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REGULAR ARTICLE

Influence of interactions between litter decomposition and rhizosphere activity on soil respiration and on the temperature sensitivity in a subtropical montane forest in SW China

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Abstract
Aims The aims were to identify the effects of interactions between litter decomposition and rhizosphere activity on soil respiration and on the temperature sensitivity of soil respiration in a subtropical forest in SW China.
Methods Four treatments were established: control (CK), litter removal (NL), trenching (NR) and trenching together with litter removal (NRNL). Soil CO_2 efflux, soil temperature, and soil water content were measured once a month over two years. Soil respiration was divided into four components: the decomposition of basic soil organic matter (SOM), litter respiration, root respiration, and the interaction effect between litter decomposition and rhizosphere activity. A two-factor regression equation was used to correct the value of soil CO_2 efflux.
Results We found a significant effect of the interaction between litter decomposition and rhizosphere activity (R_{INT}) on total soil respiration, and R_{INT} exhibited significant seasonal variation, accounting for 26 and 31 % of total soil respiration in the dry and rainy seasons, respectively. However, we found no significant interaction effect on the temperature sensitivity of soil respiration. The temperature

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sensitivity was significantly increased by trenching compared with the control, but was unchanged by litter removal.

Conclusions Though the interaction between litter decomposition and rhizosphere activity had no effects on temperature sensitivity, it had a significant positive effect on soil respiration. Our results not only showed strong influence of rhizosphere activity on temperature sensitivity, but provided a viable way to identify the contribution of SOM to soil respiration, which could help researchers gain insights on the carbon cycle.

Keywords Q_{10} · Root respiration · Litter respiration · Soil organic matter decomposition · Soil respiration

Introduction

Soil is the largest organic carbon pool in terrestrial ecosystems (Lal 2004). Global soil respiration (R_S), which has been estimated to be 98±12 Pg C yr^{-1} in 2008 (Bond-Lamberty and Thomson 2010), is an important source of atmospheric CO_2 (Raich and Schlesinger 1992; Friedlingstein et al. 2006). Soil respiration contains many components that are difficult to distinguish (Kuzyakov 2006). However, to obtain a better understanding of C-cycling on regional and global scales, previous studies have developed methods to quantify the components of R_S (Hanson et al. 2000; Kuzyakov 2006; Subke et al. 2006). Soil respiration is usually divided into autotrophic respiration (R_A) and heterotrophic respiration (R_H) (Hanson et al. 2000; Subke et al. 2006). In forest ecosystems, trenching (or girdling) has been widely used to partition R_A and R_H (Hogberg et al. 2001; Subke et al. 2006; Li et al. 2010; Sayer and Tanner 2010), and the contribution of R_H was 45–70 % of R_S, which declined with increasing annual R_S (Subke et al. 2006) . Since litter decomposition commonly makes a significant contribution to R_S, litter removal has been used to quantify the contribution of aboveground litter decomposition (R_{AL}) to R_S (C_{AL}) in forest ecosystems (Bowden et al. 1993; Sulzman et al. 2005; Sayer 2006; Wang et al. 2013). Combining the above, the decomposition of soil organic matter (SOM) can thus be calculated as follows: $R_{SOM} = R_S – R_A – R_{AL}$, thereby enabling estimates of the contribution of SOM decomposition to R_S (C_{SOM}) (Rey et al. 2002; Sulzman et al. 2005; Chang et al. 2008).

However, the above equation may underestimate the contribution of SOM to $R_{S.}$ For example, Rey et al. (2002) reported lower estimated values of C_{SOM} compared with measured values based on experiments combining trenching with litter removal. This discrepancy is due to the priming effect caused by both rhizosphere activity (Fu and Cheng 2002; Kuzyakov 2002) and litter decomposition (Park et al. 2002; Kalbitz et al. 2007). Subke et al. (2004) indicated that since both litter decomposition and rhizosphere activity can promote SOM decomposition, they may positively interact. Therefore, to correctly partition the components of R_S, it is important to quantify this interaction. However, few studies have investigated this interaction in forest ecosystems (see Subke et al. 2004).

