

## Soil respiration in an old-growth subtropical forest: Patterns, components, and controls

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Received 6 December 2012; revised 20 January 2013; accepted 18 February 2013; published 4 April 2013.

[1] The patterns, components, and controls of soil respiration in an old-growth subtropical forest were investigated using an automatic chamber system. We measured soil respiration in three treatments (control, trenching, litter removal) over 15 months. The annual total soil respiration ( $1248 \text{ gC m}^{-2} \text{ yr}^{-1}$ ) showed considerable spatial variation (coefficient of variation = 27.8%) within the forest. Thirty samples were required to obtain results within 10% of the mean value at a 95% confidential level. A distinctive cosine-like diel pattern of soil respiration was observed; the time lag between gross primary production and soil respiration at this scale was calculated to be 4–5 h. Seasonality of soil respiration was strong ( $\sim 1 \mu\text{mol m}^{-2} \text{ s}^{-1}$  near the end of winter;  $\sim 6 \mu\text{mol m}^{-2} \text{ s}^{-1}$  in midsummer). No time lag was discerned between gross primary production and soil respiration at the seasonal scale. Soil temperature at 5 cm below surface can explain most (>91%) of the observed annual variation in soil respiration. The apparent respiration temperature sensitivity index ( $Q_{10}$ ) was 3.05. The lowest  $Q_{10}$  value was observed in winter, when soil moisture was low. Soil respiration was overestimated by a  $Q_{10}$  function during both dry and wet periods. The relative contributions of soil organic matter ( $R_{\text{SOM}}$ ), litterfall decomposition ( $R_{\text{L}}$ ), and root respiration ( $R_{\text{R}}$ ) to total soil respiration are 65.25%, 18.73%, and 16.01%, respectively; the temperature sensitivity of these components differ:  $R_{\text{L}}$  ( $Q_{10} = 7.22$ ) >  $R_{\text{SOM}}$  (2.73) >  $R_{\text{R}}$  (1.65). This relationship between  $Q_{10}$  values for litter respiration, soil organic matter decomposition, and root respiration still holds after minimizing the confounding effect of moisture. A relatively constant substrate supply and/or thermal acclimation could account for the observed low-temperature sensitivity in root respiration. Given the high carbon stocks and fluxes, the old-growth subtropical forests of China seem important in the global carbon budget and climate change.

**Citation:** Tan, Z.-H., et al. (2013), Soil respiration in an old-growth subtropical forest: Patterns, components, and controls, *J. Geophys. Res. Atmos.*, 118, 2981–2990, doi:10.1002/jgrd.50300.

### 1. Introduction

[2] Human activity has significantly altered global carbon cycling [Magnani et al., 2007; Vitousek et al., 1997]. Large amounts of carbon ( $\sim 375$  billion tons) have been released into the atmosphere through fossil fuel combustion, cement manufacturing, and tropical deforestation. Around half of this carbon dioxide has been absorbed by the ocean and terrestrial biosphere, the remaining half remains in the atmosphere. Atmospheric carbon dioxide has increased from 280 ppm in the preindustrial era to 390 ppm in 2011 [WMO, 2012]. Carbon dioxide is one of many long-lived greenhouse gases. An increase in its atmospheric concentration changes Earth's radiation balance and climate system and leads to so-called global climate change.

[3] In the study of climatic change and carbon cycling interaction, there are two main research issues. One is the “missing sink” in global carbon cycling [Pan et al., 2011; Woodwell et al., 1978]. The other is the feedback between climatic change and carbon cycling [Cox et al., 2000]. As

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2169-897X/13/10.1002/jgrd.50300

mentioned earlier, the ocean and terrestrial biosphere are natural carbon sinks and have absorbed nearly half of all artificial carbon dioxide emissions. In attempts to find the size and location of terrestrial carbon sinks, the “missing sink” issue has been raised. It is still not well addressed and remains full of uncertainties [Pan *et al.*, 2011]. The feedback issue is to understand whether global climatic change has a positive or negative impact on natural carbon sinks [Denman *et al.*, 2007]. If natural carbon sinks are enhanced in climatic change, an increase in atmospheric carbon dioxide will be mitigated and negative feedback will occur. The opposite holds true as well. The presence of feedback is commonly accepted and plays a crucial role in predicting future climate trends. However, our understanding of them is still highly limited.

[4] Soil is the largest carbon pool in terrestrial ecosystems, containing 2700 Gt of carbon. This amount is more than the sum of carbon in atmosphere (780 Gt) and biomass (575 Gt) [Lal, 2008]. Around 60–80% of photosynthetic production is respired into the atmosphere through soil respiration [Bond-Lamberty and Thomson, 2010]. The magnitude of soil respiration ( $R_s$ ) is about 13 times that of fossil fuel combustion. Therefore, a slight variation of soil respiration caused by biotic or abiotic factors can exert a strong impact on global carbon balance [Davidson and Janssens, 2006]. Although numerous studies have been carried out to investigate the soil respiration of different vegetation types, the regional or global pattern of soil respiration, and its components and environmental controls, still needs to be addressed [Bond-Lamberty and Thomson, 2010].

[5] Region-wide field measurements in soil respiration employ the same standards and, combined with manipulation treatments, could be used to address the “missing sink” on the one hand and to quantify climate change carbon-cycle feedbacks on the other. Thus, we established a soil respiration measurement network in Asia. An automatic soil respiration chamber was applied to all the measurement sites in the network. The network covers nearly all terrestrial ecosystems in Asia, from tropical rainforest in Southeast Asia, to subtropical forest, temperate forest, boreal forest and tundra in west Siberia. At some of the sites, soil was heated using infrared lamps to model a warming effect.

[6] In this study, we report on the soil respiration measurements taken from one site of the network located in an old-growth subtropical forest of China. Soil respiration data collected in this area are very important for synthetic studies; i.e., studies by Bond-Lamberty and Thomson [2010] and Mahecha *et al.* [2010]. Furthermore, they are important because these forests serve as regional carbon sinks. In Asia, mainly in China, there is the dry belt that is controlled by a subtropical high pressure resulting from the effect caused by the Tibetan Plateau [Kira, 1991]. Subtropical evergreen forests are potential vegetations in the area, but not deserts or subtropical savannas. These subtropical forests were largely destroyed by humans in the past years. Only in the mountainous areas that are difficult to access are old-growth forests still found. In previous studies, these old-growth forests were reported to be strong carbon sinks [Zhou *et al.*, 2006]. Whether these carbon sinks persist or weaken under a warming climate is uncertain [Tan *et al.*, 2012].

[7] We tried to investigate all aspects of the components, patterns, and controls of soil respiration at the study location with field data collected from a soil automatic chamber, a nearby eddy flux system, and a nearby climate station. The main hypotheses of this study are:

[8] 1. Due to high soil-carbon densities and well-watered conditions, the annual total soil respiration of the forest will be higher than the predicted value based on a global MAT- $R_s$  (MAT: mean annual temperature) relationship [Raich and Schlesinger, 1992].

