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Effects of litter inputs on soil aggregate C turnover and flow differ among three natural forest ecosystems along a climate gradient in China

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Abstract

Background Plant litter input plays an important role in controlling soil organic carbon (SOC) turnover and the flow of carbon (C) among different pools. However, the relative effects of aboveground and belowground root litter on soil aggregate C dynamics across different forest types and along climate gradients remain poorly understood. In this study, we examined changes in soil aggregate mass proportion, litter-derived and native C contents of macro-aggregate, micro-aggregate and silt + clay fractions, and C flow among these fractions during 2 years of litter input, using ¹³C isotope tracing technique in tropical, temperate and boreal forests along a climate gradient in China.

Results The results showed that belowground root litter input enhanced soil aggregation across all three forests, but aboveground litter input had no significant effect. Belowground root litter input increased total and litter-derived C content across aggregate fractions compared to aboveground litter input in the tropical forest, while it decreased native C content in the same forest. However, the effects of litter input on total and litter-derived C contents were minimal in the boreal and temperate forests. In addition, patterns of soil C flow among aggregates varied depending on both litter input type and forest type.

Conclusions Our results imply that belowground root litter enhances soil aggregation and aggregate C turnover compared to aboveground litter input. Moreover, the effects of root litter input on soil aggregate C turnover and C flow depend on forest types along the climatic gradient.

Keywords Climatic gradient, Forest type, Litter input, Soil aggregation, Soil carbon turnover, Soil carbon flow

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Introduction

Plant litter is the key factor controlling the size and stability of the soil organic carbon (SOC) pool in terrestrial ecosystems (Leff et al. 2012; Cao et al. 2020). During litter decomposition, most plant C is released back as atmospheric CO₂ (Rubino et al. 2010; Steffens et al. 2015), but a small portion of litter C can transfer into soils through two main pathways: (1) the dissolved organic matter-microbial pathway occurring at an early stage, and (2) the physical-transfer pathway occurring when litter fragments are transferred directly to soils

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(Cotrufo et al. 2015). To understand soil C sequestration, accurate knowledge is necessary on how litter-derived C transfers into soils and on the stabilization pathways through which C flows among SOC pools.

Over the past several decades, the effects of litter input on SOC pool size have been widely studied. A large number of previous studies have found lower SOC accumulation induced by aboveground leaf litter compared to the belowground roots (Bird et al. 2008; Schmidt et al. 2011; Berhongaray et al. 2019; Huang et al. 2021; Wang et al. 2023; Zhang et al. 2023a), with root litter input leading to higher biochemical recalcitrance and thus more C retention in soils (Fulton-Smith and Cotrufo 2019). In contrast, some studies showed that leaf litter input was more important in maintaining SOC (Cao et al. 2020; Zhang et al. 2023b). Using global data of litter manipulation experiments, Wu et al. (2023) found that the input of leaf litter contributed more to stable soil carbon accumulation than living roots in broadleaved forests the input of plant litter had a similar contribution to SOC accumulation across forest types. Several studies have demonstrated that SOC pool size differs among forests along climatic zones, with the varied annual precipitation and temperature (Sayer et al. 2012; Tamura and Tharayil 2014; Villarino et al. 2021). Moreover, there is a great difference in plant litter quantity and quality among forests, which control soil microbial activity (Tamura and Tharayil 2014; Mou et al. 2021), and ultimately affects SOC turnover (Mou et al. 2021; Chen et al. 2022; Wu et al. 2018). Although the distinct effects of plant leaf and root litter input on the size of SOC pools and turnover have been well studied in some forests (Wu et al. 2023), it is not yet clear how SOC turnover induced by different litter types changes among forest types and along climatic gradients (Leff et al. 2012). In addition, it is generally difficult to interpret short-term changes in the total SOC pool (Lajtha et al. 2018), because plant litter input can not only transform into soil as newly-derived SOC, but can also stimulate native SOC mineralization via priming effects (Dijkstra et al. 2020; Shi et al. 2023). The isotopic abundance of ^{13}C has been widely used to trace SOC turnover of litter-derived C formation and native SOC mineralization (Crow et al. 2009; Lajtha et al. 2018; Sokol and Bradford 2019). The isotopic abundances of ^{13}C are different in C3 ($\delta^{13}\text{C} = -28.1 \pm 2.5\%$) and C4 ($\delta^{13}\text{C} = -13.5 \pm 1.5\%$) plants because the C3 and C4 photosynthetic pathways show characteristically different discriminations against ^{13}C during photosynthesis (O'Leary 1981). Capitalizing on this natural difference in $\delta^{13}\text{C}$, soil transplantation has been widely used in agricultural (Balesdent and Balabane 1996) and

grassland (Huang et al. 2021) ecosystems to trace plant-derived C vs. existing SOC in situ.

The persistence of SOC is not primarily determined by its molecular structure, but rather by its immediate biotic and abiotic environment (Schmidt et al. 2011). On the one hand, soil aggregation plays an important role in controlling SOC stabilization due to the physical protection of SOC mineralization mediated by soil microorganisms (Spohn and Giani 2011). On other hand, soil aggregation in turn depends on the input of organic materials that provide organic binding agents, e.g., polysaccharides, roots and fungal hyphae, and resistant aromatic components (Tisdall and Oades 1982). Therefore, the quality of plant litter plays a key role in controlling soil aggregate formation (Mizuta et al. 2015; Parwada and Van Tol 2019; Baumert et al. 2021; Sarker et al. 2022), as well as the pathways of litter-derived C transforming into soils (Cotrufo et al. 2013, 2015; Huang et al. 2021). Furthermore, the natural differences in the abundance of ^{13}C between aggregate size classes can provide information about the direction and intensity of C flow indicating the stabilization pathways (Gunina and Kuzyakov 2014; Shi et al. 2023; Werth and Kuzyakov 2008). For example, Shi et al. (2023) found that the plant-derived C flowed directly or indirectly from macro-aggregates to silt + clay size classes via micro-aggregates, but the intensity of C flows decreased as forest succession progressed. Similarly, Gunina and Kuzyakov (2014) suggested that C stabilization was not different among coniferous, deciduous forests and arable cropland, and that the main direction of C flows within aggregates was from the macro-aggregate-free particulate organic matter to the mineral microaggregate fraction. In contrast, Atere et al. (2020) found that the C flowed from heavy to light (mineral to occluded light) fraction in paddy soils under long-term fertilization, a pathway that was opposite to that observed in upland soils (Gunina and Kuzyakov 2014). Though several studies have reported the C flow pathways among forest types under the same environmental conditions (Gunina and Kuzyakov 2014; Shi et al. 2023), it is not yet clear how C stabilization pathways change among forests along a climatic gradient.

In the present study we aimed to disentangle the relative effects of aboveground and belowground litter input on the formation of newly litter-derived C and the retention of soil native C in aggregate fractions, as well as the C flow between soil aggregate classes in three forest types along a climatic gradient. To this end, a 2-year ^{13}C isotopic tracing experiment with sugarcane (C4 plant) cropland soils transplanted to forest soils (C3 plant) was conducted in boreal, temperate and tropical forests in China. We measured the C and $\delta^{13}\text{C}$ content in the soil macro-aggregate ($>250 \mu\text{m}$), micro-aggregate

(53–250 μm) and silt+clay (<53 μm) fractions. We hypothesized that (1) belowground root litter enhances soil aggregation compared to aboveground litter input, and thus results in C flow from a smaller size to a larger size aggregate fractions; (2) belowground root litter induces greater changes in aggregate C turnover with higher litter-derived C and lower native C content; and (3) changes in aggregate C turnover and flow differ among forest types, and the response sensitivity increases from boreal to tropical forest along the climatic gradient.

Materials and methods

Study sites

In this study, three natural forests (boreal, temperate and tropical) were selected along a climatic gradient from a cold temperate to a tropical climate in China (Fig. 1). The boreal forest is located at Mohe County (52.92°N, 122.79°E), Heilongjiang Province, northeastern China. The climate is of a cold temperate continental monsoon type, characterized by mean annual precipitation (MAP) of 436 mm and mean annual air temperature (MAT) of -4.14 °C. The dominant tree species in the boreal forest are *Larix gmelinii* and *Betula platyphylla*. The temperate forest is located at Qingyuan County (41.85°N, 124.93°E), Liaoning Province, northeastern China. The climate is characterized by a mid-temperate continental monsoon type, with MAP of 794 mm and MAT of 5.19 °C, and the forest features the dominant tree species *Quercus mongolica*, *Acer mono* and *Carpinus cordata*. The tropical forest is located at Ledong County (18.44°N, 108.01°E), Hainan Province, southern China. The climate is tropical monsoon with MAP of 2499 mm and MAT of 19.8 °C. The dominant tree species in the tropical forest are

Castanopsis hystrix, *Cyclobalanopsis glauca* and *Machilus pauhoi*.

Soil transplantation experiment

We set up four litter treatments, including aboveground litter input (AL), belowground root litter input (BL), aboveground plus belowground litter input (AL + BL) and no litter input as control (NL) at each forest site. At each site, four 20 m × 20 m plots were selected (four replicates per site), with a distance between plots of at least 100 m.

The method of natural ¹³C isotopic abundance was used to trace litter C input into soils and the transfer among soil aggregate fractions. For the soil transplant experiment, we collected sugarcane (a C₄ plant) soils at 0–20 cm in a cropland continuously planted with sugarcane for more than 20 years in the Experimental Farm of Fujian Agriculture and Forestry University (26.08°N, 119.23°E), located in Fuzhou, southeastern China. The plant residues in the C₄ soil were picked out, and air dried soils were passed through a 3 mm mesh sieve. The sugarcane soil is classified as Argi-Udic Ferrosol, and the texture was loam soil with 40.1% sand, 42.8% silt and 17.1% clay. Soil pH was 4.87, and soil C and N contents were 9.41 and 0.71 g kg⁻¹, respectively.

