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Impacts of changed litter inputs on soil CO₂ efflux in three forest types in central south China

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Climate change is expected to cause the alteration of litter production in forests, which may result in substantial changes in soil CO_2 efflux (FCO₂) process as litter represents a major pathway of carbon from vegetation to the soils. In this study, we conducted an aboveground litter manipulation experiment to examine the influence of litter addition and exclusion on soil FCO₂ in Camphor tree, Masson pine, and mixed Camphor tree and Masson pine forests in central south China. Litter input manipulation included three treatments: non-litter input (litter exclusion), double litter input (litter addition), and natural litter input (control). On average, litter exclusion significantly reduced soil FCO₂ rate by approximately 39%, 24% and 22% in Camphor tree forests, the Mixed forests, and Masson pine forests, respectively. On a yearly basis, double litter addition significantly increased soil CO₂ by 12% in the Mixed forests (*P*=0.02) but not in both Camphor tree and Masson pine forests (*P*>0.05), when compared with their corresponding control treatments. However, litter addition increased soil FCO₂ rates in the months of June–August in Camphor tree and Masson pine forests, coinciding with high soil temperature of summer conditions. Litter exclusion reduced soil FCO₂ more than litter addition increased it in the study sites. Responses of soil respiration to litter input treatments varied with forest types. Litter input treatments did not alter the seasonal patterns of soil temperature and soil water content. Our results indicated that changes in aboveground litter as a result of global climate change and/or forest management have a great potential to alter soil respiration and soil carbon balance in forest ecosystems.

soil respiration, litter exclusion, litter addition, subtropical forests, soil environmental factors

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Soil is the second largest carbon pool and has a great potential to affect global climate change through carbon release and sequestration. Soil carbon, being about twice as much carbon $(1580 \times 10^{15} \text{ g})$ as the atmosphere $(750 \times 10^{15} \text{ g})$ or terrestrial vegetation $(610 \times 10^{15} \text{ g})$ is a large component of the global carbon cycle [1,2]. The amount of soil carbon in forest ecosystems is determined by carbon inputs from aboveground litter and belowground root turnover, and carbon outputs from soil respiration and runoff with dissolved organic carbon [3,4]. The emission of CO₂ from forested soils (also called soil respiration) represents the largest terrestrial CO₂ flux to the atmosphere [5]. As a result, soil CO₂ efflux (FCO₂) is an important regulator of climate change and plays a critical role in carbon balance in the local, regional and global scales [6,7]. Soil temperature (T_{soil}) and soil moisture (W_{soil}) have been widely reported as the major factors to influence soil respiration [8]. Soil FCO₂ rates are also affected by many biotic and abiotic factors, such as fine root production [9], microbial activity [10,11], soil organic matter [12], soil pH [8,13], soil type, nutrient availability,

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vegetative cover type [14], as well as forest management practices [15,16].

Elevated atmospheric greenhouse gases, particularly CO₂ concentration likely result in the increment of net primary production of plant communities [17,18] and thus aboveground litter production in forest ecosystems [19]. Litter and its decomposition represent the major pathway of carbon and other nutrients from plant components to the soils [20]. In addition, litter layer on the forest floor helps to maintain favorable micro-environmental conditions for decomposition process by regulating the microclimate in forests [21]. Thus, the amount of litter accumulated in the forests is expected to affect soil organic matter content and underground processes. It was reported that litter removal and litter addition treatments affected the number of decomposer organisms in forests, such as arthropods [22] and fungi [23,24]. Therefore, changes in amount of litter on the stand floor will alter the amounts of available nutrients [21] and decomposition rates [25] in the soils. Particularly, increased litter resulted from global climate change would cause the alterations of soil microbial community, which further result in an excess of soil respiration from both newly added carbon sources and existed soil organic matter [18,26]. This process, termed as 'priming effect', is mainly attributed to dissolved organic carbon from aboveground added litter and recently has received increased attention [27,28]. Despite attention given recently to examining influences of aboveground litter changes on soil FCO₂ due to global climate change and forest management practices, there still exists great uncertainty and variability among measurements in different forest ecosystems [18,26,29,30].

