Temperature and substrate availability regulate soil respiration in the tropical mountain rainforests, Hainan Island, China

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Abstract

Aims
Tropical forest plays a key role in global C cycle; however, there are few studies on the C budget in the tropical rainforests in Asia. This study aims to (i) reveal the seasonal patterns of total soil respiration (R7), litter respiration (R4) and soil respiration without surface organic litter (Rsol) in the primary and secondary Asian tropical mountain rainforests and (ii) quantify the effects of soil temperature, soil moisture and substrate availability on soil respiration.

Methods
The seasonal dynamics of soil CO2 efflux was measured by an automatic chamber system (Li-8100), within the primary and secondary tropical mountain rainforests located at the Jianfengling National Reserve in Hainan Island, China. The litter removal treatment was used to assess the contribution of litter to belowground CO2 production.

Important Findings
The annual R7 was higher in the primary forest (16.73 ± 0.87 Mg C ha⁻¹) than in the secondary forest (15.10 ± 0.26 Mg C ha⁻¹).

The rates of R7, Rsol and R4 were all significantly higher in the hot and wet season (May–October) than those in the cool and dry season (November–April). Soil temperature at 5 cm depth could explain 55–61% of the seasonal variation in R7, and the temperature sensitivity index (Q10) ranked by R7 (Q10 = 3.39) > R4 (2.17) > Rsol (1.76) in the primary forest and by R4 (4.31) > R7 (1.86) > Rsol (1.58) in the secondary forest. The contribution of R4 to R7 was 22–23%, while litter input and R7 had 1 month time lag. In addition, the seasonal variation of R7 was mainly determined by soil temperature and substrate availability. Our findings suggested that global warming and increased substrate availability are likely to cause considerable losses of soil C in the tropical forests.

Keywords: soil respiration, soil temperature, litter, tropical mountain rainforest

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INTRODUCTION
Soil respiration annually releases C of about 98 Pg (1 Pg = 10¹⁵ g) to the atmosphere at the global scale (Bond-Lamberty and Thomson 2010a) and ranks the second among the terrestrial C fluxes (Denman et al. 2007; Raich et al. 2002), whose magnitude is much larger than that of the fossil fuel combustion (Boden et al. 2012). Therefore, the small variation of soil respiration can exert the strong influence on the global C balance. Many studies have reported the soil respiration of different vegetation types (Li et al. 2013; Raich et al. 2002), but the regional or global pattern of soil respiration, and its components and environmental controls, is yet to be clarified (Bond-Lamberty and Thomson, 2010b).
Total soil respiration ($R_T$) is the sum of all CO$_2$ effuxes produced by litter, soil organic matter and roots, and the considerable uncertainties on the relative contribution of these components to $R_T$ were reported across the world. For example, the contribution of root respiration to $R_T$ within forest ecosystems varies from 5 to 90% (Hanson et al. 2000; Wang et al. 2010), while aboveground litter respiration ($R_L$) contributes 16–37% (Abido Valentin et al. 2008; Rey et al. 2002; Singh et al. 2008; Sulzman et al. 2005; Wang et al. 2012; Zimmermann et al. 2009). Soil respiration is influenced by biotic factors (e.g. substrate and ecosystem productivity) and abiotic factors (e.g. soil temperature, soil moisture, oxygen, nitrogen (C:N ratio), soil texture and soil pH) (Luo and Zhou 2006). Aboveground litter is an important biotic factor influencing soil respiration because it provides the main aboveground C source to soil respiration. At the global scale, the averaged contribution of aboveground litter to forests is 33% (Raich et al. 1989), and in the tropical forests, aboveground litter decomposition has been estimated to comprise 16–37% of soil respiration (Atarashi-Andoh et al. 2012; Zimmermann et al. 2009). Changes in the inputs of litter and detritus to the soil are likely to affect the rates of soil respiration and therefore influence the relative contribution of different components to the total soil CO$_2$ efflux (Högberg et al. 2001; Wang et al. 2003). For instance, many studies showed that litter removal decreased soil flux in the forest ecosystem (Atarashi-Andoh et al. 2012; Deng et al. 2007; Li et al. 2004). Soil respiration is also influenced by abiotic factors, among which temperature is the most important factor. $Q_{10}$, a quotient indicating the temperature sensitivity of soil respiration, varies among ecosystems and across temperature ranges, partly because various components of soil respiration have different sensitivities (Chen et al. 2000; Cui et al. 2013; Fang et al. 2001; Kirschbaum 2000; Simmons et al. 1996). Globally, the mean $Q_{10}$ value is estimated to be approximately 3.0 for temperature ranging 0 to 20°C, whereas 3.3 with a range of 1.4–4.6 in the tropical forests (Bond-Lamberty and Thomson 2010a).