[9] 2. For an evergreen canopy and a year-long growing season, the seasonal variation of root respiration, both growth and maintenance, will not be as strong as that of a temperate or boreal forest [Bååth and Wallander, 2003; Boone *et al.*, 1998]. Meanwhile, a low-temperature sensitivity of root respiration is expected in the subtropical forest.

[10] 3. Soil water content covaried with temperature in the studied forest, which is influenced by a monsoon climate. Water will have a strong confounding effect on the derived apparent temperature sensitivity of litterfall and soil organic matter decomposition.

## 2. Materials and Methods

### 2.1. Site Description

[11] The study site is located in the Mt. Ailao Nature Reserve (24°32'N, 101°01'E; 2476 m elevation) in Yunnan Province, SW China. In this area, an old-growth subtropical evergreen broadleaved forest is spread widely and well protected. This forest has a stand age that exceeds 300 years and is free of management. The dominant vegetation species in this forest are *Lithocarpus chintungensis*, *Rhododendron leptothrium*, *Vaccinium duclouxii*, *Lithocarpus xylocarpus*, *Castanopsis wattii*, *Schima noronhae*, *Hartia sinensis*, and *Manglietia insignis*. The tree density of the forest is 2728 ha<sup>-1</sup>; the median tree height is 9.0 m; median tree diameter at breast height is 9.5 cm; and the median basal area in the forest is 91 m<sup>2</sup> ha<sup>-1</sup>. The leaf area index measured by the canopy analyzer (LAI-2000, Li-Cor Inc., Lincoln, NE, USA) is ~5.0. The estimated total stand biomass is 499 t ha<sup>-1</sup>. Mean annual air temperature is 11.3°C, with monthly mean values ranging from 5.4 to 23.5°C. The site receives an annual average of 1840 mm of precipitation, based on more than 20 years of data collected at a meteorological station. The region has two distinct seasons influenced by a monsoon climate. The wet season occurs from May through October, and the dry season occurs from November to April. The soils are loamy Alfisols. An organic carbon horizon is located 3–7 cm below ground surface. It has a pH of 4.5 and organic carbon and total nitrogen contents of 304 and 18 g kg<sup>-1</sup>, respectively [Tan *et al.*, 2011].

### 2.2. Experimental Design and Soil Respiration Measurement

[12] Twenty chambers were divided into four treatments (five chambers per treatment): control, trenching, above-ground litter removal, and infrared light warming. Locations of the chambers are shown in Figure S1 in the auxiliary material. A warming treatment was not included in this study. For the trenching treatments, we excavated trenches down to 50 cm in depth, lined them with plastic sheets,

and then refilled and packed them carefully with the original soil. The trench depth of 50 cm was based on:

[13] i. The soil profile data showed that the main root system of the studied forest trees is seldom deeper than 1.5 m.

[14] ii. Soil respiration was mainly contributed by fine root but not coarse root. And the active fine root could also be reflected by the water uptake. A previous study in the same forest showed that 82% water abstraction by roots 40 cm or shallower [Liu *et al.*, 2003]. We could then believe a trench of 50 cm could at least exclude over 82% of the root respiration.

[15] The aboveground litter was removed every two weeks in the aboveground litter removal treatment.

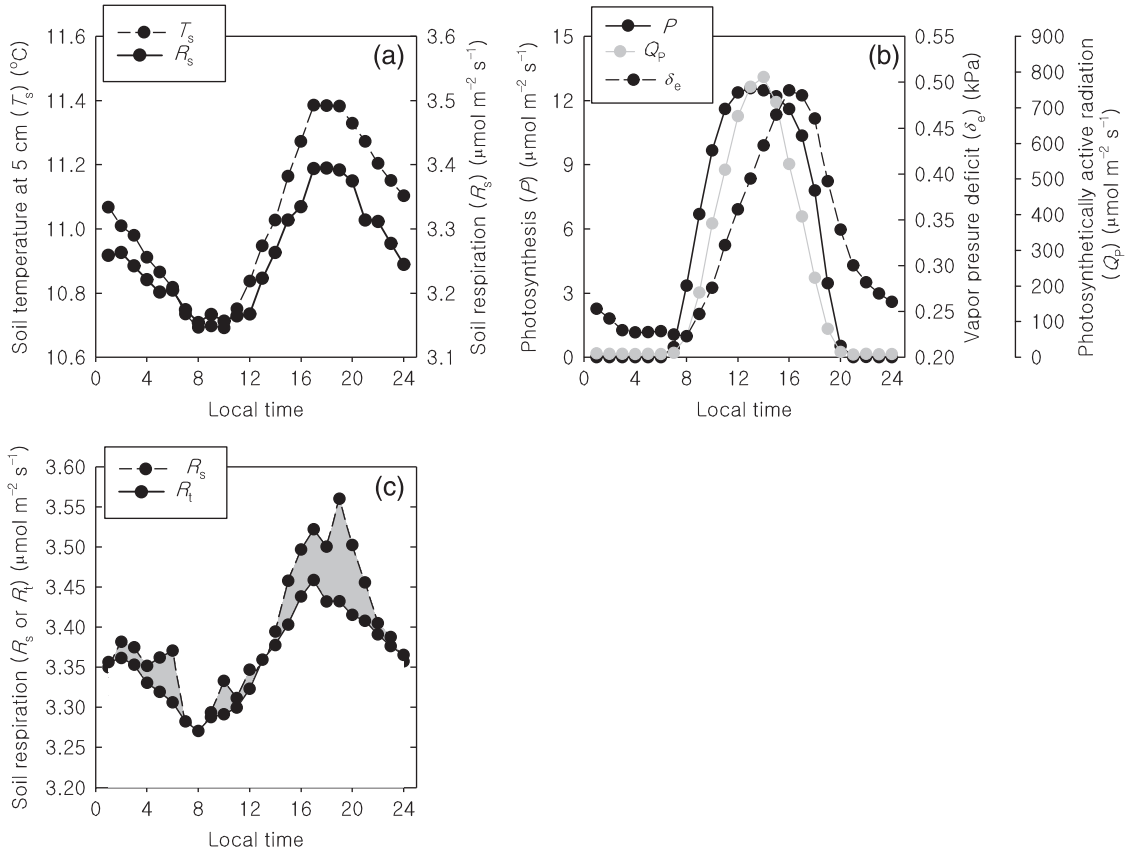
[16] Soil efflux was monitored by a multichannel automated measurement system developed by Liang at the Japan National Institute for Environmental Studies. The system measured soil efflux in a flow-through and non-steady-state manner, and was comprised of 20 automatic chambers and a control box. The chambers (90 cm × 90 cm × 50 cm) were made from clear PVC. The system incorporates several design features to prevent gas outlet [Liang *et al.*, 2003]. Two lids at the top of the chamber can be raised or closed; they are operated by compressed air (MAX-E-12, Techno Fronto) regulated by a four-way valve (BK120, Techno Fronto). Two fans (KMFH-12B, Kyoei, Tokyo, Japan) mounted in each chamber ensure sufficient mixing of air during measurement.