In this study, we investigated the responses of soil respiration to aboveground litter input manipulation in three common forest types in central south China. The camphor tree (Cinnamomum camphora) is a dense evergreen broadleaves tree species and is commonly planted as shaded, windbreak and timber forests. Additionally, camphor tree forests represent one of the most important climax vegetation communities in subtropical region of China. Masson pine (Pinus massoniana) is an evergreen conifer tree species and often cultivated for timber production. Because of characteristics of strong tolerance to infertile and drought soils, Masson pine forests have been widely planted in southern China and the total area of theplantations was around 2×10^6 km² [31]. In the past years, several studied were conducted to examine aboveground processes in these forests, such as allocation of aboveground biomass and productivity, seasonal patterns of tree photosynthesis, and decomposition of litter [16,31,32]. However, few studies were carried out to examine belowground processes in these forests, such as soil respiration. Here we document dynamics of soil FCO₂ response to increased and decreased litter inputs treatments in three common types of forests in the region. The purpose of the study is to test the hypothesis that changes in aboveground litter inputs determine the variations of soil CO₂ rates in the dominant forest types. The specific objectives of the paper were to: (1) quantify annual and seasonal variations of soil FCO₂ rates following litter exclusion and addition treatments in the Camphor tree, Masson pine, and the mixed Camphor tree and Masson pine forests; (2) estimate relative contributions of litter composition on soil respiration in the three types of forests; and (3) examine the effects of litter input changes on T_{soil} and M_{soil} , which are the dominant abiotic factors controlling soil FCO₂ rates in the forests.

2 Methods

2.1 Study area

The study was carried out at Hunan Forest Botanic Garden, Changsha City, Hunan Province, China (113°02'-113°03'E, $28^{\circ}06'-28^{\circ}07'N$). The garden covered about 140 ha and the study area was a typical moist subtropical zone with a mean annual temperature of 17.2°C and mean monthly temperatures of 4.7°C and 29.4°C in January and July, respectively. Annual precipitation ranged from 1200 to 1700 mm. Mean annual relative humidity was >80%. The frost-free period was 270-310 d per year. Elevation was 46-114 m with an average site slope of 5–15°. Soil pH on the surface (0–10 cm) was acidic with an average pH of 5.0. Three dominate forest types in the garden were selected in the research project. Masson pine forests were planted in 1980 with an initial stand density of 2 m×2 m. Camphor tree forests were established in 1982 with a tree density of 2 m×3 m. The Masson pine and Camphor tree mixed forests (thereafter as the Mixed forest) were planted in 1982 with an initial density of 2 m×3 m and using a proportion of 50%: 50% for the two tree species. The general characters of the three stands are listed in Tables 1 and 2. Understorey species in these forests were Sassafeas tsumu Hemsl.; Cinnamomum camphora; Symplocos caudata Wall. ex A. DC.; Clerodendron cyrtophyllum Turcz; Nephrolepis auriculata Trimen; Lophantherum gracile Brengn.; Miscanthus floridulus Warband

Table 1 Characteristics of the Camphor tree, Mixed forest and Masson pine forests in Hunan Forest Botanic Garden, Changsha, Hunan Province, China

Forest types	Planted time	Stand density (tree ha ⁻¹)	Mean DBH (cm)	Mean tree height (m)
Camphor tree	1982	1600	14.9	12.5
Mixed forest	1982	1600	16.9	12.7
Masson pine	1980	1600	15.2	12.3

Forest types	Soil density (g cm ⁻³)	Soil pH	Total C (mg C g ⁻¹))	Total N (mg N g ⁻¹)	Litter production (t $ha^{-1}a^{-1}$)
Camphor tree	1.50±0.11	3.9±0.18	9.45±1.01	0.81±0.18	3.26±0.17
Mixed forest	1.36±0.26	4.2±0.20	11.02±1.88	1.03±0.24	4.30±0.22
Masson pine	1.57±0.33	3.7±0.15	8.38±0.32	0.67 ± 0.67	3.41±0.25

 Table 2
 Soil properties and litter production in the Camphor tree, Mixed forest and Masson pine forests in Hunan Forest Botanic Garden, Changsha, Hunan Province, China (mean±SE)

and Phytolacca acinosa Roxb. Firmiana simplex.

