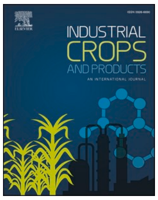
Industrial Crops & Products 225 (2025) 120518

Contents lists available at ScienceDirect

Industrial Crops & Products

journal homepage: www.elsevier.com/locate/indcrop



Mitigation of soil organic carbon mineralization in tea plantations through replacement of pruning litter additions with pruning litter derived biochar and organic fertilizer

Shaobo Zhang [a], Fuyin Huang [b], Shuai Guo [c], Ying Luo [a], Liping Zhang [a], Lan Zhang [a], Zhenzheng Li [a], Shibei Ge [a], Huasen Wang [d], Jianyu Fu [a], Xin Li [a], Peng Yan [a,*]

[a] *Tea Research Institute, Chinese Academy of Agricultural Sciences, Hangzhou 311300, China*
[b] *College of Horticulture Science, Zhejiang A&F University, Hangzhou 311300, China*
[c] *Hangzhou Botanical Garden (Hangzhou West Lake Academy of Landscape Science), Hangzhou 311300, China*
[d] *School of Mathematics and Computer Science, Zhejiang A&F University, Hangzhou 311300, China*

ARTICLE INFO

Keywords:
Pruning litter
Tea plantation
Microbial community
Functional genes
Carbon emission

ABSTRACT

Tea pruning litter is frequently added to soil to improve soil fertility and the C pool in tea plantations. However, the effects of different methods of incorporating tea pruning litter, such as direct return to the field, processing to organic fertilizer, and biochar, on soil organic carbon mineralization and its underlying mechanisms, especially microbial mechanisms, are still poorly understood. Therefore, we conducted an incubation experiment to explore the efficacy of tea pruning litter and its derivatives, biochar, and organic fertilizer, on the mineralization and chemical composition of soil organic C (SOC), labile organic C, functional gene abundance, microbial community composition, and activities of enzymes associated with C cycling in tea plantation soil. The results indicated that cumulative soil CO_2 emissions were ranked as pruned litter > organic fertilizer > biochar > control soil. The cumulative soil CO_2 emissions was decreased significantly by decreasing of the content of O-alkyl C and microbial biomass carbon, β-glucosidase/cellobiohydrolase activities, and the abundance of *GH48* and *cbh*I ($P < 0.05$). This indicates that lower CO_2 emissions following organic fertilizer and biochar addition (cf. pruned litter) were associated with a decrease in O-alkyl C content, β-glucosidase and cellobiohydrolase activities, as well as the abundance of *GH48* and *cbh*I. More interestingly, changes in the microbial community structure, especially in some key species, such as *Acidobacteria*, *Actinobacteria*, *Sordariomycetes*, and *Mortierellomycetes*, can significantly affect the rate of SOC mineralization. Our study demonstrates that applying organic fertilizer and biochar derived from pruned litter significantly mitigated SOC mineralization compared to pruned litter application alone, and both have great potential for maintaining soil C stock in tea plantation soil.

1. Introduction

The soil C pool, as a major component of terrestrial ecosystem C cycling, maintaining the global C balance and mitigating C emissions are crucial functions of it (Rocci et al., 2021; Wei et al., 2021). However, unsustainable land-use practices, such as excessive fertilization, improper cultivation methods, and frequent soil tillage, can significantly increase the loss of soil C pools, thereby reducing the capacity of soils to sequester C (Cates et al., 2016; Denvir et al., 2024). Research has shown that the main measures for increasing soil organic carbon (SOC) storage include reducing the disintegration of native SOC and increasing the input of soil organic matter (Li et al., 2018; Berhane et al., 2020; Zhou et al., 2020). Agricultural and forestry ecosystems frequently increase SOC storage through the input of organic material (Yu et al., 2020; Ni et al., 2021), and this has been widely recommended to sustain and rise soil fertility (Liu et al., 2019; Wu et al., 2019). However, the quality of these organic inputs is one of the main factors determining the dynamic transformation of SOC (Lu et al., 2014; Liang et al., 2021). Therefore, selecting the appropriate exogenous organic matter to increase SOC storage is important for enhancing the soil C sequestration capacity.

Owing to the higher content of easily decomposable C, such as cellulose, in agricultural and forestry waste, returning this waste to fields

---

* Corresponding author.
E-mail address: yanpengzn@tricaas.com (P. Yan).

https://doi.org/10.1016/j.indcrop.2025.120518
Received 30 August 2024; Received in revised form 8 January 2025; Accepted 10 January 2025
Available online 21 January 2025

can significantly increase short term SOC storage, however its rapid decomposition will also lead to a significant increase in C emissions (Fan et al., 2019; Hall et al., 2020; Miao et al., 2022). For example, Zhang et al. (2021) found that the application of bamboo leaves to Moso bamboo soil forests can significantly increase the water-soluble organic carbon (WSOC), microbial biomass carbon (MBC), and total carbon (TN), content in the soil, while also contributing to an increase in C emissions. However, biochar produced from agricultural and forestry waste under high-temperature and oxygen-limited conditions has been found to effectively enhance SOC storage and relieve greenhouse gas emissions from the soil (Zimmerman et al., 2011; Chen et al., 2021a; Zhang et al., 2021). Besides, organic fertilizers prepared from agricultural and forestry waste through fermentation and other methods can significantly reduce the cellulose content, thereby slowing down C emissions from the soil (Gao et al., 2019; Awasthi et al., 2020). Therefore, studying the impact of different utilization methods of agricultural and forestry waste on SOC dynamics is extremely important for promoting the accumulation of soil SOC.

As a key process influencing the transformation of SOC, SOC mineralization can significantly affect SOC storage depending on the rate and direction of the mineralization (Lal et al., 2018; Olayemi et al., 2022). Research has shown that the application of different types of extrinsic C can significantly influence the rate of SOC mineralization, which is attributed to differences in the labile C content and the availability of nutrients (Mitchell et al., 2015; Wang et al., 2015; Li et al., 2018). For example, the addition of fresh agricultural and forestry waste can significantly increase the amount of particulate organic carbon (POC), WSOC, and MBC in the soil, thereby promoting the SOC mineralization (Wang et al., 2018; Hao et al., 2022), while the application of biochar demonstrably reduces the rate of SOC mineralization by diminishing the content of labile SOC within the soil matrix (Li et al., 2018; Dai et al., 2021). In addition, the rate of SOC mineralization is significantly affected by changes in the chemical composition of SOC, particularly in the ratio of O-alkyl C to aromatic C (Ling et al., 2021; Zhang et al., 2021). Previous research has indicated that elevated levels of O-alkyl C can accelerate the rate of SOC mineralization, whereas the mineralization of SOC tends to decrease as the content of aromatic C rises (Sjöberg et al., 2004; Chen et al., 2019). Furthermore, microorganisms are the primary drivers of C cycling in soil ecosystems (Lin et al., 2019; Sokol et al., 2019; Soong et al., 2020). Different types of exogenous organic matter, when added to soil, can significantly influence nutrient availability and utilizable carbon content, leading to alterations in microbial community composition and structure (Lin et al., 2019; Bello et al., 2020). Shifts in the makeup and organization of soil microbiota, especially some key species relative abundance and functional genes abundance (e.g., *GH48* and *cbh*I), can significantly affect the enzyme activities related to SOC decomposition (e.g., β-glucosidase, dehydrogenase, and invertase), this leads to changes in SOC decomposition, consequently impacting the rate at which SOC mineralizes (Zhang et al., 2017; Duan et al., 2021a). For example, tea pruning litter contains high C and N, which can provide sufficient C and N sources for microorganisms after being added to the soil, thereby affecting the community composition and structure of microorganisms, especially the abundance of functional microbial flora related to C decomposition, resulting in changes in the enzyme activities related to C decomposition in the soil, and then affecting the mineralization rate of SOC (Wang et al., 2015; Wu et al., 2019; Yang et al., 2022; Zhang et al., 2023). Nevertheless, there is insufficient research exploring the impact of different types of exogenous C application on SOC mineralization through a comprehensive analysis of changes in SOC composition, microbial communities, carbon cycling functional gene abundance, and enzyme activities.

As an integral component of terrestrial ecosystems, tea plantations play a crucial role in mitigating greenhouse gas emissions and maintaining the global C balance (Fan et al., 2020; Du et al., 2023). Statistical data indicate that China has the longest history of tea cultivation and the largest tea production worldwide (Yan et al., 2020; Xie et al., 2021). By 2022, the area of tea plantations had reached 3.3303 million hectares (Annual Bulletin of Statistics, ITC, 2023). Previous studies have found that although the area of tea plantation is smaller than that of forests and grasslands, the average SOC density in Chinese tea plantation is approximately 59.17 Mg ha^{-1}, and the SOC storage reaches 207.13 Tg (Wang et al., 2023). Therefore, tea plantations have a significant prospective for C sequestration and emission reduction, conducive to regulating the C balance in terrestrial ecosystems (Li et al., 2011; Zhang et al., 2017). Tea tree pruning is an important measure in tea plantation management to ensure a high yield and quality of tea (Yang et al., 2022; Zhang et al., 2023). Tea pruning litter is one of the main sources of SOC in tea plantation soils (Li et al., 2011; Yang et al., 2022). Research indicates that directly returning tea pruning litter to the soil can significantly increase SOC content in the short term (Yang et al., 2022). However, as tea pruning litter decomposes, it releases nutrients that can modify the microbial community structure and composition in the soil of tea plantations, affecting greenhouse gas emission rates and thereby altering the C balance in the tea plantation (Pramanik et al., 2020; Luo et al., 2023). Therefore, adopting a scientific approach to return tea pruning litter to fields is crucial for enhancing soil fertility and the C sequestration function of tea plantation ecosystems.

