

The manipulation of aboveground litter input affects soil CO₂ efflux in a subtropical liquidambar forest in China

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Litters on the forest floor represent an important organic carbon (C) sources from aboveground plants to the soil, which therefore have a significant influence on belowground processes such as soil respiration. In this study, dynamic property of soil respiration was investigated under aboveground litter manipulation treatments in a liquidambar forest in subtropical China. The purpose of this study was to examine the impacts of changing aboveground litter inputs on soil CO₂ emission in forests. The litter manipulation included litter addition (LA), litter removal (LR) and litter control (LC) treatments. Each litter treatment had six replications. Soil respiration rates were measured using an infrared gas analyzer system (LI-COR 8100) with soil chambers. The results showed that mean soil respiration rates increased significantly in LA plots (mean \pm SE: $2.21 \pm 0.44 \mu\text{mol m}^{-2} \text{s}^{-1}$; $P < 0.05$) and decreased slightly in LR plots ($1.17 \pm 0.16 \mu\text{mol m}^{-2} \text{s}^{-1}$) when compared to control plots ($1.42 \pm 0.20 \mu\text{mol m}^{-2} \text{s}^{-1}$). On average, LA treatment significantly increased annual soil respiration by about 56% ($837.5 \pm 165 \text{ gC m}^{-2} \text{ year}^{-1}$), while LR treatment decreased soil respiration by approximately 17% ($443.1 \pm 61.7 \text{ gC m}^{-2} \text{ year}^{-1}$) compared with the control ($535.5 \pm 75.7 \text{ gC m}^{-2} \text{ year}^{-1}$). The “priming effect” was a primary contributor to the increase of soil respiration in LA treatments and the reduction of soil CO₂ efflux was mainly ascribed to the elimination of organic C sources in LR treatments. Soil temperature was the main factor affecting seasonal variation in soil respiration. Up to the 90% to 95% seasonal variation in soil respiration is explained by soil temperature within each of the litter treatments. Our study indicated that changes in litter inputs due to climate change and human practices would significantly affected soil CO₂ emission and would subsequently affect C balance in subtropical forests.

Keywords: Soil CO₂ Emission, Annual Litter Input, Deciduous Forests, Soil Temperature, Soil Water Contents, Subtropical China

Introduction

Soil respiration is commonly defined as the total CO₂ efflux (FCO₂) from the soil-litter surface and is one of the largest CO₂ fluxes from land to the atmosphere (Davidson et al. 2006, Taneva et al. 2006). It has been estimated that soil FCO₂ is about 75 PgC year⁻¹ (Raich & Tufekcioglu 2000), which is about ten times the flux of CO₂ to the atmosphere contributed by the combustion of fossil fuels (Rustad et al. 2000). Therefore, this flux represents a major component of the global carbon (C) cycle

that can directly affect atmospheric CO₂ concentration and thereby the global climate systems (Schlesinger & Andrews 2000, Marland et al. 2001).

Carbon dioxide emission from forest soils vary considerably, depending upon forest types (Raich & Tufekcioglu 2000, Yan et al. 2014, Wang et al. 2016), stand composition and structure (Han et al. 2015, Coletta et al. 2017), growth and development stages (Irvine & Law 2002), as well as litter amount on the floor (Zimmermann et al. 2009, Yan et al. 2013). Aboveground litterfall repre-

sents a major pathway of C from plant to the soil, and thus the litter amount accumulated on forest floor plays a critical role in maintaining forest production and regulating belowground processes such as soil respiration. Litter amount directly or indirectly affect soil respiration by regulating microclimatic conditions on the floor (Sayer 2006), modifying microbial community structure and function (Frey et al. 2004, Waldrop et al. 2004, Brant et al. 2006), changing the number of decomposer organisms (Cullings et al. 2003), affecting de-

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composition rates (Hobbie & Vitousek 2000, Rothstein et al. 2004) and altering the amounts of available nutrients in the soil (Sayer 2006). As a consequence, changes in litter amount on soil surface might result in a significant alteration of soil respiration in forests (Brecht et al. 2017, Wu et al. 2017).

