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Influence of rhizosphere activity on litter decomposition in subtropical forest: implications of estimating soil organic matter contributions to soil respiration

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Abstract

Litter decomposition plays an important role in the carbon cycle and is affected by many factors in forest ecosystems. This study aimed to quantify the rhizosphere priming effect on litter decomposition in subtropical forest southwestern China. A litter decomposition experiment including control and trenching treatments was conducted using the litter bag method, and the litter decomposition rate was calculated by litter dry mass loss. Trenching did not change soil temperature, but increased the soil water content by 14.5%. In this study, the interaction of soil temperature and soil water content controlled the litter decomposition rate, and explained 87.4 and 85.5% of the variation in litter decomposition in the control and trenching treatments, respectively. Considering changes in soil environmental factors due to trenching, the litter decomposition rates were corrected by regression models. After correction, the litter decomposition rates of the control and trenching treatments were 32.47 ± 3.15 and 25.71 ± 2.72% year^{-1}, respectively, in the 2-year period. Rhizosphere activity significantly primed litter decomposition by 26.3%. Our study suggested a priming effect of rhizosphere activity on litter decomposition in the subtropical forest. Combining previous interaction effect results, we estimated the contributions of total soil organic matter (SOM) decomposition, total litter decomposition, and root respiration to soil respiration in the subtropical forest, and our new method of estimating the components of soil respiration provided basic theory for SOM decomposition research.

Introduction

Soil respiration (R_S) is an important source of atmospheric CO_2 and a regulator of climate change. R_S is affected by interaction effect among factors (Cui *et al.* 2021, Wu *et al.* 2014) and has several components that are notoriously difficult to partition (Hanson *et al.* 2000, Kuzyakov 2006). The isotope technique is an efficient tool for partitioning the components (Pries *et al.* 2013, Rodeghiero *et al.* 2013, Whitman & Lehmann 2015); however, a large knowledge gap regarding R_S partitioning in forest ecosystems remains. In forest ecosystems, traditional methods involve trenching or girdling (Hogberg *et al.* 2001, Jovani-Sancho *et al.* 2018) and model method based on root allometry and spatial distribution (Zhao *et al.* 2021) were used to separate R_S into autotrophic respiration (R_A) and heterotrophic respiration (R_H), or litter removal treatment was used to divide R_S into aboveground litter decomposition (R_{AL}) and belowground CO_2 efflux (R_{NL}) (Chang *et al.* 2008, Sayer *et al.* 2011, Tan *et al.* 2013). Based on carbon pools with different turnover rates, R_S can be grouped into plant-derived CO_2 and soil organic matter (SOM)-derived CO_2 combinations (Kuzyakov 2006). Considering the turnover rate, only SOM-derived CO_2 has a potential effect on the atmospheric CO_2 level (Kuzyakov 2006). Therefore, it is important to partition R_S and further quantify the contribution of SOM decomposition.

The rate of SOM decomposition can be calculated as $R_{SOM} = R_S - R_A - R_{AL}$ (Sulzman *et al.* 2005, Tan *et al.* 2013) and $R_{SOM} = R_{NRNL}$ (trenching with litter removal) (Rey *et al.* 2002) with traditional methods, thereby enabling estimates of the contribution of SOM decomposition to R_S. However, these methods do not consider the interaction of litter decomposition and rhizosphere activity. A previous study showed a significant interaction between litter decomposition and rhizosphere activity (Wu *et al.* 2014), and R_S was divided into four components: basic SOM respiration, litter respiration without an effect of rhizosphere activity, root respiration, and the interaction between litter decomposition and rhizosphere activity (Figure 1a). Notably, the interaction effect may include two components: SOM decomposition primed by both litter