2.2 Experimental design

The study was a nested design in which forest type (Camphor tree forest, Masson pine forest, and Mixed forest) was the main factor, and the changed litter input treatments were the sub-factor nested in the main factor. One site (with the area of 50 m×50 m) was chosen for each of the three forest types in the study area. Three changed litter input treatments were employed for each forest type. Six replicated plots (each with the size of 3 m×4 m) were set up as the measurement points for each of the three litter input treatments within for each forest type. Therefore, the total number of measurement points was $3 \times 3 \times 6 = 54$.

The changed litter input treatments, including non-litter input (litter exclusion), double litter input (litter addition) and natural litter input (as control), were conducted for each of the forest types. The non-litter input treatment was performed to remove all litter materials from the floor in the plot 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 plot to prohibit litter falling on the floor. All litter was collected and removed from the mesh collection twice a month. The double litter input treatment was performed to transfer and evenly distribute litter materials obtained from a non-litter input plot described above on a double litter input plot. The double litter input treatment was carried out twice a month. The natural litter input treatment, as a control treatment, was performed to keep the natural status of litter on the floor and the normal litter-fall process was allowed, neither removal nor addition. The study was initiated in June of 2009. All treatments were usually conducted at the beginning of each month, approximately one week prior to the measurement of soil FCO₂.

2.3 Soil FCO₂ rate measurements

Soil FCO₂ rates were measured on a biweekly basis from June of 2009 to May of 2010 using a portable infra-red gas analyzer (LI-COR 8100A) with soil CO₂ flux chamber (LI-8100-09). In order to minimize soil disturbance effects from the utilization of the flux chamber, PVC collars were inserted into the soil one week prior to the first measurement of FCO₂, and kept in place through the entire study. The PVC collars used were 20.0 cm in diameter and 4.4 cm in

height, and were installed to leave 2.5 cm protruding above the soil surface. The FCO₂ value at each measurement point was the mean of three sequential flux estimates at each sampling interval; values are expressed as μ mol CO₂ m⁻² s⁻¹. The monthly data collection was timed to span a few days with similar weather patterns since it was not possible to obtain all measurements in a single day [33].

2.4 Soil temperature and moisture measurements

 $T_{\rm soil}$ and $M_{\rm soil}$ were measured at the same time during the measurements of soil FCO₂ using a soil thermocouple probe (LI-COR 8100-201) and a water content probe (LI-COR 8100-202) at 5 cm below the soil surface. $M_{\rm soil}$ was presented as volumetric soil moisture content.

2.5 Date analysis

The effects of forest types, litter input treatments, temporal variation (month-to-month), and their interactions on soil FCO₂, T_{soil} , and M_{soil} statistically tested using analysis of variance (ANOVA). The original FCO₂ data were log-transformed to satisfy the normality and homogeneous assumptions of ANOVA. Multiple comparisons were conducted to identify the differences in FCO₂ and T_{soil} , and M_{soil} among the forest types. A Tukey-Kramer test was used to compare the variation of soil FCO₂ in each forest types due to the changed litter input treatments. Exponential regression analysis was employed to examine relationships between soil FCO₂ and T_{soil} . Statistical analyses were conducted using the SAS statistical package.

3 Results

Soil FCO₂ rates were significantly different among the forest types for the control plots over the year (P<0.0001) (Table 3). On average, Camphor tree forests had the highest soil respiration rate (3.16±1.60 µmol m⁻² s⁻¹) (mean±SE) during the study period, the next was the Mixed forests (2.16±0.84 µmol m⁻² s⁻¹) and the lowest values were found in Masson pine forests (1.91±0.70 µmol m⁻² s⁻¹). In other words, soil FCO₂ rates were about 1.7 and 1.1 times higher in Camphor tree and the Mixed forest sites than that in Masson pine sites.

Non-litter input treatments had a significant effect on soil

Table 3 Annual averages of Soil FCO₂ rates in the three types of forest under litter treatments in Hunan Forest Botanic Garden, Changsha, Hunan Province, China (μ mol m⁻² s⁻¹) (mean±SE)^a)

Forest types	Treatments			
	Control	Double litter	Non-litter	
Camphor tree	$3.16 \pm 1.60^{A,a}$	3.11±1.79 ^a	1.93±1.01 ^b	
Mixed forest	$2.16 \pm 0.84^{B,a}$	2.29 ± 0.96^{b}	$1.68 \pm 0.78^{\circ}$	
Masson pine	$1.91 \pm 0.27^{C,a}$	1.82 ± 0.85^{a}	1.49±0.61 ^b	

a) Different capital letters in the Control column indicate significant difference among the forest types (P<0.0001); different small letters in a row indicate significant difference between different treatments in each forest type (P<0.05).