Elevated atmospheric CO₂ concentration could stimulate plant growth and thereby increase litterfall production in forest ecosystems (Finzi et al. 2001, Sayer et al. 2007). Such increases of aboveground litter are likely to lead to changes in soil microbial community structure and activity, which could constitute an important positive feedback to soil respiration process (Waldrop & Firestone 2004, Sayer 2006). A number of researchers have investigated the responses of soil FCO₂ process to the changes in litter amount on forest floor. Sayer et al. (2007) reported that increased litter in tropical forests boosts the transfer of soil CO₂ to the atmosphere. Zimmermann et al. (2009) indicated that litter amount on soil surface made a large contribution to diurnal and annual patterns of soil respiration process in a tropical montane cloud forest. Our previous work has shown that when litter inputs were double, soil respiration increased about by 12% in a Masson pine and Camphor tree mixed forest. However, such effect of increasing soil FCO₂ was not found both in a pure Camphor tree forest and in a pure Masson pine forest. In contrast, litter exclusion significantly reduced soil FCO₂ rates by approximately 20-40% in these subtropical evergreen forests (Yan et al. 2013). Such variable results suggest that more studies are required to further understanding of the impacts of changing litter inputs on soil respiration in forests. It is a particular case for deciduous forests, because less study has been conducted in terms of litter-soil respiration relation in this forest type, despite deciduous forests are important components of subtropical forest communities (Polyakova & Billor 2007, Prevost-Bouere et al. 2010, Chen & Chen 2018).

Here, we conducted an aboveground litter input manipulation experiment to examine the impact of changes in litter inputs on soil respiration rates in liquidambar forests in the subtropical region of China. We hypothesized that litter manipulation treatments would affect soil FCO₂ rates due to changes in carbon inputs in soil. The liquidambar forests are a common timber and green-garden deciduous forest type in southern China. The litter manipulation experiments were designed to address the following questions: (i) Do the changes in litter amount affect soil respiration rates in this deciduous forest? (ii) Do the litter manipulation treatments alter the seasonal patterns of soil FCO₂ process? (iii) Do the relationships among soil respiration, soil temperature and moisture vary due to the change of litter inputs?

Materials and methods

Study site

The study was carried out at Hunan Botanical Garden in Changsha city, Hunan Province, China (113° 02' - 113° 03' E, 28° 06' - 28° 07' N). The study area is a typical moist subtropical zone with a mean annual temperature of 17.2 °C and mean temperatures of 4.7 and 29.4 °C in January and July, respectively. Annual precipitation is 1200-1700 mm and the average annual rainfall is 1422 mm, most of which occurring from April to August. Mean annual relative humidity is >80%. The frost-free period is 270-310 days per year. The garden covers about 140 ha, with elevation of 50-110 m a.s.l. and an average site slope of 5-15°. Soil is classified as a typical red earth developed from slate parent rock, which is equal to Allit-Udic Ferrosols according to the World Reference Base for Soil Resources (CRG-CST 2001). Soil texture ranges from clay loam to sandy loam. pH on the topsoil (0-10 cm) was acidic with an average pH of 5.0. The concentration of organic carbon and nitrogen in the top 20 cm of the soil were 23.1% and 1.57%, respectively.

The liquidambar (*Liquidambar formosana* Hance) forests were planted in 1986 with an initial stand density of 2 × 2 m. When the current study started in 2013, the average height of the trees was 14.8 m, the average diameter at breast height 16.8 cm, the stand density 1100 trees per hectare and the stand crown density 0.9. Understorey consisted of *Sassafras tsumu* Hemsl., *Cinnamomum camphora*, *Symplocos caudata* Wall. ex A. DC., *Clerodendron cyrtophyllum* Turcz., *Nephrolepis auriculata* Trimen, *Lophantherum gracile* Brengn., *Miscanthus floridulus* Warband and *Phytolacca acinosa* Roxb. T.