The aim of this incubation experiment was to: (1) examine the impact of pruned litter, pruned litter-derived organic fertilizer, and pruned litter-derived biochar on soil organic carbon mineralization in tea plantation ecosystems; and (2) explore how tea-pruned litter, its biochar derivative, and organic fertilizer amendments influence the biotic and abiotic mechanisms of SOC mineralization. Specifically, we hypothesized the following:

(1) Pruned litter and its derivatives promote the rate of SOC mineralization, whereas pruned litter biochar and organic fertilizers significantly mitigate the rate of SOC mineralization.
(2) Pruned litter biochar and organic fertilizers mitigate the rate of SOC mineralization compared to pruned litter because of alterations in the microbial community structure and key microbial taxa, especially reduced functional gene abundance and enzyme activity associated with C decomposition.

2. Materials and methodologies

2.1. Soil, pruned litter, biochar, and organic fertilizer characterization

From a tea plantation in Xihu District, soil samples were extracted from the uppermost 20 cm layer, Hangzhou City, China. The area experiences a subtropical monsoon climate, where temperatures average 17.0 °C annually and precipitation reaches 1533 mm per year. The soil is categorized as Ultisol (US Taxonomy) and originated from anshan porphyritic bedrock lacking quartz. The basic properties of the soil were: pH 3.95; SOC 3.69 %; TN 0.38 %; available P (AP) 0.0192; available K (AK) 0.0082 %.

Soil pH, SOC, and TN levels were measured using a pH meter and an elemental analyzer, respectively. The Bray technique, utilizing a combination of NH_4F and HCl as the extractant, was employed to quantify the AP content (Bray and Kurtz, 1945). Flame photometry was employed to assess the AK content following extraction with an NH_4OAc solution (Zhang et al., 2021).

Pruned litter was collected from the tea plantations. The total C and N concentrations in the tea pruned litter were 45.8 % and 3.39 %, respectively. To form the biochar, tea pruned litter (< 2 mm) underwent slow pyrolysis for 2 h at 500 °C in an oxygen-restricted environment, and the C and N concentrations were 62.0 % and 3.38 %, respectively. Organic fertilizers were prepared from tea pruned litter through natural fermentation, and the C and N concentrations were 29.7 % and 1.49 %, respectively. The C and N levels of the three materials were determined utilizing an elemental analyzer.

2.2. The experimental incubation encompassed four distinct protocols

No pruned litter added (control), pruned litter application, biochar application, and organic fertilizer application. Three replications were performed for each treatment. Pruned litter, biochar, and organic fertilizer were added as equivalent C bases, that is, 7 g C kg^{-1} soil.

For the incubation experiment, the following materials were pulverized to a particle size smaller than 2 mm: pruned litter, pruned litter biochar, pruned litter fertilizer, and unmodified soil. The pruned litter, pruned litter biochar, and pruned litter fertilizer were homogeneously blended with a newly collected soil specimen (equating to 400 g oven-dried mass) in a pair of glass containers, the soil's water content was adjusted to 60 % of its field capacity (Throughout the study duration) and a bulk density of 1.32 g cm^{-3} (500 mL). A dark environment at 25 °C was maintained for the soil mixtures, which were enclosed in airtight glass containers. Each treatment's duplicates comprised two soil quantities: one portion (200 g) was utilized to assess CO_2 release, while remaining 200 g portion was utilized to evaluate soil physicochemical attributes, SOC chemical structure, enzymatic activities, C-degrading functional gene abundance, and microbial community makeup after the experimentation concluded.

2.3. Quantification of soil CO_2 emission

Soil-emitted CO_2 was quantified utilizing an alkali-trapping technique. In brief, A small glass container with 10 mL of 0.4 mol L^{-1} NaOH solution was placed in each glass container to trap CO_2 released during SOC mineralization. The exchange of NaOH traps followed a specific schedule, occurring on days 2, 4, 6, 8, 10, 15, 20, 25, 30, 35, 40, and 45 of the incubation process. Three supplementary glass containers (sans soil) were employed to compute the CO_2 absorption of the NaOH solution from the surrounding atmosphere. A titration technique employing HCl solution was used to measure the amount of CO_2 absorbed by the NaOH solution.

2.4. Determination of soil physicochemical properties, enzyme activities, and chemical composition of SOC

For soil pH identification, the study employed a 1:2.5 (w/v) soil-water ratio. AP was determined by HCl-NH_4F extraction. Soil WSOC and MBC were analyzed following the methods of Song et al. (2019). POC and mineral-associated organic carbon (MAOC) were analyzed following the method described by Cambaradella and Elliott. The molecular structure of the SOC was quantified utilizing a ^{13}C NMR spectrometer (Zhang et al., 2021). The spectral ranges of alkyl C are 0–46 ppm, O-alkyl C is 46–114 ppm, aromatic C is 114–164 ppm, and carbonyl C is 164–220 ppm, respectively.

The methods for measuring β-glucosidase and cellobiohydrolase activities in soil were adopted from Alef and Nannipieri (1995) and Zhang et al. (2017), respectively. See supplementary information for further details.

2.5. Determination of the soil microbial community characteristics

A Fast DNA SPIN kit (MP Biomedicals, USA) was employed to isolate DNA ($n = 3$) from 0.2 g fresh soil, and the further details on microbial determination and analysis, etc., can be found in the supplemental information. All unprocessed sequences were submitted to the NCBI Sequence Read Archive (ID SRP507209 and SRP507218). Details of the determination of *GH48* and *cbh*I gene copy numbers are provided in the supplemental information.

2.6. Statistical analysis

To determine whether experimental treatments differed significantly, the study utilized a single-factor ANOVA in conjunction with the least significant difference test. Before performing ANOVA, data normality and variance homogeneity were assessed, and logarithmic transformation was applied to mitigate variance heterogeneity. Spearman's correlation analysis was utilized to determine the correlation coefficients among cumulative CO_2 emissions, keystone microbial taxa, and soil properties. SPSS version 20.0 was the statistical software employed for data analysis. To analyze the effects of pruned litter, organic fertilizer, and biochar applications on bacterial and fungal community composition, the study employed non-metric multidimensional scaling (NMDS) (Zhang et al., 2023).

R software (Team, 2013) was utilized to perform a structural equation model (SEM) analysis, aiming to explore the influence of soil modifications from pruned litter, biochar, and organic fertilizer application on the aggregate SOC mineralization process. Initially, we identified two enzymes in the soil (β-glucosidase and cellobiohydrolase) as crucial elements governing SOC mineralization, given that the total SOC mineralization exhibited significant correlations ($P < 0.01$) with the functionality of these enzymes. Second, we chose five crucial soil characteristics (O-alkyl C content, *GH48*, *cbh*I abundance, fungal Chao1, and Shannon indices) based on the ANOVA results. Finally, structural equation models were established using the soil properties selected through the preceding steps.

3. Results

3.1. FTIR analysis

The functional groups of pruned litter (PL), biochar (B), and organic fertilizer (OF) are shown in Table S1. The functional groups in the PL treatment were -OH, -CH_3, C=C/C=O, C-O, C-O-C, aromatic C-H, and C=C. The functional groups in treatment B included -OH, -CH_3, C=O, C-H deformation, C-O-C, aromatic C-H, and C=C groups. The functional groups in the OF treatment included -OH, -CH_3, C=O, C-H deformation, and C-O-C groups (Fig. 1).

3.2. The rate of SOC mineralization

After the 60-day incubation study, the aggregate CO_2 released from SOC mineralization varied between 416 and 2158 mg CO_2 kg^{-1} soil (Fig. 2a). Relative to the control, the aggregate CO_2 emissions were enhanced under the PL, OF, and B treatments by the rates of 419 %, 162 %, and 62 %, respectively (Fig. 2b). Additionally, the aggregate CO_2 emissions was reduced following the addition of OF and B than in PL and

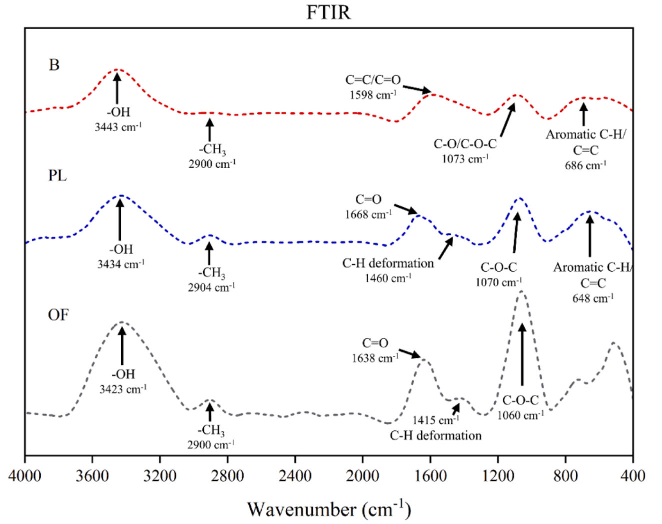


Fig. 1. FTIR spectra of pruned litter, organic fertilizer, and pruned litter biochar.

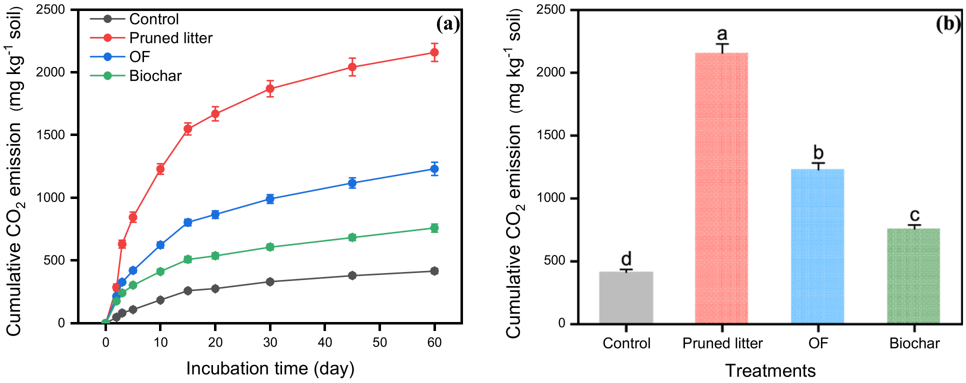


Fig. 2. Dynamics of aggregate CO_2 release from tea plantation soil with, and without, the addition of modifiers (pruned litter, organic fertilizer and pruned litter biochar) during the 60 days incubation period. (a) Dynamics of aggregate CO_2 release and (b) aggregate CO_2 release after 60 days of incubation. Standard deviations are represented by error bars, while lowercase letters signify significant differences between treatments ($P < 0.05$) (The same applies hereinafter).

was ranked PL > OF > B > Control (Fig. 2b).