 FCO_2 process (P<0.05) in all studied forests (Table 3). By comparing with control treatments, soil FCO₂ rates were decreased by 39.2 (±6.8)%, 24.1 (±12.3)% and 22.3 (±7.0)% under non-litter input treatments in Camphor tree, Mixed forest, and Masson pine plots, respectively. In other words, approximate 39%, 24% and 22% of the total soil FCO₂ were litter-derived in the three forest types, respectively. Double litter input treatments likely had no obvious impacts on soil FCO_2 in Camphor tree and Masson pine forests (P>0.05) when compared with their corresponding litter control treatments, but litter addition increased soil FCO₂ rates in the months of June-August in the two forest types, coinciding with high T_{soil} of summer conditions (Table 3, Figures 1 and 2). On a yearly basis, double litter treatments significantly increased soil CO₂ by 12% when compared with litter control treatments in the Mixed forests (P=0.02) (Table 3).

The three forest types exhibited similar seasonal variations of soil FCO₂ rates, with lowest values occurring during the winter months of December-February and greatest rates during the months of June-August for control treatment (Figure 1). On a monthly basis, the mean soil FCO_2 rates were 1.21–5.47, 1.11–3.48 and 0.84–2.85 μ mol m⁻² s⁻¹ in control plots, and 0.64-3.40, 0.66-2.87 and 0.64-2.26 µmol m⁻² s⁻¹ in non-litter input plots in Camphor tree, Mixed forest, and Masson pine forests, respectively. Nonlitter input and double litter input treatments did not modify the seasonal patterns of soil FCO₂ in the study sites. At most measurement dates, there were no significant differences of soil FCO₂ rates between double and control litter input sites. But soil FCO₂ rates were obviously lower in non-litter input sites than in both double and control litter input plots throughout the whole course of the study. Particularly, variations in monthly soil FCO₂ rates were large among the three stands in the growing season, but small in the winter times (Figure 1).

There were similar seasonal patterns in T_{soil} in all control sites of the three forest types (Figure 2). The highest and lowest values were observed in months of July–August and January, respectively, in Camphor tree, the Mixed forest, and Masson pine forests. T_{soil} was not affected by litter input treatments for the three forest types (Table 4). Non-litter



Figure 1 The seasonal patterns of soil FCO_2 in response to litter treatments in three stand types in Hunan Forest Botanic Garden, Changsha, Hunan Province, China during the time period of June of 2009 to May of 2010. (a) Camphor tree forests; (b) the Mixed forests; (c) Masson pine forests. Data were no available in the month of January of 2010 in Masson pine forests.

input treatments reduced monthly mean values in $M_{\rm soil}$ compared to control treatments in the studied forests, but the differences in $M_{\rm soil}$ were not significant between the two treatments (*P*>0.05) (Table 5). No statistically significant differences in $M_{\rm soil}$ were found between double litter input plots and control plots in the three forest types during the study times.

Soil FCO₂ rates were strongly correlated with T_{soil} (*P*< 0.0001) (Figure 3), but not with M_{soil} (*P*>0.05) (Figure 4). In the study site, T_{soil} was selected as the signal dominant independent valuable to describe the dynamics of soil FCO₂, and accounted about 90%, 89% and 93% variability in soil FCO₂ rates in Camphor tree, Mixed forest and Masson pine forests respectively.



Figure 2 Seasonal patterns of soil temperature in response to litter treatments in three types of forest stand type in Hunan Forest Botanic Garden, Changsha, Hunan province, China during the time period of June of 2009 to May of 2010. (a) Camphor tree forests; (b) the Mixed forests; (c) Masson pine forests. Data were no available in the month of January of 2010 in Masson pine forests.