Experimental design

The experiment was a completely randomized design (CRD) initiated in May 2013. Three plots (each with 20 × 20 m in size) were chosen within the liquidambar forests in the study site. Six 3 × 4 m subplots were set up in each of the plots, where litter manipulation treatments were performed. Among these six subplots in a plot, two subplots were subject to one of the three litter manipulation treatments. Thus, there were six replications (six subplots) for each litter treatment in this study.

Three litter manipulation treatments were used in this study: litter removal (LR), litter addition (LA) and litter control (LC) treatments. The LR treatment was performed to remove all litter materials from the floor in the subplot at the beginning of the study. Then a 1-mm-mesh collection was installed about 0.8 m height above the forest floor on the subplot to prevent litter falling on the floor. All litter was collected and removed from the mesh collection twice a month. The LA treatment was performed by transferring and evenly dis-

tributing litter materials obtained from a LR subplot described above on LA subplots. The LA treatment was carried out twice a month. In the LC treatment, the natural status of litter on the floor was kept and the normal litter-fall process was allowed, excluding any removal or addition. The monthly litter-fall production varies greatly in the studied forests, ranging from about 180 to 1100 kg ha⁻¹ year⁻¹. Two PVC collars were established at each litter treatment subplot as the measurement points of soil respiration, and the mean value taken from these two PVC collars was considered to represent soil respiration from this subplot.

Soil FCO₂ measurements

Soil FCO₂ was measured on a biweekly basis from January 2013 to December 2014, using a portable infra-red gas analyzer (LI-COR 8100 with chamber (LI-COR Inc., Lincoln, Nebraska, USA). The measurements were delayed by 2-3 days when the designed time was a rainy day. At each measurement point, a PVC collar (11.7 cm in diameter, 4.4 cm in height) was installed into the soil, leaving 2.5 cm protruding above the soil surface. In order to minimize soil disturbance from the deployment of the flux chamber, PVC collars were placed into the soil at least one week prior to the first field measurement and remained in place through the course of the study. In each measurement date, soil FCO₂ measurements were taken twice between 9:00 AM and 6:00 PM at each measurement points. The soil FCO₂ value at each measurement point was the mean of the three sequential flux estimates at each sampling interval. Soil FCO₂ was calculated from the change in CO₂ concentration in the chamber during each flux measurements and the chamber height. Soil FCO₂ is expressed as μmol m⁻² s⁻¹. The monthly data collection was timed to span a few days with similar weather patterns. A detailed description of soil FCO₂ measurements is given in Yan et al. (2013, 2014).

Soil temperature and moisture measurements

Soil temperature (T_{soil}) was measured simultaneously with soil FCO₂, using a soil thermocouple probe (LI-COR 6000-09 TC) inserted in the soil to a depth of 5 cm below the soil surface. Soil water contents (W_{soil}: volumetric soil water content, %) in the topsoil layer (0-5 cm) was measured using ECH₂O Check (Decagon Devices Inc., Pullman, WA, USA) connected with EC-5 at the vicinity of PVC collars during soil FCO₂ measurements.

Statistical analysis

Analysis of variance (ANOVA) was used to statistically assess the net effects of LR and LA on soil FCO₂ rates, and plots temporal (month-to-month) variation on soil FCO₂ rates, T_{soil}, and W_{soil}. Specifically, a mixed-design two-way repeated ANOVA was em-

ployed to test the effects of between litter treatments, measurement times, and treatment \times time interaction on soil respiration. Prior to statistical analysis, the original soil FCO_2 data were log-transformed to satisfy the normality and homoscedasticity assumptions of ANOVA. No log-transformation was performed on T_{soil} and W_{soil} data. Statistical analyses were conducted using the SAS statistical package (SAS Institute Inc. 2001).

Multiple regression analysis was employed to examine relationships between soil FCO_2 and surrounding environmental factors (T_{soil} and W_{soil}). In order to accurately describe soil FCO_2 - T_{soil} and soil FCO_2 - W_{soil} relationships, data from litter treatment plots and control plots were separately used in the development of the models related to such relationships.

