Biogeochemistry (2024) 167:1609–1617
https://doi.org/10.1007/s10533-024-01185-5

Forest types control the contribution of litter and roots to labile and persistent soil organic carbon

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Received: 16 February 2024 / Accepted: 30 September 2024 / Published online: 23 October 2024

Abstract Forest ecosystems contain a substantial terrestrial reservoir of soil organic carbon (SOC). Here, a "Detritus Input and Removal Treatments" experiment was conducted to explore the effects of litter and roots on soil labile, persistent, and total organic C (TOC) pools in the coniferous, broad-leaved, and coniferous-broad-leaved mixed forests (CF, BF, and CBF, respectively) in the subtropical and warm temperate transition zone in Henan province, eastern China. After 2–3 years of detritus manipulations, neither litter addition nor root exclusion affected soil temperature or moisture. In contrast, litter removal increased soil temperature but decreased soil moisture, regardless of forest types. Litter addition marginally decreased labile OC and TOC contents in the BF but not in the CF and CBF. Litter removal reduced labile OC and TOC contents in the CF and BF and persistent OC contents in the CF only. Root exclusion decreased labile OC contents in the CBF only, but reduced persistent OC and TOC contents in the CF and CBF. Structural equation models suggested that litter but not root manipulation altered SOC pools via changing soil temperature and moisture in the BF, whereas the effects of litter and root manipulation on SOC pools were not related to the changes in soil temperature and moisture in the CF and CBF. Our results suggest that the impact of litter and roots on SOC pools depends on forest types, which may indicate differential responses of SOC storage among forests under global change scenarios.

Keywords Above- and below-ground carbon inputs · Forest soil · Organic carbon fractions · Soil carbon storage · Soil temperature and moisture

Introduction

Forest ecosystems have the largest terrestrial reservoir of soil organic carbon (SOC) and can exert great influence on maintaining the balance of atmospheric carbon dioxide (CO_2) concentrations (Jackson et al. 2017). Previous studies have reported that forest types play an important role in SOC storage (Angst et al. 2019; Castañeda-Gómez et al. 2023). Forest types are important determinants of soil microclimates, litterfall production, root dynamics, and the quality of plant detritus (Pandey et al. 2007; Wang et al. 2008; Xu et al. 2013; Chen et al. 2014; An et al. 2017). These biotic and abiotic factors strongly influence C availability and microbial activities, consequently controlling SOC sequestration (Sokol & Bradford 2019; Sokol et al. 2019). A better understanding of how forest types affect SOC sequestration could help

Responsible Editor: Samantha R. Weintraub-Leff.

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to predict the storage of SOC under global change scenarios.

Plant organic C inputs to soil, through aboveground litter and root detritus and exudates, are the dominant sources of forest SOC pools (Juhos et al. 2021; Sayer et al. 2021; Feng et al. 2022). Growing evidence suggests that plant roots contribute more effectively to SOC sequestration than litter (Rasse et al. 2005; Jackson et al. 2017; Sokol & Bradford 2019). Several mechanisms are proposed to explain such differences. First, belowground roots typically supply much more C than aboveground litter (Rasse et al. 2005). Second, root contains 2–3 times higher concentrations of chemically complex compounds, such as lignin and tannins, than litter; therefore root-derived C has a longer mean residue time (Xia et al. 2015). Third, rhizosphere, as a microbial hotspot, can accelerate SOC formation that is driven by soil microbes (Sokol & Bradford 2019). Finally, root exudates and detritus can immediately be physically protected by their interactions with soil minerals and aggregates (Rillig et al. 2015; Jackson et al. 2017). Although these advantages of root-derived C in SOC sequestration over litter-derived C, whether the contribution of litter and roots to SOC pools follows the similar pattern under different forest types remains largely unknown.