Table 4Annual mean soil temperature in the three types of forest underlitter treatments in Hunan Forest Botanic Garden, Changsha, Hunan Prov-ince, China (°C) (mean \pm SE)

Forest types	Treatments			
	Control	Double litter	Non-litter	
Camphor tree	15.8±8.5	15.8±8.6	15.7±8.6	
Mixed forest	15.2±8.2	15.5±8.4	15.3±8.6	
Masson pine	16.5±9.0	16.4±9.9	16.6±9.2	

4 Discussion

We found that exclusion of litter inputs substantially reduced soil FCO_2 rates in the studied forests (Table 3 and Figure 1). The results were similar to that in other previous

Table 5Annual mean soil moisture in the three types of forest underlitter treatments in Hunan Forest Botanic Garden, Changsha, Hunan Prov-ince, China (%) (mean±SE)

Forest types	Treatments			
	Control	Double litter	Non-litter	
Camphor tree	16.5±4.4	17.2±4.6	12.6±3.3	
Mixed forest	15.2±4.0	13.5±3.6	14.8±3.9	
Masson pine	15.1±4.0	15.4±4.1	14.1±3.7	



Figure 3 The relationships between soil FCO_2 and soil temperature in control plots of the three forest types in Hunan Forest Botanic Garden, Changsha, Hunan Province, China. (a) Camphor tree forests; (b) the Mixed forests; (c) Masson pine forests.

litter manipulation experiments [12,29,34,35]. Sayer et al. [36] reported that soil respiration was on average 20% lower in the litter removal plots than in the control plots from a long-term litter manipulation study in tropical forests. Zimmermann et al. [37] pointed out that litter layer contributed 37% of total soil FCO₂ in a tropical montane cloud forest in



Figure 4 The relationships between soil FCO_2 and soil moisture in control plots of the three forest types in Hunan Forest Botanic Garden, Changsha, Hunan Province, China.

Peru. Exclusion of litter from soil surface reduced soil FCO₂ by 17%-44% in three successional subtropical forests in southern China [38]. Removal of litter result in a decline of soil FCO₂ rates by about 22% in temperate forests [34,39]. Although the contribution of surface litter to the soil respiration could be as high as 54%-68% [29], the proportion of aboveground litter on the total soil respiration, on a global scale, was 20% to 30% [14]. Our estimates, about 22%-39% of soil FCO₂ was reduced following litter exclusion in the three forests, fall within the range of these published values. CO₂ from soil surface includes the sum of autotrophic respiration (root and rhizosphere) and heterotrophic respiration (microbes and soil fauna). Litter falling and thereafter its decomposition represent a major pathway of carbon and other nutrients from vegetation to the soil, meaning to provide raw food resources for soil fauna and microbial. Thus, prohibiting aboveground litter inputs or litter removal would be expected to greatly reduce soil FCO₂ rates in forest ecosystems [37,40]. In the current study, litter input treatments did not significantly modify seasonal patterns of T_{soil} and $M_{\rm soil}$ in the three forests (Tables 4 and 5), while dynamics of soil FCO₂ were tightly correlated to the changes in T_{soil} (Figure 3). As a result, the negative effect of litter removal on soil FCO₂ was likely attributed to the reduction of the amount of available respiratory substrates, which may cause the changes in composition and activity of soil microbial community. Li et al. [29] reported that microbial biomass was greatly reduced (about 68%) from tropical forests due to litter exclusion. The changes in the composition and activity of microbial community were observed following litter removal [41,42]. Therefore, the reduction in soil FCO₂ following litter exclusion was mainly attributed to a direct effect, available substrates limitation which can decrease the heterotrophic respiration. In our previous study at the same sites, we found that heterotrophic respiration made a major contribution (more than 70% of total soil respiration) in an adjacent stand of Chinese fir plantations [30].

In the present study, the percentage of reduction in soil FCO₂ rates following litter exclusion decreased in an order Camphor tree forests>Mixed forests>Masson pine forests

(Table 3). The results suggested that the tree species and forest type itself played a critical role in the responses of soil FCO₂ to litter exclusion because these forests located in the same site with similar micro-environmental condition and soil type and had the same stand aging (Tables 1 and 2). Li et al. [29] conducted a long-term litter manipulation experiment in Puerto Rico and found that litter removal decreased soil FCO₂ by 68% in a pine plantation and 54% in a secondary forest. Bréchet et al. [43] reported that differences in soil respiration were related to the quantity of litter biomass in 16 tree species planted in mono-specific plots, highlighting the role of tree species as a source of variation of soil FCO₂. Moreover, different tree species, such as faster and slower growing tree species, produces variable amount of litter contained different concentrations of C, nitrogen and other nutrient elements, which make different contributions to soil respiration and affects the abundance, composition, and activity of soil microbial communities [35]. This is particularly true in our case as the microenvironment factors were not significantly affected by litter input treatments. Litter on the forest floor was effective mulch on the soil surface that regulated the microenvironment. Soils were exposed following litter exclusion, and the bare soil should have higher T_{soil} and lower M_{soil} . However, our results showed that litter exclusion had no obvious effects on $T_{\rm soil}$ and $M_{\rm soil}$ in three forest types, which may be attributed to the closed canopy of these forests that made a mulch effect in migrating microclimate in mature stands [13].