Results

Litter manipulation treatments significantly changed soil FCO_2 rates ($P < 0.001$) during this 2-year experiment. This effect was not significantly different between the measurement time of 2013 and 2014 ($P > 0.05$). Specifically, litter addition (LA) treatments significantly increased soil FCO_2 rates ($P = 0.0017$) while litter removal (LR) treatments significantly reduced soil FCO_2 rates ($P = 0.0199$) compared to litter control (LC) treatments during the study period. On average, soil FCO_2 rates increased by approximately 56% in LA plots (mean \pm SE: $2.21 \pm 0.44 \mu\text{mol m}^{-2} \text{s}^{-1}$) and reduced by about 17% in LR plots ($1.17 \pm 0.16 \mu\text{mol m}^{-2} \text{s}^{-1}$) when compared to the LC plots ($1.42 \pm 0.20 \mu\text{mol m}^{-2} \text{s}^{-1}$). Based on biweekly measurements, the cumulative annual mean soil FCO_2 was 535.5 ± 75.7 , 837.5 ± 165.0 , and $443.1 \pm 61.7 \text{ gC m}^{-2} \text{ year}^{-1}$ in LC, LA and LR plots, respectively.

The dynamic patterns of soil FCO_2 rates were similar in the three litter manipulation treatment plots during the study period (Fig. 1). The soil FCO_2 rates increased in the spring and reached their peaks during the summer times with a short falling-rising process in July. Soil respiration then decreased in the autumn and reached its minimum in the winter. The soil FCO_2 rates varied substantially, ranging from 0.21 - 2.66 , 0.36 - 4.58 , and 0.27 - $2.38 \mu\text{mol m}^{-2} \text{s}^{-1}$ in LC, LA and LR plots, respectively (Fig. 1).

On average, the maximum mean monthly soil FCO_2 rates appeared in June and minimum in February. There were likely two peaks in terms of annual soil FCO_2 process in liquidambar forests: one appeared in the months of June and July and another in October. LA treatments significantly increased monthly mean soil FCO_2 rate during the whole course of the study when compared to the control, while LR treatments reduced monthly mean soil FCO_2 rates significantly for all months, except in the winter times when the difference was not significant between the treated plots and control plots (Fig. 2).

There were similar seasonal patterns in

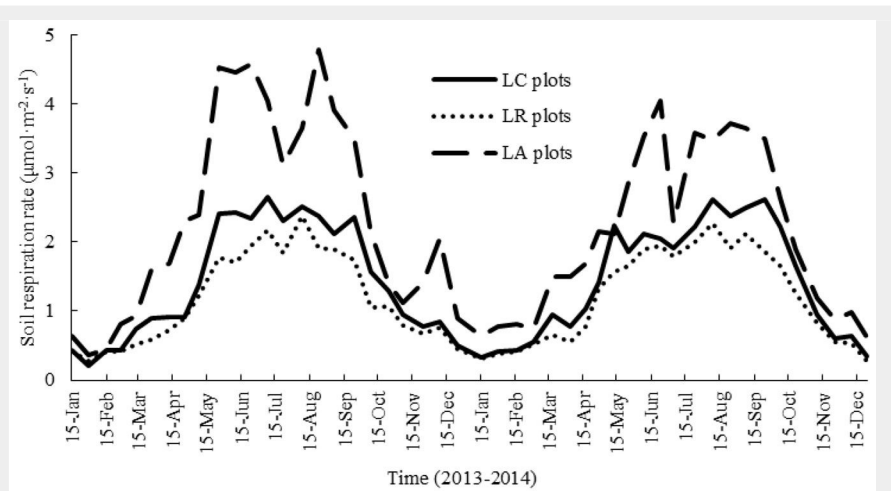


Fig. 1 - Dynamics of soil respiration in the liquidambar forests with different litter manipulation treatments from January 2013 to December 2014.