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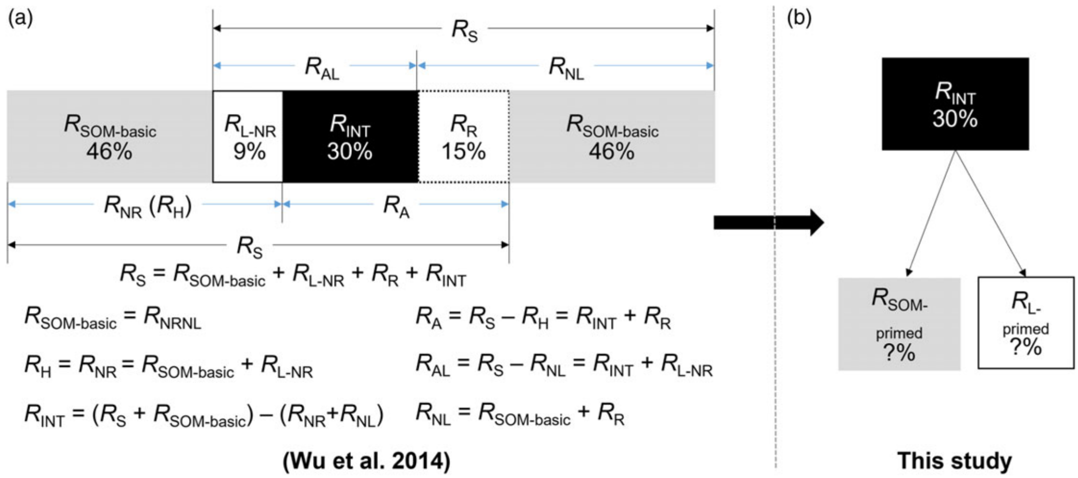

Figure 1. Soil respiration components and their calculations, modified from Wu *et al.* 2014 (a); aim of this study (b).

and rhizosphere activities ($R_{SOM\text{-}primed}$) and litter decomposition primed by rhizosphere activity alone ($R_{L\text{-}primed}$) (Figure 1b). To further quantify the contributions of specific components of SOM, determining the effect of rhizosphere activity on litter decomposition in detail is necessary. Previous studies have shown a rhizosphere priming effect on the litter decomposition rate (Subke *et al.* 2011, Wang *et al.* 2016). Therefore, our hypothesis was that rhizosphere activity would promote litter decomposition in a subtropical forest southwestern China. Our aims were to quantify the priming effect and further quantify the contribution of total SOM decomposition.

The litter bag method has been widely used to investigate litter decomposition. In this study, we prepared litter bags for decomposition experiments lasting 2 years in control and trenching plots, thereby enabling us to determine whether rhizosphere activity had a priming effect on litter decomposition in the subtropical forest.

Materials and methods

Site description

This experiment was performed at the Ailaoshan Station for Subtropical Forest Ecosystem Studies (24°32′N, 101°01′E; 2480 m above sea level) of the Chinese Ecological Research Network, which is located in Jingdong County, Yunnan Province. The annual mean air temperature is 11.3 °C (Wu *et al.* 2014). Mean rainfall from 2013 to 2015 is 1598.5 mm and 86.0% of rainfall occurs during the rainy season (May to October) (Huang *et al.* 2020). The soils are Alfisols, which have a pH of 4.5 (Chan *et al.* 2006). In the study plots, surface soil organic carbon (0~10 cm) was 129.7 ± 27.1 g kg^{-1} (mean ± standard deviation (SD), n=3). The dominant tree species in this forest are *Vaccinium duclouxii*, *Lithocarpus chintungensis*, and *Schima noronhae*, and the litterfall totals 864 g m^{-2} yr^{-1} (Wu *et al.* 2014).