Soil temperature and moisture can affect SOC pools through changing the activities of microorganisms and faunas. The alterations of detrital input can influence soil temperature and moisture (Xu et al. 2013), which, consequently, affects CO_2 emissions and SOC pools. Weintraub et al. (2013) found that in a lowland wet tropical forest, C-cycling enzyme activities were associated with soil moisture during litter manipulation. This indicates that soil moisture regulates microbial activities that largely control SOC turnover. Fekete et al. (2014) found that the effect of soil moisture on CO_2 emissions was weakened but that of soil temperature was promoted in a Central-European deciduous forest when the roots were excluded, implying differential effects of soil temperature and moisture on SOC sequestration. To the best of our knowledge, it remains unclear how soil temperature and moisture differentially affect SOC pools among forest types.

Accordingly, the objective of this study was to investigate how SOC pools and soil temperature and moisture respond to litter and root manipulations with varying forest types. To do this, we chose an experimental site that had adjacent coniferous, broad-leaved, and coniferous-broad-leaved mixed forests (CF, BF, and CBF), then the "Detritus Input and Removal Treatments" (DIRT) experiments were performed in each forest. We analyzed labile and persistent OC, and TOC contents, and soil temperature and moisture after 2–3 years of detritus manipulations.

Methods

Site description

The DIRT experiment is located at the Mountain Xian (32°06'N, 114°01'E, and 204 m a.s.l.) of Nanwan Forest Service, Xinyang, Henan, China. The climate in this region belongs to subtropical and warm temperate transition zone, with mean annual precipitation (1951–2014) and temperature being 1063 mm and 15.2 °C, respectively. The experimental site has three forest types, that is, a coniferous forest (CF), a broad-leaved forest (BF), and a coniferous-broad-leaved mixed forest (CBF). The CF is dominated by *Pinus massoniana* Lamb., the BF by *Quercus acutissima* Carruth., and the CBF by both *P. massoniana* and *Q. acutissima*. The forest floor is approximately 4.6, 5.5 and 4.8 cm for CF, BF and CBF, respectively. The average amounts of litterfall of the CF, BF, and CBF was 546.97, 1642.38 and 707.92 g m^{-2} y^{-1}, respectively. The foliar C-to-nitrogen (N) ratio is 63.88 for *P. massoniana* and 45.64 for *Q. acutissima*. The soil at the experimental site is classified as a Haplic Luvisols (FAO classification). The pH is 4.20, 4.49, and 4.21 for the CF, BF, and CBF soil, respectively.

Experimental design and measurements

For each forest type, the DIRT experiment was established in September 2015 and was laid out as a randomized block design. It included six treatments: control (C), litter addition (LA), litter removal (LR), root exclusion (RE), root exclusion plus litter addition (RELA), and root exclusion plus litter removal (RELR). Each treatment had four replicate plots and the area of each plot was 4 m^2 (2 m × 2 m) with a 2-m buffer zone between adjacent plots (Fig. 1). The plots were intentionally placed

Fig. 1 A photo of the plots in the broad-leaved forests (**a**). A plot that was trenched to a depth of 0.5 m for installing 100-mesh nylon cloth (**b**). The construction of experimental plots (**c**). Routine measurement with a portable device (**d**)

between trees, that is, there were no trees growing in the plots, as shown in Fig. 1. We designed small plots so as to protect the roots from damage because of the trenching manipulation and focus on soil responses. Similar plots were also used in other DIRT experiments (Huang & Spohn 2015; Guo et al. 2021; Castañeda-Gómez et al. 2023). Therefore, 72 plots were included: three forest types × six treatments × four replicates. For the LR and RELR treatments, litter on the forest floor was manually removed every month. The resulting litter was then added to the corresponding LA and RELA plots. For the RE, RELA, and RELR treatments, the plots were trenched to a depth of 0.5 m and insulated with 100-mesh nylon cloth to prevent roots from entering the plots (Fig. 1b), as depicted in previous studies (Feng et al. 2009a, 2009b; Zhang et al. 2023). We cannot exclude the possibility that very few roots may enter the plots from below 0.5 m depth. However, the amounts must be very small, given that most of the tree roots distribute in the 0–0.5 m soil layer. This is particularly true for the fine roots that are strongly associated with SOC sequestration (Xia et al. 2015). Therefore, the very few roots that entered the plots can barely affect the results. The plots without litter and root manipulations were prepared as the controls.