Using experimental data collected from a subtropical montane cloud forest in SW China, this study tested the hypothesis that litter decomposition and rhizosphere activity has a positive interaction effect on soil respiration. In this forest, SOM mainly comes from roots and aboveground litter. Since roots release both low- and high-weight substances, such as sugars, amino acids, enzymes, and mucilage (Nguyen 2003), and litter decomposition percolates dissolved organic carbon into the mineral soil (Kalbitz et al. 2000), the trenching and litter removal treatments prevented labile input. Temperature-quality hypothesis suggests that old, low-quality SOM causes higher temperature sensitivity (Q_{10}) due to the higher activation energy required for the decomposition of low-quality SOM (Bosatta and Agren 1999); previous studies have supported this hypothesis (Davidson and Janssens 2006; Conant et al. 2008; Wetterstedt et al. 2010; Suseela et al. 2013). Therefore, we also hypothesized negative effects of litter decomposition and rhizosphere activity on the temperature sensitivity of R_S.

Materials and methods

Site description

This experiment was conducted at the Ailaoshan Station for Subtropical Forest Ecosystem Studies (24°32′N, 101°01′E; 2,480 m above sea level) of the Chinese Ecological Research Network, which is located in Jingdong County, Yunnan Province. Over the past 10 years (2002–2011), the annual mean air temperature was 11.3 °C, with a minimum monthly mean temperature of 5.7 °C in January and a maximum monthly mean temperature of 15.6 °C in July. The average annual rainfall was 1,778 mm, with 86.0 % falling in the rainy season (May–October) (Fig. 1). The forest is influenced by the southwest monsoon and is exposed to frequent and intense wind and mist events throughout the year. The forest is described as a subtropical cloud forest, given the abundant moisture and persistent cloud cover (Song et al. 2012; Zhang et al. 2012). The dominant tree species in the forest are *Vaccinium duclouxii*, *Lithocarpus chintungensis*, and *Schima noronhae*, along with *Sinarundinaria nitida* in the shrub layer, and the litterfall is 864 g m^{-2} $year^{-1}$. The soils are Alfisols, which have a pH value of 4.5, soil organic carbon 304 g kg^{-1}, and total nitrogen 18 g kg^{-1} in the humus horizon (Chan et al. 2006).

Experiment design

Three plots (10 × 10 m) were selected in the forest, and four subplots were established in each plot: control (CK), litter removal (NL), trenching (NR) and trenching with litter removal (NRNL). Cover structures (i.e., a bamboo framework covered with 1-mm nylon mesh, 1 × 1 m) were established in the NL subplots at a height of 1.2 m above the ground to prevent new litter dropping. Visible litter in the subplots was removed at the beginning of this experiment. In the NR subplots, PVC pipes (diameter 630 mm, height 500 mm) were used for trenching. A circular trench (width about 300 mm) was dug to 500 mm, to form a cylinder of soil contained by the PVC pipe; soil was backfilled by its original layers with topsoil over subsoil (see Fig. S1). NRNL plots were established by combining the NL and NR treatments. In the center of each subplot, one PVC connector was permanently inserted into the soil to a depth of 20 mm at the beginning of the experiment, and a PVC top-closed pipe (diameter 200 mm, height 200 mm) was mounted on the connector, constituting a respiration chamber when we measured soil CO_2 efflux.

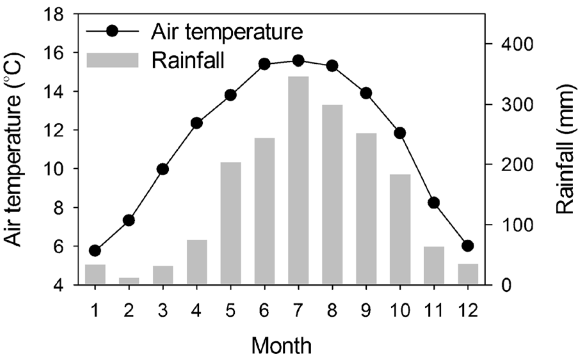


Fig. 1 Seasonal variations in air temperature and rainfall averaged from 2002 to 2011 at the Ailaoshan Station for Subtropical Forest Ecosystem Studies

Data collection

The experimental setup was finished on 15 January 2010 and measurements began on 7 February 2010, continuing for two years. Soil CO_2 efflux was measured monthly using a gas analyzer (LI-840; Li-cor, Lincoln, NE, USA) between 9:00 and 11:00 (Beijing Time) to avoid diurnal fluctuations. Soil temperature (T, °C) was measured at 50 mm depth with a digital thermometer (6310; Spectrum, Illinois, USA) and soil water content (W, %) was measured by time domain reflectometry (MP-KIT; Beijing Channel, Beijing, China).