Experimental design

In the subtropical forest, three plots (10 × 10 m) were selected, and four subplots were established in each plot in January 2010: control (CK), litter removal (NL), trenching (no roots, NR), and trenching with litter removal (NRNL). Soil CO_2 efflux was measured from February 2010 to January 2012. Based on the interaction design between litter and root, R_S was divided into four components, namely, basic SOM respiration ($R_{SOM\text{-}basic} = R_{NRNL}$), litter respiration without an effect of rhizosphere activity ($R_{L\text{-}NR}$), root respiration (R_R), and the interaction between litter decomposition and rhizosphere activity (R_{INT}), and their contributions ($C_{SOM\text{-}basic}$, $C_{L\text{-}NR}$, C_R, and C_{INT}) were 46 %, 9 %, 15 %, and 30 %, respectively (for details, see Wu *et al.* 2014). However, the components of R_{INT} were unclear (Figure 1b).

Therefore, at the previously mentioned research site, we selected two subplots (1 m × 1 m) in each of the three studied plots. One subplot acted as a control (CK), and the trenching treatment (NR) was applied in the other subplot. Along the edge of the trenching plot, a square trench (approximately 30 cm wide) was dug to 50 cm to obtain a cubic soil core. We placed two layers of 40-mesh nylon around the core to prevent new root growth. The soil was backfilled to the original level with topsoil over the subsoil. The trenching treatment was completed at the beginning of June 2013. In each subplot, we prepared five nylon mesh (2 mm) litter bags (15 cm × 20 cm) marked with numbers (Figure S1). In detail, fresh foliage litter samples were collected using 1 m × 1 m nylon nets hanging 1 m above the ground at several locations from January to July 2013. We collected, air dried, and stored foliage litter every month. In August, we mixed foliage litters and dried them at 60 °C for 72 hours before experimentation. Then, we weighed and recorded the initial dry mass (M_i, approximately 10.0 g of dry mixed foliage litter) for each litter bag. On 31 August 2013, visible litter was carefully removed from the experimental plots, and litter bags were placed on the surface. The litter bags were not moistened as in the rainy season.

Data collection and analysis

Following the experimental setup, we collected the decomposed litter bags on five dates (Figure S1): (1) 29 October 2013, (2) 29 December 2013, (3) 30 April 2014, (4) 30 August 2014, and (5) 31 August 2015. We collected one litter bag from each of the subplots each time (3 for the control and 3 for the trenching treatment). After collection, the litter was removed from the bags, placed onto screens, and cleaned via brushing and shaking in water in a large basin. After cleaning, the foliage litter was dried (as above) and weighed to obtain the final litter dry mass (M_f). The accumulated litter decomposition rate (ALDR, %) was calculated as follows:

$$\mathrm{ALDR} = \left(1 - \frac{M_f}{M_i}\right) \times 100\% \quad (1)$$

The litter decomposition rate at each stage (SLDR, % yr^{-1}) was calculated as follows:

$$\mathrm{SLDR}_j = \frac{\mathrm{ALDR}_j - \mathrm{ALDR}_{j-1}}{t_j - t_{j-1}} \times 365 \quad (2)$$

where j is the litter bag collection time (from 1 to 5).

Every month, we measured the soil temperature (°C) and soil water content (% (v/v)) at a 5-cm depth using a digital thermometer (6310; Spectrum, Illinois, USA) and the time domain reflectometry (MP-KIT; Beijing Channel, Beijing, China) three times. The means of soil temperature (ST, °C) and the soil water content (SW, %) during each decomposition stage were also calculated.

Linear regression models were used to display the relationships of SLDR with ST and SW (Wu *et al.* 2014):

$$SLDR = a \cdot ST + b \quad (3)$$

$$SLDR = a \cdot SW + b \quad (4)$$

$$SLDR = a \cdot ST \cdot SW + b \quad (5)$$

where a and b are parameters from the models.