In mid-August of 2017 and 2018, soil temperature at the depth of 10 cm was measured using a thermocouple probe (Li-8100–201) attached to the Li-8100 (LI-COR, Lincoln, USA). Volumetric soil water content (0–10 cm) was measured by using a portable Time Domain Reflectometer equipment (Soil moisture equipment Corp., Santa Barbara, CA, USA). Thereafter, two soil cores (10 cm in depth) were randomly sampled in each plot with a soil auger (10 cm in diameter). The two soil cores were mixed together, sieved with a 2-mm mesh to remove the roots and stones. Soil labile OC was then extracted by using two-step acid hydrolysis method (Zhou et al. 2012). Labile OC pools 1 and 2 in the extracts and SOC in the residues was determined with TOC analyzer (Vario MACRO CUBE, Elementar Inc., Hanau, Germany). The labile OC pools 1 and 2 were summed up as total labile C pools; SOC in the residues were considered as persistent OC. Soil TOC were calculated as the sum of labile and persistent OC pools.

Statistical analyses

A three-way analysis of variance (ANOVA) was performed to test the effects of forest types, and litter and root manipulations on soil temperature and moisture, and the contents of labile and persistent OC, and TOC. The analyses were conducted using PASW Statistics 18 (SPSS Inc., Armonk, NY, USA). When no significant interactions between forest types, and litter and root manipulations were observed, the data were pooled according to the corresponding treatments. Then the significance was tested by using Duncan's Multiple Range Test or Student's t-test. Structural equation models (SEMs) were performed to test how litter and root manipulations altered SOC pools among forests using AMOS 21.0 (SPSS Inc., Armonk, NY, USA).

Results

Changes in soil temperature and moisture

There were no significant interactions between forest types, and litter and root manipulations on soil temperature and moisture (Table 1; $P > 0.05$). The BF soils had the highest temperature and the lowest moisture, while the CBF soils had the lowest temperature and intermediate moisture (Fig. 2a, d; $P < 0.05$). Litter removal decreased soil moisture (Fig. 2b, e; $P < 0.05$) but had no effects on soil temperature. Litter addition and root exclusion did not affect soil moisture and temperature (Fig. 2b, c, e, f).

Changes in SOC pools

Labile and persistent OC and TOC contents were greater in the CF and CBF soils than in the BF soils (Table 1; Fig. 3; $P_{\text{forest}} < 0.001$). The litter addition treatment demonstrated decreased labile OC and TOC contents in the BF soils but not in the CF and CBF soils (Fig. 3a, c). The litter removal treatment demonstrated reduced soil labile OC contents in the CF and BF but not in the CBF soils (Fig. 3a; $P < 0.05$), however, the interactions between forest types and litter manipulation were not observed (Table 1; $P_{\text{forest} \times \text{litter}} > 0.05$). The interactive effects between forest types and litter manipulation on persistent OC and TOC contents were significant (Table 1; $P_{\text{forest} \times \text{litter}} < 0.01$). Litter removal treatment caused reductions in persistent OC contents in the CF but not in the BF and CBF soils (Fig. 3b), whereas it decreased TOC contents in the CF and BF but not in the CBF soils (Fig. 3c).

Significant interactive effects between forest types and root exclusion were observed on labile OC and TOC contents (Table 1; Fig. 3a, c). Root exclusion treatment decreased labile OC contents in the CBF but not in the CF and BF soils ($P_{\text{forest} \times \text{root}} < 0.05$). It decreased TOC contents in the CF and CBF but not in the BF soils ($P_{\text{forest} \times \text{root}} < 0.01$). In contrast, root exclusion treatment decreased persistent OC contents, regardless of forest types ($P_{\text{root}} = 0.001$). Compared with root exclusion alone, both litter and root exclusion had no significant effects on SOC pools in the CBF but caused declines in labile and persistent OC,

Table 1 Three-way analysis of variance for soil temperature (ST), soil moisture (SM), labile OC, persistent OC, and total organic carbon (TOC) as affected by forest types, and litter and root manipulations

