

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 ± 30 g C·m⁻²·year⁻¹, with a range of 706–790 g C·m⁻²·year⁻¹. Although this forest was characterized by a humid climate with high precipitation (1469 mm·year⁻¹), 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 ± 30 g C·m⁻²·an⁻¹ avec une étendue de 706–790 g C·m⁻²·an⁻¹. Bien que cette forêt soit caractérisée par un climat humide avec de fortes précipitations (1469 mm·an⁻¹), 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.

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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 CO₂ 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; Boroken 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

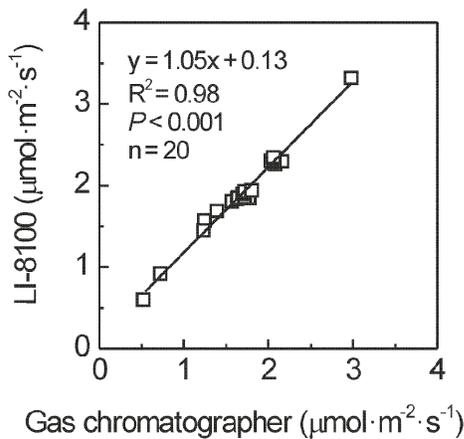
This study was conducted in a subtropical evergreen coniferous plantation at Qianyanzhou Ecological Station ($26^{\circ}44'39''\text{N}$, $115^{\circ}03'33''\text{E}$, elevation 102 m) in southeast China. The slash pine plantation was established in 1985. A few Masson's pine (*Pinus massoniana* Lamb.) 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 $17.9 \text{ }^{\circ}\text{C}$, 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 CO_2 efflux

Soil CO_2 efflux was measured using a static closed chamber – gas chromatography system from January 2004 to July 2007. Subsequently, an automated soil 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 CO_2 concentration was determined by a gas chromatographer (HP4890D; Agilent Technologies, Inc., Wilmington, Delaware) equipped with a flame ionization detector. Soil CO_2 emission was then calculated from a linear regression of temporal changes of 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 ($\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$), Δm refers to an increase in CO_2 in the chamber (μmol), Δc and Δt are changes of 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 (m^3), A is ground area covered by the chamber (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 10×10 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 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