To set up the four litter input treatments, four holes (6 cm diameter, 20 cm depth) were drilled using a soil auger, with two PVC tubes inserted into two holes, and two nylon net pipes with a 3 mm mesh size inserted into the other two holes. Two groups of all litter microcosms (a total of 8 holes) were set up in each plot to allow for two sampling times of sampling back the C₄ soils. The previously collected sugarcane (C₄) soils were filled into the PVC tubes for the NL and AL treatment,

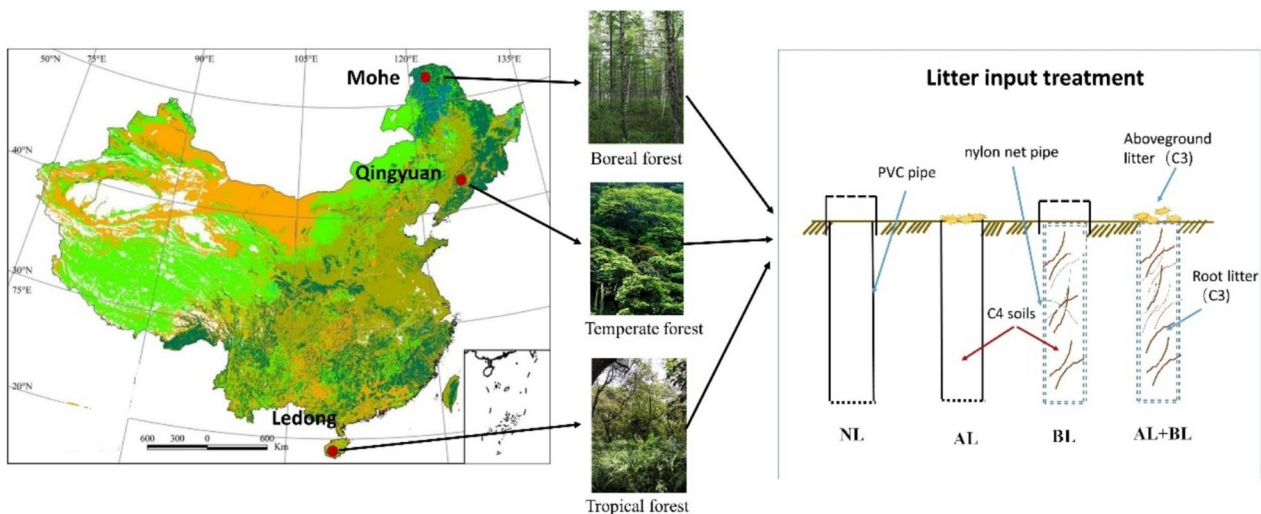


Fig. 1 Site location and litter input treatments in boreal, temperate and tropical forest along a climatic gradient in China. NL non-litter input, AL aboveground litter input, BL belowground litter input, AL + BL aboveground plus belowground litter input

or nylon net pipes for the BL and AL + BL treatment to allow roots to grow into soils (Fig. 1). For the AL and AL + BL treatments, the previously removed forest floor litter was carefully placed back onto the soil surface. For the NL and BL treatments, the forest floor litter was removed and a larger PVC collar (>6 cm diameter, 5 cm height) covered with a nylon net (mesh size: 1 mm × 1 mm) was placed on top of the inserted PVC tube to prevent fresh litter from falling on the soil. In our experiment, the leached C from forest canopies was ignored as we considered it a negligible C input source. At the start of the experiment, we took three samples of aboveground forest floor litter and root (0–20 cm layer) samples in each plot for measuring litter $\delta^{13}\text{C}$.

Soil sampling and soil aggregate fractionation

After 1 and 2 years, soils in each treatment were sampled. The previously replaced C4 soils were dug out from the PVC pipes, all plant residues and in-growing roots in soils were picked out by hand, and air dried for soil aggregate fractionation according to Six et al. (2000). Briefly, 50 g of air-dried soil was soaked slowly using distilled water, and allowed slaking for 10 min. Then, samples were placed on a set of 250 and 53 μm sieves and shaken uniformly for 10 min (30 times/min). The remaining size fractions on the 250 μm and 53 μm sieves were collected to obtain macro-aggregate (>250 μm) and micro-aggregate (53–250 μm), respectively. The unsettled portion of the suspension passed through the 53 μm sieve was decanted and centrifuged to obtain the sediment, which was combined with the settled suspension to obtain the silt + clay fraction (<53 μm). The separated aggregates were oven-dried at 60 °C, and weighed to determine the mass proportion of each fraction and C and ^{13}C contents.

Litter and soil C content and $\delta^{13}\text{C}$ analyses

Plant litter samples were oven-dried at 50 °C for 48 h and ball-milled for measuring C and ^{13}C abundance. Soil samples of each aggregate fraction were ball-milled and passed through a 0.25 mm sieve, and treated with 10% HCl for 24 h to remove carbonates before SOC and $\delta^{13}\text{C}$ analysis. The C content and $\delta^{13}\text{C}$ of soil and litter samples were analyzed using a stable isotope ratio mass spectrometer (Isoprime 100, Elementar, Germany) connected to an elemental analyzer (vario MICRO cube, Elementar, Germany). The C isotope ratios were expressed relative to the international PDB limestone standard as $\delta^{13}\text{C}$. Standards of acetanilide, L-histidine, D-glutamic acid and glycine were used to calibrate the data, and the analytical precision for $\delta^{13}\text{C}$ was <0.2‰.

Data calculation

The litter-derived C in soils was calculated using a two-source mixing model according to the difference in soil $\delta^{13}\text{C}$ values between the litter input treatment ($\delta^{13}\text{C}_{\text{treatment}}$) and control ($\delta^{13}\text{C}_{\text{control}}$) as follows (Balesdent and Balabane 1996):

$$F_i = \frac{\delta^{13}\text{C}_{\text{treatment}} - \delta^{13}\text{C}_{\text{control}}}{\delta^{13}\text{C}_{\text{litter}} - \delta^{13}\text{C}_{\text{control}}} \quad (1)$$

where F_i represents the proportion of litter-derived C in aggregate fraction i , which ranges from 0 to 1. No litter-derived C is assumed to be contained in soils when F_i is 0, and all soil C is assumed to be derived from litter C input when F_i is 1. In addition, $\delta^{13}\text{C}_{\text{litter}}$ in the equation is the value of $\delta^{13}\text{C}$ in locally present aboveground and/or belowground litter.

The litter-derived (LitC_i) and native (NatC_i) C content (g kg^{-1}) of each aggregate fraction was calculated by multiplying total C content of fraction i (TC_i) with F_i or $(1 - F_i)$ as in Eqs. (2) and (3), respectively.

$$\text{LitC}_i = \text{TC}_i \times F_i \quad (2)$$

$$\text{NatC}_i = \text{TC}_i \times (1 - F_i) \quad (3)$$

The C flow pathway between the aggregates was determined using a previously described method considering that the increasing $\delta^{13}\text{C}$ in the fraction corresponds to the degree of its microbial transformation (Gunina and Kuzyakov 2014). Firstly, the difference ($\Delta^{13}\text{C}$) was calculated as the $\delta^{13}\text{C}$ of the aggregates minus the corresponding $\delta^{13}\text{C}$ of the bulk soil. According to increasing $\Delta^{13}\text{C}$ values, we directed the arrows between the aggregate size classes, and the fractions at the start of the arrow were considered as “source” and at the end as “product”. Thereafter, the $\Delta^{13}\text{C}$ of the “product” was subtracted from the $\Delta^{13}\text{C}$ of the “source” for each fraction, with a decreasing difference in $\Delta^{13}\text{C}$ indicating a proportionally higher the probability of C flow between the fractions.

Statistical analysis

Data were analyzed using the software R (version 4.4.1). A two-way analysis of variance (two-way ANOVA) was conducted to test the effects of litter type and forest type on the mass proportion, and the total, litter-derived and native C content after 1 and 2 years. Then the Tukey’s honestly significant difference (HSD) test was performed for post hoc pairwise comparisons. Data were tested for normality and homogeneity of variances and transformed whenever necessary. If not otherwise stated, the significance level was set to $p = 0.05$.

Table 1 Two-way ANOVA analysis of litter input and forest type on soil aggregate mass proportion after 1 and 2 years

Factors	df	1 year			2 years		
		Macro-aggregate	Micro-aggregate	Silt + Clay	Macro-aggregate	Micro-aggregate	Silt + Clay
Litter input	3	<0.001	<0.001	0.14	0.53	0.09	0.99
Forest type	2	<0.001	<0.001	0.001	0.002	0.003	0.02
Litter input × Forest type	6	0.44	0.55	0.87	0.72	0.44	0.76

Data in table are the *p* values

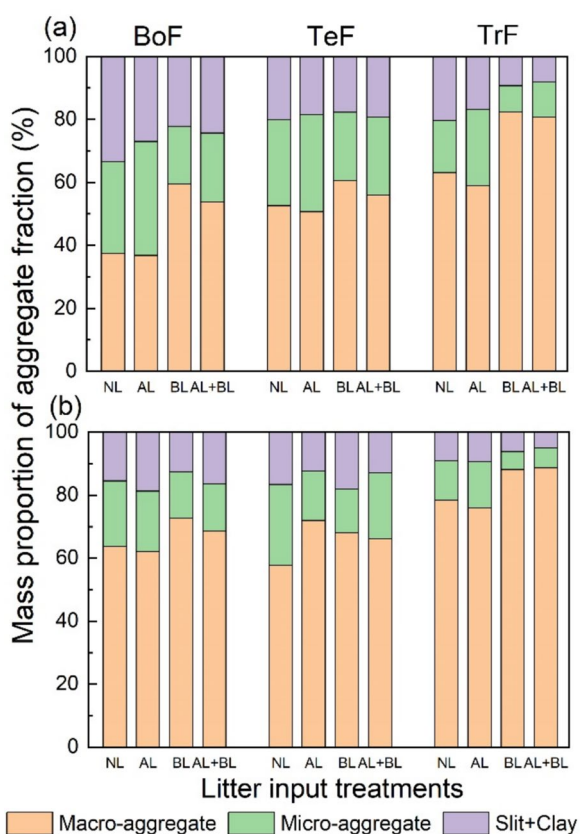


Fig. 2 Effects of litter input on aggregate mass proportion in the boreal, temperate and tropical forests along a climatic gradient after **a** 1 and **b** 2 years. *NL* non-litter input, *AL* aboveground litter input, *BL* belowground litter input, *AL + BL* aboveground plus belowground litter input, *BoF* boreal forest, *TeF* temperate forest, *TrF* tropical forest