Tropical forests play a key role in global C cycling, which contain about 40% of the global terrestrial biomass C stock (Field et al. 1998; Phillips et al. 1998) and contribute 67% of the global annual total soil flux (Bond-Lamberty and Thomson 2010b). Nevertheless, due to the most intense contemporary land use change, tropical forests exhibited the greatest uncertainty of C sink (Mallhi 2012; Pan et al. 2011). In Asia, deforestation is rapidly changing the intact tropical forests into the secondary forests or plantations, causing an increase in annual C release from land use change in tropical Asia from 0.88 Pg C yr$^{-1}$ in the 1980s to 1.09 Pg C yr$^{-1}$ in the 1990s (Houghton 2005). Several studies showed that the tropical mountain rainforest served as a net C sink (Chave et al. 2005; Chen et al. 2010; Fehse et al. 2002), but the pattern and magnitude of soil CO$_2$ dynamics within the Asian tropical mountain rainforests still remain poorly documented. It is, therefore, of great importance to explore the spatiotemporal patterns and determinants of soil respiration in the tropical mountain rainforest in this region.

In this paper, we are to investigate the patterns of soil respiration and its components, and their biotic and abiotic drivers, based on the field data collected from soil automatic chamber and nearby forest microclimate station at the Jianfengling National Reserve in Hainan Island, China. We hypothesize that: (i) due to the differences in soil characteristics, microclimate and stand structure, the annual total soil respiration would be different between the primary forest and the secondary forest; and (ii) soil temperature and substrate availability would control the temporal variation of soil respiration, and the time lag may exist between substrate availability and soil respiration.

**MATERIALS AND METHODS**

**Site description**

The study was conducted in Jianfengling National Natural Reserve (18°23′–18°50′N, 108°36′–109°05′E), which is located at the southwestern part of Hainan Island, China. The total area of the reserve is about 470 km$^2$, where mountain rainforest (with an altitude of 800–1000 m) covers about 163 km$^2$ (Du et al. 2013; Li et al. 2002), with two major forest types—primary and secondary mountain rainforest (Table 1). The primary forest is dominated by species in families Lauraceae and Fagaceae (such as Malletus hookerianus, Gironniera subaequale, Cryptocarya chinesis, Cyclobalanopsis patelliformis and Nephe (iumtopengii). The secondary forest had naturally developed on the intact forest cut down in 1960s to 1970s, dominated by species in families Rubiaceae, Fagaceae and Myrtaceae (such as Castanopsis tonkinensis, Schefflera octophylla, Alniphyllum fortunei, Psychotria rubra and Blasts cochinchinensis) (Fang et al. 2004; Li et al. 2002). Mean annual air temperature is 19.8°C, ranging from 14.8 (January) to 23.3°C (June), and the annual precipitation averages 2449 mm (Zhou et al. 2009). Influenced by a tropical monsoon climate, the region has two seasons, wet and dry season; the former starts from May to October and the latter occurs from November to April. The soils are lateritic yellow soil (Chen et al. 2010).

**Experiment design**

Three random plots with a size of 20×20 m were established in September 2010 in the primary and secondary tropical mountain rainforests, respectively. Six 1×1 m subplots were set randomly within each plot, with a half for the control treatment (normal litter inputs) and another half for non-litter (NL) treatment (aboveground litter was removed from subplots). For the NL treatment, doubled nylon nets (2-mm mesh screen) were placed 1 m above the ground surface in each subplot to prohibit fresh litter falling on the floor. The litter on roofs of the nets was cleared every 7 days to allow sunlight to reach the soil surface covered by the net.