Soil CO_2 efflux (R) was calculated as follows:

$$R = \frac{M}{V_0} \cdot \frac{P}{P_0} \cdot \frac{T_0}{Ta} \cdot H \cdot \frac{dc}{dt} \qquad (1)$$

where R is the soil CO_2 efflux (μmol m^{-2} s^{-1}); M is the CO_2 molar mass; V_0, P_0 and T_0 are constants (22.4 L·mol^{-1}, 1013.25 hPa, and 273.15 K, respectively); Ta is air temperature (K); H is the height of the respiration chamber (m); and dc/dt is the slope of CO_2 concentration variation with time over the measurement period.

Calculations

As soil temperature and soil water content affected soil respiration in forest ecosystems, previous studies have developed two-factor regression models to reflect the relationship of soil respiration with soil temperature and soil water content (Xu and Qi 2001; Qi et al. 2002). At the present site, soil temperature and soil water content showed similar seasonal variations (Fig. 2). Considering their interaction effect on soil CO_2 effluxes, their product was taken as variable. Thus, a two-factor regression model was developed to reveal the relationship of soil CO_2 efflux with soil temperature and soil water content, and given high regression coefficients of determination (R^2 values) ranged from 0.76 to 0.93 (Fig. S2). The two-factor regression model equation was as follow:

$$R = \mathrm{a} \cdot T \cdot W + \mathrm{b} \qquad (2)$$

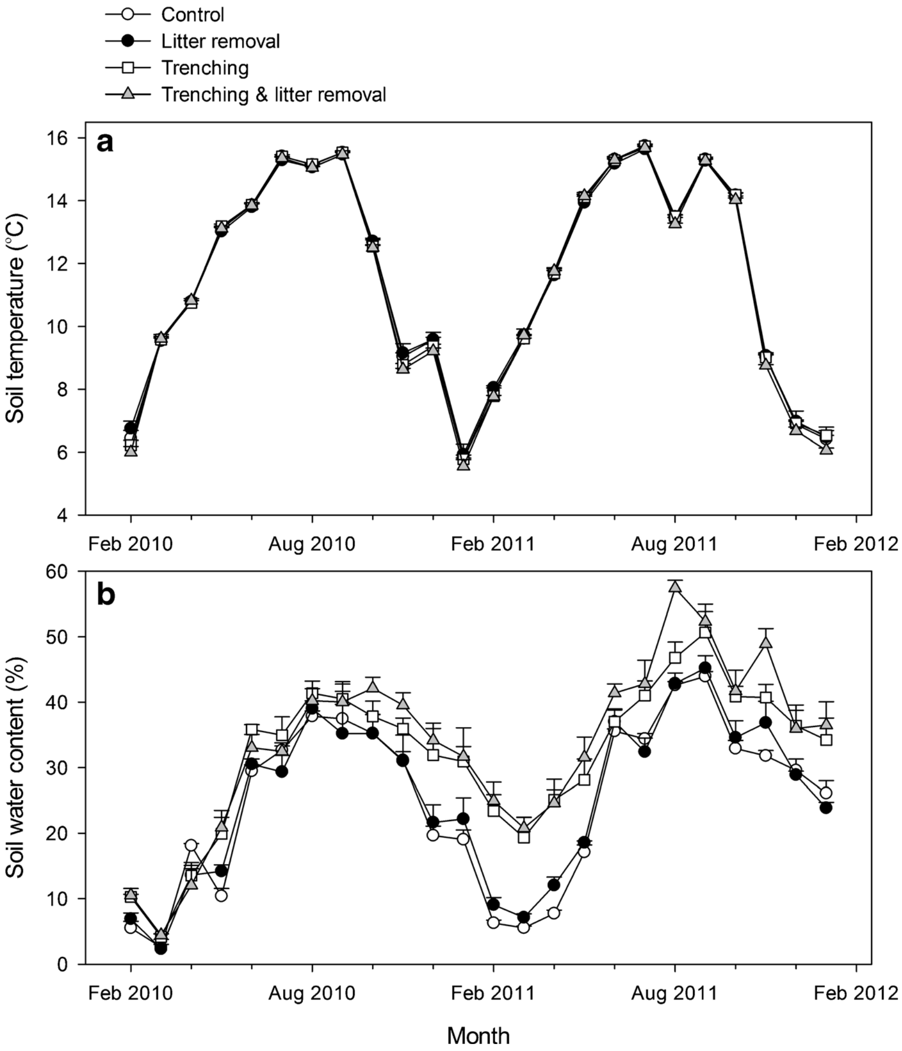
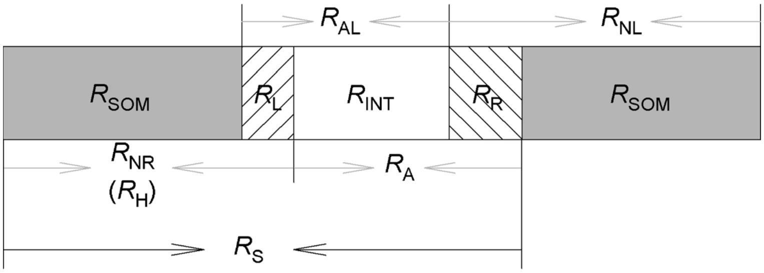