3.3. SOC pool

In comparison with control, POC content decreased ($P < 0.05$) after B supplementation on day 15 and elevated ($P < 0.05$) following the PL and OF treatments (OF > PL) on day 60. The MAOC content elevated ($P < 0.05$) subsequent to B addition on day 15 and day 60 (Table 1).

In addition, relative to the control, the WSOC content decreased under the PL, OF, and B treatments and ranked Control > PL > OF > B on day 15, and decreased following the addition of OF, but increased by B addition on day 60. In contrast, relative to the control, MBC levels rose after PL and B application but decreased with the addition of organic fertilizer on day 15, and that was increased under the PL, OF, and B treatments, while PL was higher than OF and B treatments on day 60 (Table 1).

Compared to control, OF treatment resulted in a 25 % reduction in soil alkyl carbon content, as observed on day 60 of the experiment (Fig. 3b). O-alkyl C content was increased with the addition of PL (9.3 % on day 15 and 9.8 % on day 60) and OF (8.7 % on day 15 and 10.5 % on day 60) (Fig. 3c, d) and was decreased with B on day 15 (Fig. 3c). In addition, B notably enhanced aromatic C content by 23.3 % and 31.9 % on day 15 and day 60, respectively (Fig. 3e, f), whereas OF addition enhanced aromatic C by 16.4 % on day 60 (Fig. 3f). Furthermore, the Carbonyl C content decreased under the PL and OF treatments, increased under the B treatment on day 15, and decreased under the PL and B treatments on day 60 (Fig. 3g, h).

3.4. Soil enzyme activity

Compared to the control soil, β-glucosidase activity was elevated ($P < 0.05$) after PL application, rising by 208 % and 107 % at day 15 and day 60, respectively, and was increased ($P < 0.05$) following the OF addition by 21 % on day 60 (Fig. 4a, b).

In addition, as compared to the control soil, cellobiohydrolase activity was increased ($P < 0.05$) following the PL addition by 205 % and 145 % on day 15 and day 60, respectively, and was increased ($P < 0.05$) following OF incorporation, showing a 21 % enhancement at day 60 (Fig. 4a, b).

3.5. Microbial C-cycling genes

In contrast to the control soil, PL markedly elevated the abundance of *cbh*I by 1065 % and 170 % on day 15 and day 60, respectively (Fig. 4e, f), and the *cbh*I abundance was increased by the OF addition on day 60 and was lower in the OF treatment compared to the PL treatment (Fig. 4f). In addition, *GH48* abundance was increased by the PL and OF additions by 211 % and 144 % on day 15, respectively (PL > OF) (Fig. 4g), and was increased by PL addition on day 60 (Fig. 4h).

3.6. Soil microbial community characteristics

Non-metric multidimensional scaling (NMDS) showed that bacterial ($R = 0.4054$, $P < 0.01$, stress $= 0.095$) and fungal ($R = 0.5103$, $P < 0.01$, stress $= 0.072$) communities were significantly altered by the addition of pruned tea litter and its derivatives (Fig. 5a, b). Specifically, the bacterial community changed significantly ($P < 0.05$) after the three exogenous C additions on day 15 and day 60, and the treatments with PL and OF did not change significantly on day 60 (Fig. 5a). In addition, the fungal community changed remarkably ($P < 0.05$) after the addition of PL and OF, but no significant change was observed after the addition of B on day 15 and day 60 (Fig. 5b).

The Shannon index of the bacteria was not affected by the three exogenous C additions on day 15 and day 60; however, the OF treatment yielded higher results compared to the PL treatment. The Chao1 index of the bacteria exhibited the same trend on day 15. In addition, the Shannon index of the fungi was significantly decreased by the addition of PL on day 60 (Table 2).

Table 1
Pruned litter, pruned litter biochar, and organic fertilizer effects on soil particulate organic carbon (POC), mineral-associated organic carbon (MAOC), water-soluble organic C (WSOC), and microbial biomass C (MBC) in tea plantation soil. The mean values after "± " are the standard deviation.

	Day 15				Day 60			
	POC (g kg^{-1})	MAOC (g kg^{-1})	WSOC (mg kg^{-1})	MBC (mg kg^{-1})	POC (g kg^{-1})	MAOC (g kg^{-1})	WSOC (mg kg^{-1})	MBC (mg kg^{-1})
Control[†]	13.0 ± 0.6a[‡]	13.4 ± 0.5b	288 ± 8a	639 ± 40b	12.4 ± 0.7c	13.6 ± 1.1bc	129 ± 12b	470 ± 22c
PL	13.6 ± 0.8a	14.2 ± 0.9b	218 ± 7b	755 ± 41a	15.1 ± 0.7b	12.1 ± 0.4c	127 ± 6b	760 ± 70a
OF	13.8 ± 0.6a	14.7 ± 1.3b	188 ± 12c	450 ± 26c	19.1 ± 1.4a	15.4 ± 1.5b	75 ± 3c	650 ± 30b
B	11.0 ± 0.5b	17.8 ± 1.1a	210 ± 12d	813 ± 43a	11.7 ± 1.0c	18.0 ± 0.7a	176 ± 16a	604 ± 52b

[†] Control, PL, OF, and B represent the treatments of no additions, pruned litter, organic fertilizer, and pruned litter biochar additions, respectively.
[‡] Significant variances between treatments are indicated by lowercase letters ($P < 0.05$) (The same applies hereinafter).

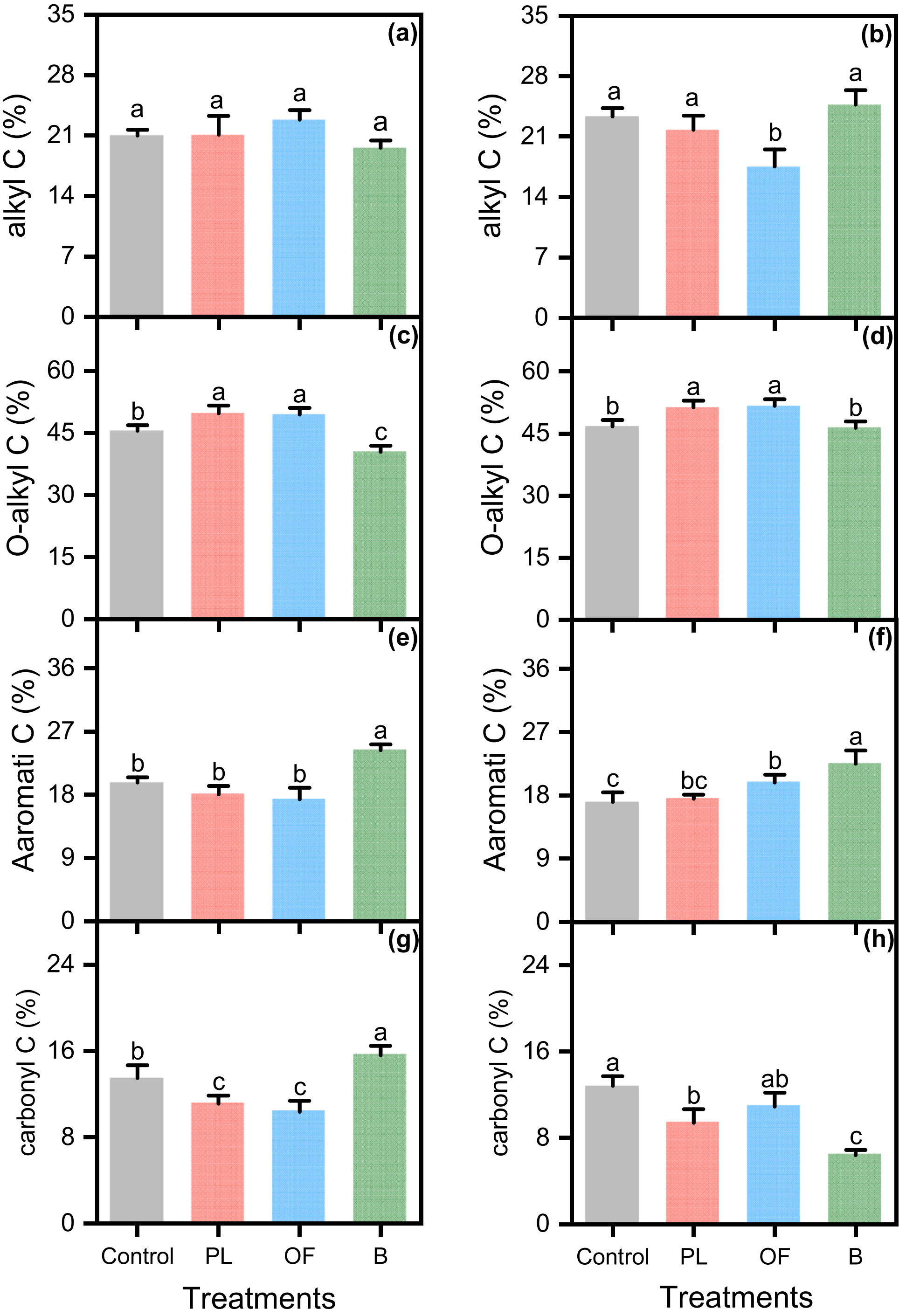


Fig. 3. Chemical composition of organic C in tea plantation soil amended with pruned litter, pruned litter biochar, and organic fertilizer.