**Soil respiration measurement**

At each subplot, one PVC collar (19.6 cm inner diameter, 5.0 cm height) was permanently installed to a depth of 3.0 cm
**Table 1:** main characteristics of vegetation, microclimate, root and soil properties (mean ± 1SE) in our study sites

<table>
<thead>
<tr>
<th>Variable</th>
<th>Primary forest</th>
<th>Secondary forest</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Main characteristics</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Location</td>
<td>E 108°53′, N 188′4′</td>
<td>E 108°52′, N 188′44′</td>
</tr>
<tr>
<td>Elevation (m)</td>
<td>870</td>
<td>880</td>
</tr>
<tr>
<td>Gradient (°)</td>
<td>&lt;3</td>
<td>10–20</td>
</tr>
<tr>
<td>Annual mean air temperature (°C)</td>
<td>19.66±0.85 a</td>
<td>20.00±0.67 a</td>
</tr>
<tr>
<td>Annual mean precipitation (mm)</td>
<td>2198</td>
<td>2198</td>
</tr>
<tr>
<td>Annual mean relative humidity (%)</td>
<td>89.36±0.83 a</td>
<td>94.95±0.66 b</td>
</tr>
<tr>
<td>Annual mean VPD (kPa)</td>
<td>0.26±0.03 a</td>
<td>0.12±0.02 b</td>
</tr>
<tr>
<td>Annual mean PAR (µmol m⁻² s⁻¹)</td>
<td>311.58±21.30 a</td>
<td>235.70±15.43 b</td>
</tr>
<tr>
<td><strong>Stand characteristics</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Tree density (stems ha⁻¹)</td>
<td>4092</td>
<td>7717</td>
</tr>
<tr>
<td>Leaf area index</td>
<td>5.58±0.19</td>
<td>5.01±0.24</td>
</tr>
<tr>
<td>Basal area (m² ha⁻¹)</td>
<td>52.3</td>
<td>45.3</td>
</tr>
<tr>
<td>Litterfall (Mg ha⁻¹ yr⁻¹)</td>
<td>8.19±0.36 a</td>
<td>7.97±0.87 a</td>
</tr>
<tr>
<td><strong>Soil characteristics</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Annual mean soil temperature (°C)</td>
<td>19.94±0.71 a</td>
<td>20.44±0.70 a</td>
</tr>
<tr>
<td>Annual mean soil moisture (%)</td>
<td>29.12±1.84 a</td>
<td>28.02±2.11 a</td>
</tr>
<tr>
<td>Bulk density (g cm⁻³)</td>
<td>1.15±0.05 a</td>
<td>1.21±0.03 a</td>
</tr>
<tr>
<td>pH</td>
<td>4.48±0.06 a</td>
<td>4.21±0.09 b</td>
</tr>
<tr>
<td>Soil organic C (mg g⁻¹)</td>
<td>31.20±1.59 a</td>
<td>36.60±2.23 a</td>
</tr>
<tr>
<td>Soil total N (mg g⁻¹)</td>
<td>1.60±0.17 a</td>
<td>1.65±0.10 a</td>
</tr>
<tr>
<td>Soil C/N</td>
<td>21.32±2.43 a</td>
<td>24.19±2.63 a</td>
</tr>
</tbody>
</table>

Different letters indicate significant differences in primary and secondary forest at *P* < 0.05. SE of microclimate is differences among 12 months, and SE of other factors is differences among three plots. The chemical characteristics of soil come from our unpublished data (Zhou et al., unpublished data).

RESULTS

**Seasonal variations in environmental factors**

Total annual precipitation was approximately 2200 mm in 2012. Intense typhoon or tropical storms occurred frequently between June and October, and nearly two-thirds of the annual rainfall occurred in this period. The temporal trends of soil water content in both forests were correlated with that of rainfall. The maximum value was in October 2012, with 37.8% in the primary forest and 35.4% in the secondary forest (Fig. 1a). In both forests, soil temperature was lowest in January (14.4 and 14.7°C) and highest in June and July (23.1 and 23.6°C; Fig. 1b), which corresponded to the wet seasons. Soil temperature in the secondary forest was slightly higher than that in the primary forest. For example, in January, the mean soil temperature was 14.4°C in the primary forest and 14.7°C in the secondary forest. In June and July, the mean soil temperature was 23.1°C in the primary forest and 23.6°C in the secondary forest.