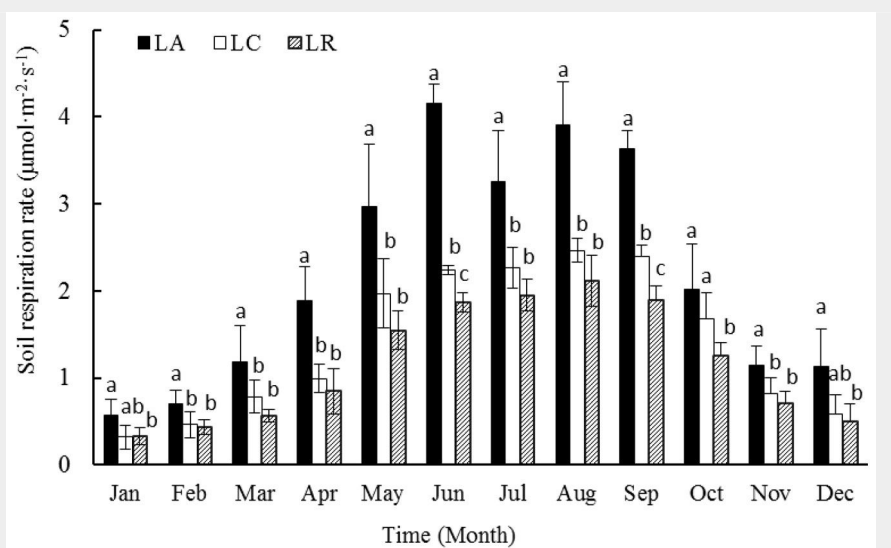


Fig. 2 - Monthly mean soil respiration of the liquidambar forests with various litter manipulation treatments during the period 2013-2014. Different letters above the bars in the same month indicate significant differences ($P < 0.05$) among treatments after ANOVA.

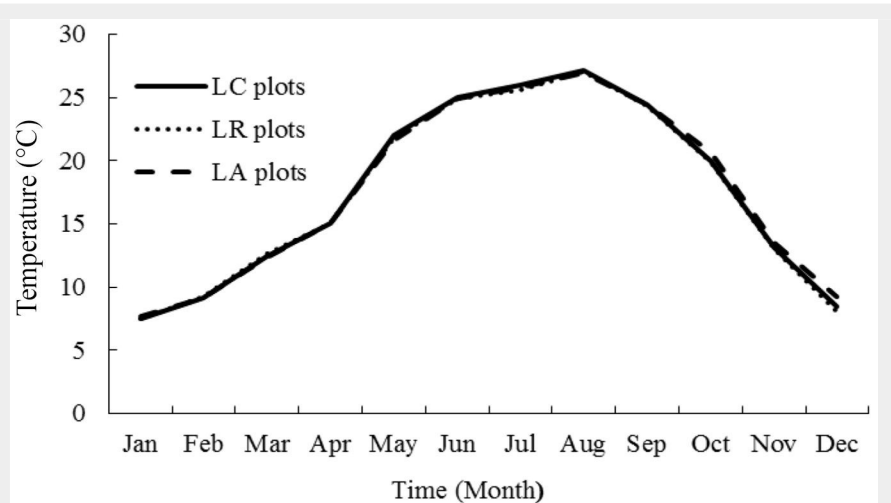


Fig. 3 - Monthly mean soil temperature of the liquidambar forests with various litter manipulation treatments during the period 2013-2014.

T_{soil} in the three litter manipulation treatment plots, with the highest during summer and the lowest during the winter (Fig. 3). Litter manipulation treatments did not significantly change both T_{soil} ($P > 0.05$) and W_{soil} ($P > 0.05$). Soil FCO_2 rates were strongly correlated with T_{soil} ($P = 0.0205$ – Fig. 4), but not with W_{soil} ($P = 0.2630$ – Fig. 5) in all studied plots. The relationship between soil FCO_2 rates and T_{soil} can be described using an exponential function as follows. In LA plots (eqn. 1):

$$Soil\ FCO_2 = 0.3552e^{0.0901T_{soil}} \quad (1)$$

where the corresponding Q_{10} was 2.52 ($R^2 = 0.903$). In LR plots (eqn. 2):

$$Soil\ FCO_2 = 0.2015e^{0.0901T_{soil}} \quad (2)$$

where the corresponding Q_{10} was 2.46 ($R^2 = 0.966$). In LC plots (eqn. 3):

$$Soil\ FCO_2 = 0.2195e^{0.0944T_{soil}} \quad (3)$$

where the corresponding Q_{10} was 2.57 ($R^2 = 0.945$).