For bacterial community (class level), as compared to the control, B addition decreased the relative abundance of *Acidobacteria* on day 15 and day 60, and that was increased by the PL and OF addition on day 60; PL and OF addition decreased the relative abundance of *Alphaproteobacteria*, *Thermoleophilia*, and *Bacilli* on day 15 and day 60; PL addition increased the relative abundance of *Actinobacteria* on day 15 and day 60, and decreased the relative abundance of *Acidimicrobiia* on day 15; PL and OF amendment increased the *Verrucomicrobiae* relative abundance on day 15 and day 60 (Fig. 6a).

For fungi (class level), when contrasted with the control, the relative abundance of *Sordariomycetes* was increased by PL and OF addition, and it was decreased by B addition on day 15 and day 60; the relative abundance of *Leotiomycetes* and *Dothideomycetes* decreased under all three treatments on day 15 and day 60; the relative abundance of *Mortierellomycetes* and *Rozellomycotina_cls_Incertae_sedis* decreased with the addition of PL and OF, regardless of incubation time; PL increased the relative abundance of *Umbelopsidomycetes* (Fig. 6b).

3.7. *Relationships between soil factors and soil CO_2 emissions*

On day 15 and day 60, the aggregate soil CO_2 release increased significantly ($P < 0.05$) with an increase in the O-alkyl C content, β-glucosidase and cellobiohydrolase activities, and the abundance of *GH48* and *cbh*I. In addition, on day 60, a marked elevate in aggregate

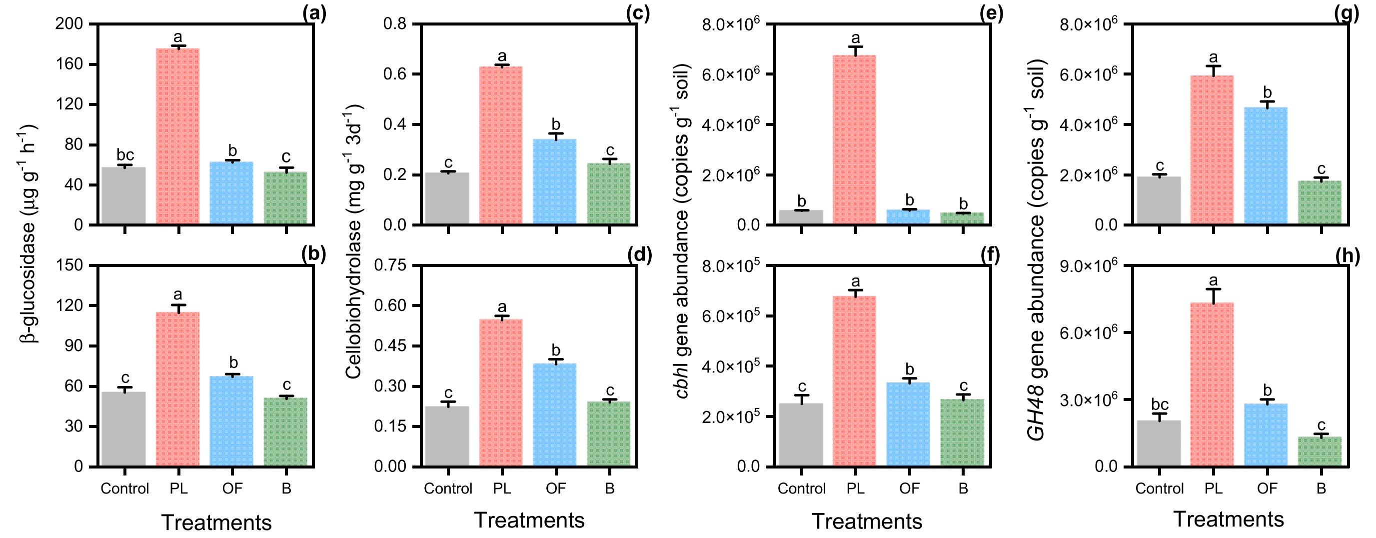


Fig. 4. β-glucosidase (a, b) and cellobiohydrolase (c, d) activities, and *GH48* (e, f) and *cbh*I (g, h) abundance in tea plantation soil amended with pruned litter, pruned litter biochar, and organic fertilizer.

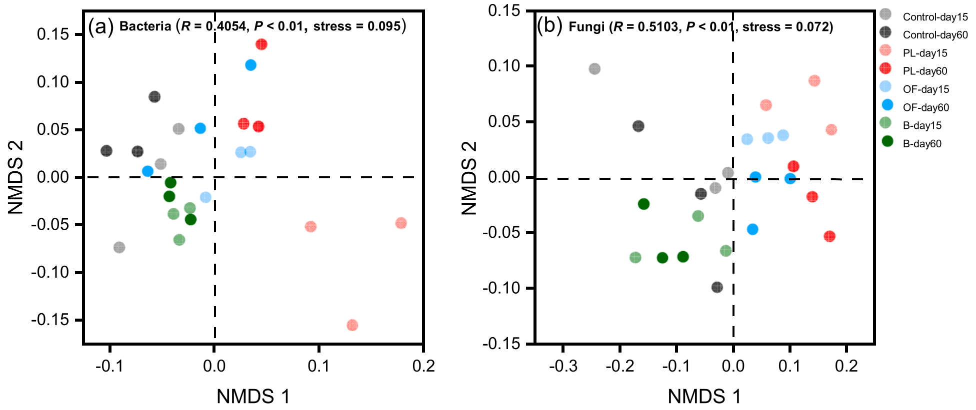


Fig. 5. Non-metric multidimensional scaling ordination based on the Bray-Curtis distance representing illustrating differences (a) bacterial, and (b) fungal community structures in tea plantation soil amended with pruned litter, pruned litter biochar, and organic fertilizer.

Table 2
Pruned litter, organic fertilizer and pruned litter biochar, effects on the microbial diversity after 15 and 60 days of incubation in the tea plantation soil microbiome. The mean values after "± " are the standard deviation.

	Bacterial Shannon index		Bacterial Chao1 index	
	Day 15	Day 60	Day 15	Day 60
Control[†]	2.65 ± 0.04ab[‡]	2.58 ± 0.04ab	71.8 ± 1.1ab	68.1 ± 0.9a
PL	2.43 ± 0.06b	2.54 ± 0.04b	67.2 ± 3.9b	68.2 ± 0.3a
OF	2.68 ± 0.02a	2.69 ± 0.06a	75.9 ± 0.7a	73.5 ± 0.9a
B	2.56 ± 0.17ab	2.63 ± 0.07ab	71.0 ± 1.0ab	67.5 ± 5.3a
	Fungal Shannon index		Fungal Chao1 index	
	Day 15	Day 60	Day 15	Day 60
Control[†]	2.02 ± 0.26a	1.96 ± 0.22a	33.7 ± 4.2a	31.8 ± 3.8a
PL	1.58 ± 0.20a	1.44 ± 0.21b	28.3 ± 3.1a	27.1 ± 0.9a
OF	1.70 ± 0.13a	1.71 ± 0.17ab	32.0 ± 3.0a	28.7 ± 0.6a
B	1.96 ± 0.21a	2.03 ± 0.11a	32.0 ± 5.2a	31.3 ± 1.5a

[†] Control, PL, OF, and B represent the treatments of no additions, pruned litter, organic fertilizer, and pruned litter biochar additions, respectively.

soil CO_2 emissions was observed as MBC levels rose ($P < 0.05$) (Fig. 7).

In addition, irrespective of the incubation time, at the class level for bacteria, the cumulative CO_2 emissions showed positive associations with the proportional presence of *Acidobacteria*, *Actinobacteria*, and *Verrucomicrobiae*, but demonstrated while displaying negative correlations with the proportional representation of *Alphaproteobacteria*, *Thermoleophilia*, *Bacilli*, and *Acidimicrobiia* ($P < 0.01$) (Table 3). For fungi, the total CO_2 released exhibited a positive association with *Sordariomycetes* and *Umbelopsidomycetes.* Conversely, it showed an inverse relationship with the Chao1 and Shannon indices and the relative abundance of *Leotiomycetes*, *Dothideomycetes*, *Mortierellomycetes*, and *Rozellomycotina_cls_Incertae_sedis* ($P < 0.01$) (Table 3).

Furthermore, the SEM results showed that the aggregate soil CO_2 release following PL application was driven by the activities of β-glucosidase/cellobiohydrolase ($P < 0.01$). In addition, *GH48* and *cbh*I gene abundance was indirectly increased by the total soil CO_2 release, which was a result of modified β-glucosidase/cellobiohydrolase activities (Fig. 8a). For the OF amendment, aggregate soil CO_2 release was influenced by cellobiohydrolase activity ($P < 0.01$). Through modifying cellobiohydrolase function, aggregate soil CO_2 release indirectly increased O-alkyl C content (Fig. 8b). Interestingly, the results of SEM showed that the aggregate soil CO_2 release following the B application was not influenced by β-glucosidase and cellobiohydrolase activities (Fig. 8c).