Fig. 2 Seasonal variability in soil temperature and soil water content of each treatment (mean + SE). *Open circles* represent control (CK), *black circles* represent litter removal (NL), *open squares* represent trenching (NR), and *triangles* represent trenching together with litter removal (NRNL)



$$R_s = R_{SOM} + R_L + R_R + R_{INT}$$
$$R_{NL} = R_R + R_{SOM}$$
$$R_{NR} = R_L + R_{SOM}$$
$$R_A = R_R + R_{INT}$$
$$R_{AL} = R_L + R_{INT}$$
$$R_{INT} = (R_S + R_{SOM}) - (R_{NR} + R_{NL})$$

Fig. 3 Soil respiration divided into four components: basic SOM decomposition (R_{SOM}), litter respiration (R_L), root respiration (R_R), and interaction (R_{INT}). R_A is autotrophic respiration including R_R and R_{INT}, R_{AL} is aboveground litter decomposition including R_L and R_{INT}, R_H is heterotrophic respiration including R_{SOM} and R_L, and R_{NL} is soil CO_2 efflux after litter removal including R_{SOM} and R_R

where a and b are constants estimated from regression model (details see Fig. S2), T is soil temperature (°C), and W is soil water content (%).

R_S, R_{NL}, R_{NR}, and R_{NRNL} represent the soil CO_2 effluxes of CK, NL, NR, and NRNL, respectively. We divided soil respiration into four components: basic SOM respiration (R_{SOM}), litter respiration (R_L), root respiration (R_R), and a component representing the interaction between litter decomposition and rhizosphere activity (R_{INT}) (Fig. 3). The two-factor regression model showed that both T and W had positive effects on soil CO_2 efflux (Fig. S2), while the treatments affected the soil microclimate (Sayer 2006; Sayer and Tanner 2010), especially W (Fig. 2). Therefore, to eliminate the biases due to soil microclimate change, effluxes should be compared under the same environmental conditions. Accordingly, the mean soil temperature and soil water content measured in control subplots were used to correct the values of R_S, R_{NL}, R_{NR}, and R_{NRNL} by Eq. (2). The same T and W variables, but different parameters (a and b) for each subplot, were used for this correction (Fig. S2). The correction did not change R_S and R_{NL}, but it reduced R_{NR} and R_{NRNL} (Fig. S3).

We calculated the components as follows (details see Fig. 3):

$$\text{Soil total respiration}: R_S = R_{SOM} + R_L + R_R + R_{INT} \lim_{x\to\infty} \quad (3)$$

$$\text{Basic SOM respiration}: R_{SOM} = R_{NRNL} \quad (4)$$

$$\text{Litter respiration}: R_L = R_{NR} - R_{NRNL} \quad (5)$$

$$\text{Root respiration}: R_R = R_{NL} - R_{NRNL} \quad (6)$$

$$\text{Interaction}: R_{INT} = (R_S + R_{NRNL}) - (R_{NR} + R_{NL}) \quad (7)$$

Temperature sensitivity (Q_{10}) was calculated from R_{T+10}/R_T; R_T was a regression model of efflux with soil temperature in field experiments. For example, an exponential equation ($Q_{10} = e^{b*T}$) was used to estimated Q_{10} previously, which was derived from a one-factor regression model ($R = R_0*e^{b*T}$). However, one-factor regression model could not well reveal the relationship of efflux with soil temperature. Therefore, as mentioned above, two-factor regression models were developed for better understanding of the relationship. Q_{10} was not a constant; it changed with the variations of soil temperature and soil water (Davidson and Janssens 2006).