Discussion

Climate change includes correlated increases of atmospheric CO_2 concentration and temperature on the Earth, which may increase forest productivity, including litterfall. But the consequences for soil FCO_2 process remain poorly understood. The present experiment was designed to address how changes in aboveground litter inputs affect CO_2 emission from the soil in deciduous liquidambar forests. Our results showed that soil FCO_2 rates significantly increased by about 39% due to LA treatments and declined by 10% in LR plots when compared to the LC. These results were consistent with other previous findings (Schaefer

et al. 2009, Sayer et al. 2011). For instance, Sulzman et al. (2005) reported that doubling needle litter addition caused a 34% increase in the total C efflux in an old growth coniferous forest. Li et al. (2004) found that soil CO_2 efflux decreased considerably by 54% and 68% on average in a secondary forest and a plantation, respectively, compared to the control. Chemidlin Prevost-Boure et al. (2010) carried out a litter manipulation treatment in a temperate deciduous forest and found that soil FCO_2 significantly increased by 60-120% in LA treatment, but significantly decreased by 25-45% in a litter exclusion treatment when compared to the control. They attributed the effect of litter treatment on the variations in soil FCO_2 to the alteration of soil activity mediated by the quantity of fresh litter. Litterfall and litter decomposition constitute a linkage between aboveground portion of the plants and the soil and are a key

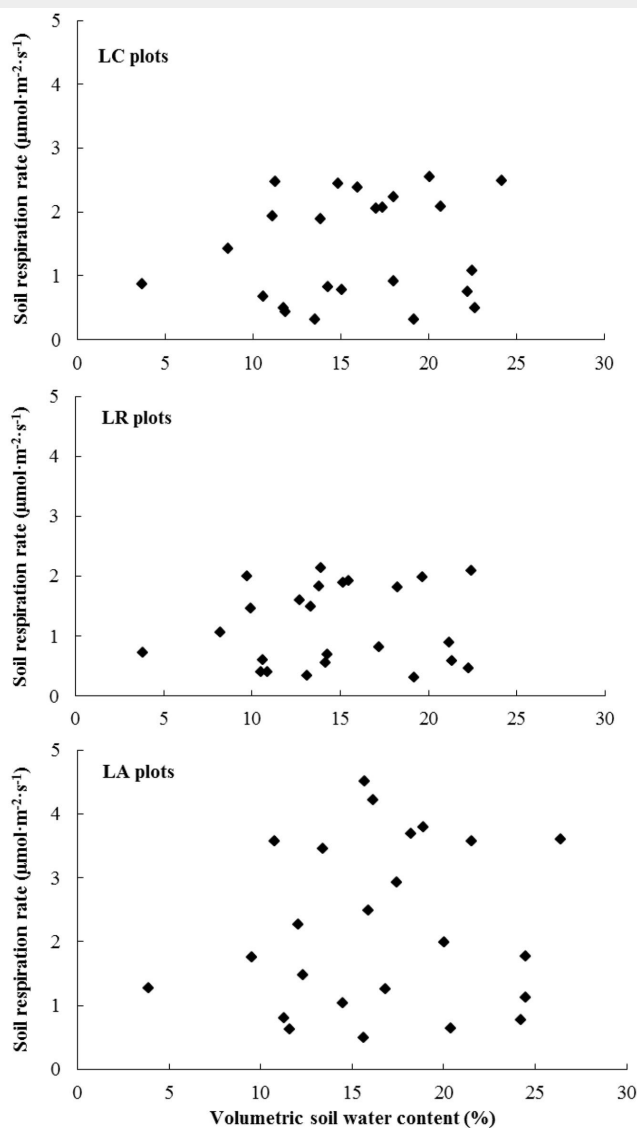


Fig. 4 - The relationships between soil respiration rates and volumetric soil water content of the liquidambar forests with various litter manipulation treatments during the period of time of 2013 and 2014.