Results

Soil aggregate mass proportion

Litter input and forest type had significant impacts on soil aggregate mass proportions, but their interactive effects were not significant (Table 1). The mass proportion of macro-aggregate across three forests was higher in the BL (67.48%) than that in both the NL (51.06%, *p*=0.03) and AL (48.8%, *p*=0.03) treatment after 1 year

of litter input (Fig. 2a). However, in tropical forests, 1 year after litter input the mass proportion of micro-aggregate across the three forests was lower in both the BL (16.1%, *p*<0.001) and AL+BL (19.23%, *p*<0.001) than in the AL treatment (30.39%). Additionally, after 1 year, the BL treatment had a lower micro-aggregate mass proportion than the NL treatment (24.34%, *p*=0.04) (Fig. 2a). The mass proportion of the silt + clay fraction among litter input treatments did not differ significantly after 1 year (Fig. 2a), and the mass proportions of all aggregate fractions were not significantly different between litter input treatments after 2 years (Fig. 2b). The macro-aggregate mass proportion in the tropical forest was significantly higher than that in both the boreal and temperate forests after 1 and 2 years, while the mass proportion of micro-aggregate was opposite (Fig. 2a, b). Moreover, in the tropical and temperate forests, the mass proportions of the silt + clay fraction was lower than that in the boreal forest after 1 year (Fig. 2a), but lower in the tropical forest than in both the boreal and temperate forests after 2 years (Fig. 2b).

Soil aggregate δ¹³C and total, litter-derived and native C contents

Soil aggregate δ¹³C was significantly affected by litter input, forest type and their interaction (Table 2; Fig. 3). The δ¹³C values of macro-aggregate in the AL + BL treatment were lower than under both the NL (*p*=0.006) and AL (*p*=0.007) treatments after 1 year (Fig. 3a), and lower than under the NL treatment after 2 years in the boreal forest (Fig. 3d). For the temperate forest, we only observed lower micro-aggregate δ¹³C in the BL and AL + BL treatments compared to the NL treatment after 1 year of litter input (Fig. 3b). The values of δ¹³C of each fraction and bulk soil were all lower in both the BL and the AL + BL treatments than in the NL and AL treatments in the tropical forest after 1 and 2 years (Fig. 3c, f). The average δ¹³C values of both bulk soil and aggregate fractions of litter input treatments were all significantly lower in the tropical forest compared to the boreal and temperate forests, but there were no differences in δ¹³C values between the boreal and temperate forests.

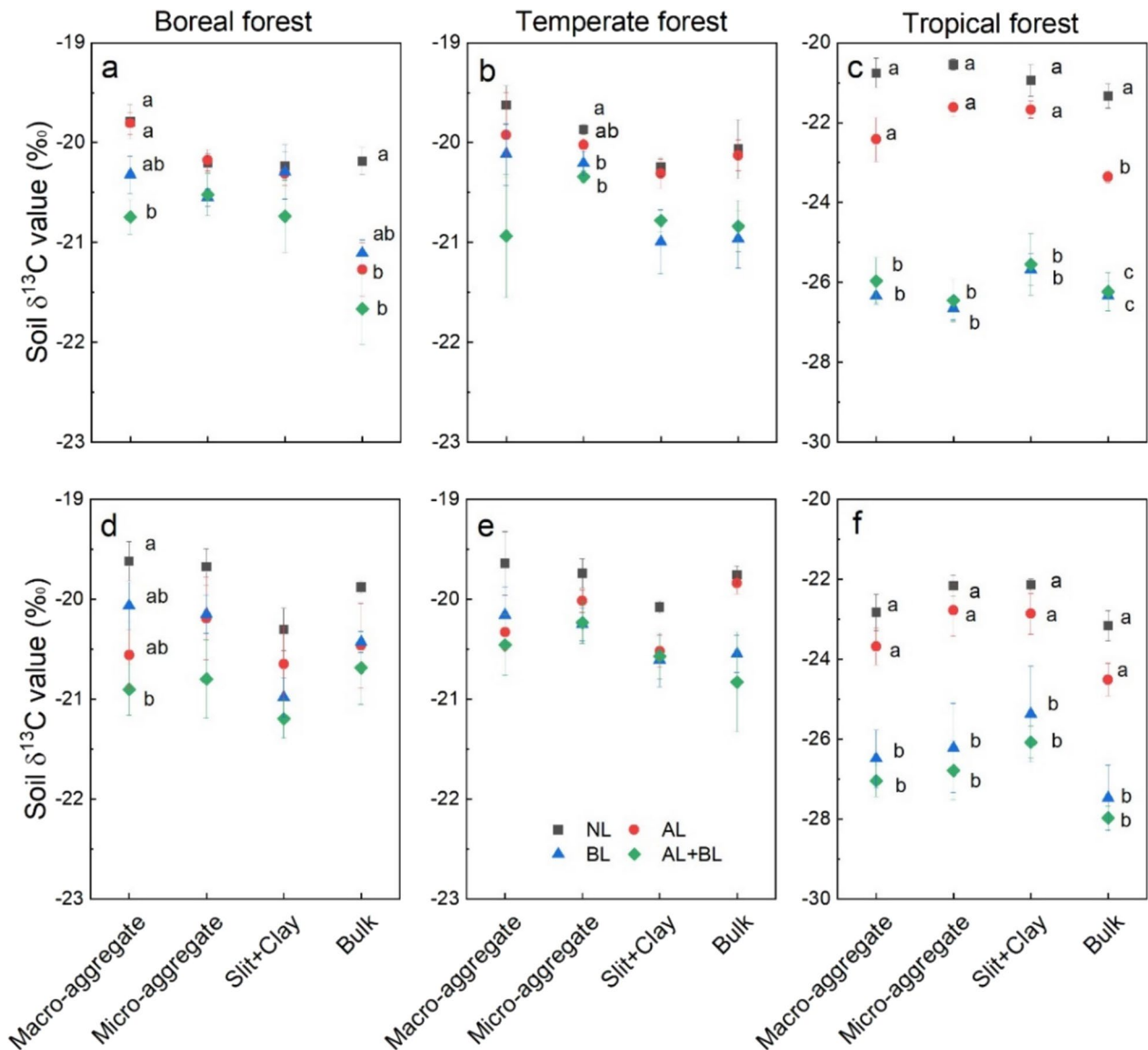


Fig. 3 Changes of soil bulk and aggregate $\delta^{13}\text{C}$ among litter input treatments in **a** boreal, **b** temperate and **c** tropical forest after 1 year, and **d** boreal, **e** temperate and **f** tropical forest after 2 years. NL non-litter input, AL aboveground litter input, BL belowground litter input, AL + BL aboveground plus belowground litter input

Table 2 Two-way ANOVA analysis of litter input and forest type on total C content and $\delta^{13}\text{C}$ of each aggregate fraction after 1 and 2 years

Factors	Soil $\delta^{13}\text{C}$				Total C content			
	df	Macro-aggregate	Micro-aggregate	Silt + Clay	Bulk soil	Macro-aggregate	Micro-aggregate	Silt + Clay
Litter input	3	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
Forest type	2	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
Litter input x Forest type	6	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
Litter input	3	<0.001	0.001	<0.001	<0.001	<0.001	0.02	0.006
Forest type	2	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
Litter input x Forest type	6	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001

Data in table are the *p* values

Table 3 Two-way ANOVA analysis of litter input and forest type on litter-derived and native C content of each aggregate fraction after 1 and 2 years

Factors	df	Litter-derived C content			Native C content		
		Macro-aggregate	Micro-aggregate	Silt + Clay	Macro-aggregate	Micro-aggregate	Silt + Clay
Litter input	3	<0.001	<0.001	<0.001	<0.001	<0.001	0.23
Forest type	2	<0.001	<0.001	<0.001	<0.001	<0.001	0.59
Litter input × Forest type	6	<0.001	<0.001	<0.001	0.001	<0.001	0.08
Litter input	3	0.009	0.008	0.006	0.06	0.04	0.008
Forest type	2	<0.001	<0.001	<0.001	0.07	0.006	0.002
Litter input × Forest type	6	<0.001	<0.001	<0.001	0.16	0.04	0.04

Data in table are the *p* values

The effects of litter input on total, litter-derived and native C contents varied among forest types (Tables 2, 3; Fig. 4), except for the native C content of the silt + clay fraction after 1 year and the native C content of macro-aggregate fraction after 2 years. Compared to the AL treatment, the belowground root litter input (i.e., BL and AL + BL treatments) had the higher litter-derived C contents of all aggregate fractions in the tropical forest, which led to higher total C contents in both BL and AL + BL treatments than that in the NL and AL treatments after 1 and 2 years (Fig. 4a–f). However, soil native C content of the macro- and micro-aggregate fractions in both the BL and AL + BL treatments were lower than that in the NL and AL treatments in the tropical forest (Fig. 4a, b). For the boreal forest, the total C content of the macro-aggregate in the BL treatment was significantly higher than that in the NL treatment after 1 year (Fig. 4a), and the total C content of the silt + clay fraction in the BL treatment was higher than that in the AL treatment after 2 years (Fig. 4f). In addition, the native C content of the silt + clay fraction in the AL + BL treatment was significantly lower than that in the NL treatment in the boreal forest after 2 years (Fig. 4f). There were no changes in total, litter-derived, and native C content in all aggregate fractions in the temperate forest (Fig. 4a–f).