Base on the two-factor regression model (Eq. 2), we could get R_T and R_{T+10}.

$$R_T = a \cdot T \cdot W + b \quad (8)$$

$$R_{T+10} = a \cdot (T + 10) \cdot W + b = a \cdot T \cdot W + b + 10a \cdot W \quad (9)$$

where W in R_T was the same to R_{T+10}, because R_{T+10} meant efflux rate after increasing 10 °C soil temperature, and thereby soil water content should keep the same compared to R_T. Therefore, we developed Q_{10} equation as follow:

$$Q_{10} = \frac{RT + 10}{RT} = 1 + \frac{10a \cdot W}{a \cdot T \cdot W + b} \quad (10)$$

where a and b are as estimated by Eq. (2) for each subplot (Fig. S2). Eq (10) revealed the relationship of Q_{10} with soil temperature and soil water content as reviewed by Davidson and Janssens (2006); Q_{10} should be compared under the same environmental conditions for different treatments. Therefore, the mean soil temperature and soil water content measured in control subplots were used to calculate Q_{10} values of all subplots for each measurement time.

Statistical analysis

All the data were subjected to tests for normality and homoscedasticity before ANOVA analyses. Univariate general linear modeling (GLM) was used to test the interaction effect of litter and root treatments. All differences were tested for statistical significance at the 95 % level. Statistical analyses were performed with SPSS 13.0 (SPSS Inc., Chicago, IL, USA).

Results

Influence of interaction between litter and rhizosphere on soil respiration

The Univariate GLM analyses showed that both rhizosphere activity and litter decomposition had significant effects on R_S, and there were significant interactions between them (Table 1A).

R_{INT} exhibited seasonal variation, increasing rapidly from the dry season to the rainy season (Fig. 4a). The average value in dry season ($0.82 \pm 0.28\ \mu mol \cdot m^{-2} \cdot s^{-1}$) was significantly different from that in rainy season ($2.55 \pm 0.50\ \mu mol \cdot m^{-2} \cdot s^{-1}$) (Fig. 4b).

The contribution of R_{INT} to R_S (C_{INT}) showed a similar pattern to its flux; i.e., higher contributions in

Table 1 *F* and *p* values of univariate GLM analyses on soil CO_2 efflux (A) and temperature sensitivity (B)

Source	Dry-season		Rainy-season		Annual	
	F	*p*	*F*	*p*	*F*	*p*
A: Respiration						
Root	94.184	<0.001	99.016	<0.001	111.924	<0.001
Litter	33.772	<0.001	85.742	<0.001	74.722	<0.001
Litter × Root	12.686	0.007	32.400	<0.001	29.596	0.001
B: *Q*10						
Root	16.794	0.003	28.090	0.001	17.963	0.003
Litter	0.004	0.988	0.250	0.631	0.003	0.960
Litter × Root	1.089	0.327	1.690	0.230	1.095	0.326

the rainy season (Fig. 4c). However, C_{INT} in dry season (27±8 %) did not significantly differ to that in rainy season (31±6 %). R_{INT} contributed 30±7 % to R_S as the annual mean (Fig. 4d).

Single-factor regressions of R_{INT} as a linear function of T only, and as a linear function of W only, showed that T and W explained 64 and 85 % of the variation in R_{INT}, respectively. Linear regression of T with C_{INT} and logarithmic regression of W with C_{INT} showed that T and W explained 41 and 93 % of the variation in C_{INT}, respectively (Fig. 5).

Comparisons to other components

R_{SOM} showed similar patterns to those for R_{INT}; i.e., higher fluxes in the rainy season. R_L showed minor seasonal variations whereas R_R was largely unchanged

