [[Crossref](#)]
24. Mingjie Xu, Xuefa Wen, Huimin Wang, Wenjiang Zhang, Xiaoqin Dai, Jie Song, Yidong Wang, Xiaoli Fu, Yunfen Liu, Xiaomin Sun, Guirui Yu. 2014. Effects of Climatic Factors and Ecosystem Responses on the Inter-Annual Variability of Evapotranspiration in a Coniferous Plantation in Subtropical China. *PLoS ONE* **9**:1, e85593. [[Crossref](#)]
25. Yidong Wang, Huimin Wang, Zhong-Liang Wang, Zeqing Ma, Xiaoqin Dai, Xuefa Wen, Yunfen Liu. 2014. Effect of litter layer on soil-atmosphere N<sub>2</sub>O flux of a subtropical pine plantation in China. *Atmospheric Environment* **82**, 106-112. [[Crossref](#)]
26. D. Gaumont-Guay, T.A. Black, A.G. Barr, T.J. Griffis, R.S. Jassal, P. Krishnan, N. Grant, Z. Nescic. 2014. Eight years of forest-floor CO<sub>2</sub> exchange in a boreal black spruce forest: Spatial integration and long-term temporal trends. *Agricultural and Forest Meteorology* **184**, 25-35. [[Crossref](#)]
27. Yidong Wang, Huimin Wang, Zeqing Ma, Xiaoqin Dai, Xuefa Wen, Yunfen Liu, Zhong-Liang Wang. 2013. The litter layer acts as a moisture-induced bidirectional buffer for atmospheric methane uptake by soil of a subtropical pine plantation. *Soil Biology and Biochemistry* **66**, 45-50. [[Crossref](#)]
28. Wenzhong You, Wenjun Wei, Huidong Zhang, Tingwu Yan, Zhaokai Xing. 2013. Temporal patterns of soil CO<sub>2</sub> efflux in a temperate Korean Larch (*Larix olgensis* Herry.) plantation, Northeast China. *Trees* **27**:5, 1417-1428. [[Crossref](#)]
29. Daniel Bini, Cristiane Alcantara dos Santos, Kellen Banhos do Carmo, Nagomi Kishino, Galdino Andrade, Waldemar Zangaro, Marco Antonio Nogueira. 2013. Effects of land use on soil organic carbon and microbial processes associated with soil health in southern Brazil. *European Journal of Soil Biology* **55**, 117-123. [[Crossref](#)]
30. Yidong Wang, Huimin Wang, Zhong-Liang Wang, Wenjiang Zhang, Changcheng Guo, Xuefa Wen, Yunfen Liu. 2012. Optimizing manual sampling schedule for estimating annual soil CO<sub>2</sub> efflux in a young exotic pine plantation in subtropical China. *European Journal of Soil Biology* **52**, 41-47. [[Crossref](#)]
31. Wang Yidong, Wang Zhong-Liang, Wang Huimin, Guo Changcheng, Bao Wankui. 2012. Rainfall pulse primarily drives litterfall respiration and its contribution to soil respiration in a young exotic pine plantation in subtropical China. *Canadian Journal of Forest Research* **42**:4, 657-666. [[Abstract](#)] [[Full Text](#)] [[PDF](#)] [[PDF Plus](#)]