We compared the SLDR of the control and trenching treatments ($\mathrm{SLDR_{CK}}$ and $\mathrm{SLDR_{NR}}$, respectively) during the whole 2-year period. The rhizosphere priming effect on litter decomposition ($\mathrm{RPE_{LD}}$, %) was calculated as follows:

$$\mathrm{RPE_{LD}} = \frac{\mathrm{SLDR_{CK}} - \mathrm{SLDR_{NR}}}{\mathrm{SLDR_{NR}}} \times 100\% \quad (6)$$

Combined with the $\mathrm{RPE_{LD}}$ results, the contributions of total l itter decomposition ($C_{\text{L-total}}$) and total SOM decomposition ($C_{\text{SOM-total}}$) were calculated as follows:

$$C_{L-total} = C_{L-NR} + C_{L-NR} \times RPE_{LD} \quad (7)$$

$$C_{SOM-total} = C_{SOM-basic} + (C_{INT} - C_{L-NR} \times RPE_{LD}) \quad (8)$$

where ($C_{\text{L-NR}} \times \mathrm{RPE_{LD}}$) is the contribution of primed litter decomposition ($R_{\text{L-primed}}$) and ($C_{\text{INT}} - C_{\text{L-NR}} \times \mathrm{RPE_{LD}}$) is the contribution of primed SOM decomposition ($R_{\text{SOM-primed}}$). Finally, we divided the three components of R_S, namely, total SOM decomposition, total litter decomposition, and R_R, and estimated their contributions (mean values were used for the $C_{\text{SOM-total}}$ and $C_{\text{L-total}}$ calculations).

We used a *t* test to test for differences in annual mean soil temperature and soil water content values, mean soil temperature, soil water content, and litter decomposition rate values at each stage; and corrected annual mean litter decomposition rate values between the control and trenching treatments (the R version 4.0.5, packages readxl, ggplot2, lubridate, ggpmisc, and ggpubr were used).

Results

Effect of trenching on soil microenvironmental factors

Trenching did not change the variation patterns of soil temperature or soil water content during the 2-year period. The soil temperature did not change, but the soil water content increased under trenching (Figure 2a, c). In the whole 2-year period, the annual mean soil temperatures were 11.66 ± 0.06 and 11.53 ± 0.11°C (mean ± SD) for the control and trenching treatments, respectively. However, the annual mean soil water contents were 22.07 ± 1.22 and 25.26 ± 1.42% (v/v), respectively, indicating a significant ($p = 0.0419$) increase of 14.5% (%/%) in response to trenching. Considering each decomposition stage, the trenching also did not change soil temperature except in the first stage (2013/9–2013/10, significantly decreased by 0.11°C) (Figure 2b). However, the soil water content increased, especially in dry season, such as in the third stage (2014/1–2014/4, significantly increased by 58.0%) (Figure 2d).

Effect of trenching on litter decomposition

The accumulated litter decomposition rates increased during the decomposition period; however, the third stage showed nearly zero in both the control and trenching treatments (Figure 3a, b). In each stage, the trenching treatment had a higher decomposition rate than the control treatment, except in the first stage (2013/9~2013/10) (Figure 3b). The annual mean decomposition rates were 30.59 ± 1.79 and 31.35 ± 2.78% in control and trenching treatments, respectively. Trenching increased the annual mean decomposition rate non-significantly by 2.5%.

Effect of the soil microenvironment on litter decomposition

Variations in SLDR, ST, and SW showed the same pattern (Figures 2b, d & 3b), and linear regression models showed that SLDR had a significant relationship with ST, SW, and ST×SW both in control and trenching treatments. Variations in ST, SW, and ST×SW explained 63.0 and 63.9%, 74.3 and 70.2%, and 87.4 and 85.5% of the variation in SLDR in the control and trenching treatments, respectively (Figure 4).

Result based on the corrected decomposition rate

Figure 4 shows that the interaction of ST and SW controlled litter decomposition. Considering the increase in soil water content in trenching plots, we corrected the litter decomposition rates of the control and trenching treatments (Figure S2). After correction, the annual mean decomposition rate increased by 6.1% (before: 30.59 ± 1.79%, after: 32.47 ± 3.15%) ($p > 0.1$) and decreased by 18.0% (before: 31.35 ± 2.78%, after: 25.71 ± 2.72%) ($p = 0.066$) in the control and trenching treatments, respectively. Therefore, the corrected results showed that rhizosphere activity had a significantly priming effect on litter decomposition (26.3%) (Figure 5).