As soil FCO_2 rates were reduced by 20%–40% from the non-litter input plots in the studied forests, we expected that the similar percentage would be gained in the double litter input plots compared to the control treatments. Surprisingly, double litter input treatments did not significantly alter soil FCO₂ rates in both Camphor tree and Masson pine forests, but in the Mixed forests, when compared to the corresponding control treatments (Table 3, Figure 1). Many previous studies reported that litter additions often increased soil FCO₂ rates [21,40,44], mostly due to 'priming effect', an increase in soil organic carbon mineralization following the input of fresh organic carbon residues [27,28]. Crow et al. [26] reported that double needle litter inputs increased actual soil respiration and the priming effect accounted for up to 19% of total soil FCO₂ from litter addition sites in an undisturbed old-growth western hemlock and Douglas fir stand. Sayer et al. [36] performed a litter-manipulation treatments project in a tropical forest, and they found that the total annual soil FCO₂ increased from 10.0±0.5 t C ha⁻¹ a⁻¹ in control plots to 13.8±1.2 t C ha⁻¹ a⁻¹ in litter addition plots. In the current study, litter addition indeed increased soil respiration by about 12% in the mixed forests on a yearly basis, showing a positive priming effect [26]. It is worthy to note that double litter inputs had no significant impact on soil FCO2 in Camphor tree and Masson pine forests on a yearly basis, but litter addition increased soil FCO₂ rates in the months of June-August in the two forest types,

coinciding with high T_{soil} of summer conditions. Our data did not allow us to directly determine the mechanisms controlling the response to additional litter inputs. However, a number of factors were likely attributed to the result. Firstly, the availability of respiratory substrates was not limited to microbial community for decomposition in Camphor tree and Masson pine forests during the study period and thus microbial respiration was not greatly enhanced by additional aboveground litter inputs. Second, litter addition effect did not completely occur within one-year experiment in the study site. Third, the temporal scales of soil priming effect should be considered when assessing the effect of litter changes in forest ecosystems. The influence of litter treatments on dynamics of belowground parts including soil microbial activity and soil FCO₂ might be dependent upon the time period following the treatments. Park and Matzner [45] reported that litter additions did not alter the amount of microbial biomass in a temperate deciduous forest two years later following the treatment. Nadelhoffer et al. [41] indicated that total fungal biomass in the forest floor increased, but total fungal biomass and active bacterial biomass in the mineral soil decreased after five years of litter addition. Crow et al. [26] performed a Detritus Input Removal and Transfer Experiment and pointed out that high rates of soil priming effect observed in July-August were not directly caused by addition of litter, but were due to the cumulative added litter over six years and higher temperature, increased enzyme activity, and greater root activity.

5 Conclusions

Based on field measurements of soil FCO₂ rates under litter input treatments in Camphor tree, Mixed forest, and Masson pine forest types, we conclude that changes in litter inputs influence soil respiration significantly in these forests. Litter contributed 20%–40% of total soil respiration in the common forest types in southern China. The exclusion of litter from forest floor would lead to a reduction of available substrates in soils, which might affect soil microbial communities and cause decline of soil FCO₂. It seems that litter exclusion had more effects in reducing soil FCO₂ than litter addition in increasing it in the study sites. Responses of soil respiration to litter input treatments varied with forest types. Further research is required to clarify the long-term effects of climate change via litter input alteration on soil FCO₂ and soil carbon balance in various forest ecosystems.