Modified exponential model was used to fit the daily soil temperature data, where *y* = *a* *e*⁻¹⁰⁺*b*, where *y* is the daily mean of soil temperature, *a* is the fitted parameter, and *b* is the fitted parameter, and *T* is the soil temperature. The model equation is:

For sampling soil CO₂ efflux, about 2 weeks before the first measurement. Soil respiration was measured between 8:30 AM and 12:30 PM using a Li-8100 automated soil CO₂ flux system (LI-COR Inc., Lincoln, NE). Total soil respiration (*Rₜ*) in the control subplot was measured monthly from January 2011 to December 2012. Measurement of *Rₜ* in the NL subplot was carried out monthly from January to December 2012. Soil temperature (*Tₛ*) at 5 cm depth and volumetric water content (VWC) at 10 cm depth was measured adjacent to each respiration collar with a portable temperature probe provided with the Li-8100.

**Measurement of climate and driving factors**

Within two forests, sensors were placed on two microclimate towers to continually measure 30-min mean air temperature (*Tₘₐₜ*), air relative humidity (RH, %), *Tₛ* at 5 cm depth (°C), soil VWC at 10 cm depth (%) and photosynthetically active radiation (PAR). The vapor pressure deficit (VPD) was calculated by the methods described by Campbell and Norman (1998). RH and *Tₛ* were measured by humidity sensors HMP45C (Vaisala, Helsinki, Finland); *Tₛ* and VWC were measured with thermocouples T-107 (Campbell Scientific Inc., Logan, UT) and time-domain reflectometers CS-616 (Campbell Scientific Inc.). Leaf area index was measured on a typical cloudy day during the dry and wet season with a canopy analyzer LAI-2000 (Li-Cor Inc., Lincoln, NE). PAR was measured with photo quantum sensor PAR LITE (Kipp & Zonen Inc, the Netherlands) above canopy from the micro-climate tower. Four litter traps (0.5 m²) with a mesh size of 2 mm were placed randomly in each plot about 0.5 m above the ground surface. Litter accumulated in each trap was collected monthly since April 2011; separated by leaves, twigs, flowers and fruits; dried 65°C for 48 h; and weighed on a digital balance. The C content of the mixed litter was 50.77% in the primary forest and 51.66% in the secondary forest (Li et al. 1998).

**Statistical analyses**

The contribution of litter to soil CO₂ efflux was calculated as the differences in soil CO₂ efflux between the control and NL treatments. One-way ANOVA was used to compare soil characteristics and stand structure between the primary forest and the secondary forest. Paired samples T-test was performed to assess the effect of forest type on CO₂ efflux (*Rₜ*, *Rₘₐₜ*, and *Rₚₐ*) and microclimate factors (*Tₛ*, *Tₘₜ*, RH, VWC, VPD and PAR) between the primary and secondary forests. Unless otherwise stated, the level of statistical significance was set at *α* = 0.05. To test the effects of the factors on soil respiration and its components, linear relationships between soil CO₂ efflux (*Rₜ*, *Rₘₜ*, and *Rₚₐ*) and the driving factors (*Tₛ* and VWC) were analysed at the seasonal scale. Soil respiration was fitted to an exponential model as *y* = *a* *e*⁻¹⁰⁺*b*, where *y* is soil respiration, *a* and *b* are fitted parameters, and *T* is soil temperature. *Q₁₀* values were calculated as *Q₁₀* = *e*⁻¹⁰⁺*b* Statistical analyses were conducted in SPSS 20.0 (SPSS Inc., IL).
than that in the primary forest, especially in the wet season (Fig. 1b). The rates (means ± SE) of total litter fall (leaves, twigs, flowers and fruits) were 8.19 ± 0.36 Mg ha⁻¹ in the primary and 7.97 ± 0.87 Mg ha⁻¹ in the secondary forest in 2012. During the dry season, total litter fall fluctuated by 0.5–0.6 Mg ha⁻¹ per month. During the wet season, monthly litterfall varied dramatically, due to the disturbance from typhoons or tropical storms, which reached the maximum values of 2.36 and 2.20 Mg ha⁻¹ in October in the primary and secondary forests, respectively (Fig. 1c).