Compared to both boreal and temperate forests, total and litter-derived C content was generally higher in the tropical forest (Fig. 4). However, the native C contents of the macro- and micro-aggregates in the tropical forest were lower than that in the boreal and temperate forests after 1 year (Fig. 4a, b). Moreover, the native C content of the micro-aggregate in the boreal forest was lower than that in the temperate forest (Fig. 4e), and the native C content of the silt + clay fraction in the boreal forest was lower than that in both temperate and tropical forests after 2 years (Fig. 4f).

Pathways of C flow among aggregate fractions

The pathway of C flow between soil aggregates differed among litter input and forest type. In general, soil C flowed directly from the silt + clay fraction or indirectly via the micro-aggregate to macro-aggregate fractions in both the boreal and temperate forests. The pathway of C flow was opposite from the macro-aggregate to the silt + clay or micro-aggregate fraction in the BL and AL + BL treatments after 1 year (Fig. 5a, b). For the tropical forest, however, soil macro-aggregates generally served as a C “source” (lighter $\Delta^{13}C$) for the silt + clay fraction (heaviest $\Delta^{13}C$), except for the NL treatment after 1 year (Fig. 5c).

Discussion

Effects of litter input and forest type on soil aggregation

Our results showed that soil aggregation was affected by the belowground root litter rather than the aboveground litter input, considering the higher mass proportions of macro-aggregate in the BL treatment than in the NL and AL treatments (Fig. 2). This result supported our first hypothesis that belowground root litter enhances soil aggregation compared to aboveground litter input. Similarly, several previous studies also observed that plant roots and mycorrhizal fungi play a dominant role in soil aggregation (Siddiky et al. 2012; Morris et al. 2019; Rillig et al. 2015), because roots exert an entanglement effect, pushing soil particles together to form macro-aggregates (Poirier et al. 2018; Baumert et al. 2021). Furthermore, root mucilage and exudates, mainly composed of polysaccharides, can enhance the growth of different microbes, which contributes to the formation of macro-aggregates (Mizuta et al. 2015). The biochemical quality of organic matter can impact differently on soil aggregation, with a rapid but short- and medium-term aggregate stability induced by organic matter rich in carbohydrate C, while organic matter rich in aromatic C barely enhances soil aggregation (Sarker et al. 2022). In contrast

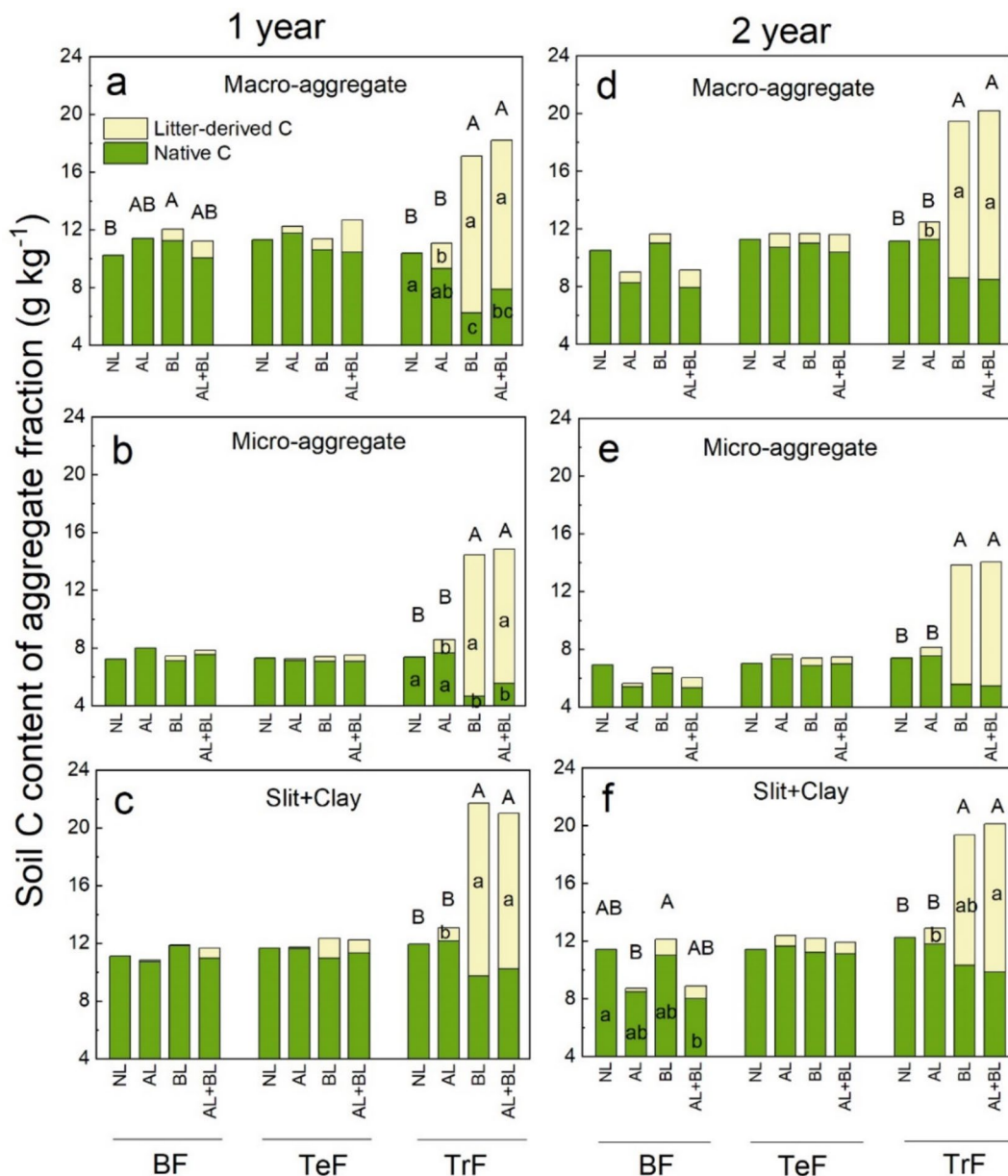


Fig.4 Changes of the total, litter-derived and native C content of **a** macro-aggregate, **b** micro-aggregate and **c** slit + clay fraction after 1 year, and **d** macro-aggregate, **e** micro-aggregate and **f** silt + clay fraction after 2 years of litter input in boreal, temperate and tropical forest. *NL* non-litter input, *AL* aboveground litter input, *BL* belowground litter input, *AL + BL* aboveground plus belowground litter input, *BoF* boreal forest, *TeF* temperate forest, *TrF* tropical forest. The litter-derived C in different treatments are as follows: AL treatment refers to carbon produced by the decomposition of aboveground leaf litter, BL treatment refers to carbon produced by the decomposition of belowground root litter, and AL + BL treatment refers to carbon produced by the combined decomposition of aboveground leaf litter and belowground root litter. Different capital letters on bars indicate significant differences of total aggregate C content among litter input treatments at a level of $p < 0.05$. Different lowercase letters on bars indicate significant differences in the litter-derived C or native C contents among litter input treatments at a level of $p < 0.05$

(See figure on next page.)

Fig.5 Effects of litter input on C flow in **a** boreal forest, **b** temperate forest and **c** tropical forest after 1 and 2 years. The numbers in figures (clouds) indicate the difference ($\Delta^{13}C$) of $\delta^{13}C$ values between each aggregate fraction and bulk soil. The arrows indicate the direction of C flow between aggregates according to increasing $\Delta^{13}C$ values. These numbers above the arrows indicate relative probability of C flow between soil aggregate fractions. The smaller the number on the arrow, the smaller the difference between $\Delta^{13}C$ values, and the higher the probability of C flow. The wider the arrow, the greater the probability