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- Johnson D W, Cutis P S. Effects of forest management on soil C and N storage: Meta analysis. For Ecol Manag, 2001, 140: 227–238
- 2 Lal R. Soil carbon sequestration to mitigate climate change. Geoderma, 2004, 123: 1–22
- 3 Davidson E A, Richardson A D, Savage K E, et al. A distinct seasonal pattern of the ratio of soil respiration to total ecosystem respiration in a spruce-dominated forest. Glob Change Biol, 2006, 12: 230–239
- 4 Epron D, Nouvellon Y, Deleporte P, et al. Soil carbon balance in a clonal Eucalyptus plantation in Congo: Effects of logging on carbon inputs and soil CO₂ efflux. Glob Change Biol, 2006, 12: 1021–1031
- 5 Berger T W, Inselsbacher E, Boltenstern S Z. Carbon dioxide emissions of soil under pure and mixed stands of beech and spruce, affected by decomposing foliage litter mixtures. Soil Biol Biochem, 2010, 42: 986–997
- 6 Chen X, Hutley L B, Eamus D. Carbon balance of a tropical savanna of northern Australia. Oecologia, 2003, 137: 405–416
- 7 Baggs E M. Partitioning the components of soil respiration: A research challenge. Plant Soil, 2006, 284: 1–5
- 8 Raich J W, Schlesinger W H. The global carbon dioxide flux in soil respiration and its relationship to vegetation and climate. Tellus, 1992, 44B: 81–99
- 9 Chen X, Eamus D, Hutley L B. Seasonal patterns of soil carbon dioxide efflux from wet-dry tropical savanna of northern Australia. Aust J Bot, 2002, 50: 43–51
- 10 Chen C R, Condron L M, Xu Z H, et al. Root, rhizosphere and root-free respiration in soils under grassland and forest plants. Eur J Soil Sci, 2006, 57: 58–66
- 11 Mariani L, Chang S X, Kabzems R. Effects of tree harvesting, forest floor removal, and compaction on soil microbial biomass, microbial respiration, and N availability in a boreal aspen forest in British Columbia. Soil Biol Biochem, 2006, 38: 1734–1744
- 12 Ewel K C, Cropper W P Jr, Gholz H L. Soil CO₂ evolution in Florida slash pine plantations. II. Importance of root respiration. Can J For Res, 1987, 17: 330–333
- 13 Peng Y Y, Thomas S C. Influence of non-nitrogenous soil amendments on soil CO₂ efflux and fine root production in an N-saturated northern hardwood forest. Ecosystems, 2010, 13: 1145–1156
- 14 Raich J W, Nadelhoffer J. Belowground carbon allocation in forest ecosystems: Global trends. Ecology, 1989, 70: 1346–1354
- 15 Peng Y Y, Thomas S C, Tian D. Forest management and soil respiration: Implications for carbon sequestration. Environ Rev, 2008, 16: 96–111
- 16 Tian D L, Peng Y Y, Yan W D, et al. Effects of thinning and litter fall removal on fine root production and soil organic carbon content in Masson pine plantations. Pedosphere, 2010, 20: 486–493
- 17 Delucia E H, Hamiltom J G, Naidu S L, et al. Net Primary Production of a Forest Ecosystem with Experimental CO₂ Enrichment. Science, 1999, 284: 1177–1179
- 18 Sayer E J, Powers J S, Tanner E V J. Increased litterfall in tropical forests boosts the transfer of soil CO₂ to the atmosphere. PLoS One, 2007, 12: e1299
- 19 Finzi A C, Allen A S, DeLucia E H, et al. Forest litter production, chemistry, and decomposition following two years of free-air CO₂ enrichment. Ecology, 2001, 82: 470–484
- 20 Vitousek P, Sanford Jr L. Nutrient cycling in moist tropical forest. Annu Rev Ecol Syst, 1986, 17: 137–167
- Sayer E J. Using experimental manipulation to assess the roles of leaf litter in the functioning of forest ecosystems. Biol Rev, 2006, 81: 1–31
- 22 David J F, Ponge J F, Arpin P, et al. Reactions of the macrofauna of a forest mull to experimental perturbations of litter supply. Oikos, 1991, 61: 316–326
- 23 Tyler G. Effects of litter treatments on the sporophore production of beech forest macrofungi. Mycol Res, 1991, 95: 1137–1139
- 24 Cullings K W, New M H, Makhija S, et al. Effects of litter addition on ectomycorrhizal associates of a lodgepole pine (*Pinus contorta*) stand in Yellowstone National Park. Appl Environ Microb, 2003, 69: 3772–3776
- 25 Rothstein D E, Vitousek P M, Simmons B L. An exotic tree alters

decomposition and nutrient cycling in a Hawaiian montane forest. Ecosystems, 2004, 7: 805-814