Discussion

Effect of rhizosphere activity on litter decomposition

Litter decomposition is controlled by litter quality (Cordova *et al.* 2018, Hoorens *et al.* 2003, Keiser *et al.* 2013, Sánchez-Silva *et al.* 2018), Home-field advantage (Fanin *et al.* 2016, Fanin *et al.* 2021, Luai *et al.* 2019), and soil environmental factors (Deltedesco *et al.* 2020, Li *et al.* 2021, Wang *et al.* 2010). Studies have shown that litter diversity has a mixed effect, enhancing

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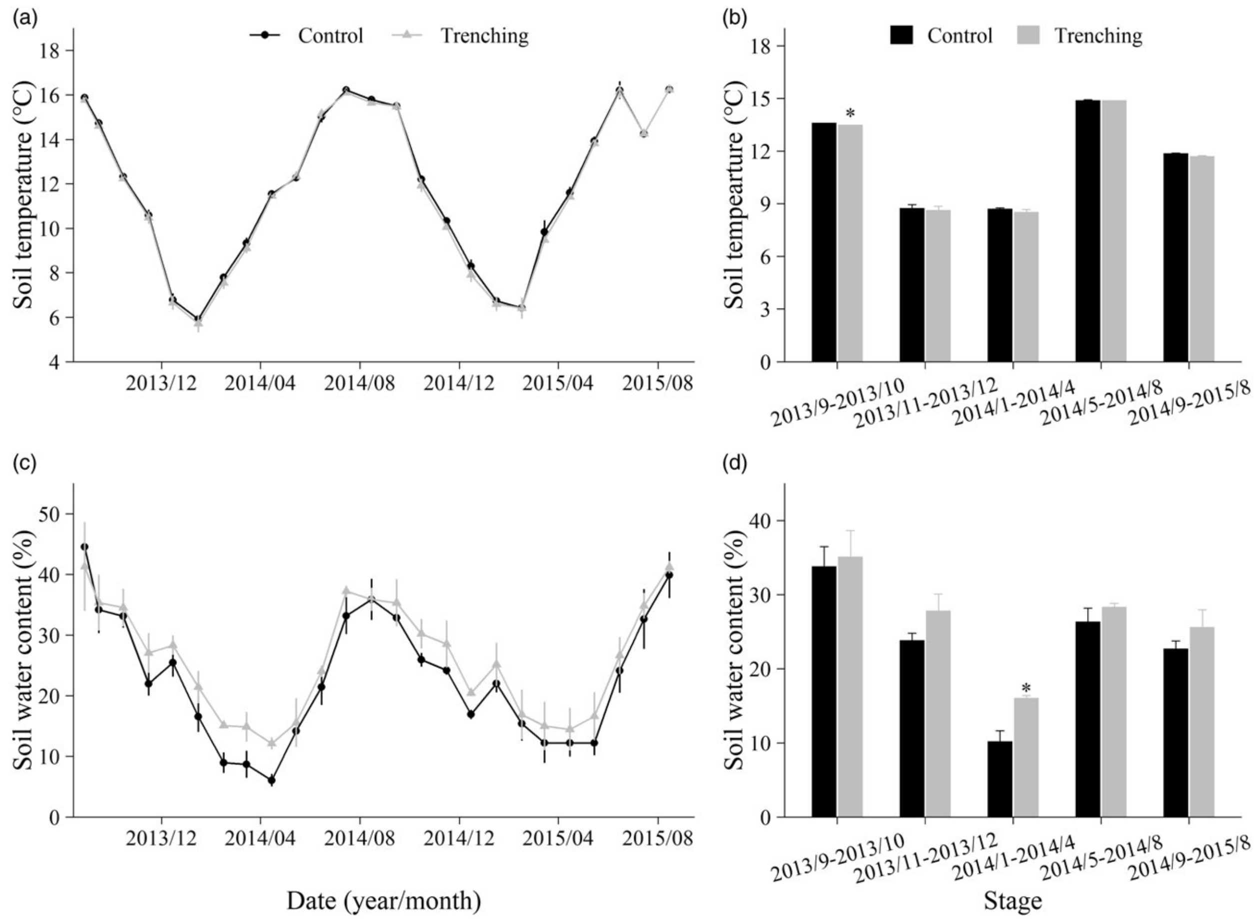