[17] The main components of the control box are an infrared gas analyzer (IRGA; Li-840, Li-Cor Inc.) and a data logger (CR10X, Campbell Scientific Inc.). During measurement, air in the closed chamber is circulated through the IRGA by a microdiaphragm pump (CM-50, Enomoto Ltd., Tokyo, Japan). The 20 chambers are closed sequentially by a home-made relay board controlled by the data logger. The data logger acquires output signals from the IRGA every second and records an average value every 10 s; the total sampling period for each chamber was 180 s. For each chamber, 1 efflux value was obtained per hour. The efflux was calculated from 18 records, as shown in equation (1):

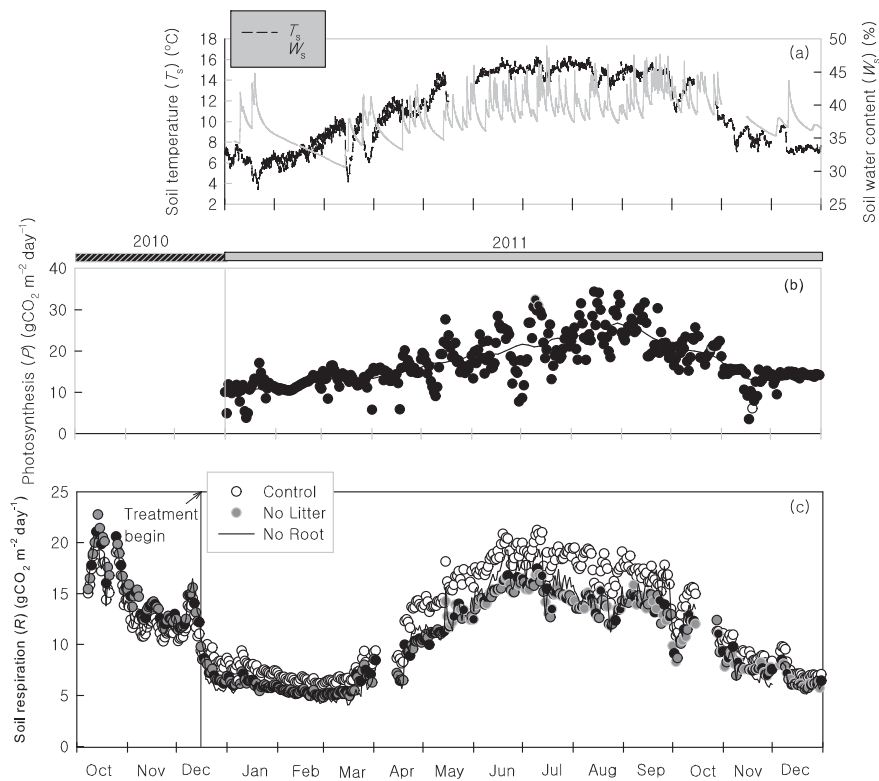
$$R_s = \frac{VP(1 - W)}{RST} \frac{\partial c}{\partial t} \quad (1)$$

where  $V$  is volume of the chamber ( $m^3$ );  $S$ , the base area of the chamber ( $m^2$ );  $R$ , a gas constant ( $8.314 \text{ Pa } m^3 \text{ K}^{-1}$ );  $T$ , the air temperature in the chamber (K);  $P$ , the air pressure (Pa);  $W$ , the water vapor mole fraction; and  $\partial C/\partial t$ , the rate of increase in carbon dioxide mole fraction ( $\mu\text{mol } \text{mol}^{-1} \text{ s}^{-1}$ ) in the chamber calculated by the least squares method.

[18] Soil temperature at 5 cm depth and air temperature inside each chamber were measured with self-made thermocouples. Soil moisture at 10 cm depth was monitored with time-domain reflectometers (CS-616, Campbell Scientific



**Figure 1.** (a) Diel pattern of soil respiration ( $R_s$ ) and soil temperature ( $T_s$ ) for 2011; (b) diel pattern of gross primary production derived from eddy covariance observations ( $P$ ), photosynthetically active radiation ( $Q_p$ ), and atmospheric vapor pressure deficit ( $\delta_e$ ); and (c) diel pattern of  $R_s$  and modeled soil respiration ( $R_t$ ) in autumn. In Figure 1c, the grey area shows the difference between observed and modeled soil respiration.



**Figure 2.** (a) Annual variation of  $T_s$  and soil volumetric water content ( $W_s$ ) measured at 5 cm in depth each hour, and (b) daily binned gross primary production ( $P$ ) derived from eddy covariance observations. The grey line in Figure 2b shows results after smoothing. Daily binned respiration is shown for different treatments: control (open circles), no litter (grey circles), and no root (solid line).

Inc., Logan, UT, USA). Air pressure at 30 cm height in the center of the plot was measured by a pressure transducer (PX2760, Omega Engineering, Inc., Stamford, CT, USA).

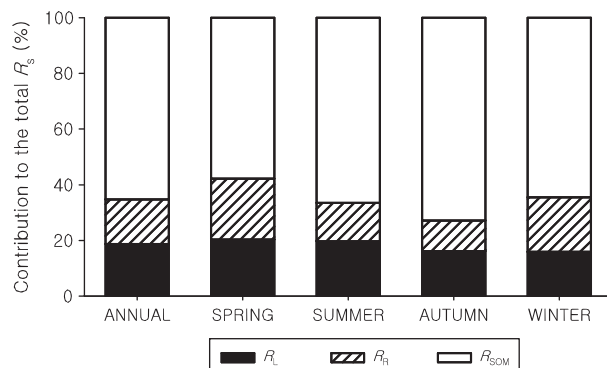
### 2.3. Complementary Measurements

[19] The eddy covariance system was comprised of an open-path IRGA (LI-7500, Li-Cor Inc., Lincoln, NE, USA) and a three-dimensional sonic anemometer (CSAT-3, Campbell Scientific Inc., Logan, UT, USA). The system was

mounted at the height of 34 m. Eddy flux data were first controlled and assessed; i.e., spike removal, coordinate rotation, storage-flux correction, low friction velocity filtering, density correction [Tan *et al.*, 2011]. Gap filling and flux partitioning were completed through an online procedure that is maintained by Max Planck Institute (<http://www.bgc-jena.mpg.de/~MDIwork/eddyproc/index.php>). Gross primary production ( $P$ ) was the same as the gross primary production that was derived from flux partitioning ( $GPP$ ).

[20] Soil temperature was measured at a depth of 5 cm with a self-made thermometer and a time-domain reflectometer. Data were collected at hourly intervals, as controlled by a data logger (CR-1000, Campbell Scientific Inc., Logan, UT, USA).

[21] Leaf area index was measured on a typical cloudy day each month with a canopy analyzer (LAI-2000, Li-Cor Inc., Lincoln, NE, USA). Aboveground litter was collected with 25 litter traps (1 m  $\times$  1 m in area) every month. Litter was taken into the laboratory for analysis. Photosynthetic active radiation ( $Q_p$ ) was measured at a height of 34 m from the eddy flux tower. Air humidity and air temperature was measured by humidity sensors (HMP45C, Vaisala, Helsinki, Finland). The vapor pressure deficit ( $\delta_e$ ) was calculated using the approach described by Campbell and Norman [1998].