Sources of variation	*df*	ST		SM		Labile OC		Persistent OC		TOC	
		F	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*
Forest	2	**281.80**	**< 0.001**	**57.10**	**< 0.001**	**26.45**	**< 0.001**	**30.26**	**< 0.001**	**46.63**	**< 0.001**
Litter	2	**5.90**	**0.005**	**5.76**	**0.005**	**15.63**	**< 0.001**	**5.52**	**0.007**	**14.71**	**< 0.001**
Root	1	0.95	0.334	1.59	0.212	**10.47**	**0.002**	**11.22**	**0.001**	**19.28**	**< 0.001**
Forest × Litter	4	1.97	0.112	1.16	0.339	1.52	0.209	**4.60**	**0.003**	**5.33**	**0.001**
Forest × Root	2	0.67	0.516	1.65	0.202	**3.88**	**0.027**	2.75	0.073	**5.42**	**0.007**
Litter × Root	2	1.00	0.373	0.02	0.983	0.12	0.891	1.57	0.218	1.09	0.345
Forest × Litter × Root	4	0.23	0.922	1.04	0.397	1.39	0.251	0.44	0.778	0.94	0.447
Error	54										

Significant test results ($P < 0.05$) are given in bold

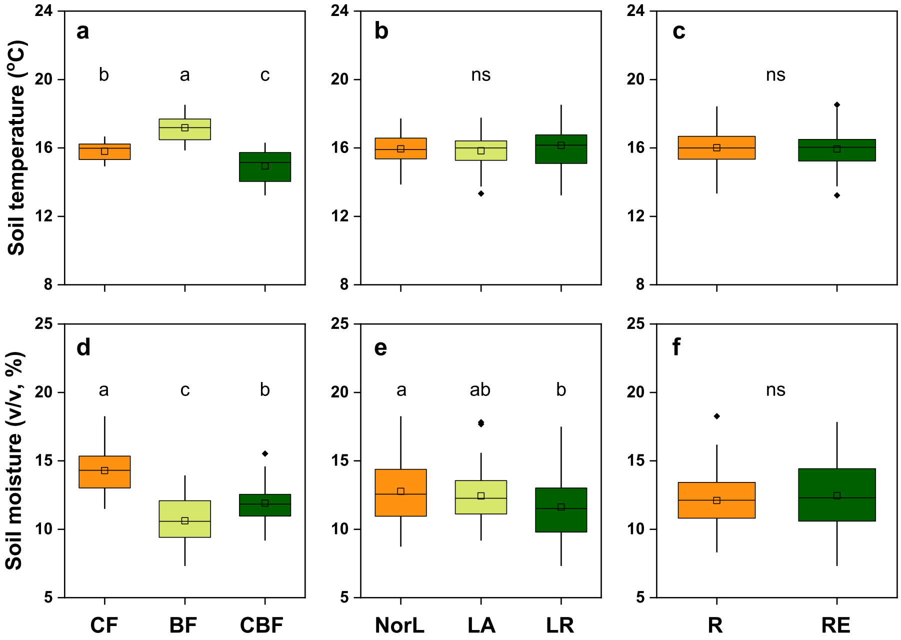

Fig. 2 Soil temperature (**a**, **b**, **c**) and moisture (**d**, **e**,**f**) as affected by forest types (**a**, **d**), and litter (**b**, **e**) and root (**c**, **f**) manipulation (n = 48 for a, b, and d, and e; n = 72 for c and f). Different lower letters indicate significance at $P < 0.05$ among forest types and litter manipulations (Duncan's Multiple Range Test) and between root manipulations (Student's t-test); ns, not significant. CF, coniferous forest; BF, broad-leaved forest; CBF, coniferous-broad-leaved mixed forest; NorL, normal annual aboveground litter inputs; LA, litter addition; LR, litter removal; R, the presence of roots; RE, root exclusion. Box plots show the mean (square), median (horizontal line), 25 and 75% quartile (rectangle), 1.5 × interquartile range (whiskers), and outliers (isolated points)

and TOC contents in the CF and labile OC contents in the BF.