Figure 2. Seasonal variations in soil temperature (a) and soil water content (c), and mean values in each decomposition stage (b, d). * indicates $p < 0.05$.

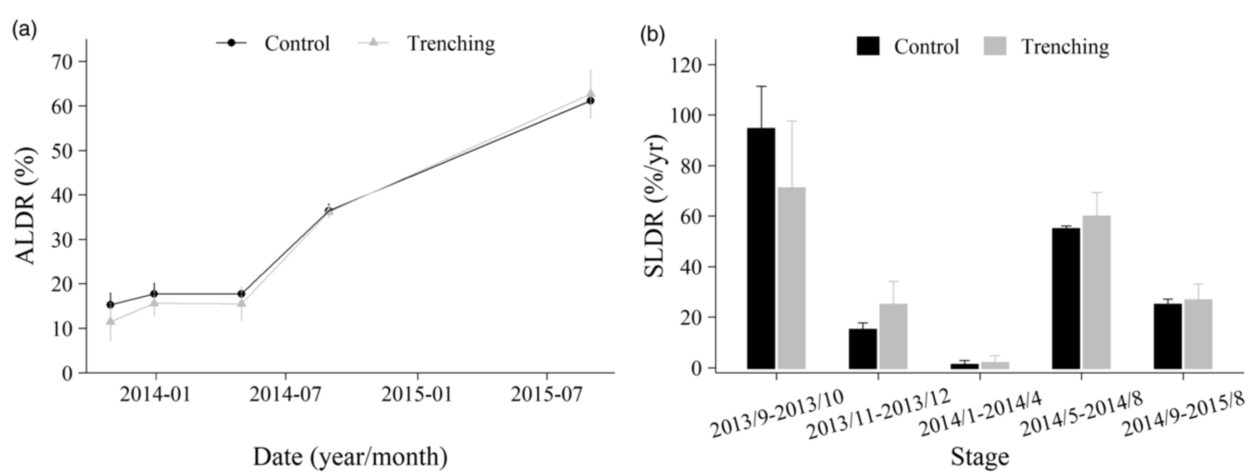

Figure 3. Accumulated litter decomposition rate (ALDR, %) (a), and litter decomposition rate at each stage (SLDR, % yr^{-1}) (b).

the litter decomposition rate (Butenschoen *et al.* 2014, Lecerf *et al.* 2011), most likely due to nitrogen transfer in litter mixtures (Bonanomi *et al.* 2014, Handa *et al.* 2014, Lummer *et al.* 2012), and thereby changes microbial communities and activities (Pei *et al.* 2017, Santonja *et al.* 2017). Wang *et al.* (2010) suggested that soil environmental factors, especially the soil surface water content, affected the litter decomposition process, because of soil microclimatic effects on soil microbial composition and activities (Allison & Treseder 2008, Bray *et al.* 2012, Fang *et al.* 2016, Supramaniam *et al.* 2016). Our results showed that variation of the soil water content had a greater explanation in litter decomposition rate than soil temperature (Figure 4). In addition, rhizosphere activities can also prime litter decomposition (Subke *et al.* 2011, Wang *et al.* 2016). Root exudation can affect the variation in and distribution of soil organic carbon (Chen *et al.* 2004), promoting microbial activities and extracellular enzyme activities that further promote litter