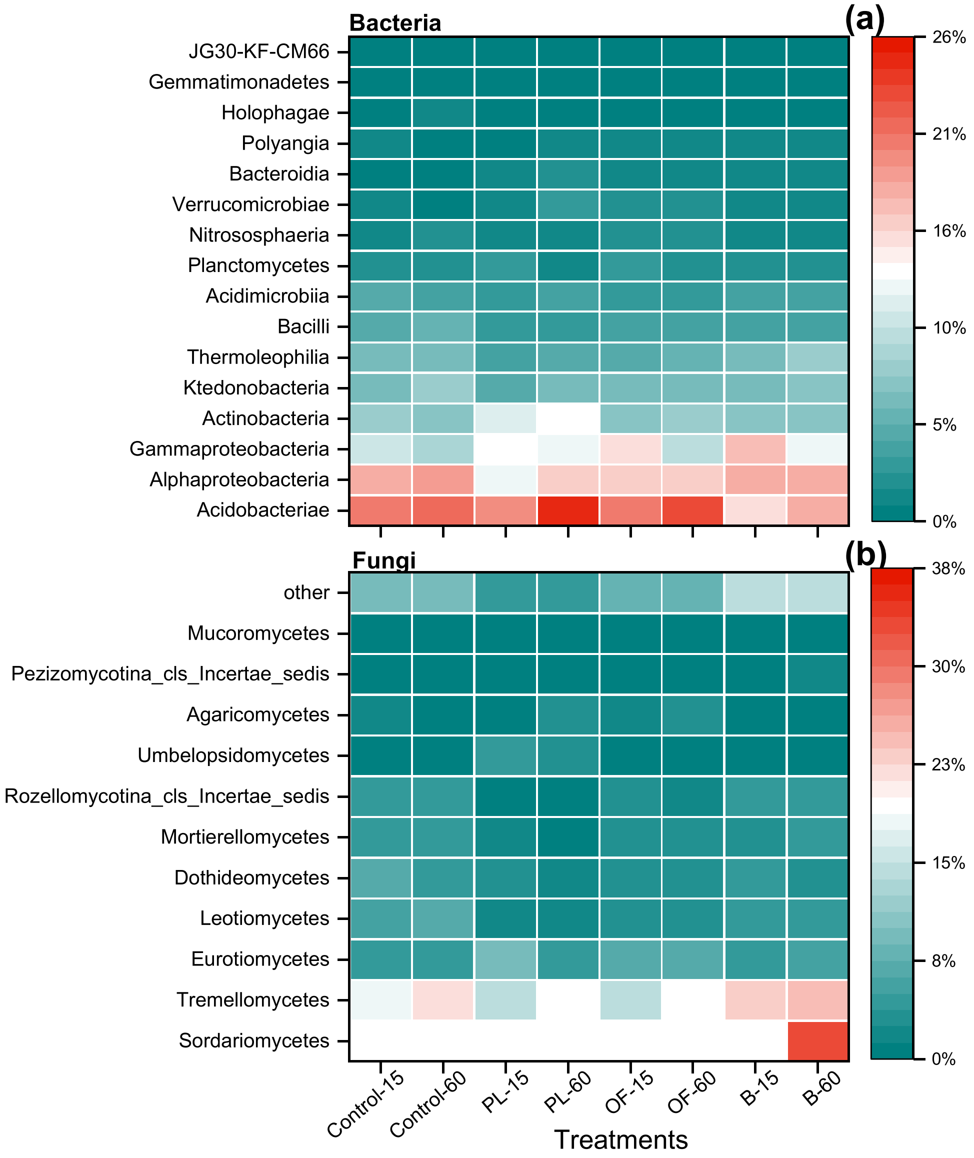


Fig. 6. Bacterial (a, b) and fungal (c, d) community compositions in tea plantation soil amended with pruned litter, organic fertilizer, and pruned litter biochar The names of the classes are shown.

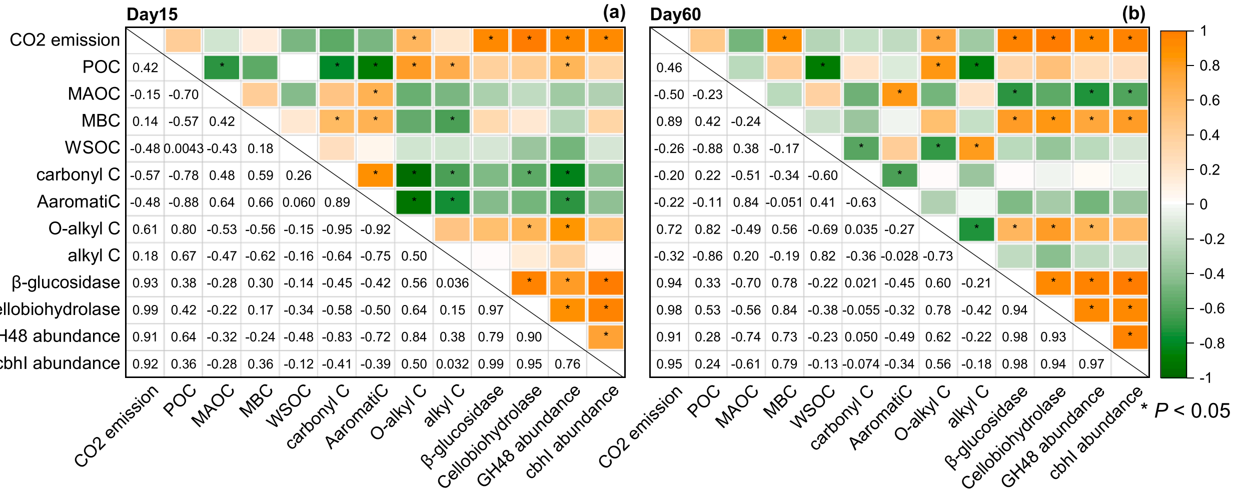


Fig. 7. Correlation coefficients betweenchemical properties, enzyme activities, functional gene abundance of soil and aggregate CO_2 release in tea plantation soil amended with pruned litter, pruned litter biochar, and organic fertilizer.

Table 3

Correlation coefficients between the relative abundance of soil bacterial and fungal classes and cumulative CO_2 emissions in tea plantation soil amended with pruned litter.

Bacterial	Cumulative CO_2 emission	Fungal	Cumulative CO_2 emission
Chao1 index	0.263	Chao1 index	−0.605***
Shannon index	0.101	Shannon index	−0.733***
Acidobacteria	0.485 *	*Sordariomycetes*	0.705**
Alphaproteobacteria	−0.584 * *	*Tremellomycetes*	−0.235
Gammaproteobacteria	0.325	*Eurotiomycetes*	0.156
Actinobacteria	0.799 * *	*Leotiomycetes*	−0.799**
Ktedonobacteria	−0.342	*Dothideomycetes*	−0.712**
Thermoleophilia	−0.576 * *	*Mortierellomycetes*	−0.786**
Bacilli	−0.616 * *	*Rozellomycotina_cls_Incertae_sedis*	−0.897**
Acidimicrobiia	−0.504 *	*Umbelopsidomycetes*	0.640**
Planctomycetes	−0.307	*Agaricomycetes*	0.345
Nitrososphaeria	−0.345	*Pezizomycotina_cls_Incertae_sedis*	−0.037
Verrucomicrobiae	0.823 * **	*Mucoromycetes*	0.069

4. Discussion

4.1. Changes in soil organic carbon mineralization rate from incorporation of pruned litter and its derivatives

In this study, we found that the cumulative SOC mineralization was increased relative to the control following the addition of pruned litter, organic fertilizer, and biochar, while it was lower in the organic fertilizer and biochar treatments than in the pruned litter treatment. This result aligns with both our initial hypothesis and the discoveries of Zhang et al. (2021), who reported that the rate of mineralization was significantly enhanced by 122 % and 30.1 % following the bamboo leaves and their biochar amendment in bamboo forest soil, and the mineralization lower after biochar amendment than it was after amendment with bamboo leaves. Similarly, Whitman et al. (2016) reported the application of pyrogenic organic matter may result in less SOC loss than the application of an equivalent amount of fresh stover to Mardin soil. Interestingly, we found that the amendment of organic fertilizer mitigated the rate of SOC mineralization, although it was still higher than in the case of biochar addition.

The possible mechanisms by which biochar and organic fertilizer additions reduce the rate of SOC mineralization include: 1) Compared to pruned litter, biochar and organic fertilizers have a low content of easily decomposable C (cellulose, etc.), which abates microbial growth and activities, thereby decreasing the mineralization rate of SOC (Fan et al., 2019; Ma et al., 2020). This mechanism is evidenced by the lower concentrations of WSOC and O-alkyl C following organic fertilizer and biochar additions; 2) Due to the high content of easily decomposable C in pruned tea litter, addition thereof significantly increases the enzyme activity related to C decomposition in the soil, such as β-glucosidase and cellobiohydrolase, thereby promoting the decomposition of SOC (Nottingham et al., 2012; Lin et al., 2018). On the contrary, addition of organic fertilizer and biochar significantly reduced the activities of these two enzymes, thereby slowing down the decomposition rate of SOC (Debosz et al., 1999; Zhou et al., 2024); 3) Addition of pruned litter can significantly increase the abundance of functional genes related to C decomposition, since the pruned litter provides abundant available nutrients and energy sources for microorganisms (Kelly et al., 2021; Tang et al., 2021). Conversely, biochar and organic fertilizer have lower available nutrient and C content, reducing the number of functional genes related to C decomposition (Li et al., 2024; Zhou et al., 2024).

4.2. Relationship between soil C pool and SOC mineralization

Changes in the decomposable C content of the soil can significantly affect the rate of SOC mineralization (Wang et al., 2016; Wei et al., 2019). We have discovered that pruned litter and organic fertilizer addition (cf. control) increased the POC content, while biochar addition decreased the POC and MAOC content. Nevertheless, a notable association between the SOC mineralization rate and the POC/MAOC levels was not observed. These results indicate that POC/MAOC was not a key factor influencing SOC mineralization in this research. In addition, we found that the addition of pruned litter and its derivatives increased the MBC content, pruned litter increased the MBC content more than organic fertilizer or biochar, and a positive association among the SOC mineralization rate and MBC concentrations was evident on day 60. Microbial biomass carbon is labile organic carbon stored within microorganisms themselves, and studies have shown a positive correlation between MBC and SOC mineralization rate (Zhang et al., 2021). These findings may be explained by the abundant available nutrient and C sources for microorganisms and altered soil microbial community structure provided by pruned litter as compared to the organic fertilizer and biochar (Ridgeway et al., 2022; Du et al., 2024). Thus, we can conclude that the organic fertilizer and biochar mitigated the pace of SOC mineralization due to the reduction in MBC content.