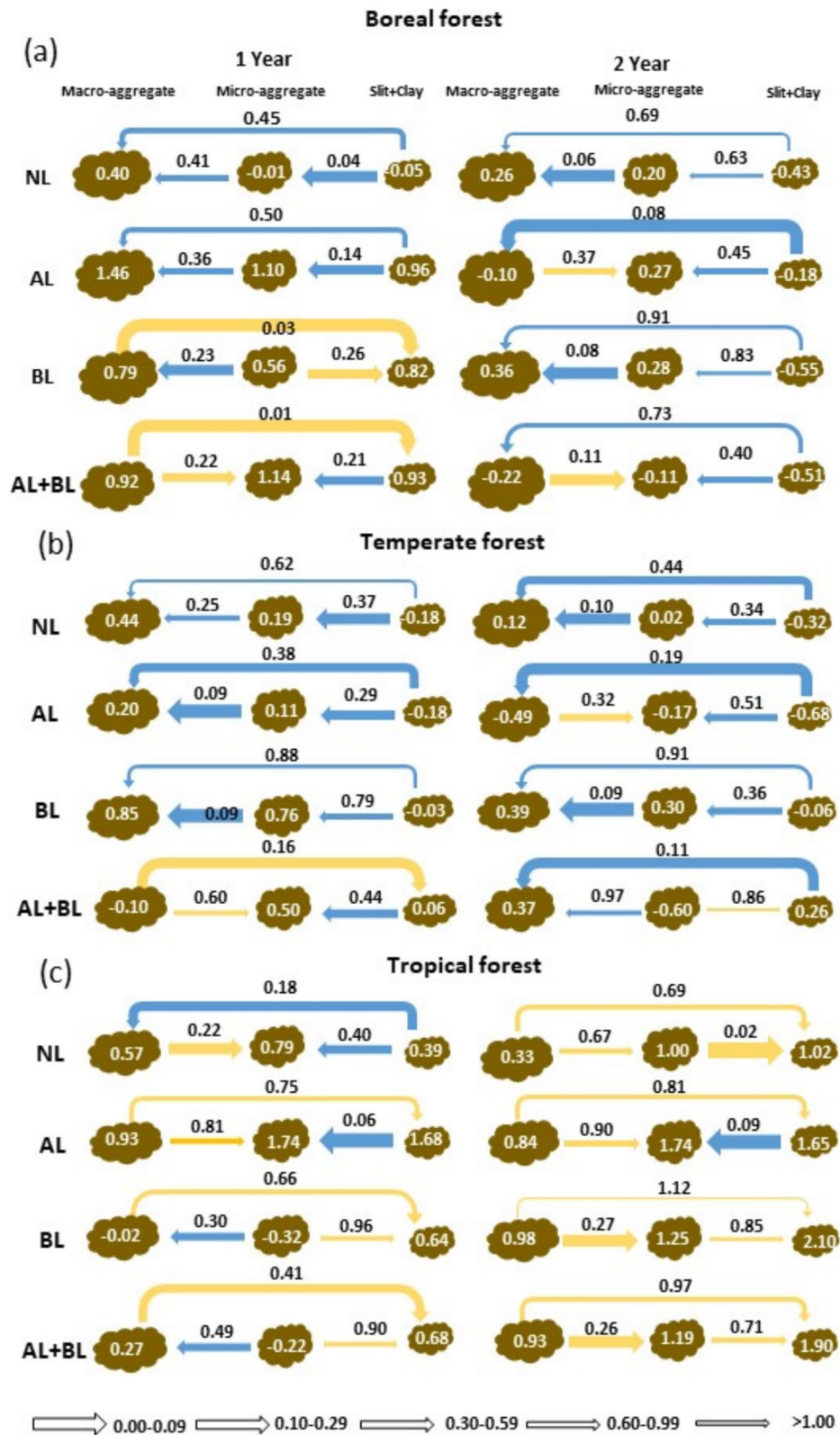


Fig. 5 (See legend on previous page.)

to the results after treatment 1 year, the effects of litter types on aggregate mass proportions were not significant after 2 years (Table 1), implying that the impact of litter type on soil aggregate structure might weaken over time. Similarly, Parwada and Van Tol (2019) found that macro-aggregate formation was a rapid process and the effects of organic matter input on soil aggregation varied over time. The rapid but short- and medium-term aggregate stability induced by root litter input might lead to a lack of difference in mass proportion of aggregates among litter input treatments after 2 years (Sarker et al. 2022). In addition, there were no significant interactions between litter input and forest type on the mass proportions of soil aggregates, indicating that the impact of litter input on soil aggregation did not vary among forest types along the climatic gradient.

We observed that the mass proportion of macro-aggregates in the tropical forest was higher than that in the boreal and temperate forests after both aboveground and belowground litter input (Fig. 2). Soil aggregation can be affected by the quantity and quality of organic matters (Abiven et al. 2009; Sarker et al. 2022), plant root morphological characteristics (Siddiky et al. 2012; Wang et al. 2017), soil bacterial or fungal-dominated community composition (Ortiz et al. 2022), as well as soil mineralogy and microclimate (Laganière et al. 2011; Toriyama et al. 2015; Shi et al. 2023). In this present study, we assumed that changes in soil aggregate mass proportion are unlikely to be mainly caused by soil properties and mineralogy as the homogenous cropland C4 soils were transplanted to forests. Moreover, the enhancement of soil aggregation in the tropical forest is unlikely explained by the higher precipitation, as a because one previous study suggested a negative correlation between macro-aggregate mass and annual precipitation, although there was a positive correlation between macro-aggregate mass and precipitation seasonality (Zhang et al. 2023a). The high temperature and humidity environment in tropical regions accelerates mineral weathering, potentially releasing more active clay minerals and metal ions such as iron and aluminum oxides, thereby enhancing soil aggregation (Siddiky et al. 2012; Morris et al. 2019). In general, productivity declined from tropical to cold temperate forest along a north–south transect in China (Wen and He 2016), which should lead to less organic bindings of soil aggregation (Forster 1990; Tisdall 1994). Supportively, we observed higher total and litter-derived C contents of aggregate fractions in the tropical forest than in the boreal and temperate forests (Fig. 4), which might account for the higher mass proportion of macro-aggregate in the tropical forest. Meanwhile, soil microbial community structure and activities play a key role in controlling soil aggregation (Helfrich et al. 2015; Ortiz et al.

2022). It has been observed that tropical forests generally show higher microbial activity and a higher fungal proportion (Wu et al. 2009), which might facilitate the decomposition of plant litter and provide more binding agents for the formation of macro-aggregates (Zhou et al. 2022).

Effects of litter input on SOC turnover vary among forest type

Plant litter C input has important impacts on the litter-derived C formation through the direct transformation of litter fragments or indirect effect of the “microbial carbon pump” (MCP) (Cotrufo et al. 2015). It also influences changes in soil native C mineralization, a phenomenon referred to as the “priming effect” (Fontaine et al. 2003; Tao et al. 2023; Jiao et al. 2024). In this present study, we found that the input of belowground root litter caused more litter-derived C formation in all fractions than aboveground litter input in the tropical forest (Fig. 4). Our results imply that the input of belowground root litter induced more C formation, supporting our second hypothesis. Fine roots are generally the major carbon sources for soil microbes (Liebmann et al. 2020), and contribute to soil C formation through the pathway of soil microbial byproducts (Mambelli et al. 2011). Moreover, root litter contains more recalcitrant compounds, such as condensed tannins, non-lignin C compounds (Sun et al. 2018; Adamczyk et al. 2019), and chitins from distal ectomycorrhizal roots (Freschet et al. 2013). These chemical properties enable root litter to resist rapid degradation even in a highly active decomposing environment. One of our previous studies also reported a higher C:N ratio of root litter than aboveground litter at the same studied sites (Chen et al. 2022). Consequently, the slower decomposition of the recalcitrant root litter may facilitate greater transfer of root litter-derived C into coarse particulate organic matter through a physical transfer pathway (Cotrufo et al. 2015). Furthermore, our results showed that belowground litter input promoted soil aggregation, potentially increasing the physical protection of SOC (Shi et al. 2023). In addition, the observed increase in litter-derived C across all three aggregate fractions suggests that both microbial and physical-transfer pathways likely contribute simultaneously to soil aggregate C formation following belowground root litter input.

It has been widely observed that the input of organic matter and rhizosphere deposition can alter native soil C mineralization by microorganisms (Kuzyakov et al. 2000; Cheng et al. 2014). In this present study, the belowground root litter input resulted in lower native C content of macro- and micro-aggregate fractions compared to the NL and AL treatments in the tropical forest (Fig. 4f), indicating a positive rhizosphere

priming effect in the tropical forest, except for aboveground litter input. Similarly, Almeida et al. (2021) observed that the presence of roots led to a lower native C content as compared to leaf, twig and bark litter. Though we did not determine root exudates in our study, the C sources from root exudates have been widely suggested to stimulate soil microbial activities, and thus induce more soil native C mineralization than aboveground residues due to the mechanism of 'stoichiometric decomposition' (Blagodatskaya and Kuzyakov 2008). On the other hand, the recalcitrant compounds from dead root residues are generally difficult to be metabolized, which can stimulate the degradation of soil native organic carbon due to the 'nutrient mining' mechanism.

Interestingly, we found that the effects of litter input on SOC turnover varied among forest types. Our results suggest that the response of SOC turnover to belowground root litter input was more sensitive in the tropical forest compared to the boreal and temperate forests. Generally, climate (e.g., MAT and MAP) is one of the most important factors influencing plant litter production and decomposition rate (Côté et al. 1995; Zhou et al. 2008; Wen and He 2016). In this present study, the greater litter-fall production and faster litter decomposition in the tropical forest should be responsible for the greater litter-derived C accumulation and native C loss. Furthermore, it has been well established that the priming effect is closely related to litter quantity and quality (Lyu et al. 2019), ecosystem type, and tree species (Lyu et al. 2018; Huo and Luo 2017; Perveen et al. 2019), as well as climatic conditions and soil properties (Lyu et al. 2019). In this present study, the favorable climatic conditions (e.g., high mean annual temperature) in the tropical site are likely to promote SOC turnover (Leff et al. 2012; Sun et al. 2019). For example, a 1 °C increase in temperature could lead to decreases in turnover time of 4–11% of the medium-active SOC and 8–16% of the stabilized SOC fractions, respectively (Hakkenberg et al. 2008). Moreover, we observed that the response of native C induced by litter input was more sensitive in the boreal forest than in the temperate forest, resulting in lower native C content of the micro-aggregate and silt + clay fractions in the boreal forest compared to the temperate forest after 2 years of litter input. In our study, species richness in the boreal forest was lower than that in the temperate and tropical forests. Plant species richness promotes soil carbon (C) and nitrogen (N) stocks via increased plant productivity (Cong et al. 2014; Chen et al. 2020), but the intensified plant-microbial competition for nitrogen can reduce the rhizosphere priming effects (Yin et al. 2018).