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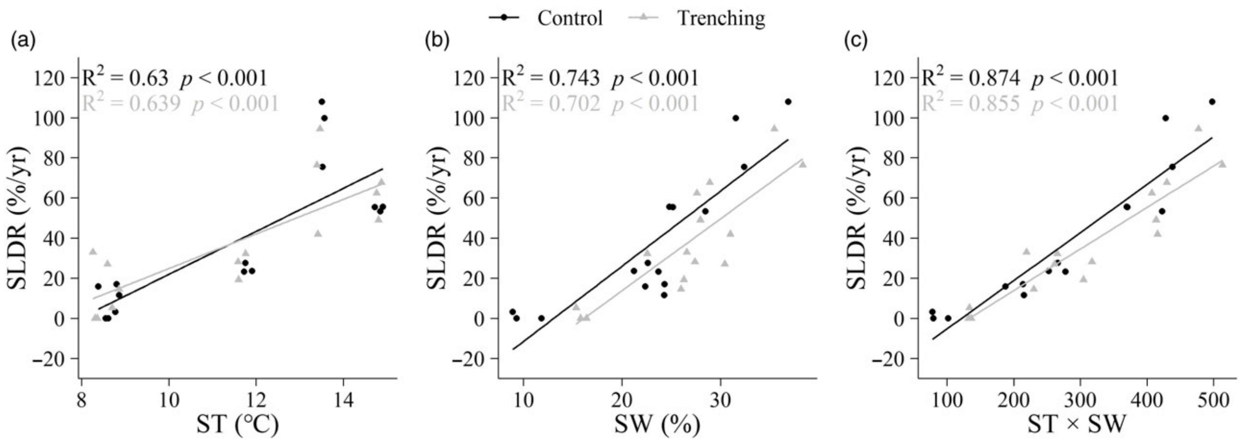

Figure 4. The relationships of SLDR with ST (a), SW (b), and the interaction of ST and SW (c).

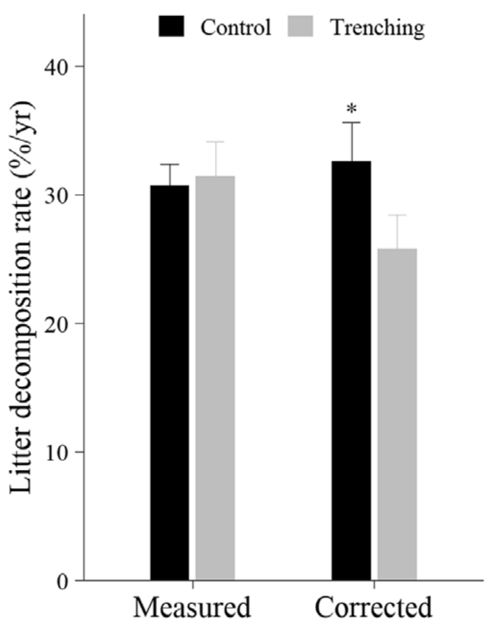

Figure 5. Measured and corrected litter decomposition rates of the control and trenching treatments.

decomposition (Brzostek *et al.* 2015, Legay *et al.* 2020, Nottingham *et al.* 2013, Shahzad *et al.* 2015, Wang *et al.* 2020). Therefore, soil microbes are the key link between litter decomposition and rhizosphere activity.

In this study, we conducted a litter decomposition experiment with control and trenching plots, including foliar litter of the same quality in both treatments. However, our measured results showed that the trenching treatment had a greater litter decomposition rate than the control treatment, suggesting no priming effects of the rhizosphere on litter decomposition (Figures 3 & 5). This was probably due to the higher soil water content in trenching plots (Figure 2). Most studies also showed that trenching could increase the soil water content (Wu *et al.* 2014, Wang *et al.* 2015, Savage *et al.* 2018) due to a reduction in water uptake in trenching plots, thus could increase litter decomposition rate. Therefore, increasing the soil water content by trenching offsets the rhizosphere activity in measured result.