Figure 1: seasonal patterns of soil respiration and environmental factors. (a) Daily rainfall and soil VWC at the 10 cm depth in the primary and secondary forest; (b) soil temperatures at the 10 cm depth in the primary and secondary forest; (c) litterfall in the primary and secondary forest; (d) soil respiration for control plots and no litter plots in the primary forest; and (e) soil respiration for control plots and no litter plots in the secondary forest. PF and SF represent primary forest and secondary forest, respectively.
Seasonal patterns of soil respiration

In 2012, the annual $R_T$ was significantly higher in the primary forest ($16.73\pm0.87$ Mg C ha$^{-1}$ yr$^{-1}$) than in the secondary forest ($15.10\pm0.26$ Mg C ha$^{-1}$ yr$^{-1}$) ($P < 0.05$). $R_T$ ranged from 3.10 to 6.15 µmol CO$_2$ m$^{-2}$ s$^{-1}$ in the primary forest (Fig. 1d) and 3.20 to 5.23 µmol CO$_2$ m$^{-2}$ s$^{-1}$ in the secondary forest (Fig. 1e). In both forests, soil respiration exhibited the similar seasonal variations as the temporal change of soil temperature. In particular, averaged soil CO$_2$ efflux was lowest in January and highest in June or July (Fig. 1d and e). The annual mean $R_{NL}$ and $R_T$ averaged 12.94 and 3.78 Mg C ha$^{-1}$ yr$^{-1}$ in the primary forest and 11.73 and 3.37 Mg C ha$^{-1}$ yr$^{-1}$ in the secondary forest (Fig. 2). The contribution of aboveground litter to annual soil respiration was 23% in the primary forest and 22% in the secondary forest. $R_T$, $R_{NL}$ and $R_L$ were higher in the wet season than in the dry season ($P < 0.05$). The averages of $R_T$ and $R_{NL}$ for the wet season in 2012 were 4.90 and 3.75 µmol CO$_2$ m$^{-2}$ s$^{-1}$ in the primary forest and 4.44 and 3.33 µmol CO$_2$ m$^{-2}$ s$^{-1}$ in the secondary forest (Fig. 1d and e).

Effects of soil temperature, soil moisture and aboveground litter on seasonal variation in soil respiration

Temporal variations of $R_T$ for the primary forest and the secondary forest were positively related to air temperature and soil temperature but were not significantly correlated with WVC, RH, VPD and PAR. Seasonal $R_T$ and $R_{NL}$ both exhibited exponential response to soil temperatures at 5 cm depth (Fig. 4a and c). In the primary forest, soil temperature explained 61, 37 and 30% of the variation in $R_T$, $R_{NL}$ and $R_L$, respectively. By contrast, the dependence of soil respiration on soil temperature was lower in the secondary forest, where soil temperature accounted for 55, 25 and 16% of the variations in $R_T$, $R_{NL}$ and $R_L$, respectively. The annual $Q_{10}$ values for soil respiration ordered $R_T > R_T > R_{NL}$, with values of 3.39, 2.17 and 1.76 in the primary forest and values of 4.39, 1.86 and 1.58 in the secondary forest (Table 2). The $Q_{10}$ values in the wet season were higher than those in the dry season. However, the simple and multiple regression analyses both showed that soil respiration was not directly affected by soil moisture, under either NL or control plots (Fig. 4b and d). Additionally, the variance inflation factor (VIF) in the multiple regression is lower than 5.0, indicative of weak collinear between the effects of soil temperature and soil moisture.

Finally, $R_T$ increased as a function of monthly total litterfall. However, soil respiration had a lagged response to the fresh litter inputs, demonstrated by a substantially higher correlation with the litterfall of the previous month (Fig. 3). For example, $R_T$ in the primary forest exhibited a positive relationship with total litter fall in the previous month ($R^2 = 0.37$, $P < 0.01$), but was independent of that in the current month ($R^2 = 0.02$, $P > 0.05$).