Effects of litter input and forest type on soil aggregate C flow

Our results showed that litter type changed soil C flow among aggregate fractions. Generally, aboveground litter input led to soil C flow from the silt + clay to the macro-aggregate fraction, or indirectly passed via the micro-aggregate to macro-aggregate fraction in both the boreal and temperate forests. This result supports an earlier concept of soil aggregation that suggests the particles of <20 µm diameter are bound to water-stable secondary particles of 20–60 µm diameter, and that these secondary particles in turn form larger aggregates (Tisdall and Oades 1982). According to the Microbial Efficiency-Matrix Stabilization (MEMS) model (Cotrufo et al. 2013), the low molecular weight compounds from the early stage of leaf litter decomposition are more likely to bond with silt and clay particles, and increase soil microbial substrate use efficiency (Cotrufo et al. 2013). Through this process, microbial cell wall components can enhance stable aggregate formation in clay soils (Tisdall and Oades 1982; Mizuta et al. 2015). In contrast to aboveground litter, soil C flowed directly from the macro-aggregate to the micro-aggregate fraction or indirectly passed via the silt + clay fraction to the micro-aggregate fraction in the AL + BL treatment in both the boreal and temperate forests after 1 year of litter input, reflecting that the micro-aggregates were formed inside the macro-aggregates (Gunina and Kuzyakov 2014). In this present study, the belowground root litter input had a fast enhancement of soil macro-aggregate formation, which might mainly account for the change of C flow from the macro-aggregate to the micro-aggregate fraction. Furthermore, the releases of organic acids from plant root can increase the surface charge density of colloidal particles (e.g., iron and aluminum oxides, montmorillonite and other clay minerals) in macro-aggregates through coordination adsorption or ion exchange (Huang et al. 2021; Wiesenbauer et al. 2025), accelerating the formation of 'organic-mineral complexes' in micro-aggregates. It has also been shown that the decomposition products of belowground root residues provide more binders for further connecting structurally stable micro-aggregates (Gunina and Kuzyakov 2014; Lajtha et al. 2018).

In contrast to the boreal and temperate forests, soil C flowed mainly from the macro-aggregate to the micro-aggregate and silt + clay fractions in the tropical forest. This is consistent with several previous studies that found that the main direction of C flows within the aggregates was from the free POM to the mineral micro-aggregate fractions in both coniferous and deciduous forests (Gunina and Kuzyakov 2014), and from the macro-aggregate to the silt + clay fraction in forests along a secondary successional chronosequence (Shi et al. 2023). Generally,

litter decomposition and SOC turnover are relatively fast in tropical sites (Leff et al. 2012), which leads to the formation of more litter residue C via a physical-transfer path and thereby enhances soil aggregation (Cotrufo et al. 2015). Consequently, the litter-derived C flows from the macro-aggregate to the micro-aggregate or silt + clay fractions.

Collectively, we quantified the importance of different plant C inputs to soil aggregation, SOC formation and flow across different forests along a climate gradient, which contributes to understanding future SOC accumulation and stabilization. Yet, our study has limitations that should be noted. First, the soil sieving and re-packing process during the transplantation of C4 soil to forest sites disturbed the original soil physical structure and aggregation formation and protection (Hassink 1992). This disturbance may interfere with the litter input and forest type treatment effects on soil aggregation and thereby SOC turnover and flow. Second, the ingrowth cores may impact root and mycorrhizal fungal growth, thereby affecting contributions of roots and mycorrhizal fungi to SOC turnover (Huang et al. 2021). Third, the difference of soil microbial community in C4 soil may lead to reduced litter decomposition due to the lack of 'home-field advantage' (HFA) that microbes might decompose litter originating from their own community more easily than from elsewhere (Pugnaire et al. 2023). Additionally, our study only used ^{13}C isotopic tracing that can not to distinguish and quantify the relative contribution of aboveground and belowground root litter to SOC turnover. Future studies that use the ingrowth core approach to quantify the impacts of litter input on SOC turnover along climatic gradients are recommended to use undisturbed soils, and should apply the coupling isotopic tracing technique (e.g., ^{13}C and ^{15}N) in a field experiment.

Conclusion

Our study demonstrates that belowground root litter input enhances soil aggregation in forests along a climatic gradient compared to aboveground litter input. Moreover, belowground root litter promotes greater litter-derived C accumulation and reduces native C content more markedly than aboveground litter in the tropical forest. However, the effects of litter input on soil aggregate carbon turnover are less evident in the boreal and temperate forests. Our results imply that the impacts of litter input on soil carbon turnover depend on the forest type, and the response of SOC turnover to the belowground root litter is more sensitive in the tropical forest than in the temperate forest. In addition, our results show that the direction and probability of C flow among aggregate fractions differ among litter type and forest types, implying that litter input and forest type can alter

soil C transfer among aggregate fractions, and thereby the pathway of soil carbon stabilization. Collectively, our results suggest that quantifying contributions of aboveground and belowground litter C input to SOC turnover in different forest types is clearly needed for better understanding and projection of SOC sequestration and stability in global forests.

Abbreviations

C	Carbon
SOC	Soil organic carbon
MAP	Mean annual precipitation
MAT	Mean annual air temperature
AL	Aboveground litter input
BL	Belowground litter input
AL + BL	Aboveground plus belowground litter input
NL	No litter input as control

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Author contributions

Qinqin Xu: Data curation; formal analysis; writing—original draft. Wei Zhang, Junkai Hu, Xiyue Wang: Data curation, supervision, editing. Yalin Hu: Data curation, supervision, editing, resources, project administration, funding acquisition. Sebastian Leuzinger and Yong Zheng: Review & editing.

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Availability of data and material

Data sets generated during the current study are available from the corresponding author on reasonable request.

Declarations

Ethics approval and consent to participate

Not applicable.

Consent for publication

All authors approved the manuscript for publication in the *Ecological Processes*.

Competing interests

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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References

- Abiven S, Menasseri S, Chenu C (2009) The effects of organic inputs over time on soil aggregate stability—a literature analysis. *Soil Biol Biochem* 41:1–12. <https://doi.org/10.1016/j.soilbio.2008.09.015>
- Adamczyk B, Sietiö O, Biasi C, Heinonsalo J (2019) Interaction between tannins and fungal necromass stabilizes fungal residues in boreal forest soils. *New Phytol* 223:16–21. <https://doi.org/10.1111/nph.15729>