**Figure 3.** Relative contribution of aboveground litter decomposition ( $R_L$ ), root respiration ( $R_R$ ), and soil organic matter decomposition ( $R_{SOM}$ ) to  $R_s$  in the year 2011 (annual) and in winter (December–February), spring (March–May), summer (June–August), and autumn (September–November).

### 2.4. Calculations

[22] We calculated soil respiration components from measurements obtained under different treatments. These components are related mathematically as



$$R_R = R_c - R_{NR} \quad (2)$$

$$R_L = R_c - R_{NL} \quad (3)$$

$$R_{SOM} = R_c - R_R - R_L \quad (4)$$

where  $R_R$ ,  $R_L$ ,  $R_{SOM}$ ,  $R_c$ ,  $R_{NR}$ , and  $R_{NL}$  are, respectively, respiration of root, aboveground litter, soil organic matter, control, no-root, and no-aboveground litter treatments.

[23] A  $Q_{10}$  function and Lloyd-Taylor equation [Lloyd and Taylor, 1994] were used to obtain a temperature-respiration relationship. These equations are given as

$$R_s = R_{10} \cdot Q_{10}^{(T_s - 10)/10} \quad (5)$$

$$R_s = R_{283} \cdot \exp(E_0(1/(283.16 - T_0) - 1/(T_s - T_0))) \quad (6)$$

where  $R_s$  is soil respiration,  $T_s$  is soil temperature at 5 cm depth,  $R_{10}$  is the fitted  $R_s$  at a soil temperature of 10°C,  $Q_{10}$  is a temperature sensitivity index of  $R_s$ ,  $R_{283}$  is the fitted  $R_s$  at a temperature of 10°C (283 K), and  $E_0$  and  $T_0$  are two fitted parameters. The index  $Q_{10}$  is defined as the  $R_s$  at one temperature over the flux at a temperature 10°C lower.

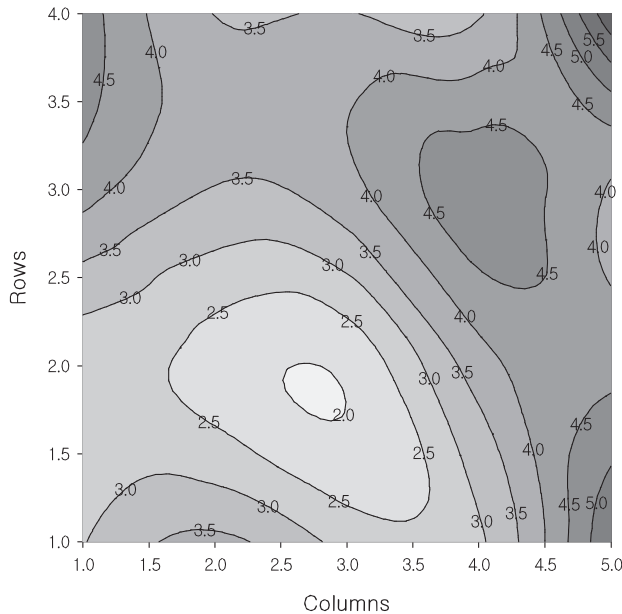
[24] A two-parameter exponential equation was also used to obtain a temperature-respiration relationship. This equation can be expressed as

$$R_s = a \cdot \exp(bT_s) \quad (7)$$

$$Q_{10} = \exp(10b) \quad (8)$$

where  $a$  and  $b$  are fitted parameters.

[25] Two approaches were taken to separate the confounding effects of temperature and water. One is called well-watered regression, which determines a temperature response after leaving out measurements when soil moisture is too low or too high (determined by temperature model residuals near to zero). The other is a multivariate regression that uses a multivariate mixed model. This approach takes soil moisture into



**Figure 4.** Spatial pattern of soil respiration before treatments (from 8 October 2010 to 16 December 2010). There were a total of 20 permanent chambers with 5 rows and 4 columns.

account during regression. After separating the confounding effects,  $Q_{10}$  values were calculated based on the fitted parameters. The model here is a typical multiplicative model of temperature and soil moisture and is given as

$$R_s = R_{\text{ref}} \cdot \exp(\ln(Q_{10}) \cdot T_s / 10) \quad (9)$$

$$Q_{10} = a_1 - a_2 \cdot T_s + a_3 \cdot S_w + a_4 \cdot S_w^2 \quad (10)$$

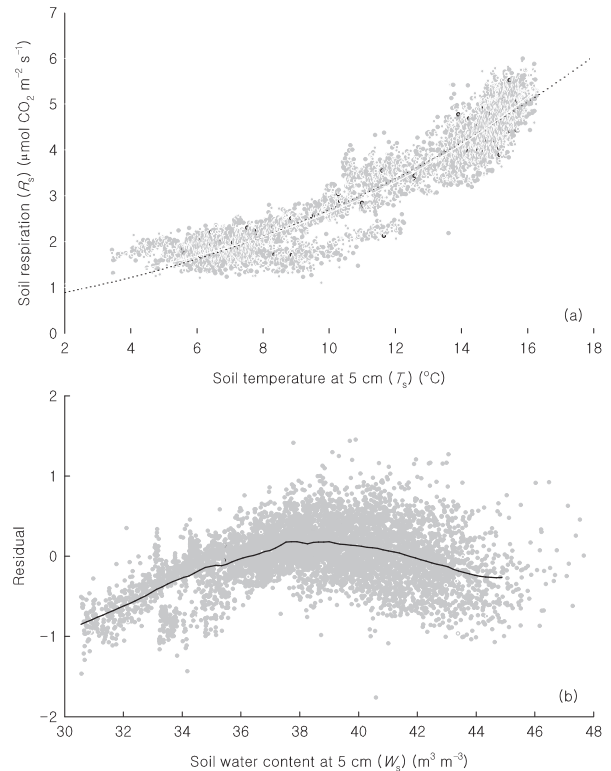
where  $R_{\text{ref}}$  and  $a_i$  where  $i = 1, 2, 3, 4$  are fitted parameters.  $S_w$  is volumetric soil water content at 5 cm depth. Initial parameter values are 0.1, 3.0, 0.1, 10, and 0.1, respectively.

[26] Nonlinear regressions, both univariate and multivariate, were accomplished by using the `nlinfit` command in Matlab 7.1. The confidence interval of regression parameters was estimated with the `nlparci` command.