In addition, alterations in the SOC's chemical makeup can significantly affect the rate of SOC mineralization (de la Rosa et al., 2018; Chen et al., 2019). Zhang et al. (2021) found that O-alkyl C, which are easily decomposed by enzymes and microbial respiration, lead to an increased rate of soil carbon mineralization, in contrast, aromatic carbons, being more difficult to decompose, are beneficial for the stabilization of soil carbon. The findings of our study indicate that pruned litter and organic fertilizer application markedly elevated the content of O-alkyl C on day 15 and day 60, and there was an increase in the aromatic C content due to the application of organic fertilizer, which aligns with prior research outcomes (Li et al., 2017; Sarker et al., 2018). In addition, our investigation found that biochar application decreased the content of O-alkyl C on day 15 and increased the content of aromatic C on day 15 and day 60, which was primarily due to the higher content of recalcitrant C in the biochar (Chen et al., 2019; Chen et al., 2021b). Furthermore, our outcomes demonstrate that the cumulative CO_2 emissions elevated markedly with an increase in O-alkyl C content, but this was not related to changes in aromatic C content. These observations imply that the enhancement of the SOC mineralization rate by pruned litter and organic fertilizer application (cf. control) could be linked to an elevate in O-alkyl C content, and the decrease in SOC mineralization by biochar (cf. pruned litter and organic fertilizer) is attributed to the decrease in O-alkyl C. The findings from SEM analysis also suggested that the application of organic fertilizer led to an increase in soil O-alkyl C content, which indirectly resulted in higher CO_2 emissions compared to the control treatment. Importantly, the effect of both of these additions on SOC mineralization was not associated with altered aromatic C content.

4.3. Relationship between soil microbial community and SOC mineralization

The current research showed that bacterial and fungal communities

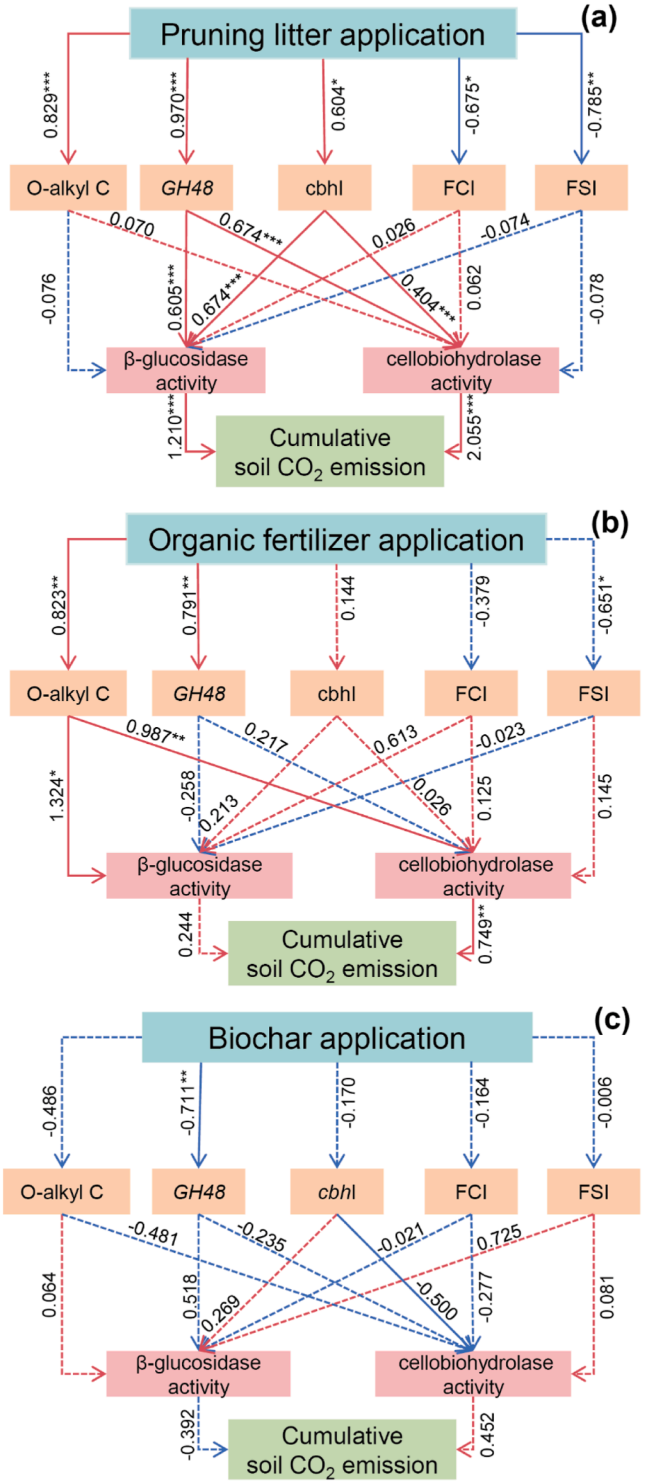


Fig. 8. A structural equation model demonstrating the direct and indirect impacts of integrating (a) pruned litter, (b) organic fertilizer, and (c) pruned litter biochar on O-alkyl C, *GH48*, *cbh*I, FCI, FSI, and the activities of β-glucosidase and cellobiohydrolase on the aggregate CO_2 release from SOC mineralization in tea plantation soil amended with pruned litter and its derivatives. *GH48*, *GH48* gene abundance; *cbh*I, *cbh*I gene abundance; FCI, fungal Chao1 Index; FSI, fungal Shannon Index. Coefficients that differ markedly from zero are denoted by * * and * ** , indicating $P < 0.01$ and 0.001, respectively.

were markedly altered by the application of tea-pruned litter and its derivatives. Our study revealed that pruned litter addition decreased the Shannon index of fungi and there was a negative relationship among the SOC mineralization rate and the fungi Shannon index. These outcomes indicate that the elevated SOC mineralization rate by pruned litter application (cf. control) was likely attributable to the reduction in the Shannon index of fungi.

In addition, the incorporation of organic substances and their derivatives significantly affects SOC mineralization by altering the abundance of some key microbial species in the soil, especially those associated with the conversion of SOC (Zhou et al., 2016; Duan et al., 2019; Wang et al., 2019). Our investigation revealed that tea pruning litter and organic fertilizer application increased the proportional presence of *Acidobacteria*, *Actinobacteria*, and *Verrucomicrobiae*, while both decreased *Alphaproteobacteria*, *Thermoleophilia*, and *Bacilli*. The incorporation of biochar diminished the relative prevalence of *Acidobacteria* and *Bacilli*. The SOC mineralization rate positively correlated with the proportional presence of *Acidobacteria*, *Actinobacteria*, and *Verrucomicrobiae*, and negatively correlated with the proportional presence of *Alphaproteobacteria*, *Thermoleophilia*, *Bacilli*, and *Acidimicrobiia*. These findings align with those of Wang et al. (2024), who showed that *Acidobacterium* is mainly involved in the decomposition of easily decomposed C. With a decrease in soil pH, it also decomposes some recalcitrant C, and an increase in its abundance promotes the decomposition of SOC. Previous studies have also shown that *Verrucomicrobiae*, *Alphaproteobacteria*, and *Thermoleophilia* play important roles in C cycling and that all of them mainly degrade recalcitrant C components in soils (Fierer et al., 2013; Ling et al., 2022; Liu et al., 2023). Furthermore, Ling et al. (2022) discovered that *Bacilli* typically utilize labile carbon from the soil, and the abundance of *Bacilli* is greater when the soil is amended with organic matter that has a higher content of easily decomposable carbon. In this study, changes in the abundance of *Bacilli* have been shown to be significantly correlated with cellulase activity, which affects the decomposition of C in the soil. These findings indicate that *Acidobacteria*, *Actinobacteria*, *Verrucomicrobiae*, *Alphaproteobacteria*, *Thermoleophilia*, *Bacilli*, and *Acidimicrobiia* represent pivotal bacterial groups influencing the SOC mineralization rate at the class level, and changes in the proportional presence of these bacteria can significantly affect the decomposition and conservation of C in tea plantation soil.

The addition of pruned litter and organic fertilizer enhanced the proportional presence of *Sordariomycetes*, whereas both interventions diminished the relative prevalence of *Rozellomycotina_cls_Incertae_sedis*, *Leotiomycetes*, *Dothideomycetes*, and *Mortierellomycetes*. Additionally, biochar addition decreased the abundance of *Sordariomycetes*, *Leotiomycetes*, and *Dothideomycetes*. Our study showed that aggregate CO_2 release was positively linked to *Sordariomycetes* and *Umbelopsidomycetes* but negatively linked to the relative abundance of *Leotiomycetes*, *Dothideomycetes*, *Mortierellomycetes*, and *Rozellomycotina_cls_Incertae_sedis*. This aligns with prior studies indicating that *Sordariomycetes* and *Mortierellomycetes* affect the decomposition of SOC by influencing the enzyme activity associated with C decomposition (Chen et al., 2015; Liu et al., 2021). Furthermore, *Umbelopsidomycetes* promote the decomposition of C by converting stubborn organic matter into organic matter, which is easily decomposed in the soil (Muszewska et al., 2021). All the aforementioned results indicate that the elevated SOC mineralization rate discovered in the pruned litter and organic fertilizer treatments was attributed to an elevation in the proportional presence of *Sordariomycetes* and *Umbelopsidomycetes*, and a reduction in the proportional presence of *Leotiomycetes*, *Dothideomycetes*, *Mortierellomycetes*, and *Rozellomycotina_cls_Incertae_sedis*. The lower SOC mineralization rate for biochar addition was due to a decline in the proportional presence of *Leotiomycetes* and *Dothideomycetes*.