Multivariate effects on SOC pools among forests

The SEMs showed that litter and root manipulations explained a significant proportion of the variance in the contents of labile and persistent OC contents, with their effects varying among forest types (Fig. 4). The changes in labile and persistent OC contents because of litter and root manipulations were not related to changes in soil temperature and moisture in the CF and CBF (Fig. 4a, c). Although root exclusion increased soil moisture in the CF, but moisture-induced changes in labile and persistent OC contents were not evident (Fig. 4a). Litter but not root manipulation had indirect effects on labile and persistent OC contents via altering soil moisture in the BF (Fig. 4b). Moreover, litter manipulation can alter soil moisture directly or indirectly through changing soil temperature.

Discussion

Forest dependence of SOC responses to litter and root C inputs

Litter C inputs have been considered as an important contributor to the fractions and contents of SOM in forests (Fekete et al. 2014; Wu et al. 2018; Zhang et al. 2023). However, in the present study a marginal decrease in labile OC and TOC contents was observed because of litter addition in the BF soils. Similar changes were also reported in a BF that was dominated by northern red oak and paper birch (Pisani et al. 2016). However, such decreases in SOC because of litter addition were not found in the CF and CBF. This could be partly attributed to the differences of quality and quantity of litter among forest types. The

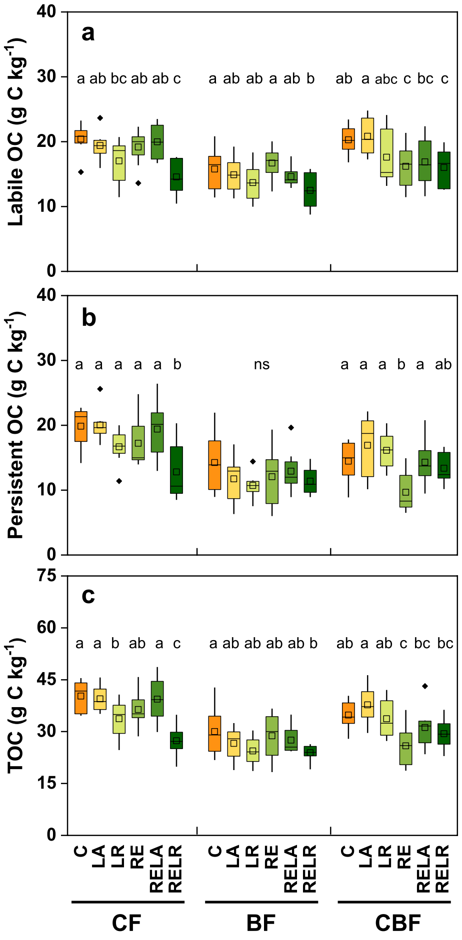

Fig. 3 Contents of labile (**a**), persistent (**b**), and total (**c**) soil organic C as affected by forest types, and litter and root manipulation (n = 8). Different lower letters indicate significance at $P < 0.05$ between litter and root manipulations within each forest type; ns, not significant. *C* control. *LA* litter addition, *LR* litter removal, *RE* root exclusion, *RELA* root exclusion plus litter addition, *RELR* root exclusion plus litter removal, *CF* coniferous forest, *BF* broad-leaved forest, *CBF* coniferous-broad-leaved mixed forest. Box plots show the mean (square), median (horizontal line), 25 and 75% quartile (rectangle), 1.5 × interquartile range (whiskers), and outliers (isolated points)

BF soils received more and higher-quality (lower C:N ratio) litter than the CF and CBF soils. Therefore, litter addition in the BF could potentially stimulate microbial activity and consequently increase SOM decomposition because of priming effect (Crow et al. 2009; Karhu et al. 2016). This could also be attributed to the duration of our study. Here, the amount of SOC and its fractions were analyzed after 2–3 years of litter manipulations. Perhaps, such short-term litter addition was not sufficient to induce significant changes in SOC pools in the CF and CBF. For example, after two years of litter addition, SOC contents were not altered in a subtropical coniferous forest (Wu et al. 2018).