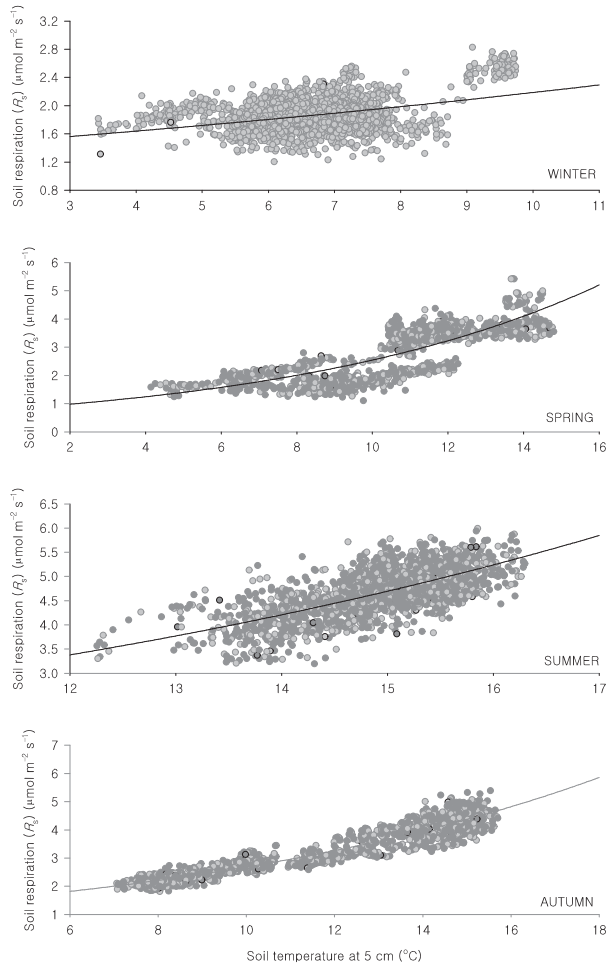
### 3. Results

#### 3.1. Diel Pattern of Soil Respiration and Related Ecological Variables

[27] An obvious cosine-like diel pattern of soil respiration ( $R_s$ ) was observed and is shown with hourly data in Figure 1a. Respiration peaks in late afternoon (between 17:00 and 19:00 h) and is lowest in early morning (between 08:00 and 10:00 h). The daily range of  $R_s$  is around



**Figure 5.** Explanation of the temporal variation of soil respiration with (a) soil temperature and (b) soil water content. Black circles represent raw hourly data in 2011. In Figure 5a, solid and dashed lines are fitted by the  $Q_{10}$  function and Lloyd-Taylor equation. In Figure 5b, the residual values of observed soil respiration and modeled values from the  $Q_{10}$  function were related to soil water content at 5 cm. The grey line indicates smoothing results.



**Figure 6.** Relationship between soil respiration rate ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ ) and  $T_s$  ( $^{\circ}\text{C}$ ) for different seasons. Black circles represent raw hourly data. The solid line was fitted using the two-parameter exponential equation ( $R_s = a * \exp^{(bT_s)}$ ).

$0.25 \mu\text{mol m}^{-2} \text{s}^{-1}$  and accounts for  $\sim 7\%$  of the mean respiration rate. A similar diel pattern of soil temperature at 5 cm depth ( $T_s$ ) was observed, suggesting that  $T_s$  plays a strong role in controlling  $R_s$  at the diel scale. Gross primary production ( $P$ ), derived by the eddy-covariance method, showed a

different diel pattern. Its peak value occurred in midday (between 13:00 and 14:00 h) when the highest photosynthetically active radiation ( $Q_p$ ) occurred (Figure 1b). The diel pattern observed for  $P$  also occurred for  $Q_p$  but not for atmospheric water vapor deficit ( $\delta_e$ ). The peak of  $R_s$  occurred 4 or 5 h after the peak of  $P$ . The relationship between  $R_s$  and  $P$  at the diel scale is comparable, roughly, to that between radiation intensity and temperature. The observed autumn soil respiration ( $R_s$ ) is higher than the modeled soil respiration ( $R_t$ ), especially during the latter afternoon (Figure 1c). The difference between  $R_s$  and  $R_t$  did not show a diel pattern that was similar to that of gross primary production ( $P$ ) or radiation flux ( $Q_p$ ).

**3.2. Annual Pattern of Soil Respiration and Related Ecological Variables**

[28] Soil temperature varied markedly with season as shown in Figure 2a. The annual mean and range of soil temperature over the period of observation was  $11.02^{\circ}\text{C}$  and  $\sim 10^{\circ}\text{C}$ . Maximum soil temperature coincided with the highest summertime soil water content. The minimum soil water content occurred when temperature increased rapidly in early spring. The annual mean and range of soil water content was 38.14% and  $\sim 11\%$ . This feature indicates a mild seasonal variation of soil water content. Gross primary production ( $P$ ), derived from eddy-covariance observations, ranged from  $10 \text{ gCO}_2 \text{ m}^{-2} \text{ d}^{-1}$  in winter to  $30 \text{ gCO}_2 \text{ m}^{-2} \text{ d}^{-1}$  in summer (Figure 2b). It increased gently from a moderate level in winter to a peak value during late summer and early autumn (August and September) and then declined smoothly. There is a similar and distinct seasonal pattern of soil respiration among all treatments: control, no litter, and no root (Figure 2c). Soil temperature increased after mid-January, but it did not induce a corresponding increase in soil respiration. A slight decline of soil respiration was observed despite an increase in temperature until mid-March. The decline of soil respiration was temporally correlated with a decrease of soil water content in this period (from mid-January to mid-March). This correlation suggests that soil water content plays a leading role in regulating soil respiration during the period (Figures 2a and 2c). Afterward, soil respiration increased rapidly under the well-watered condition and in the warm climate of late spring and early summer (during April and June) and peaked in midsummer.

**Table 1.** (a) Parameters of the Relationship Between Soil Respiration Rate ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ ) and Soil Temperature ( $^{\circ}\text{C}$ ) at 5 cm ( $R_s = a * e^{(bT_s)}$ ) for Different Seasons; (b) Parameters of the Relationship Between Soil Respiration Rate and Different Soil Respiration Components: Total Soil Respiration ( $R_s$ ), Derived Root Respiration Calculated as the Difference Between Control and No Root Treatment ( $R_R$ ), Derived Above Ground Litter Decomposition Calculated as the Difference Between Control and No Litter Treatment ( $R_L$ ), and Derived Soil Organic Matter Decomposition Defined as Control Minus the Sum of  $R_R$  and  $R_L$  ( $R_{SOM}$ )

	<i>a</i>	<i>b</i>	<i>p</i>	<i>r</i> <sup>2</sup>	<i>Q</i> <sub>10</sub> (Confidence Interval at 0.05)
<b>(a) Season</b>					
WINTER (December–February)	1.3536	0.0479	<0.0001	0.1338	1.61(1.53–1.69)
SPRING (March–May)	0.7712	0.1193	<0.0001	0.6488	3.29(3.12–3.46)
SUMMER (June–August)	0.9054	0.1097	<0.0001	0.4795	2.99(2.84–3.14)
AUTUMN (September–November)	1.0135	0.0975	<0.0001	0.9130	2.65(2.60–2.69)
<b>(b) Component</b>					
<i>R</i> <sub>s</sub>	0.8626	0.1117	<0.0001	0.9168	3.05(3.02–3.08)
<i>R</i> <sub>R</sub>	0.2924	0.0501	<0.0001	0.1220	1.65(1.59–1.70)
<i>R</i> <sub>L</sub>	0.0591	0.1978	<0.0001	0.7160	7.22(6.91–7.54)
<i>R</i> <sub>SOM</sub>	0.6460	0.1005	<0.0001	0.7545	2.73(2.68–2.77)