4.4. Contribution of soil microbial C-cycling genes and enzymes activities to SOC mineralization

In this study, the addition of pruned litter elevated the activities of β-glucosidase and cellobiohydrolase, while the addition of organic fertilizer enhanced the activity of cellobiohydrolase. Furthermore, the combined increase in activities of β-glucosidase and cellobiohydrolase enzymes led to an escalation in aggregate soil CO_2 release. This aligns with the observations of Luo et al. (2019) and Zhang et al. (2021), which show that the soil β-glucosidase and cellobiohydrolase exhibited a connection to SOC mineralization. These results suggest that the increased rate of SOC mineralization after pruned litter application is associated with higher activities of β-glucosidase and cellobiohydrolase, while the decreased rate of SOC mineralization after the addition of organic fertilizer and biochar is related to lower activities of β-glucosidase and cellobiohydrolase. The SEM outcomes also indicated that pruned litter increased the rate of SOC mineralization by boosting the activities of β-glucosidase and cellobiohydrolase, whereas organic fertilizer solely increased the rate of SOC mineralization by enhancing the activity of cellobiohydrolase.

Previous studies have found that *GH48* and *cbh*I play crucial roles in soil carbon decomposition (Grover et al., 2020; Duan et al., 2021b). Alterations in the abundance of *GH48* and *cbh*I genes had a significant influence on the functions of β-glucosidase and cellobiohydrolase within the soil (Li et al., 2024; Zhou et al., 2024), in line with our research findings, the correlation remains intact, showing that the levels of *GH48* and *cbh*I correspond positively with the enzymatic activities of β-glucosidase and cellobiohydrolase. In this study, pruned litter addition increased the abundance of *GH48* and *cbh*I, whereas *GH48* and *cbh*I gene abundance was lower in the organic fertilizer and biochar treatments than in the pruned litter treatment. Moreover, soil CO_2 release was higher following the addition of pruned litter than with organic fertilizer and biochar addition, and there was a positive association between soil CO_2 release and *GH48/cbh*I gene abundance. These outcomes suggest that the elevated SOC mineralization rate following the addition of pruned litter was associated with an increase in the abundance of *GH48* and *cbh*I under the pruned litter treatments, whereas the reduced SOC mineralization rate following the application of organic fertilizer and biochar was due to the lower *GH48* and *cbh*I abundance under the two treatments. Furthermore, our SEM analysis showed that pruned litter promoted enzyme activity by increasing the abundance of *GH48* and *cbh*I, thereby increasing the rate of SOC mineralization.

5. Conclusions

Our study indicated that, compared to the control, the application of pruned litter dramatically increased SOC mineralization, while the pruned litter derivative organic fertilizer and biochar addition could effectively mitigate the rate of SOC mineralization, and the mitigating effect of biochar was more intense (cf. organic fertilizer). In addition, pruned litter enhanced C emission primarily by increasing the O-alkyl C content and β-glucosidase/ cellobiohydrolase activities, as well as enhancing the abundance of *GH48* and *cbh*I. In contrast, the pruned litter derivative organic fertilizer and biochar mitigated the C emission mainly by reducing the content of MBC and O-alkyl C, β-glucosidase/ cellobiohydrolase activities, as well as the abundance of *GH48* and *cbh*I. More interestingly, our study indicated that the mitigation of the SOC mineralization rate by organic fertilizer and biochar addition was associated with alterations in the makeup and arrangement of microbial populations, especially the relative abundance of some key species, such as bacterial taxa (*Acidobacteria*, *Actinobacteria*, and *Verrucomicrobiae*) and fungal taxa (*Sordariomycetes* and *Umbelopsidomycetes*). These results suggest that processing tea tree pruning litter into organic fertilizer and biochar, especially biochar, can effectively mitigate the loss of C from tea plantation soils by reducing the content of easily degradable C, the abundance of functional genes and enzyme activities associated with C decomposition, and "altering the characters of soil microbial communities". This provides new ideas for optimizing the use of tea pruning litter to improve SOC content. The outcomes of our research predominantly originated from the incubation trial, and should these findings be confirmed through a field experiment, it will be beneficial for the construction of ecologically low-C tea plantations.

CRediT authorship contribution statement

Shaobo Zhang: Methodology, Formal analysis, Investigation, Resources, Data curation, Writing – original draft, Visualization. **Fuyin Huang:** Investigation, Data curation, Writing – review & editing. **Shuai Guo:** Writing – review & editing. **Ying Luo:** Writing – review & editing. **Liping Zhang:** Writing – review & editing. **Lan Zhang:** Writing – review & editing. **Zhenzheng Li:** Writing – review & editing. **Shibei Ge:** Writing – review & editing. **Huasen Wang:** Writing – review & editing. **Jianyu Fu:** Writing – review & editing. **Xin Li:** Writing – review & editing. **Peng Yan:** Conceptualization, Validation, Writing – review & editing, Supervision, Funding acquisition.

Declaration of Competing Interest

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.

Acknowledgements

This research was funded by the Key Research and Development Project of Science and Technology Department of Zhejiang Province (2022C02046), Key R&D Program of Zhejiang (2023C02019), Zhejiang Province Science and Technology Cooperation Project for Nine Affiliations of Agriculture, Rural Affairs, and Farmers (2024SNJF031, and 2023SNJF037), and the Agricultural Science and Technology Innovation Program (CAAS-ZDRW202417).

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.indcrop.2025.120518.

Data availability

Data will be made available on request.

References

Alef, P., Nannipieri, P., 1995. Enzyme Activities. Methods in Applied Soil Microbiology and Biochemistry. Academic Press, London, pp. 311–373.

Awasthi, M.K., Duan, Y., Awasthi, S.K., Liu, T., Zhang, Z., 2020. Effect of biochar and bacterial inoculum additions on cow dung composting. Bioresour. Technol. 297, 122407.

Bello, A., Han, Y., Zhu, H.F., Deng, L.T., Yang, W., Meng, Q.X., Sun, Y., Egbeagu, U.U., Sheng, S.Y., Wu, X.T., Jiang, X., Xu, X.H., 2020. Microbial community composition, co-occurrence network pattern and nitrogen transformation genera response to biochar addition in cattle manure-maize straw composting. Sci. Total Environ. 721, 137759.

Berhane, M., Xu, M., Liang, Z., Shi, J., Wei, G., Tian, X., 2020. Effects of long-term straw return on soil organic carbon storage and sequestration rate in North China upland crops: a meta-analysis. Glob. Change Biol. 26, 2686–2701.

Bray, R.H., Kurtz, L.T., 1945. Determination of total, organic, and available forms of phosphorus in soils. Soil Sci. 59, 39–46.

Cates, A.M., Ruark, M.D., Hedtcke, J.L., Posner, J.L., 2016. Long-term tillage, rotation and perennialization effects on particulate and aggregate soil organic matter. Soil Tillage Res 155, 371–380.

Chen, J.H., Chen, D., Xu, Q.F., Fuhrmann, J.J., Li, L.Q., Pan, G., Li, Y.F., Hua, Q., Liang, C.F., Sun, X., 2019. Organic carbon quality, composition of main microbial groups, enzyme activities, and temperature sensitivity of soil respiration of an acid paddy soil treated with biochar. Biol. Fertil. Soils 55, 185–197.

Chen, G., Fang, Y., Van Zwieten, L., Xuan, Y., Tavakkoli, E., Wang, X., Zhang, R., 2021b. Priming, stabilization and temperature sensitivity of native SOC is controlled by microbial responses and physicochemical properties of biochar. Soil Biol. Biochem. 154, 108139.

Chen, W.H., Lin, B.J., Lin, Y.Y., Chu, Y.S., Ubando, A.T., Show, P.L., Ong, H.C., Chang, J. S., Ho, S.H., Culaba, A.B., Pétrissans, A., Pétrissans, M., 2021a. Progress in biomass torrefaction: principles, applications and challenges. Prog. Energy Combust. Sci. 82, 100887.

Chen, L., Xu, J., Feng, Y., Wang, J., Yu, Y., Brookes, P.C., 2015. Responses of soil microeukaryotic communities to short-term fumigation-incubation revealed by MiSeq amplicon sequencing. Front. Microbiol. 6, 1149.

Dai, Z.M., Xiong, X.Q., Zhu, H., Xu, H.J., Leng, P., Li, J.J., Tang, C., Xu, J.M., 2021. Association of biochar properties with changes in soil bacterial, fungal and fauna communities and nutrient cycling processes. Biochar 3, 239–254.

Debosz, K., Rasmussen, P.H., Pedersen, A.R., 1999. Temporal variations in microbial biomass C and cellulolytic enzyme activity in arable soils: effects of organic matter input. Appl. Soil Ecol. 13, 209–218.

Denvir, A., García-Oliva, F., Arima, E.Y., Latorre-Cárdenas, M.C., González-Rodríguez, A., Young, K.R., De La Cruz, L.I.L., 2024. Sustainability implications of carbon dynamics on the avocado frontier. Agric. Ecosyst. Environ. 359, 108746.

Du, S., Wang, L., Yang, H., Zhang, Q., 2024. Tree phylogeny predicts more than litter chemical components in explaining enzyme activities in forest leaf litter decomposition. Microbiol. Res., 127658

Du, L., Zheng, Z.C., Li, T.X., Wang, Y.D., Huang, H.G., Yu, H., Ye, D.H., Liu, T., Zhang, X. Z., 2023. Aggregate-associated carbon compositions explain the variation of carbon sequestration in soils after long-term planting of different tea varieties. Sci. Total Environ. 856, 159227.

Duan, Y.M., Awasthi, S.K., Liu, T., Verma, S., Wang, Q., Chen, H., Ren, X.N., Zhang, Z.Q., Awasthi, M.K., 2019. Positive impact of biochar alone and combined with bacterial consortium amendment on improvement of bacterial community during cow manure composting. Bioresour. Technol. 280, 79–87.

Duan, Y., Chen, L., Li, Y.M., Wang, Q.Y., Zhang, C.Z., Ma, D.H., Li, J.Y., Zhang, J.B., 2021a. N, P and straw return influence the accrual of organic carbon fractions and microbial traits in a Mollisol. Geoderma 403, 115373.