DISCUSSION

Annual soil respiration in tropical mountain forests

We compiled data of annual soil respiration from 12 tropical mountain forests over the world (Table S1, see online supplementary material). Annual soil respiration of tropical mountain forests averaged 1445 g C m$^{-2}$ yr$^{-1}$, which is higher than that of tropical forests (1260 g C m$^{-2}$ yr$^{-1}$) reported by Raich and Schlesinger (1992); 1286 g C m$^{-2}$ yr$^{-1}$ calculated based on the updated data from the Bond-Lamberty and Thomson (2010a). On average, during 2012, soils released 1510–1673 g C m$^{-2}$ in the Jianfengling tropical mountain forest. However, this value was smaller than that of tropical montane cloud forest (1812 g C m$^{-2}$ yr$^{-1}$) in Peru (Zimmermann et al. 2009).

Figure 2: annual total soil respiration ($R_T$), soil mineral respiration ($R_{NL}$) and litter respiration ($R_L$) in tropical mountain rainforest Hainan, China, in 2012.
Table 2: correlation coefficients between soil respiration and microclimate factors

<table>
<thead>
<tr>
<th></th>
<th>Factors</th>
<th>$T_6$</th>
<th>$T_5$</th>
<th>VWC</th>
<th>RH</th>
<th>VPD</th>
<th>PAR</th>
</tr>
</thead>
<tbody>
<tr>
<td>Primary forest $R$</td>
<td>0.83*</td>
<td>0.83*</td>
<td>0.52</td>
<td>-0.41</td>
<td>0.61</td>
<td>0.51</td>
<td></td>
</tr>
<tr>
<td>$P$ value</td>
<td>0.001</td>
<td>0.001</td>
<td>0.078</td>
<td>0.183</td>
<td>0.051</td>
<td>0.088</td>
<td></td>
</tr>
<tr>
<td>Secondary forest $R$</td>
<td>0.87*</td>
<td>0.86*</td>
<td>0.40</td>
<td>-0.19</td>
<td>0.37</td>
<td>0.52</td>
<td></td>
</tr>
<tr>
<td>$P$ value</td>
<td>0.000</td>
<td>0.000</td>
<td>0.190</td>
<td>0.568</td>
<td>0.210</td>
<td>0.082</td>
<td></td>
</tr>
</tbody>
</table>

*Significant correlation between $R_I$ and factors at $P = 0.05$.

but larger than in the Hawaiian tropical montane forest (973 g C m$^{-2}$ yr$^{-1}$) in USA (Koehler et al. 2009).

Vegetation structure and species composition strongly influence C allocation patterns (Adachi et al. 2006), the quantity and quality of detritus production (Rustad et al. 2000), soil microclimate and structure (Butler et al. 2012; Raich et al. 2000) and consequently the soil respiration. On the one hand, the differences of soil respiration between the primary forest and the secondary forest were caused by different microclimate (Table 1). Compared to the secondary forest, VPD and PAR were significantly higher while RH was significantly lower in the primary forest. Furthermore, soil pH in the primary forest was significantly lower than in the secondary forest. Soil pH regulates chemical reactions and a multiplicity of enzymes in microorganisms. Xu and Qi (2001) found that pH values in the top 10 cm correlated negatively with soil CO$_2$ efflux, accounting for 34% of variation in soil CO$_2$ efflux. In the primary forest during the wet season, the lower soil pH had a positive effect on soil microbial activity so as to increase the production of soil CO$_2$ efflux. As a result, the mean and maximal values of $R_I$ in the primary forests were significantly higher than that in the secondary forest.

**Contribution of litter to total soil CO$_2$ efflux**

A range of values for the relative contribution of litter respiration to total CO$_2$ efflux have been reported among different forest ecosystems (Table S2, see online supplementary material). Globally, the relative contribution of $R_I$ varied within a range from 19% in the temperate forest (Sulzman et al. 2005) to 37% in the tropical forest (Zimmermann et al. 2009). Our results showed that the contributions of $R_I$ to $R_T$ in both forests were near to 23%, which indicated that the main factor contributing to $R_T$ in both forests was $R_{eff}$. This seasonal variation in $R_T$ is mainly related to the timing of litterfall ($P < 0.01$; Fig. 3), as the input of fresh organic matter to the forest floor leads to the incorporation of soluble C and readily decomposable organic matter (Schlesinger et al. 2000). During the wet season with higher temperature and humidity, the heavy inputs of litter to the forest floor result in the increase of litter decomposition and activities of microbial; therefore, the contribution of aboveground litter to soil respiration is larger.