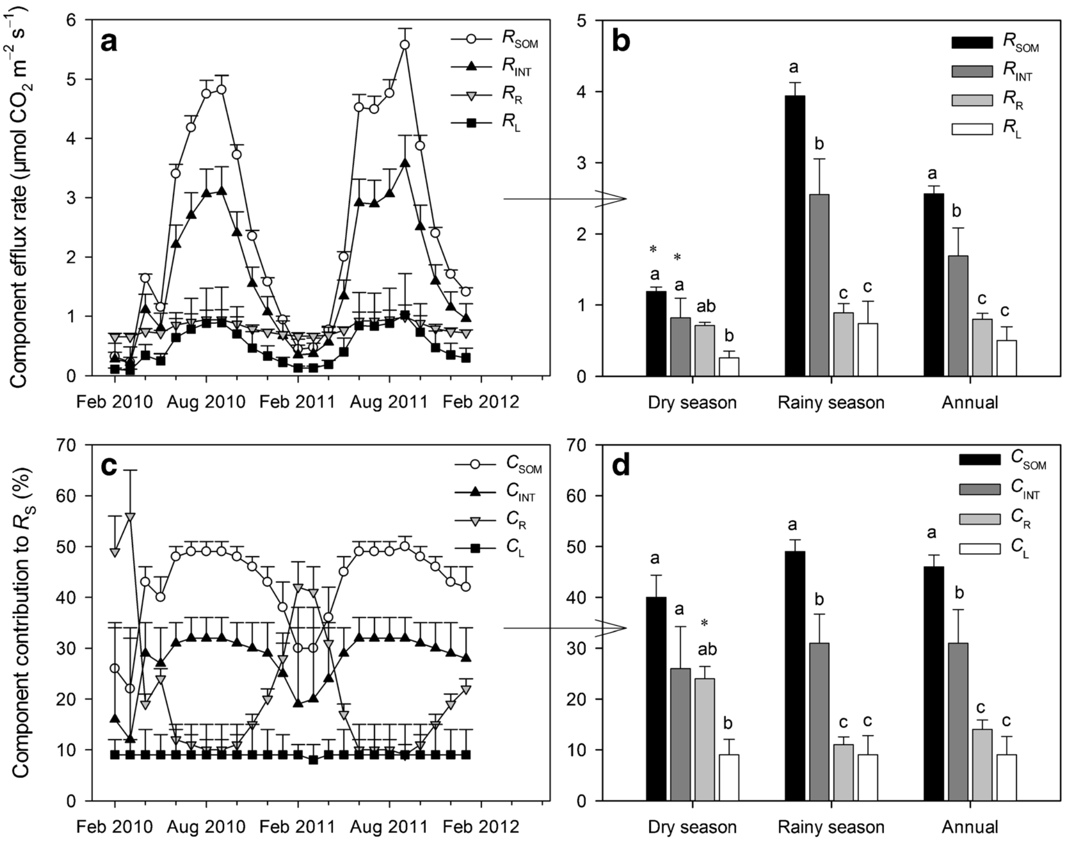


Fig. 4 Seasonal variability in soil respiration components **a** and their contributions to soil respiration **c**: *open circles* represent R_{SOM} or C_{SOM}, upward-facing triangles represent R_{INT} or C_{INT}, downward-facing triangles represent R_R or C_R, and squares represent R_L or C_L. Comparisons among components in dry season average, rainy season average, and annual mean **b, d**: *black vertical* bar represents R_{SOM} or C_{SOM}, dark gray represents R_{INT} or C_{INT}, gray represents R_R or C_R, and white represents R_L or C_L; all data passed the normality and homoscedasticity tests before one-way ANOVA analysis; different letters for the same measurement time indicate significant differences (as indicated by LSD's post-hoc test); *means significant difference between dry and rainy seasons (independent t testes). Data are mean + SE (n=3)