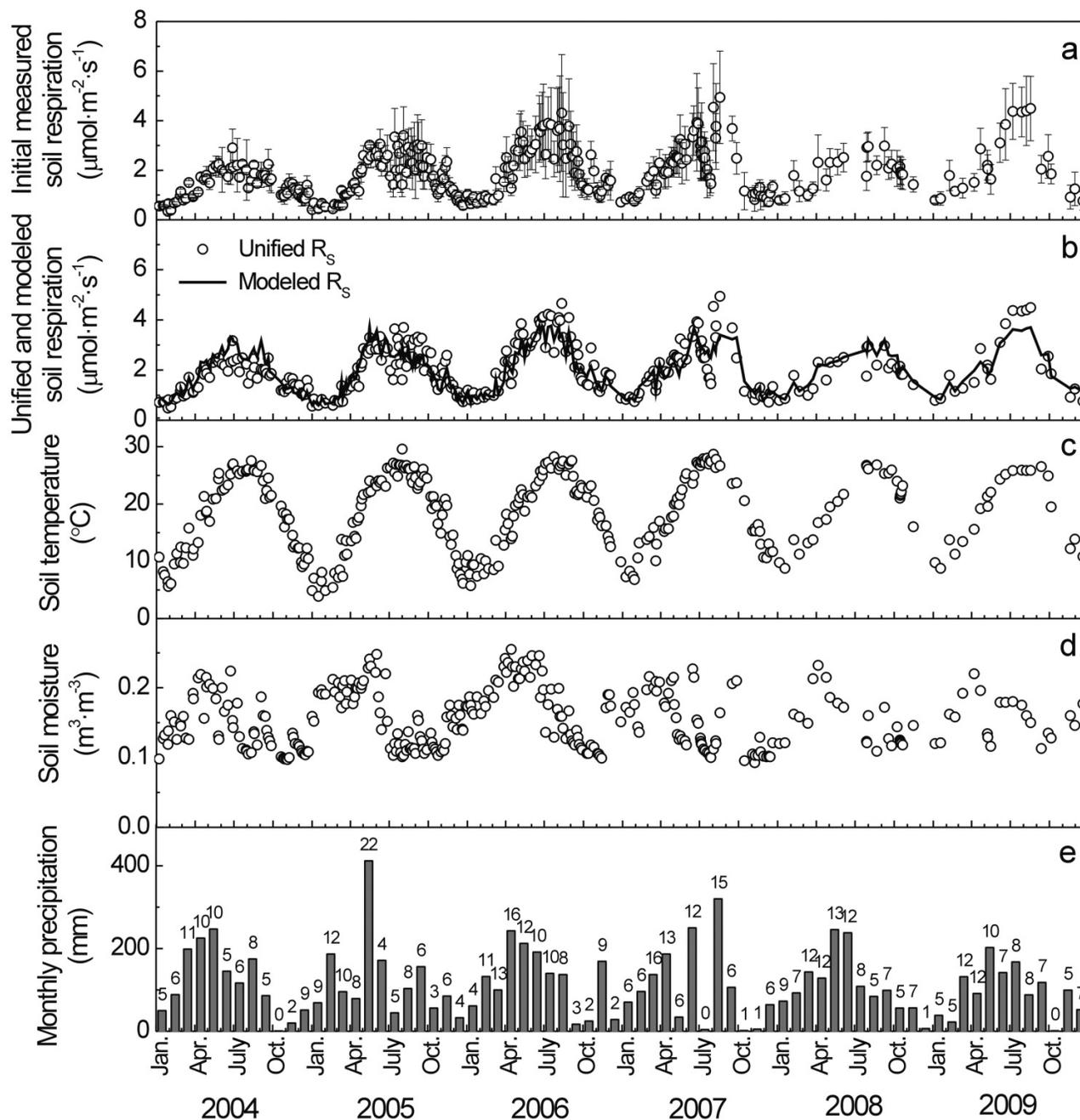
Litterfall was collected monthly by placing 14 litter traps (1 m^2 square) around the study area and then was separated into leaves, branches, flowers, and fruit. Each sample was oven-dried at 65 °C until constant mass was obtained. Litterfall carbon input was calculated according to the mass and carbon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



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

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

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

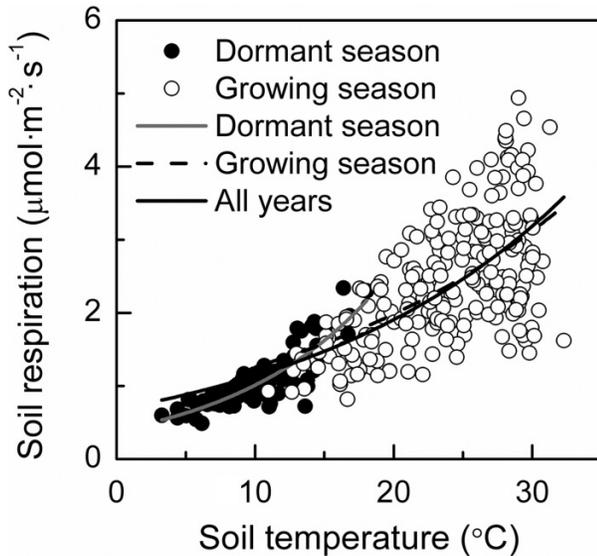
where R_S is soil respiration, $R_{S,15}$ is normalized soil respiration at 15 °C, T_S is soil temperature, SWC is volumetric soil moisture, and α , β , γ , and δ are fitted parameters.

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.