Our results supported the positive relationship between soil respiration and aboveground litterfall (Davidson et al. 2002; Raich et al. 1989). On the basis of the annual soil C efflux and litterfall C estimates in our study, we obtained a mean ratio for C efflux to litterfall C of 4.02 for our control plots in the primary forest, higher than the mean value of 2.80 for global mature forests (Davidson et al. 2002). The ratio of our control plots in the secondary forest was 3.66, lower than in the primary forest (4.02). This may suggest a lower level of belowground C allocation in the secondary forest, or a larger amount of root respiration (decomposition of root litter) contributing to soil respiration, compared to the decomposition of aboveground litter in the primary forest.

Our study site was disturbed by tropical storms or typhoon during the wet season, resulting in more fresh litter input to the forest floor, which will cause a number of C substrates in soil organic matter and thus regulate soil respiration (Franzluebbers et al. 2001). Soil respiration is a composite of multiple processes, consuming substrates from various sources. Aboveground litter is an important source of C substrate for microbial respiration. The majority of energy for litter respiration is derived from litter decomposition. Besides

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**Figure 3:** Total soil respiration as a function of total litterfall of the current month (open circles) and previous month (solid circles) in (a) primary forest and (b) secondary forest.
changes in soil C pools, changing leaf litter inputs also had strong effects on soil CO$_2$ fluxes (Fig. 3). Litter removal drove declines in soil respiration similar to those reported in other studies of tropical ecosystems (e.g. Boone et al. 1998; Fanin et al. 2011; Sayer et al. 2011). The litter decomposition itself is governed by substrate quality and quantity. As a consequence, soil respiration usually increases with the amount and quality of litter (Leff et al. 2012; Sayer et al. 2007; Vasconcelos et al. 2004). In the Luquillo Experimental Forest, soil respiration was significantly reduced in the litter and root exclusion plots, and litter exclusion reduced soil microbial biomass by 70% (Li et al. 2004). The individual numbers of microbes in the forest litters in Jianfengling tropical forests varied in different seasons with the seasonal variations of litterfall (Wang et al. 2005).

**Effects of soil temperature, soil moisture and litterfall on soil CO$_2$ efflux**

We observed greater seasonal variations in soil respiration ($R_T$, $R_{SL}$ and $R_b$), with higher rates in the wet season than in the dry season, which is similar to previous studies in other tropical forests (Davidson et al. 2000; Hashimoto et al. 2007; Sotta et al. 2004). Tropical forests often exhibit an increase in soil respiration during the wet season, suggesting that soil microorganisms may be limited by water during the dry season (Li et al. 2005; Yi et al. 2007).

We observed a high correlation between soil temperature and soil respiration (Fig. 4a and c). Although the temperature dependence varied across forests (Table S2, see online supplementary material), soil temperature explained 55–61% of temporal variation of $R_T$ among forests. Therefore, the seasonal variations in $R_T$ rate are dominated by soil temperature both in the primary and secondary forests, which agreed with other studies carried out in the Asian tropical forests (Hashimoto et al. 2004; Sha et al. 2005). The most likely mechanisms are because of the direct effects of temperature on the capacities of respiratory enzymes (Stone et al. 2012) and the enzyme substrate supply (Allison et al. 2008; Wang et al. 2012).

It is commonly recognized that soil respiration depends on temperature (Yvon-Durocher et al. 2012). Subsequently, soil C release is expected to increase with global warming, despite an acclimatization (Luo et al. 2001) and substrate limit (Knorr et al. 2005). However, our sites showed that temperature sensitivity of soil respiration is largely different in different forests during different seasons and under different component values. In this study, $Q_{10}$ values for control plots in the primary and secondary forests are 2.17 and 1.86, respectively, which are slightly lower than global mean values (1.9–4.1) but fell in the range of the tropical forest (1.2–4.6; Bond-Lamberty and Thomson 2010a). Although tropical mountain rainforest is evergreen, the seasonal variation of