Litter removal reduced soil labile OC and TOC contents in the CF and BF soils; it also reduced persistent OC contents in the CF soils (Fig. 3). It is likely that litter removal led to a direct reduction in C sources and nutrient availability (Huang & Spohn 2015), thereby limiting microbial activity and C turnover (Men et al. 2023). However, the decrease in C and nutrient availability as a result of litter removal cannot explain the changes in SOC pools in the CBF. Considering the differences in the forest stands, we would expect intermediate responses of SOC pools to litter removal in the CBF relative to the CF and BF. Unexpectedly, litter removal had no effects on SOC in the CBF. This may be attributed to the lowest soil temperature in the CBF (Fig. 2a), which slowed down the turnover of SOC by microbes, thereby failing to cause significant reductions in SOC in the litter removal plots.

Plant roots can remarkably contribute to SOC storage through secreting organic compounds and root sloughing (Feng et al. 2022; Zhang et al. 2023). In the present study, root exclusion suppressed labile and persistent OC, and TOC contents in the CBF, and persistent OC and TOC contents in the CF (Fig. 3). This may result from the absence of root-derived C inputs (Zhang et al. 2023). Previous studies suggested that roots are more effective contributors to SOC than litter (Rasse et al. 2005; Jackson et al. 2017; Sokol & Bradford 2019). However, we found that the relative contribution of litter and roots to SOC pools was inconsistent among forest types. SOC sequestration in the BF was primarily controlled by litter, but that in the CBF by roots and in the CF by litter and roots (Fig. 4). Here, we cannot entirely explain such differences. Maybe this resulted from the combined effects of microbial activities, the quality and quantity of litter and root, and complex interactions between input C and soil minerals and inhabitants. Interestingly, soil microclimates, particularly soil moisture, mediated C sequestration in the BF but not in the CF and CBF. A possible explanation is that soil moisture is a limiting factor in SOC formation in the BF, since the BF soil had the highest temperature but the lowest moisture. A lower soil moisture decelerated microbial

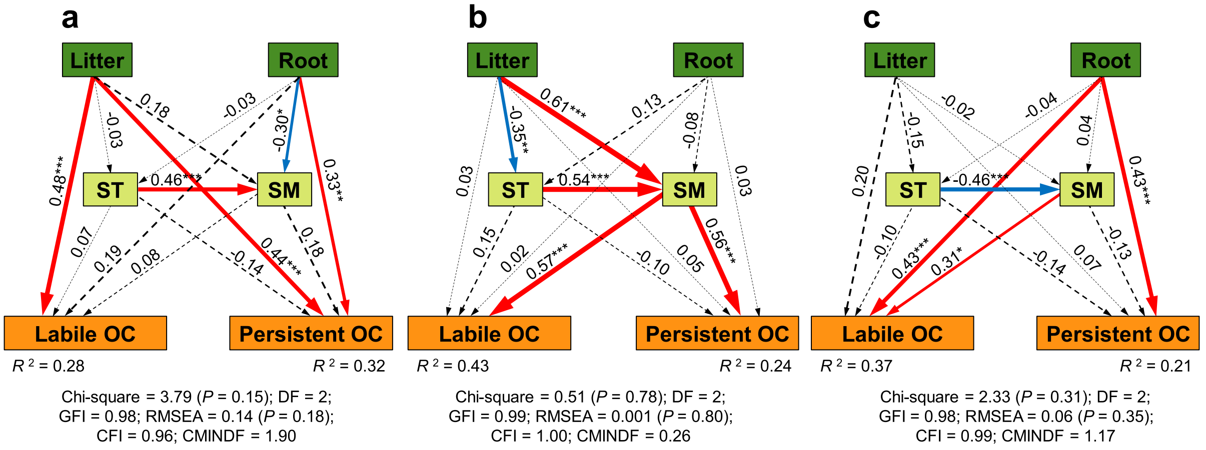

Fig. 4 Structural equation models showing indirect and direct effects of litter and root manipulation on labile and persistent soil organic C for coniferous (a), broad-leaved (**b**), and coniferous-broad-leaved mixed (**c**) forests. Red and blue arrows indicate significant positive and negative relationships, respectively. Dashed arrows indicate nonsignificant relationships. Arrow width corresponds to absolute values of standardized path coefficients that are adjacent to the arrows and indicative of the effect size of the relationships (*$P < 0.05$, **$P < 0.01$, ***$P < 0.001$). R^2-values denote the amount of variance explained by the model for labile and persistent OC. *ST* soil temperature, *SM* soil moisture

transformation of SOC and made microbial activities more sensitive to its further decline as a result of litter removal.