**3.3. Relative Contribution of Components to Total Soil Respiration**

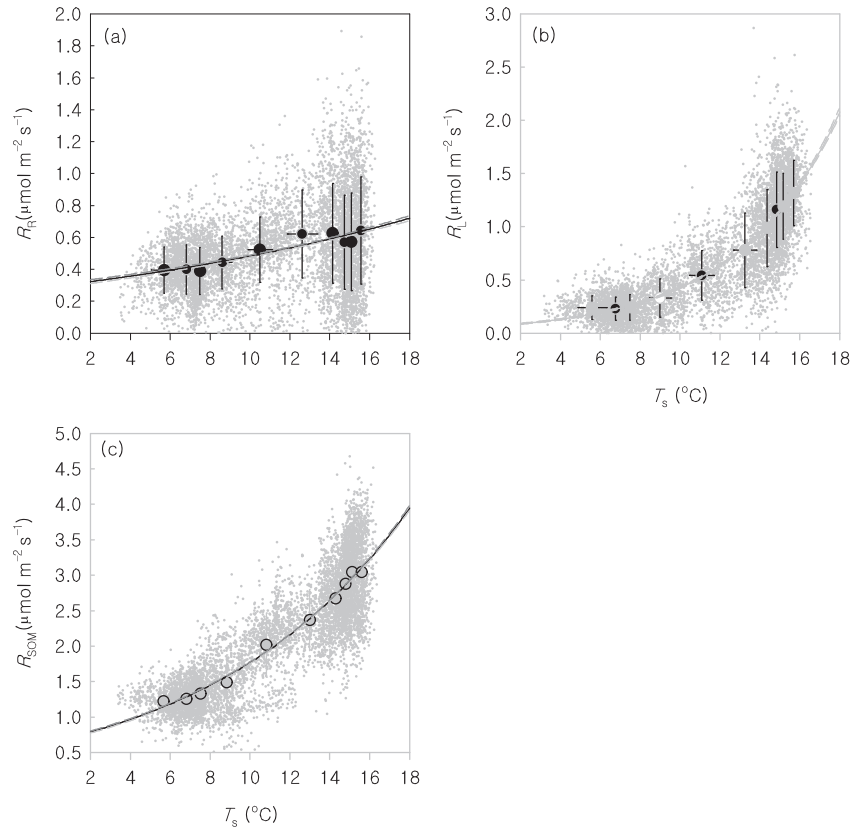
[29] The relative contribution of  $R_R$ ,  $R_L$ , and  $R_{SOM}$  to total soil respiration is shown in Figure 3. The main component contributing to total soil respiration is  $R_{SOM}$ , which accounts for up to 65.25% annually. Component  $R_L$  contributed 18.73% to total soil respiration, and component  $R_R$  contributed 16.01%. The relative contribution of  $R_L$  is higher during summer and autumn, while that of  $R_R$  is higher during spring and winter.

**3.4. Spatial Variation of Soil Respiration**

[30] Respiration measurements were recorded before we started treatments to investigate the spatial variation of soil respiration in the forest. A contour map of soil respiration illustrates that there was considerable spatial variation in soil respiration (Figure 4). The mean soil respiration rate for all 20 chambers during this period is  $3.74 \pm 1.04 \mu\text{mol m}^{-2} \text{s}^{-1}$ , where the second number denotes standard deviation. The dimensionless coefficient of variation was estimated to be 27.80%. The number of samples needed to estimate soil respiration within 10% of its mean value, at a 95% confidential level, was calculated to be 30.

**3.5. Environmental Controls on Soil Respiration**

[31] A strong dependence of soil respiration on temperature was detected ( $r^2=0.91$ ,  $n=7113$ ,  $p<0.0001$ ), based on hourly data that were averaged over five chambers in the studied forest (Figure 5a). This finding indicates that soil temperature is the dominant factor in controlling soil respiration both at diel (Figure 1a) and annual scales. The  $Q_{10}$  function and Llyod-Taylor equation describe the data set well (Figure 5a). Compared to the estimate of respiration from the Llyod-Taylor equation, the estimate calculated from the  $Q_{10}$  function was slightly higher under high- and low-temperature conditions. The residuals between observed values of  $R_s$  and those from the  $Q_{10}$  function were related to soil water content (Figure 5b). The  $Q_{10}$  function overestimates (residual  $\sim 1 \mu\text{mol m}^{-2} \text{s}^{-1}$ )  $R_s$  under dry conditions, when soil water content  $W_s$  is near 30%, and works remarkably well under moderate water conditions (residual  $\sim 0 \mu\text{mol m}^{-2} \text{s}^{-1}$ ). There is a certain level of overestimation using the  $Q_{10}$  function under wet conditions, when  $W_s$  is near 44%. The temperature sensitivity of  $R_s$ , indicated by  $Q_{10}$  values, ranges from 1.61 in winter to 3.29 in spring (Figure 6 and Table 1a). Among the respiration components, aboveground litter decomposition ( $R_L$ ) was most sensitive ( $Q_{10}=7.22$ ) to temperature variation (Figure 7 and Table 1b). On the contrary, root respiration ( $R_R$ ) showed the least sensitivity to temperature variation.



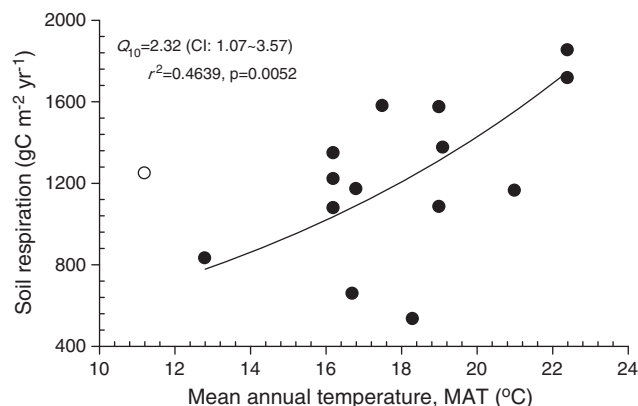
**Figure 7.** Relationship between soil respiration rate ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ ) and  $T_s$  ( $^{\circ}\text{C}$ ) for different components: (a)  $R_R$ , (b)  $R_L$ , and (c)  $R_{SOM}$ . Grey points represent raw hourly data, and black circles with error bars (standard deviation) are mean values of each 10 percentile. The solid line was fitted using the two-parameter exponential equation ( $R_s = a \cdot \exp^{(bT_s)}$ ).