- 26 Crow S E, Lajtha K, Bowden R D, et al. Increased coniferous needle inputs accelerate decomposition of soil carbon in an old-growth forest. For Ecol Manag, 2009, 258: 2224–2232
- 27 Nottingham A T, Griffiths H, Chamberlain P M, et al. Soil priming by sugar and leaf-litter substrates: A link to microbial groups. Appl Soil Ecol, 2009, 42: 183–190
- 28 Kuzyakov Y. Priming effects: Interactions between living and dead organic matter. Soil Biol Biochem, 2010, 42: 1363–1371
- 29 Li Y, Xu M, Sun O J, et al. Effects of root and litter exclusion on soil CO₂ efflux and microbial biomass in wet tropical forests. Soil Biol Biochem, 2004, 36: 2111–2114
- 30 Tian D, Wang G, Peng Y, et al. Contribution of autotrophic and heterotrophic respiration to soil CO_2 efflux in Chinese fir plantations. Aust J Bot, 2011, 59: 26–31
- 31 Tian D. Structure and Functioning of Masson Pine and Slash Pine Forest Ecosystems (in Chinese). Beijing: Science Press, 2005
- 32 Tian D. Ecology of Camphor Tree Forest Ecosystem (in Chinese). Beijing: Science Press, 2005
- 33 Laporte M F, Duchesne L C, Morrison I K. Effect of clearcutting, selection cutting, shelterwood cutting and microsites on soil surface CO₂ efflux in a tolerant hardwood ecosystem of Northern Ontario. For Ecol Manag, 2003, 174: 565–575
- 34 Rey A, Pegoraro E, Tedeschi V, et al. Annual variation in soil respiration and its components in a coppice oak forest in Central Italy. Glob Change Biol, 2002, 8: 851–866
- 35 Sulzman E W, Brant J B, Bowden R D, et al. Contribution of aboveground litter, belowground litter, and rhizosphere respiration to total soil CO₂ efflux in an old growth coniferous forest. Biogeochemistry, 2005, 73: 231–256

- 36 Sayer E J, Heard M S, Grant H K, et al. Soil carbon release enhanced by increased tropical forest litterfall. Nat Clim Change, 2011, 1: 304–307
- 37 Zimmermann M, Meir P, Bird M, et al. Litter contribution to diurnal and annual soil respiration in a tropical montane cloud forest. Soil Biol Biochem, 2009, 41: 1338–1340
- 38 Tang X, Liu S, Zhou G, et al. Soil-atmospheric exchange of CO₂, CH₄ and N₂O in three subtropical forest ecosystems in southern China. Glob Change Biol, 2006, 12: 546–560
- 39 Dong Y, Scharffe D, Lobert J M, et al. Fluxes of CO₂, CH₄, and N₂O from a temperate forest soil: The effects of leaves and humus Layers. Tellus, 1998, 50B: 243–252
- 40 Schaefer D A, Feng W, Zou X. Plant carbon inputs and environmental factors strongly affect soil respiration in a subtropical forest of southwestern China. Soil Biol Biochem, 2009, 41: 1000–1007
- 41 Nadelhoffer K J, Boone R D, Bowden R D, et al. The DIRT experiment. Litter and root influences on forest soil organic matter stocks and function. In: Foster D R, Aber J D, eds. Forests in Time. New Haven: Yale University Press, 2004. 300–315
- 42 Fontaine S, Mariotti A, Abbadie L. The priming effect of organic matter: A question of microbial competition? Soil Biol Biochem, 2003, 35: 837–843
- 43 Bréchet L, Ponton S, Roy J, et al. Do tree species characteristics influence soil respiration in tropical forests? A test based on 16 tree species planted in monospecific plots. Plant Soil, 2009, 319: 235–246
- 44 Fontaine S, Bardous G, Abbiadie L, et al. Carbon input to soil may decrease soil carbon content. Ecol Lett, 2004, 7: 314–320
- 45 Park J H, Matzner E. Controls on the release of dissolved organic carbon and nitrogen from a deciduous forest floor investigated by manipulations of aboveground litter inputs and water flux. Biogeochemistry, 2003, 66: 265–286
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