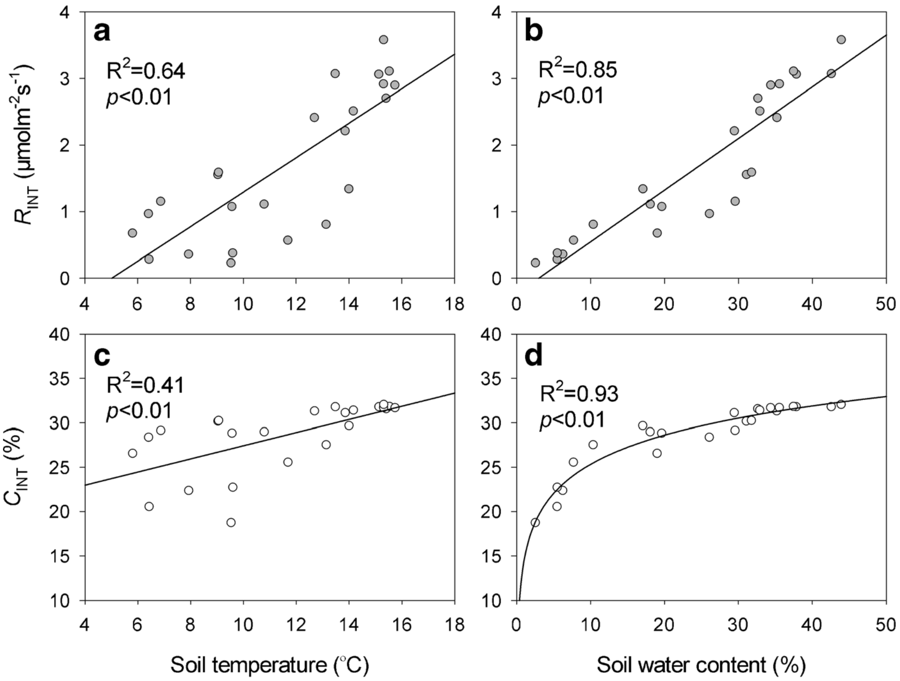


Fig. 5 **a**, **b** Linear regression of R_{INT} onto soil temperature and soil water content, **c** Linear regression of C_{INT} onto soil temperature, **d** Logarithmic regression of C_{INT} onto soil water content

throughout the year (Fig. 4a). There was significant difference for R_{SOM} between dry season and rainy season, however, no significant differences were observed for R_{R} and R_{L} (Fig. 4b).

The contribution of R_{SOM} to R_{S} (C_{SOM}) showed a similar pattern to that of C_{INT}, whereas the contribution of R_{R} to R_{S} (C_{R}) showed the opposite pattern, with large contributions during the dry season. The contribution of R_{L} to R_{S} (C_{L}) showed no seasonal variations. Values of C_{SOM}, C_{R}, and C_{L} were respectively 40±4 %, 24±2 %, and 9±3 % in the dry season, and 49±2 %, 11±2 %, and 9±4 % in the rainy season, among which only C_{R} had significant difference between dry season and rain season (Fig. 4d).

In dry season, R_{INT} only had significant difference with R_{L}, while in rainy season and annual time, it had significant differences with not only R_{L} but also R_{SOM} and R_{R} (Fig. 4b). The pattern also applied for C_{INT} that was significant different from C_{L} in dry season, while with C_{L},C_{SOM} and C_{R} in both rainy season and annual time (Fig. 4d).

Temperature sensitivity

Q_{10} showed similar seasonal patterns in CK and NL, with both lowest and highest values in dry season. The lowest values (1.35±0.06 and 1.24±0.03, respectively) appeared in March 2010 while the highest values (2.19± 0.07 and 2.06±0.03, respectively) in January 2012. Similar seasonal patterns were also observed in NR and NRNL, with lowest values (1.62±0.01 and 1.63± 0.01, respectively) in July 2011, and highest values (2.61±0.15 and 2.71±0.14, respectively) in January 2011 (Fig. 6a). Q_{10} values of CK, NL, NR, and NRNL were significantly different between dry season and rainy season (Fig. 6b).

Univariate GLM analyses showed no significant effect of interaction between litter decomposition and rhizosphere activity on Q_{10} values, but a significant effect of rhizosphere activity on Q_{10} (Table 1B). One way ANOVA analyses showed Q_{10} values were not different between CK and NL ($p>0.05$), but they were significantly higher in NR and NRNL than in CK, in dry season, rainy season, and annual time (Fig. 6b).

Discussion

As shown previously, intact rhizosphere activity is directly linked to litter decomposition (Subke et al. 2004; Subke et al. 2011). In the present study, the interaction between rhizosphere activity and litter decomposition

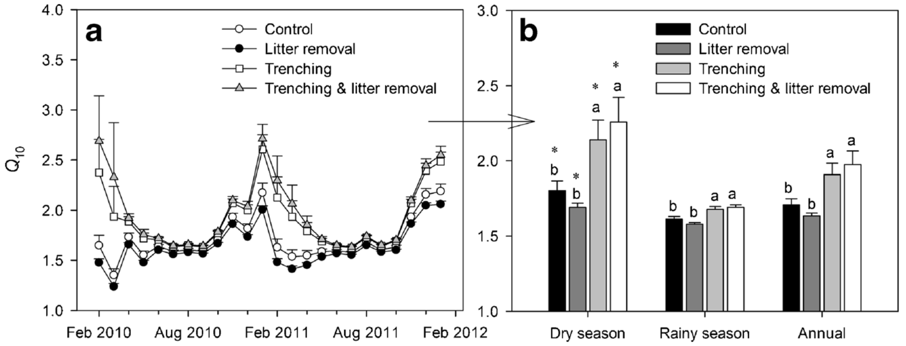


Fig. 6 Seasonal variation of Q_{10} values of the four treatments, calculated using Eq. (10) for each measurement time point **a** (mean + SE, $n=3$). Comparisons among treatments in dry season average, rainy season average and annual mean **b** (mean + SE, $n=3$): all data passed the normality and homoscedasticity tests before one-way ANOVA analysis; different letters for the same measurement time indicate significant differences (as indicated by LSD's post-hoc test); *means significant difference between dry and rainy seasons (independent t testes, $p<0.05$)