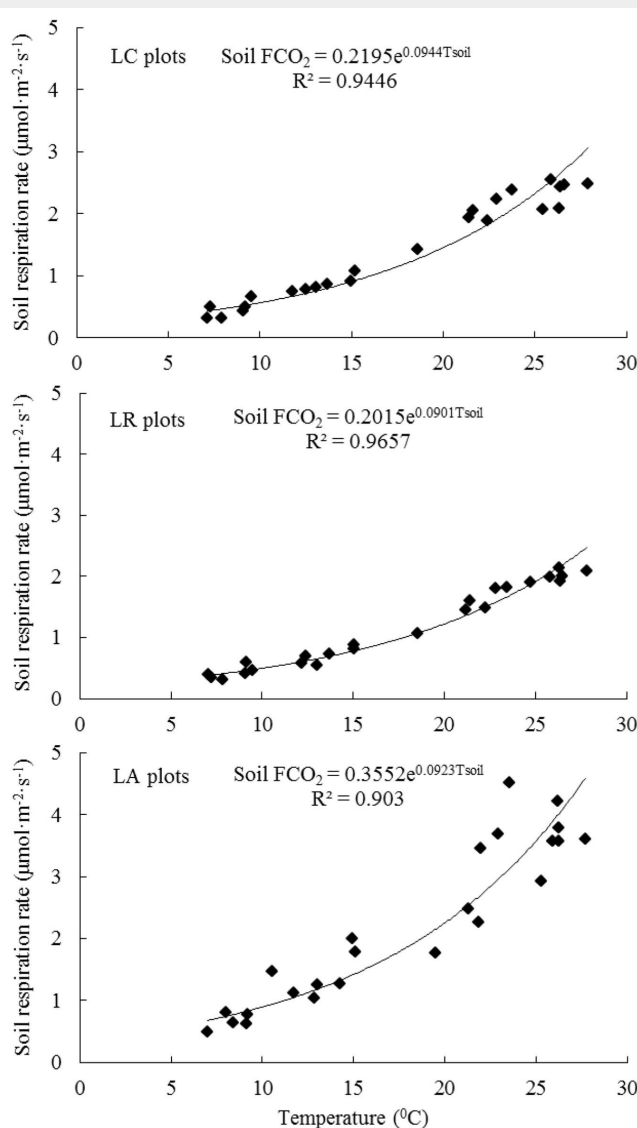


Fig. 5 - The relationships between soil respiration rates and soil temperature in the liquidambar forests with various litter manipulation treatments during the period of time of 2013 and 2014.

process in the regulation of C and nutrients cycling (Sayer et al. 2007, Wang et al. 2008, Zimmermann et al. 2009). The increase of soil respiration with LA might be attributed to several possible reasons. First, LA increased C and nutrients resources in the soil system and facilitated nutrients availability to soil organism uptake. Therefore, it would stimulate soil fauna and microbial activity, thereby increasing soil respiration processes (Crow et al. 2009, Liu et al. 2009, Li et al. 2011). Second, the inputs of fresh organic C substrates due to LA increased the leaching of organic acids, often resulting in a “priming effect”, which led an increase in soil organic C mineralization and soil FCO₂ rates (Kuzyakov 2010). Third, LA modified microclimate environments on forest floor such as T_{soil} and W_{soil} by decreasing soil exposure, which indirectly caused a change in soil FCO₂ (Sayer 2006, Yan et al. 2013). In contrast, the reduction of soil FCO₂ under LR treatments was due principally to the decline of nutrient inputs into the soil, which resulted in a suppression of food and nutrient supply to microbial communities (Vasconcelos et al. 2004, Sayer et al. 2007).