- Almeida LFI, Souza IF, Hurtarte LCC, Teixeira PPC, Inagaki TM, Silva IR, Mueller CW (2021) Forest litter constraints on the pathways controlling soil organic matter formation. *Soil Biol Biochem* 163:108447. <https://doi.org/10.1016/j.soilbio.2021.108447>
- Atere CT, Gunina A, Zhu Z, Xiao ML, Liu SL, Kuzyakov Y, Chen L, Deng YW, Wu JS, Ge TD (2020) Organic matter stabilization in aggregates and density fractions in paddy soil depending on long-term fertilization: tracing of pathways by ^{13}C natural abundance. *Soil Biol Biochem* 149:107931. <https://doi.org/10.1016/j.soilbio.2020.107931>
- Balesdent J, Balabane M (1996) Major contribution of roots to soil carbon storage inferred from maize cultivated soils. *Soil Biol Biochem* 28:1261–1263. [https://doi.org/10.1016/0038-0717\(96\)00112-5](https://doi.org/10.1016/0038-0717(96)00112-5)
- Baumert VL, Forstner SJ, Zethof JH, Vogel C, Heitkötter J, Schulz S, Kögel-Knabner I, Mueller CW (2021) Root-induced fungal growth triggers macroaggregation in forest subsoils. *Soil Biol Biochem* 157:108244. <https://doi.org/10.1016/j.soilbio.2021.108244>
- Berhongaray G, Cotrufo FM, Janssens IA, Ceulemans R (2019) Below-ground carbon inputs contribute more than above-ground inputs to soil carbon accrual in a bioenergy poplar plantation. *Plant Soil* 434:363–378. <https://doi.org/10.1007/s11104-018-3850-z>
- Bird JA, Kleber M, Torn MS (2008) ^{13}C and ^{15}N stabilization dynamics in soil organic matter fractions during needle and fine root decomposition. *Org Geochem* 39:465–477. <https://doi.org/10.1016/j.orggeochem.2007.12.003>
- Blagodatskaya E, Kuzyakov Y (2008) Mechanisms of real and apparent priming effects and their dependence on soil microbial biomass and community structure: critical review. *Biol Fertil Soils* 45:115–131. <https://doi.org/10.1007/s00374-008-0334-y>
- Cao JB, He XX, Chen YQ, Chen YP, Zhang YJ, Yu SQ, Zhou LX, Liu ZF, Zhang CL, Fu SL (2020) Leaf litter contributes more to soil organic carbon than fine roots in two 10-year-old subtropical plantations. *Sci Total Environ* 704:135341. <https://doi.org/10.1016/j.scitotenv.2019.135341>
- Chen X, Chen HYH, Chen C, Ma Z, Searle EB, Yu Z, Huang Z (2020) Effects of plant diversity on soil carbon in diverse ecosystems: a global meta-analysis. *Biol Rev* 95:167–183. <https://doi.org/10.1111/brv.12554>
- Chen T, Hong XM, Hu YL, Wang QK, Yu LZ, Wang XW (2022) Effects of litter input on the balance of new and old soil organic carbon under natural forests along a climatic gradient in China. *Biogeochemistry* 160:409–421. <https://doi.org/10.1007/s10533-022-00970-4>
- Cheng WX, Parton WJ, Gonzalez-Meler MA, Phillips R, Asao S, McNickle GG, Brzostek E, Jastrow JD (2014) Synthesis and modeling perspectives of rhizosphere priming. *New Phytol* 201:31–44. <https://doi.org/10.1111/nph.12440>
- Cong WF, Ruijven J, Mommer L, De Deyn GB, Berendse F, Hoffland E (2014) Plant species richness promotes soil carbon and nitrogen stocks in grasslands without legumes. *J Ecol* 102:1163–1170. <https://doi.org/10.1111/1365-2745.12280>
- Cotrufo MF, Wallenstein MD, Boot CM, Denef K, Paul E (2013) The microbial efficiency-matrix stabilization (MEMS) framework integrates plant litter decomposition with soil organic matter stabilization: do labile plant inputs form stable soil organic matter. *Glob Change Biol* 19:988–995. <https://doi.org/10.1111/gcb.12113>
- Cotrufo MF, Soong JL, Horton AJ, Campbell EE, Haddix ML, Wall DH, Parton AJ (2015) Formation of soil organic matter via biochemical and physical pathways of litter mass loss. *Nat Geosci* 8:776–779. <https://doi.org/10.1038/ngeo2520>
- Coûteaux MM, Bottner P, Berg B (1995) Litter decomposition, climate and litter quality. *Trends Ecol Evol* 10:63–66. [https://doi.org/10.1016/S0169-5347\(00\)88978-8](https://doi.org/10.1016/S0169-5347(00)88978-8)
- Crow SE, Lajtha K, Filley TR, Swanston CW, Bowden RD, Caldwell BA (2009) Sources of plant-derived carbon and stability of organic matter in soil: implications for global change. *Glob Change Biol* 15:2003–2019. <https://doi.org/10.1111/j.1365-2486.2009.01850.x>
- Dijkstra FA, Zhu B, Cheng W (2020) Root effects on soil organic carbon: a double-edged sword. *New Phytol* 230:60–65. <https://doi.org/10.1111/nph.17082>
- Fontaine S, Mariotti A, Abbadie L (2003) The priming effect of organic matter: a question of microbial competition? *Soil Biol Biochem* 35:837–843. [https://doi.org/10.1016/S0038-0717\(03\)00123-8](https://doi.org/10.1016/S0038-0717(03)00123-8)
- Forster SM (1990) The role of microorganisms in aggregate formation and soil stabilization: types of aggregation. *Arid Soil Res Rehabil* 4:85–98. <https://doi.org/10.1080/15324989009381236>
- Freschet GT, Cornwell WK, Wardle DA, Elumeeva TG, Liu WD, Jackson BG, Onipchenko VG, Soudzilovskaia NA, Tao JP, Cornelissen JHC (2013) Linking litter decomposition of above- and below-ground organs to plant-soil feedbacks worldwide. *J Ecol* 101:943–952. <https://doi.org/10.1111/1365-2745.12092>
- Fulton-Smith S, Cotrufo MF (2019) Pathways of soil organic matter formation from above and belowground inputs in a *Sorghum bicolor* bioenergy crop. *Glob Change Biol Bioenergy* 11:971–987. <https://doi.org/10.1111/gcbb.12598>
- Gunina A, Kuzyakov Y (2014) Pathways of litter C by formation of aggregates and SOM density fractions: implications for ^{13}C natural abundance. *Soil Biol Biochem* 71:95–104. <https://doi.org/10.1016/j.soilbio.2014.01.011>
- Hakkenberg R, Churkina G, Rodeghiero M, Börner A, Steinhof A, Cescatti A (2008) Temperature sensitivity of the turnover times of soil organic matter in forests. *Ecol Appl* 18:119–131. <https://doi.org/10.1890/06-1034.1>
- Hassink J (1992) Effects of soil texture and structure on carbon and nitrogen mineralization in grassland soils. *Biol Fertil Soils* 14:126–134. <https://doi.org/10.1007/BF00336262>
- Helfrich M, Ludwig B, Thoms C, Gleixner G, Flessa H (2015) The role of soil fungi and bacteria in plant litter decomposition and macroaggregate formation determined using phospholipid fatty acids. *Appl Soil Ecol* 96:261–264. <https://doi.org/10.1016/j.apsoil.2015.08.023>
- Huang JS, Liu WX, Yang S, Yang L, Peng ZY, Deng MF, Xu S, Zhang BB, Ahirwal J, Liu LL (2021) Plant carbon inputs through shoot, root, and mycorrhizal pathways affect soil organic carbon turnover differently. *Soil Biol Biochem* 160:108322. <https://doi.org/10.1016/j.soilbio.2021.108322>
- Huo C, Luo CW (2017) Rhizosphere priming effect: a meta-analysis. *Soil Biol Biochem* 111:78–84. <https://doi.org/10.1016/j.soilbio.2017.04.003>
- Jiao NZ, Luo TW, Chen QR, Zhao Z, Xiao XL, Liu JH, Jian ZM, Xie SC, Thomas H, Herndl GJ, Benner R, Gonsior M, Chen F, Cai WJ, Robinson C (2024) The microbial carbon pump and climate change. *Nat Rev Microbiol* 22:408–419. <https://doi.org/10.1038/s41579-024-01018-0>
- Kuzyakov Y, Friedel JK, Stahr K (2000) Review of mechanisms and quantification of priming effects. *Soil Biol Biochem* 32:1485–1498. [https://doi.org/10.1016/S0038-0717\(00\)00084-5](https://doi.org/10.1016/S0038-0717(00)00084-5)
- Laganière J, Angers DA, Paré D, Bergeron Y, Chen HYH (2011) Black spruce soils accumulate more uncomplexed organic matter than aspen soils. *Soil Sci Soc Am J* 75:1125–1132. <https://doi.org/10.2136/sssaj2010.0275>
- Lajtha K, Bowden RD, Crow S, Fekete I, Kotroczo Z, Plante AF, Simpson MJ, Nadelhoffer KJ (2018) The detrital input and removal treatment (DIRT) network: insights into soil carbon stabilization. *Sci Total Environ* 640:1112–1120. <https://doi.org/10.1016/j.scitotenv.2018.05.388>
- Leff JW, Wieder WR, Taylor PG, Townsend AR, Nemet DR, Grandy AS, Cleveland CC (2012) Experimental litterfall manipulation drives large and rapid changes in soil carbon cycling in a wet tropical forest. *Glob Change Biol* 18:2969–2979. <https://doi.org/10.1111/j.1365-2486.2012.02749.x>
- Liebmann P, Wordell-dietrich P, Kalbitz K, Mikutta R, Kalks F, Don A, Woche SK, Dsilva LR, Guggenberger G (2020) Relevance of aboveground litter for soil organic matter formation—a soil profile perspective. *Biogeosciences* 17:3099–3113. <https://doi.org/10.5194/bg-17-3099-2020>
- Lyu M, Xie J, Vadeboncoeur MA, Wang M, Qiu X, Ren Y, Jiang M, Yang Y, Kuzyakov Y (2018) Simulated leaf litter addition causes opposite priming effects on natural forest and plantation soils. *Biol Fertil Soils* 54:925–934. <https://doi.org/10.1007/s00374-018-1314-5>
- Lyu M, Nie Y, Giardina CP, Vadeboncoeur MA, Ren Y, Fu Z, Wang M, Jin C, Liu X, Xie J (2019) Litter quality and site characteristics interact to affect the response of priming effect to temperature in subtropical forests. *Funct Ecol* 33:2226–2238. <https://doi.org/10.1111/1365-2435.13428>
- Mambelli S, Bird JA, Gleixner G, Dawson TE, Torn MS (2011) Relative contribution of foliar and fine root pine litter to the molecular composition of soil organic matter after in situ degradation. *Org Geochem* 42:1099–1108. <https://doi.org/10.1016/j.orggeochem.2011.06.008>
- Mizuta K, Taguchi S, Sato S (2015) Soil aggregate formation and stability induced by starch and cellulose. *Soil Biol Biochem* 87:90–96. <https://doi.org/10.1016/j.soilbio.2015.04.011>
- Morris EK, Morris DJP, Voget S, Gleber SC, Bigalke M, Wilcke W, Rillig MC (2019) Visualizing the dynamics of soil aggregation as affected by arbuscular mycorrhizal fungi. *ISME J* 13:1639–1646. <https://doi.org/10.1038/s41396-019-0369-0>
- Mou ZJ, Kuang LH, He LF, Zhang J, Zhang XY, Hui DF, Li Y, Wu WJ, Mei QM, He XJ, Kuang YW, Wang J, Wang YQ, Lambers H, Sardans J, Peñuelas J, Liu