The responses of soil temperature and moisture to forest types, and litter and root manipulations

Previous studies suggested that forest types play an important role in affecting soil temperature and moisture (Borken & Beese 2005; Wang et al. 2008; Chen et al. 2014). In the present study, soil moisture was lower but soil temperature was higher in the BF than that in the CF and CBF (Fig. 2a, d). This can be explained by the following reasons: (1) the BF had the thickest forest floor. On the one hand, this could cause a greater heat preservation effect of the forest floor, and thus explained why its soil temperature was the greatest among the forests. Higher temperature may lead to more water loss through evaporation. On the other hand, the thicker forest floor may prevent rainwater penetrating into the mineral soils to a greater degree, that is, more rainwater may be lost through surface runoff in the BF; (2) the loss of soil moisture may also be the greatest in the BF through transpiration, given that a *Q. variabilis* dominated deciduous broad-leaved forest had greater transpiration than a *P. orientalis* dominated coniferous forest (Liu et al. 2016).

When averaged across the forests and root manipulation, litter removal decreased soil moisture (Fig. 2e). It is likely that the removal of forest litter layer bared the mineral soils, thus strengthened moisture evaporation into the air (Fekete et al. 2016). Xu et al. (2013) found that litter addition increased soil moisture and dampened fluctuations in soil temperature. On the contrary, litter addition and root exclusion did not affect soil moisture and temperature in this study (Fig. 1b, c, e, f). The thickness of litter layer in the C and RE plots ranged from 2 cm in the CF to 3 cm in the BF, possibly leading to no extra increase in the "insulating effects" of doubled litter on soil temperature and moisture. These results indicates that litter removal but not litter addition or root exclusion controlled soil microclimate in the subtropical and warm temperate transition forests.

Implications for C sequestration in the context of climate change

The BF had lower labile and persistent C and TOC contents than the CF and CBF, indicating that monoculture of coniferous trees or their mixed-culture with broad-leaved trees are more favorable for SOC sequestration in subtropical and warm temperate transition regions. Because plant above- and belowground C allocation could be altered owing to global change, the relative contribution of litter and roots to SOC pools may change under different forests. For example, elevated CO_2 and increased precipitation could facilitate belowground C allocation (Song et al. 2019), thereby improving the contribution of roots to SOC sequestration in the CF and CBF. In contrast, more carbon will be allocated to plant aboveground than belowground tissues under N addition (Song et al. 2019), indicating that N deposition would help increase the contribution of litter to SOC sequestration in the CF, particularly in the BF. Warming is predicted to have neutral effects on the root-to-shoot ratios, thus it would strengthen the contribution of litter to SOC sequestration in the BF and that of roots in the CBF. However, the effects of detritus manipulations combined with global change drivers on SOC sequestration require further study.

Conclusions

We found that labile and persistent SOC pools differentially respond to litter- and root-derived C inputs under different forest types. Moreover, plant detritus influences SOC pools through changing soil temperature and moisture for the broad-leaved forest but not for the coniferous and mixed forests. Soil microclimates, coupled with C source and nutrient availability, explain the differential responses of SOC pools to root and litter manipulations among forests. Our study provides further insight into the understanding of how litter and roots regulate SOC pools among coniferous, broad-leaved, and mixed forests, particularly in the context of global change.

Acknowledgements This study was financially supported by the National Natural Science Foundation of China (31830012), the Natural Science Foundation of Hebei Province (C2022201042) and the Collaborative Innovation Center for Baiyangdian Basin Ecological Protection and Beijing-Tianjin-Hebei Sustainable Development.

Funding This study was funded by National Natural Science Foundation of China, 31830012, Shiqiang Wan, Natural Science Foundation of Hebei Province, C2022201042, Shiqiang Wan, Collaborative Innovation Center for Baiyangdian Basin Ecological Protection and Beijing-Tianjin-Hebei Sustainable Development

Data availability Enquiries about data availability should be directed to the authors.

Declarations

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

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