## 4. Discussion

### 4.1. Annual Total of Soil Respiration in Primary Subtropical Evergreen Broadleaved Forests

[32] We compiled annual soil respiration measurements from 16 old-growth subtropical forests in China (Table S1), covering seven subtropical provinces of China. Mean annual soil respiration of old-growth subtropical forests derived from the data is  $1279 \text{ gC m}^{-2} \text{ yr}^{-1}$ . This value is very close to that of a tropical forest ( $1260 \text{ gC m}^{-2} \text{ yr}^{-1}$  reported by *Raich and Schlesinger* [1992];  $1286 \text{ gC m}^{-2} \text{ yr}^{-1}$  calculated from the *Bond-Lamberty and Thomson* [2010] data set updated in 2012). Given the high carbon dioxide fluxes observed, much more attention should be paid to old-growth subtropical forests, both in merging global carbon cycle maps and studying forest and climate interaction.

[33] There is a close relationship ( $R_s = 614.91 \times 2.32^{(\text{MAT} - 10)/10}$ ,  $r^2 = 0.46$ ,  $p < 0.01$ ) between MAT and soil respiration in a multisite plot for these forests, except for the Ailaoshan subtropical forest (Figure 8). MAT of Ailaoshan is  $11.3^\circ\text{C}$ . Soil respiration predicted by the above relationship is  $686 \text{ gC m}^{-2} \text{ yr}^{-1}$ . The observed  $R_s$  is  $1248 \pm 489 \text{ gC m}^{-2} \text{ yr}^{-1}$  (mean  $\pm$  SD) and is higher than the expectation and also higher than the modeled value ( $589 \text{ gC m}^{-2} \text{ yr}^{-1}$ ) based on a global MAT- $R_s$  relationship [*Raich and Schlesinger*, 1992]. We hypothesized that well-watered conditions would lead to a high respiration rate in Ailaoshan forest. In fact, subtropical forests are occurred nearly all under well-watered condition (Table S1). Thus, well-watered conditions appear to produce high levels of respiration in these old-growth subtropical forests. However, well-watered conditions do not explain the exceptionally high soil respiration values in Ailaoshan (Figure 8). A high soil C stock in Ailaoshan forest is probably the reason. Soil C stock of the old-growth subtropical forest in Ailaoshan ( $286 \text{ tC ha}^{-1}$ ) is largely higher than many other forests in China; i.e., rainforest in Xishuangbanna ( $95 \text{ tC ha}^{-1}$ ) and temperate forest in Changbaishan ( $118 \text{ tC ha}^{-1}$ ) [*Wang and Yang*, 2010]. It is also higher than the soil C stock in other old-growth subtropical forests; i.e.,  $97 \text{ tC ha}^{-1}$  in an old-growth forest of



**Figure 8.** Relationship between mean annual temperature and soil respiration for 16 old-growth subtropical forests in China (details of the data are shown in Table S2). Open circles represent outlier results and were obtained from the Ailaoshan subtropical forest data. These results were not included in the regression.

Dinghushan. This idea, a high soil C stock induced high soil respiration, is supported by the high proportion of decomposition SOM (65.25%) in total soil respiration in the Ailaoshan forest.

[34] The annual total of  $R_s$  estimated in this study ( $1248 \text{ gC m}^{-2} \text{ yr}^{-1}$ ) is also higher than that of a previous study ( $1055 \text{ gC m}^{-2} \text{ yr}^{-1}$ ) in the same Ailaoshan forest [*Feng et al.*, 2008]. One possible explanation for this difference is that *Feng et al.* did not account for diel variation [*Rey et al.*, 2002; *Saiz et al.*, 2006]. Measurements taken from 09:00 to 11:00 will underestimate soil respiration (Figure 1a). In addition, soil respiration measured with an automatic system will cover the full diel time period, even under bad conditions (i.e., rainy days) when manual measurements are seldom made.

[35] The other main aspect of uncertainty in estimating an annual total of soil respiration is spatial variation. Traditionally, the mean value of several fixed small soil chambers (i.e., 10 cm diameter connected with Li-6400) is used to represent the respiration of a whole stand (scales in hectare). We applied big square chambers ( $90 \text{ cm} \times 90 \text{ cm}$ ) to reduce spatial uncertainty. Nevertheless, the minimum number of samples needed to obtain results within 10% of its mean value, at a 95% confidential level, is still 30. Studies seldom take measurements from 30 chambers to obtain an annual total of soil respiration; usually, three to eight measurements are taken, with five being the average. The 95% confidence interval based on five chambers in the control treatment is  $3.30 \pm 0.86 \mu\text{mol m}^{-2} \text{ s}^{-1}$ . More attention might be needed on spatial variation, rather than temporal, to obtain an annual total of soil respiration.

### 4.2. Temperature Sensitivity of Soil Respiration and its Components

[36] It is commonly accepted that soil respiration depends on temperature [*Lloyd and Taylor*, 1994]. Subsequently, soil carbon release is expected to increase with global warming, despite an acclimatization [*Luo et al.*, 2001] and substrate limit [*Knorr et al.*, 2005]. Nonetheless, we found that temperature sensitivity of soil respiration is largely different in different seasons and under different component values. In a Danish beech forest, large seasonal changes in  $Q_{10}$  were observed [*Janssens and Pilegaard*, 2003]. Moreover, annual  $Q_{10}$  can be used as an indicator of canopy phenology [*Yuste et al.*, 2004]. The primary subtropical forest in this study is evergreen, yet seasonal variation of  $Q_{10}$  is apparent, ranging from 1.61 in winter to 3.29 in spring (Table 1a). A low soil water content restrained respiration and could account for the low  $Q_{10}$  in winter (Figure 2). A high  $Q_{10}$  in spring might be the result of leaf flushing (Figure S2) [*Zhao et al.*, 2012].

[37] We observed differences in the temperature sensitivity of soil respiration components:  $R_L$  ( $Q_{10} = 7.22$ )  $>$   $R_{\text{SOM}}$  ( $2.73$ )  $>$   $R_R$  ( $1.65$ ) (Table 1). The apparent  $Q_{10}$ , calculated by a temperature-respiration regression, often was not consistent with the definition of  $Q_{10}$  because, not only temperature, but other processes and conditions varied with time; i.e., phenophase, water condition, and photosynthesis [*DeForest et al.*, 2006; *Kuzyakov and Gavrichkova*, 2010; *Subke and Bahn*, 2010]. Our study forest was evergreen and has a year-round growing season [*Tan et al.*, 2012]. Compared to that of a temperate or boreal forest, the seasonal variation of phenophase and canopy photosynthesis



in a subtropical forest is small. Water condition, however, could act as a strong confounding factor in deriving soil respiration temperature sensitivity. Dominated by the Indian Monsoon, rainfall in the forest is mainly associated with high temperatures. We tried two methods to minimize the confounding effect of water: well-watered regression and multivariate regression. After leaving out measurements at times when moisture is too low or too high to limit respiration, the conclusion that  $R_L (Q_{10}=3.93) > R_{SOM} (3.12) > R_R (1.61)$  still held (Table 2). The multivariate model combined the effects of temperature and moisture and also gave the same results (Table 2). Meanwhile, we found that water has little confounding effect on the temperature sensitivity of root respiration, but a strong effect on litter decomposition. Temperature sensitivity of litterfall decomposition declined sharply from 7.22 to a range of 3.72 to 3.75 after minimizing the confounding effect of water.