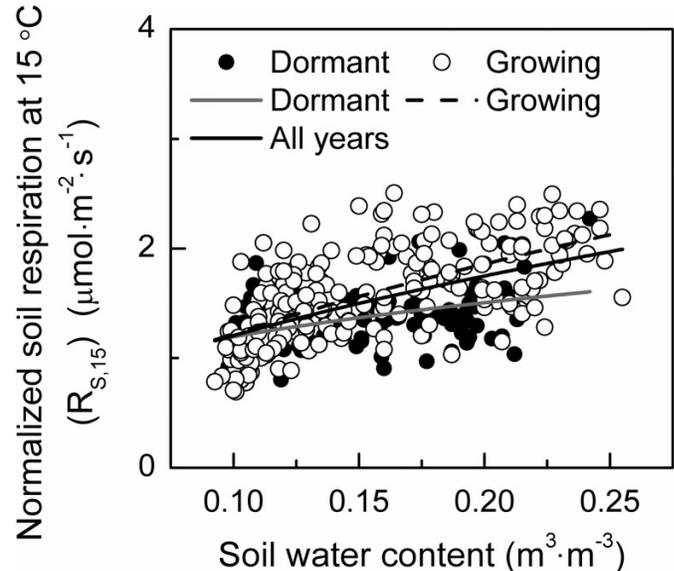
$$[7] \quad R_S = 1.996e^{0.067T_S} \text{SWC}^{0.695} \quad (R^2 = 0.65, P < 0.001)$$

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

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⁻²·year⁻¹, 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⁻²·year⁻¹. Mean annual R_S was 736 g C·m⁻²·year⁻¹, 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).

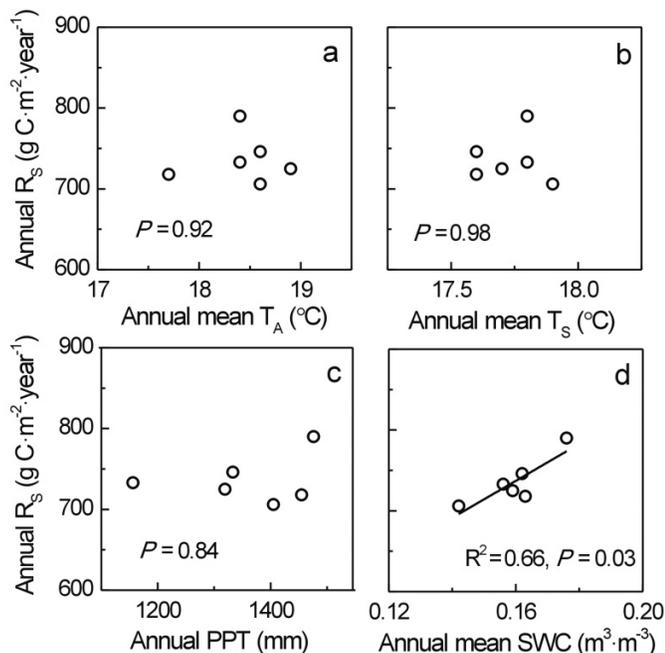
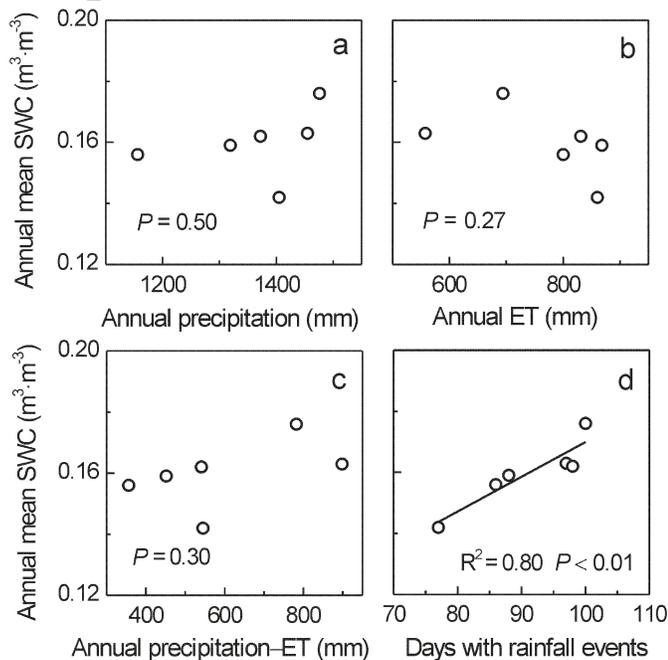