Interestingly, the alterations in soil respiration due to LA and LR treatments were not proportional in the current study. Indeed, the increase of soil FCO₂ due to LA treatments (39% on average) were much higher than the decrease of soil respiration (10%) in LR treatments when compared to the control, meaning about 29% higher than expected by the LA treatment alone. In fact, such a disproportional response in soil respiration to changes in litter inputs was a common phenomenon in forests. Han et al. (2015) investigated the effects of aboveground litter input manipulation on soil respiration in three subtropical successional forests and found that soil respiration decreased by 35% in LR plots and increased by 77% in LA sites on average. Sayer et al. (2007) reported that soil respiration was on average 20% lower in the LR and 43% higher in the LA treatment compared to the controls in a lowland tropical forest. In our previous study, we found soil FCO₂ rates were significantly decreased by about 39%, 24% and 22% in three evergreen forest types (Camphor tree forests, mixed forests, and Masson pine forest, respectively) due to LR treatments. However, LA treatments significantly increased soil CO₂ by 12% in the mixed forests, but not in both Camphor tree and Masson pine forests when compared to the control (Yan et al. 2013). Although the mechanisms underlying the different magnitudes of the effects on soil respiration in LA and LR were not clear, a number of factors were likely involved in the results. It is well-known that microorganism communities and their activity play a central role in soil organic matter decomposition. Microbial communities might respond differently to the added fresh materials and to the removal of substrates. These responses may be the result

of a different status of labile C availability for soil microorganisms (Wang et al. 2013), the utilization of different decomposed C resources (Fontaine et al. 2004, Kuzyakov 2010), the choice of specific degradable carbohydrates and water-soluble sugar components (Rasmussen et al. 2007), the presence of a particular rhizosphere and the associated mycorrhizal fungi community (Crow et al. 2009) and the employment of linear and non-linear stratagems for microbes growth and activity (Li et al. 2004).

Soil temperature (T_{soil}) is widely recognized as a major abiotic factor related to soil respiration in a single geographic area, and the seasonal variations in soil respiration process is closely linked with seasonal patterns of soil temperature (Bond-Lamberty & Thomson 2010). In the current study, soil FCO₂ rates were positively and exponentially correlated with T_{soil} (Fig. 5) and these results are in agreement with many previous studies (Bond-Lamberty & Thomson 2010, Smith & Fang 2010, Yan et al. 2014). Usually, the level of soil microorganisms' activity increased with increasing T_{soil} and the activity of soil enzymes was also enhanced under warming temperature, which caused a faster degradation of soil organic matter (Fekete et al. 2011, Beni et al. 2014). The temperature sensitivity (the Q₁₀ value) of soil respiration was often described by an exponential equation and was defined as a factor by which soil FCO₂ increase with increasing of temperature of 10 °C (Reichstein et al. 2005). Our Q₁₀ values (2.46 – 2.57) in the three litter manipulation treatments were well within the range of published Q₁₀ values widely across different forest types (Zheng et al. 2009). It is worthy to point out that the litter manipulation experiment in the present study significantly altered soil FCO₂ rates but did not affect soil temperature and Q₁₀ values, indicating the priming effect occurred in the study sites. Similar observations had been previously reported in different forests (Sulzman et al. 2005, Chemidlin Prevost-Boure et al. 2010).

Conclusions

Climate change, forest management practices, and local human activities might result in changes of litter inputs and litter amounts on forest floor, which had substantial effects on belowground processes in forests. In this study, we examined how litter input changes affect soil respiration in a liquidambar forest in a subtropical region of China. LA treatments lead to a significant increase in soil FCO₂, while LR treatments resulted in a significant reduction of soil respiration in the studied forests when compared to the control. The mechanisms of litter effects on soil respiration is very complex, but the increase or decrease in soil respiration are not likely determined by local soil microclimates (T_{soil} and W_{soil}) and temperature sensitivity (Q₁₀) because litter manipulation did not signifi-

cantly affected seasonal patterns of T_{soil} and Q₁₀ among the three litter input treatments. We proposed that the priming effect was a primary contributor to the increase of soil respiration in LA treatments and the reduction of soil FCO₂ was mainly ascribed to the elimination of organic C sources in LR treatments. Our results suggest that changes in litter inputs due to climate change and human practices will significantly affect soil CO₂ emission, thus affecting the C balance in subtropical forests.

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