- ZF (2021) Climatic and edaphic controls over the elevational pattern of microbial necromass in subtropical forests. *Catena* 207:105707. <https://doi.org/10.1016/j.catena.2021.105707>
- O'Leary MH (1981) Carbon isotope fractionation in plants. *Phytochemistry* 20:553–567. [https://doi.org/10.1016/0031-9422\(81\)85134-5](https://doi.org/10.1016/0031-9422(81)85134-5)
- Ortiz C, Fernández-Alonso MJ, Kitzler B, Díaz-Pinés E, Saiz G, Rubio A, Benito M (2022) Variations in soil aggregation, microbial community structure and soil organic matter cycling associated to long-term afforestation and woody encroachment in a Mediterranean alpine ecotone. *Geoderma* 405:115450. <https://doi.org/10.1016/j.geoderma.2021.115450>
- Parwada C, Van Tol J (2019) Effects of litter quality on macroaggregates reformation and soil stability in different soil horizons. *Environ Dev Sustain* 21:1321–1339. <https://doi.org/10.1007/s10668-018-0089-z>
- Perveen N, Barot S, Maire V, Cotrufo MF, Shahzad T, Blagodatkaya E, Stewart CE, Ding WX, Siddiq MR, Dimassi B, Mary B, Fontaine S (2019) Universality of priming effect: an analysis using thirty five soils with contrasted properties sampled from five continents. *Soil Biol Biochem* 134:162–171. <https://doi.org/10.1016/j.soilbio.2019.03.027>
- Poirier V, Roumet C, Munson AD (2018) The root of the matter linking root traits and soil organic matter stabilization processes. *Soil Biol Biochem* 120:246–259. <https://doi.org/10.1016/j.soilbio.2018.02.016>
- Pugnaire FI, Aares KH, Alifriqui M, Bärthen KA, Kindler C, Schöb C, Manrique E (2023) Home-field advantage effects in litter decomposition is largely linked to litter quality. *Soil Biol Biochem* 148:109069. <https://doi.org/10.1016/j.soilbio.2023.109069>
- Rillig MC, Antonovics J, Caruso T, Lehmann A, Powell JR, Veresoglou SD, Verbruggen E (2015) Interchange of entire communities: microbial community coalescence. *Trends Ecol Evol* 30:470–476. <https://doi.org/10.1016/j.tree.2015.06.004>
- Rubino M, Dungait JAJ, Evershed RP, Bertolini T, De Angelis P, D'Onofrio A, Lagomarsino A, Lubritto C, Merola A, Terrasi F, Cotrufo MF (2010) Carbon input belowground is the major C flux contributing to leaf litter mass loss: evidences from a ¹³C labelled-leaf litter experiment. *Soil Biol Biochem* 42:1009–1016. <https://doi.org/10.1016/j.soilbio.2010.02.018>
- Sarker TC, Zotti M, Fang Y, Giannino F, Mazzoleni S, Bonanomi G, Cai YJ, Chang SX (2022) Soil aggregation in relation to organic amendment: a synthesis. *J Soil Sci Plant Nutr* 22:2481–2502. <https://doi.org/10.1007/s42729-022-00822-y>
- Sayer EJ, Wright SJ, Tanner EVJ, Yavitt BJ, Harms KE, Powers JS, Kaspari M, Garcia MN, Turner BL (2012) Variable responses of lowland tropical forest nutrient status to fertilization and litter manipulation. *Ecosystems* 15:387–400. <https://doi.org/10.1007/s10021-011-9516-9>
- Schmidt MWI, Torn MS, Abiven S, Dittmar T, Guggenberger G, Janssens IA, Kleber M, Kögel-Knabner I, Lehmann J, Manning DAC, Nannipieri P, Rasse DP, Weiner S, Trumbore SE (2011) Persistence of soil organic matter as an ecosystem property. *Nature* 478:49–56. <https://doi.org/10.1038/nature10386>
- Shi JW, Deng L, Gunina A, Alharbi S, Wang KB, Li JW, Liu YL, Shangguan ZP, Kuz'yakov Y (2023) Carbon stabilization pathways in soil aggregates during long-term forest succession: implications from $\delta^{13}\text{C}$ signatures. *Soil Biol Biochem* 180:108988. <https://doi.org/10.1016/j.soilbio.2023.108988>
- Siddiky MRK, Schaller J, Caruso T, Rillig MC (2012) Arbuscular mycorrhizal fungi and collembola non-additively increase soil aggregation. *Soil Biol Biochem* 47:93–99. <https://doi.org/10.1016/j.soilbio.2011.12.022>
- Six J, Paustian K, Elliott ET, Combrink C (2000) Soil structure and organic matter. I. distribution of aggregate-size classes and aggregate-associated carbon. *Soil Sci Soc Am J* 64:681–689. <https://doi.org/10.2136/sssaj2000.642681x>
- Sokol NW, Bradford MA (2019) Microbial formation of stable soil carbon is more efficient from belowground than aboveground input. *Nat Geosci* 12:46–53. <https://doi.org/10.1038/s41561-018-0258-6>
- Spohn M, Giani L (2011) Impacts of land use change on soil aggregation and aggregate stabilizing compounds as dependent on time. *Soil Biol Biochem* 43:1081–1088. <https://doi.org/10.1016/j.soilbio.2011.01.029>
- Steffens C, Helfrich M, Joergensen RG, Eissfeller V, Flessa H (2015) Translocation of ¹³C-labeled leaf or root litter carbon of beech (*Fagus sylvatica* L.) and ash (*Fraxinus excelsior* L.) during decomposition—a laboratory incubation experiment. *Soil Biol Biochem* 83:125–137. <https://doi.org/10.1016/j.soilbio.2015.01.015>
- Sun T, Hobbie SE, Berg B, Hättenschwiler S (2018) Contrasting dynamics and trait controls in first-order root compared with leaf litter decomposition. *PNAS* 115:10392–10397. <https://doi.org/10.1073/pnas.1716595115>
- Sun XL, Tang ZX, Ryan MG, You YM, Sun OJX (2019) Changes in soil organic carbon contents and fractionations of forests along a climatic gradient in China. *For Ecosyst* 6:1. <https://doi.org/10.1186/s40663-019-0161-7>
- Tamura M, Tharayil N (2014) Plant litter chemistry and microbial priming regulate the accrual, composition and stability of soil carbon in invaded ecosystems. *New Phytol* 203:110–124. <https://doi.org/10.1111/nph.12795>
- Tao F, Huang YY, Hungate BA, Manzoni S, Frey SD, Schmidt MWI, Reichstein M, Carvalhais N, Ciais P, Jiang LF, Lehmann J, Wang YP, Houlton BZ, Ahrens B, Mishra U, Hugelius G, Hocking TD, Lu XJ, Shi Z, Viatkin K, Vargas R, Yigini Y, Omuto C, Malik AA, Peralta G, Cuevas-Corona R, Di Paolo LE, Luotto I, Liao CJ, Liang YS, Saynes VS, Huang XM, Luo YQ (2023) Microbial carbon use efficiency promotes global soil carbon storage. *Nature* 618:981–985. <https://doi.org/10.1038/s41586-023-06042-3>
- Tisdall JM (1994) Possible role of soil microorganisms in aggregation in soils. *Plant Soil* 159:115–121. <https://doi.org/10.1007/BF00000100>
- Tisdall JM, Oades JM (1982) Organic matter and water-stable aggregates in soils. *J Soil Sci* 33:141–163. <https://doi.org/10.1111/j.1365-2389.1982.tb01755.x>
- Toriyama J, Hak M, Imaaya A, Hirai K, Kiyono Y (2015) Effects of forest type and environmental factors on the soil organic carbon pool and its density fractions in a seasonally dry tropical forest. *For Ecol Manage* 335:147–155. <https://doi.org/10.1016/j.foreco.2014.09.037>
- Villarino SH, Pinto P, Jackson RB, Piñeiro G (2021) Plant rhizodeposition: a key factor for soil organic matter formation in stable fractions. *Sci Adv* 7:eabd3176. <https://doi.org/10.1126/sciadv.abd3176>
- Wang RZ, Dorodnikov M, Dijkstra FA, Yang S, Xu ZW, Li H, Jiang Y (2017) Sensitivities to nitrogen and water addition vary among microbial groups within soil aggregates in a semiarid grassland. *Biol Fertil Soils* 53:129–140. <https://doi.org/10.1007/s00374-016-1165-x>
- Wang JX, Lan JC, Long QX, Wang SS, Qi X, Huang MZ (2023) Soil organic carbon transfer in aggregates subjected to afforestation in karst region as indicated by ¹³C natural abundance. *For Ecol Manage* 531:120798. <https://doi.org/10.1016/j.foreco.2023.120798>
- Wen D, He N (2016) Forest carbon storage along the north-south transect of eastern China: spatial patterns, allocation, and influencing factors. *Ecol Indic* 61:960–967. <https://doi.org/10.1016/j.ecolind.2015.10.054>
- Werth M, Kuzyakov Y (2008) Root-derived carbon in soil respiration and microbial biomass determined by ¹⁴C and ¹³C. *Soil Biol Biochem* 40:625–637. <https://doi.org/10.1016/j.soilbio.2007.09.022>
- Wiesenbauer J, Gorka S, Jenab K, Schuster R, Kumar N, Rottensteiner C, König A, Kraemer S, Inselsbacher E, Kaiser C (2025) Preferential use of organic acids over sugars by soil microbes in simulated root exudation. *Soil Biol Biochem* 230:109738. <https://doi.org/10.1016/j.soilbio.2025.109738>
- Wu YP, Ma B, Zhou L, Wang HZ, Xu JM, Kemmitt S, Brookes PC (2009) Changes in the soil microbial community structure with latitude in eastern China, based on phospholipid fatty acid analysis. *Appl Soil Ecol* 43:234–240. <https://doi.org/10.1016/j.apsoil.2009.08.002>
- Wu JJ, Zhang DD, Chen Q, Feng J, Li QX, Yang F, Zhang Q, Cheng XL (2018) Shifts in soil organic carbon dynamics under detritus input manipulations in a coniferous forest ecosystem in subtropical China. *Soil Biol Biochem* 126:1–10. <https://doi.org/10.1016/j.soilbio.2018.08.010>
- Wu QX, Wu FZ, Zhu JJ, Ni XY (2023) Leaf and root inputs additively contribute to soil organic carbon formation in various forest types. *J Soils Sediments* 23:1135–1145. <https://doi.org/10.1007/s11368-022-03403-9>
- Yin L, Dijkstra FA, Wang P, Zhu B, Cheng W (2018) Rhizosphere priming effects on soil carbon and nitrogen dynamics among tree species with and without intraspecific competition. *New Phytol* 218:1036–1048. <https://doi.org/10.1111/nph.15074>
- Zhang W, Wu W, Li JW, Liu HB (2023a) Climate and topography controls on soil water-stable aggregates at regional scale: independent and interactive effects. *Catena* 228:107170. <https://doi.org/10.1016/j.catena.2023.107170>
- Zhang YX, Tang ZX, You YM, Guo XW, Wu CJ, Liu SR, Sun OJ (2023b) Differential effects of forest-floor litter and roots on soil organic carbon

formation in a temperate oak forest. *Soil Biol Biochem* 180:109017.

<https://doi.org/10.1016/j.soilbio.2023.109017>

Zhou GY, Guan LL, Wei XH, Tang XL, Liu SG, Liu JX, Zhang DQ, Yan JH (2008)

Factors influencing leaf litter decomposition: an intersite decomposition experiment across China. *Plant Soil* 311:61–72. <https://doi.org/10.1007/s11104-008-9658-5>

Zhou S, Chen L, Wang JY, He LY, Wang J, Ren CJ, Guo YX, Zhao FZ (2022)

Stronger microbial decay of recalcitrant carbon in tropical forests than in subtropical and temperate forest ecosystems in China. *Catena* 215:106351. <https://doi.org/10.1016/j.catena.2022.106351>

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