![Figure 4: relationships between soil respiration and soil temperature and soil moisture in tropical mountain forests in Hainan, China. (a) Soil respiration vs. soil temperature in the primary forest; (b) soil respiration vs. soil moisture in the primary forest; (c) soil respiration vs. soil temperature in the secondary forest; and (d) soil respiration vs. soil moisture in the secondary forest. The exponential regression lines are for $R_T$ (solid line) and $R_{SL}$ (dashed line).](https://academic.oup.com/jpe/article-abstract/6/5/325/899600)
$Q_{10}$ is obvious, ranging from 1.3–1.8 in dry season to 3.1–3.4 in wet season (Table 3). A low soil temperature and moisture in dry season and high soil temperature and moisture could account for the different $Q_{10}$ values in different seasons. The $Q_{10}$ of 3.4–4.4 for litter decomposition (Table 3) was higher than those for $R_l$ and $R_{SL}$. This is because the $R_l$ was lower than those from other components of soil respiration, and the increase from dry season to wet season, corresponding to the increase in soil temperature, was relatively high. The higher $Q_{10}$ value for litter has implications for analysis of how soil CO$_2$ efflux may be affected in a warmer world (Fang et al. 2005). The results indicate that the temperature sensitivity of soil respiration may depend on the relative contribution of litter and associate decomposition layer microbiota to total soil CO$_2$ efflux.

We found no significant linear relationships between soil respiration and soil moisture in the tropical mountain rainforest. During the wet season in 2012, with rainfall of 1941 mm, the soil moisture was above 20% for most of time. As a result, soil moisture was not a constraint factor for soil respiration, and the strong seasonal variation in soil respiration can result only from changes in substrate supply from the aboveground parts of plants and variations in soil temperature from the belowground parts of soil.

### CONCLUSIONS

Differences in aboveground vegetation structure and soil environment influenced soil CO$_2$ efflux in two tropical mountain rainforests, resulting in higher soil CO$_2$ efflux in the primary forest than in the secondary forest. Soil respiration in both forests was strongly correlated with soil temperature. Soil temperature explained 55–61% of the observed variation in $R_l$ in both forests. Soil respiration shows a positive relationship with the seasonal changes of litter input, but 1 month lag exists between soil respiration and litter input at the seasonal scale. The soil CO$_2$ efflux revealed a clear seasonal pattern, which was mainly controlled by soil temperature and substrate availability, with the fluxes significantly higher in the warm season than in the cold season. Overall, soil respiration without surface organic litter accounted for about 77% of the total C efflux, making it the dominant source of C released to the atmosphere. Furthermore, aboveground litter decomposition comprised 23% of the average annual soil respiration. The $Q_{10}$ values for different treatment plots showed that respiration by the litter layer and associated microbial activities was more temperature sensitive than $R_l$ and $R_{SL}$. The $Q_{10}$ values for different seasons revealed that respiration in the wet season was more temperature sensitive than that in the dry season. Taken together, our study suggests that climatic changes in tropical regions, which could alter the soil temperature and aboveground litter, may have significant effects on soil CO$_2$ fluxes.

### SUPPLEMENTARY MATERIAL

Supplementary material is available at Journal of Plant Ecology online.

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### REFERENCES


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**Table 3:** $R^2$ and $Q_{10}$ values for the relationship between soil respiration and temperature

<table>
<thead>
<tr>
<th>Seasons</th>
<th>$R_l$</th>
<th>$R_{SL}$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Dry</td>
<td>1.79</td>
<td>0.66</td>
</tr>
<tr>
<td>Wet</td>
<td>3.39</td>
<td>0.41</td>
</tr>
<tr>
<td>Annual</td>
<td>2.17</td>
<td>0.61</td>
</tr>
</tbody>
</table>

**Primary forest**

<table>
<thead>
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<th>$y = a e^{bT}$</th>
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<th>$R^2$</th>
<th>$P$</th>
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<td>0.002</td>
<td>1.58</td>
<td>0.53</td>
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<tr>
<td>$R_{SL}$</td>
<td>0.355</td>
<td>0.355</td>
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</table>

**Secondary forest**

<table>
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<th>$y = a e^{bT}$</th>
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<td>$R_l$</td>
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<td>0.126</td>
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<tr>
<td>$R_{SL}$</td>
<td>0.30</td>
<td>0.30</td>
<td></td>
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</tbody>
</table>

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