[38] There is no unified conclusion on the temperature sensitivity of different components of soil respiration. A litter-manipulation experiment in Harvard forest suggested that temperature sensitivity of root is stronger than that of bulk soil [Boone *et al.*, 1998]. By contrast, no different  $Q_{10}$  values were found between bulk soil and root respiration in a microcosm study [Bååth and Wallander, 2003]. A girdling experiment in a Scott pine forest of Sweden suggested that root respiration was less sensitive to that of bulk soil [Bhupinderpal *et al.*, 2003]. There was no significant correlation between root respiration and temperature in a secondary forest of Japan [Lee *et al.*, 2003]. The soil respiration component that was least sensitive to temperature in the old-growth Ailaoshan subtropical forest is root respiration (Table 1). Moreover, low temperature sensitivity was stable and did not change after minimizing the confounding effect of moisture (Table 2). There are two possible mechanisms for the low-temperature sensitivity of root respiration, compared to litter or soil organic matter decomposition. First, temperature sensitivity of root respiration is controlled by C availability and recent photosynthetic inputs to roots. The latter is rather constant over a year in the studied ecosystem (Figure 3b). Second, previous studies have shown that respiration of plants, and thus roots and mycorrhiza, acclimatizes to temperature, but there is less evidence for compensatory thermal acclimation in free-living soil microbes [Atkin and Tjoelker, 2003; Bradford *et al.*, 2008; Hartley *et al.*, 2008].

### 4.3. Photosynthesis and Soil Respiration

[39] The idea that photosynthesis drives or modulates soil respiration has been a commonly accepted view in theoretical inferences and field campaigns [Hogberg *et al.*, 2001; Tang

*et al.*, 2005]. Nevertheless, the relationship between photosynthesis and soil respiration (i.e., time lag) is still being quantified [Kuzyakov and Gavrichkova, 2010]. The relationship between photosynthesis and soil respiration at diel and annual scales was studied with a continuous data set having a high temporal resolution by combining eddy covariance and soil chamber methods. After subtracting the temperature-dependent soil respiration, the diel variation in the residuals (Figure 1c, shaded area) did not show a pattern similar to that of light intensity, which has been reported for a temperate deciduous forest in Oak Ridge, USA [Liu *et al.*, 2006]. In fact, the diel pattern between residuals and that of light intensity were similar only when photosynthetic production will immediately arrived soil and used as respiration substrate with no time lag. Nevertheless, it is consistent with observations which suggest a time lag from 7 to 12 h [Tang *et al.*, 2005] or, for a tree, from 4 to 5 days [Kuzyakov and Gavrichkova, 2010]. It makes sense that temperature was not peaked at the time of the strongest radiation, but that its peak occurred usually several hours latter [Campbell and Norman, 1998]. A very similar diel pattern was found in the relationship between soil respiration and soil temperature and in the relationship between canopy photosynthesis and light intensity. This observation suggests that peaked soil respiration will occur after the highest photosynthesis rate, like the radiation-temperature relationship in our studied forest. The time lag at the diel scale was calculated to be from 4 to 5 h. At an annual scale, soil respiration peaked earlier than that of gross primary production (Figure 2). The relationship between photosynthesis can be fitted by a four-parameter sigmoidal logistic function ( $r^2=0.6502$ ,  $p < 0.0001$ ) (Figure S3). It is not easy to obtain time lags at this scale because of the complex interaction of biotic and abiotic factors.

## 5. Conclusions

[40] We have made five conclusions:

[41] 1. Annual soil respiration in Ailaoshan forest was near the mean of 16 other old-growth subtropical Chinese forests, but high relative to its mean annual temperature. This may be due to high C stocks at this site.

[42] 2. Even though big size chambers have been introduced to make high spatial representative, the coefficient of variation of soil respiration is still 27.8%, which suggested 30 samples were required to obtain results within 10% of the mean value at a 95% confidential level. More attention to spatial variation, rather than temporal, might be needed to obtain an annual total of soil respiration.

[43] 3. Photosynthesis-respiration coupling was detected at diel scale with time lag of 4 to 5 h. The seasonality of soil respiration was strong and varied from a low value of  $\sim 1 \mu\text{mol m}^{-2} \text{s}^{-1}$  in late winter to a peak value of  $\sim 6 \mu\text{mol m}^{-2} \text{s}^{-1}$  in midsummer. A time lag between gross primary production and soil respiration at the seasonal scale was not apparent.

[44] 4. Soil temperature at 5 cm can explain more than 91% of the observed annual variation in soil respiration with a  $Q_{10}$  of 3.05. Soil respiration during winter was strongly affected by low soil water content, and the lowest  $Q_{10}$  value was detected in that time. Soil respiration was overestimated by the  $Q_{10}$  function during dry and wet periods; residuals

**Table 2.** Temperature Sensitivity ( $Q_{10}$ ) of Respiration Components  $R_R$ ,  $R_L$ , and  $R_{SOM}$

Method	$R_R$	$R_L$	$R_{SOM}$
Well water regression	1.61(1.27–1.97)	3.93(2.80–5.07)	3.12(2.88–3.37)
Multivariate regression	1.62( $\pm 0.25$ )	3.75( $\pm 0.29$ )	2.20( $\pm 0.44$ )

We applied two methods to discard the confounding effect of water on soil temperature sensitivity: well-watered regression and multivariate regression. Details on these methods are given in the text. A value in parentheses for the well-watered regression method denotes a Confidence Interval (CI), While one for the multivariate regression method denotes a Standard Deviation (SD).

between observed and temperature-dependent soil respiration illustrate this feature.

[45] 5. Temperature sensitivity differed among several components of soil respiration. The highest sensitivity occurred in aboveground litter decomposition ( $R_L$ ) ( $Q_{10}=7.22$ ), followed by decomposition of SOM ( $R_{SOM}$ ) ( $Q_{10}=2.73$ ), and then root respiration ( $R_R$ ) ( $Q_{10}=1.65$ ). The conclusion that  $Q_{10}$  for litter respiration exceeds  $Q_{10}$  of soil organic matter decomposition, which exceeds  $Q_{10}$  of root respiration holds even after minimizing the confounding effect of moisture. A rather constant substrate supply and thermal acclimation are possible mechanisms that can account for the low temperature sensitivity in root respiration.

[46] **Acknowledgments.** Funding for this study was provided by National Science Foundation of China (31200347, 41271056, 40571163, 41071071), Natural Science Foundation of Yunnan Province, China (2011FB110, 2011FA025), Development Program in Basic Science of China (2010CB833501), and Knowledge Innovation Program of the Chinese Academy of Sciences (KJCX2-YW-432-1, KZCX2-YW-Q1-05-04, KZCX1-SW-01-01A). Thanks to reviewers for their excellent comments on this work.

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