Figure 4 shows that soil temperature and soil water content, especially their interaction effect, controlled the variation in the litter decomposition rate. In the studied site, temperature and humidity levels are synchronized (Wu *et al.* 2014, Yuan *et al.* 2019), where litter decomposition is affected by soil temperature and the soil water content (Figure 4). To reveal the rhizosphere activity effect on litter decomposition, the bias due to soil microclimatic changes should be eliminated (Savage *et al.* 2018, Wu *et al.* 2014, Wang *et al.* 2015); thus, the litter decomposition rates were corrected by the model in equation (5) (Figure S2). The results showed that correction had little effect on the control treatment but had a significant effect on the trenching treatment, which was consistent with the findings of a previous study (Wu *et al.* 2014). Finally, our trenching experiment suggested a significant priming effect of rhizosphere activity on litter decomposition of 26.3% in the subtropical forest, similar to the priming effect of 30.8% (calculated by k values) observed in a temperate western hemlock forest (Subke *et al.* 2011).

The litter decomposition process plays an important role in regional and global carbon cycles and is affected by many factors. In this study, we focused on the rhizosphere activity on litter decomposition. To the best of our knowledge, we were the first to consider the effect of soil environmental factors on staged litter decomposition rates and use a regression model to correct the bias caused by environmental factor changes.

Implications of estimating soil organic matter contributions to soil respiration

Soil contains large amounts of organic carbon; climate change has caused soil carbon loss in recent decades (Bond-Lamberty *et al.* 2018), and soil carbon loss also feeds back to climate change. Hence, it is necessary to further estimate the SOM decomposition contribution to soil respiration under climate change conditions.

As shown in Figure 1, our new method of partitioning R_S includes two steps. The first step involves dividing soil respiration into four components through a factorial experiment (two factors with two levels). The second step involves partitioning the R_{INT} through the rhizosphere priming effect on litter decomposition, as described in an earlier study (Wu *et al.* 2014). Litter decomposition without an effect of rhizosphere activity accounted for 9% of R_S. Combined with the RPE_{LD} result, primed litter decomposition accounted for 2% (9% × 26.3%) of R_S; therefore, total litter decomposition contributed 11% (9% + 2%) of R_S. The interaction

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accounted for 30% of R_S; therefore, primed SOM decomposition accounted for 28% (30% − 2%) of R_S. Finally, total SOM decomposition accounted for 74%, and R_S was partitioned into three components: total SOM decomposition (74%), total litter decomposition (11%), and R_R (15%).

This is the first report to partition R_S based on the interaction of litter and the rhizosphere and rhizosphere priming effects (on litter decomposition). The contribution of SOM will be underestimated if this interaction and rhizosphere priming effects are ignored. Our results showed that total SOM decomposition contributed 74% of R_S, which was more than R_H (55%) and basic SOM (46%). Our results suggested that the rhizosphere priming effect enhanced SOM decomposition by 60.8% (28%/46%), which was consistent with a meta-analysis result of 59% (Huo *et al.* 2017). Therefore, we suggest that earlier studies likely underestimated the contribution of SOM. We also recommend that more studies be conducted on the interaction and rhizosphere priming effects under soil carbon efflux treatments that consider global warming, N deposition, precipitation changes, and other climatic changes.

Conclusion

In summary, we found a significant effect of rhizosphere activity on litter decomposition. Rhizosphere activity primed litter decomposition by 26.3%. Based on the results of this study and previous results regarding the interaction on soil respiration, we estimated that total SOM decomposition, total litter decomposition, and root respiration accounted for 74, 11, and 15%, respectively. Although the two studies of the rhizosphere priming effect on litter decomposition, and the interaction effect on R_S did not be conducted in the same period, our result can also suggest that earlier studies likely underestimated the contribution of SOM. Our result on the partitioning of R_S regarding forest soil benefits contributes to SOM decomposition research under global change.

Supplementary material. To view supplementary material for this article, please visit https://doi.org/10.1017/S0266467422000013.

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Declaration of Competing Interest. The authors declare no conflicts of interest.

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