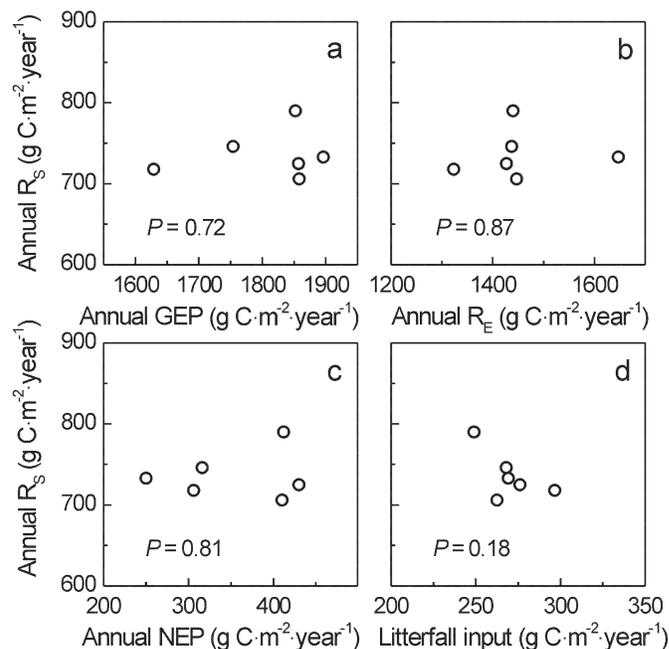
Fig. 6. Relationships between annual mean soil water content (SWC) and (a) annual precipitation, (b) annual evapotranspiration (ET), (c) annual precipitation minus ET, and (d) annual days with effective rainfall events. Effective rainfall events refer to rainfall amount ≥ 1.5 mm.



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_{Ss} 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

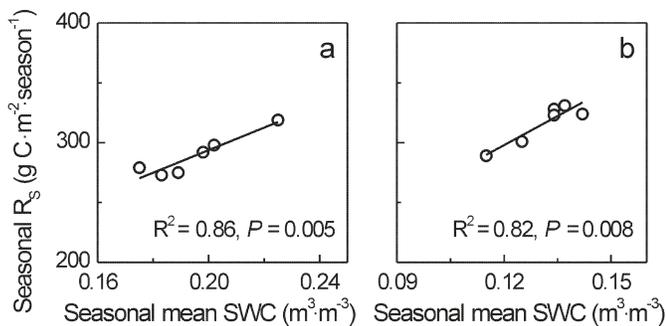
Soil temperature and moisture are usually the most important environmental factors controlling R_S (Epron et al. 2004; Martin and Bolstad 2005). In general, R_S is mainly determined by T_S , particularly under humid conditions (Wang et al. 2009; Ruehr et al. 2010). In the humid subtropical forest, we 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 ⁻²)	Mean T_S (°C)	Mean SWC (m ³ ·m ⁻³)	Rainfall (mm)	R_S (g C·m ⁻²)	Mean T_S (°C)	Mean SWC (m ³ ·m ⁻³)	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⁻²·year⁻¹, 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⁻²·year⁻¹, 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, α 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⁻²·year⁻¹, with a CV of 4%. Although this forest was characterized by a humid climate with abundant precipitation (1469 mm·year⁻¹), 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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