had a significant impact on soil respiration (Table 1A). In terms of annual mean, R_{INT} accounted for 30 % of R_{S} (Fig. 4b). Clearly, our work indicates that R_{INT} plays an important role in determining the dynamics of R_{S}. The mechanism linking litter and rhizosphere is possibly microbial activity (Li et al. 2004; Subke et al. 2004; Feng et al. 2009). Litter and roots provide easily decomposable carbon for microbial growth, which leads to a positive feedback on SOM decomposition (Dighton et al. 1987; Chapela et al. 2001). In addition, we found that R_{INT} and C_{INT} were controlled by soil moisture (Fig. 5), and the lower values we observed in the dry season are perhaps due to competition for soil moisture between roots and rhizosphere microbes (Kuzyakov 2002).

As it shown in Fig. 3, R_{INT} was in the realm of autotrophic respiration if soil respiration was divided into autotrophic and heterotrophic respiration, and was also in the realm of aboveground litter decomposition (R_{AL}) if that was divided into aboveground and belowground respiration. Conclusively, the contribution of SOM to R_{S} which was estimated from above two partition methods as mentioned in introduction would be underestimated.

R_{INT} may include two components: SOM decomposition primed by both litter and rhizosphere activities, and litter decomposition primed by rhizosphere activity alone. Previous studies have shown that rhizosphere activity (Fu and Cheng 2002; Kuzyakov 2002) and litter decomposition (Park et al. 2002; Kalbitz et al. 2007) can cause priming effects on SOM decomposition. Over short timescales (in our case, 2 years) and in small areas (in our case, 1 m^2), litter removal treatments cannot be expected to affect forest function (Sayer 2006), and nor can they be expected to influence R_{R}, because R_{R} is driven primarily by photosynthesis (Kuzyakov and Cheng 2001; Wang et al. 2010). However, rhizosphere activity can promote litter decomposition (Subke et al. 2004; Kuzyakov et al. 2007; Subke et al. 2011).

The lack of significant differences in Q_{10} values between the CK and NL treatments, combined with the significant differences between the CK and NR (and NRNL) treatments (Fig. 6b), indicate that roots have a strong effect on the Q_{10} of soil respiration; this inference was supported by the results of Univariate GLM (Table 1B). The results obtained for the NR treatment are consistent with temperature-quality hypothesis, as shown previously (Fierer et al. 2005; Knorr et al. 2005; Davidson and Janssens 2006; Conant et al. 2008; Hartley and Ineson 2008; Suseela et al. 2013), although some contrary results have also been reported (Giardina and Ryan 2000; Reichstein et al. 2000). Other studies have reported similar temperature dependences for different kinds of SOM (Cox et al. 2000; Fang et al. 2005; Jones et al. 2005), similar to our results for NL. The contrasting results we obtained for NR and NL may be explained in terms of labile carbon. The NL treatment allowed root rhizosphere activity, thereby permitting labile carbon as input into the soil. Although the NR treatment allowed litter input, little labile carbon made its way into the soil because trenching prevented the process of litter decomposition. This explanation is further supported by the fact that we observed no significant interaction between the litter and roots treatments (Table 1B). The influence of interactions between litter and rhizosphere activities on soil respiration have received little attention to date (Subke et al. 2004; Subke et al. 2011), and our study not only demonstrates the importance of such interactions, but also the need for further research to quantify these types of interactions in different ecosystems over longer timescales.

Conclusion

We found a significant positive effect of the interaction between litter decomposition and rhizosphere activity on soil respiration. The annual mean average values for C_{INT}, C_{SOM}, C_{R}, and C_{L} were 30 %, 46 %, 15 %, and 9 %, respectively. R_{INT} and C_{INT} showed seasonal variations driven by soil water content. Our finding of an interaction effect on soil respiration (R_{INT}) suggests a way to identify the contribution of SOM to soil respiration and thereby enables an improved understanding of the carbon cycle on the regional scale. Litter decomposition had no effect on the temperature sensitivity of soil respiration, whereas rhizosphere activity had a strong effect. Together, they had no significant interaction effect on temperature sensitivity. Our results provided solid results to prove the temperature-quality hypothesis and showed a viable way for further studies to gain more insights on global carbon cycle.

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