Duan, Y., Chen, L., Zhang, J.B., Li, D.M., Han, X.R., Zhu, B., Li, Y., Zhao, B.J., Huang, P., 2021b. Long-term fertilisation reveals close associations between soil organic carbon composition and microbial traits at aggregate scales. Agric. Ecosyst. Environ. 306, 107169.

Fan, L., Han, W., 2020. Soil respiration after forest conversion to tea gardens: a chronosequence study. Catena 190, 104532.

Fan, F.L., Yu, B., Wang, B.R., George, T.S., Yin, H.Q., Xu, D.Y., Li, D.C., Song, A., 2019. Microbial mechanisms of the contrast residue decomposition and priming effect in soils with different organic and chemical fertilization histories. Soil Biol. Biochem. 135, 213–221.

Fierer, N., Ladau, J.S., Clemente, J.C., Leff, J.W., Owens, S.M., Pollard, K.S., Knight, R., Gilbert, J.A., McCulley, R.L., 2013. Reconstructing the microbial diversity and function of pre-agricultural tallgrass prairie soils in the United States. Science 342, 621–624.

Gao, X.T., Tan, W.B., Zhao, Y., Wu, J.Q., Sun, Q.H., Qi, H.S., Xie, X.Y., Wei, Z., 2019. Diversity in the mechanisms of humin formation during composting with different materials. Environ. Sci. Technol. 53, 3653–3662.

Grover, S.P., Butterly, C.R., Wang, X., Gleeson, D.B., Macdonald, L.M., Hall, D., Tang, C., 2020. An agricultural practise with climate and food security benefits: "Claying" with kaolinitic clay subsoil decreased soil carbon priming and mineralisation in sandy cropping soils. Sci. Total Environ. 709, 134488.

Hall, S.J., Huang, W., Timokhin, V.I., Hammel, K.E., 2020. Lignin lags, leads, or limits the decomposition of litter and soil organic carbon. Ecology 101, e03113.

Hao, X.X., Han, X.Z., Wang, S.Y., Li, L.J., 2022. Dynamics and composition of soil organic carbon in response to 15 years of straw return in a Mollisol. Soil Tillage Res. 215, 105221.

International Tea Committee (ITC). Annual Bulletin of Statistics. Available from : https://inttea.com/wp-content/uploads/IndexABS2023.pdf.

Kelly, C.N., Schwaner, G.W., Cumming, J.R., Driscoll, T.P., 2021. Metagenomic reconstruction of nitrogen and carbon cycling pathways in forest soil: influence of different hardwood tree species. Soil Biol. Biochem. 156, 108226.

Lal, R., 2018. Digging deeper: a holistic perspective of factors affecting soil organic carbon sequestration in agroecosystems. Glob. Change Biol. 24, 3285–3301.

Li, Y., Li, Y., Chang, S.X., Liang, X., Qin, H., Chen, J., Xu, Q., 2017. Linking soil fungal community structure and function to soil organic carbon chemical composition in intensively managed subtropical bamboo forests. Soil Biol. Biochem. 107, 19–31.

Li, Y.C., Li, Y.F., Chang, S.X., Yang, Y.F., Fu, S.L., Jiang, P.K., Luo, Y., Yang, M., Chen, Z. H., Hu, S.D., Zhao, M.X., Liang, X., Xu, Q.F., Zhou, G.M., Zhou, J.Z., 2018. Biochar reduces soil heterotrophic respiration in a subtropical plantation through increasing soil organic carbon recalcitrancy and decreasing carbon-degrading microbial activity. Soil Biol. Biochem. 122, 173–185.

Li, S., Wu, X., Xue, H., Gu, B.J., Cheng, H., Zeng, J.M., Peng, C.H., Ge, Y., Chang, J., 2011. Quantifying carbon storage for tea plantations in China. Agric. Ecosyst. Environ. 141, 390–398.

Li, Y.F., Zhang, S.B., Fang, Y.Y., Hui, D.F., Tang, C.X., Van Zwieten, L., Zhou, J.S., Jiang, Z.H., Cai, Y.J., Yu, B., Hu, J.G., Zhou, G.M., Gu, B.J., Chang, S.X., 2024. Nitrogen deposition-induced stimulation of soil heterotrophic respiration is counteracted by biochar in a subtropical forest. Agric. For. Meteorol. 349, 109940.

Liang, Y., Al-Kaisi, M., Yuan, J.C., Liu, J.Z., Zhang, H.X., Wang, L.C., Cai, H.G., Ren, J., 2021. Effect of chemical fertilizer and straw-derived organic amendments on continuous maize yield, soil carbon sequestration and soil quality in a Chinese Mollisol. Agric. Ecosyst. Environ. 314, 107403.

Lin, Z.W., Li, Y.F., Tang, C.X., Luo, Y., Fu, W.J., Cai, X.Q., Li, Y.C., Yue, T., Jiang, P.K., Hu, S.D., Chang, S.X., 2018. Converting natural evergreen broadleaf forests to intensively managed moso bamboo plantations affects the pool size and stability of soil organic carbon and enzyme activities. Biol. Fertil. Soils 54, 467–480.

Lin, Y., Ye, G., Kuzyakov, Y., Liu, D., Fan, J., Ding, W., 2019. Long-term manure application increases soil organic matter and aggregation, and alters microbial community structure and keystone taxa. Soil Biol. Biochem. 134, 187–196.

Ling, L., Fu, Y.Y., Jeewani, P.H., Tang, C.X., Pan, S.T., Reid, B.J., Gunina, A., Li, Y.F., Cai, Y.J., Kuzyakov, Y., Li, Y., Su, W., Singh, B.P., Luo, Y., Xu, J., 2021. Organic matter chemistry and bacterial community structure regulate decomposition processes in post-fire forest soils. Soil Biol. Biochem. 160, 108311.

Ling, L., Luo, Y., Jiang, B., Lv, J.T., Meng, C.M., Liao, Y.H., Reid, B.J., Ding, F., Lu, Z.J., Kuzyakov, Y., Xu, J.M., 2022. Biochar induces mineralization of soil recalcitrant components by activation of biochar responsive bacteria groups. Soil Biol. Biochem. 172, 108778.

Liu, Y.Y., Dong, L.Z., Zhang, H.J., Deng, Y.Y., Hu, B., Wang, W., 2023. Distinct roles of bacteria and fungi in mediating soil extracellular enzymes under long-term nitrogen deposition in temperate plantations. For. Ecol. Manag. 529, 120658.

Liu, X.J., Hannula, S.E., Li, X., Hundscheid, M.P., klein Gunnewiek, P.J., Clocchiatti, A., Ding, W., de Boer, W., 2021. Decomposing cover crops modify root-associated microbiome composition and disease tolerance of cash crop seedlings. Soil Biol. Biochem. 160, 108343.

Liu, X., Zhou, F., Hu, G.Q., Shao, S., He, H.B., Zhang, W., Zhang, X.D., Li, L.J., 2019. Dynamic contribution of microbial residues to soil organic matter accumulation influenced by maize straw mulching. Geoderma 333, 35–42.

Lu, W., Ding, W., Zhang, J., Li, Y., Luo, J., Bolan, N., Xie, Z., 2014. Biochar suppressed the decomposition of organic carbon in a cultivated sandy loam soil: a negative priming effect. Soil Biol. Biochem. 76, 12–21.

Luo, X., Hou, E., Zhang, L., Zang, X., Yi, Y., Zhang, G., Wen, D., 2019. Effects of forest conversion on carbon-degrading enzyme activities in subtropical China. Sci. Total Environ. 696, 133968.

Luo, Y., Zhang, Y., Wang, Y., Sun, Y., Xia, X., Su, Y., Liao, W., 2023. Combined application of biochar and pruned tea plant litter benefits nitrogen availability for tea and alters microbial community structure. Agronomy 13, 1465.

Ma, Q.X., Wen, Y., Wang, D.Y., Sun, X.D., Hill, P.W., Macdonald, A., Chadwick, D.R., Wu, L.H., Jones, D.L., 2020. Farmyard manure applications stimulate soil carbon and nitrogen cycling by boosting microbial biomass rather than changing its community composition. Soil Biol. Biochem. 144, 107760.

Miao, Y.C., Lin, Y.X., Chen, Z.M., Zheng, H.J., Niu, Y.H., Kuzyakov, Y., Liu, D.Y., Ding, W., 2022. Fungal key players of cellulose utilization: Microbial networks in aggregates of long-term fertilized soils disentangled using ^{13}C-DNA-stable isotope probing. Sci. Total Environ. 832, 155051.

Mitchell, P.J., Simpson, A.J., Soong, R., Simpson, M.J., 2015. Shifts in microbial community and water-extractable organic matter composition with biochar amendment in a temperate forest soil. Soil Biol. Biochem. 81, 244–254.

Muszewska, A., Okrasińska, A., Steczkiewicz, K., Drgas, O., Orłowska, M., Perlińska-Lenart, U., Aleksandrzak-Piekarczyk, T., Szatraj, K., Zielenkiewicz, U., Piłsyk, S., Malc, E., Mieczkowski, O., Kruszewska, J.S., Bernat, P., Pawłowska, J., 2021. Metabolic potential, ecology and presence of associated bacteria is reflected in genomic diversity of Mucoromycotina. Front. Microbiol. 12, 636986.

Ni, H.W., Jing, X.Y., Xiao, X., Zhang, N., Wang, X.Y., Sui, Y.Y., Sun, B., Liang, Y.T., 2021. Microbial metabolism and necromass mediated fertilization effect on soil organic carbon after long-term community incubation in different climates. ISME J. 15, 2561–2573.

Nottingham, A.T., Turner, B.L., Chamberlain, P.M., Stott, A.W., Tanner, E.V., 2012. Priming and microbial nutrient limitation in lowland tropical forest soils of contrasting fertility. Biogeochemistry 111, 219–237.

Olayemi, O.P., Kallenbach, C.M., Wallenstein, M.D., 2022. Distribution of soil organic matter fractions are altered with soil priming. Soil Biol. Biochem. 164, 108494.

Pramanik, P., Phukan, M., 2020. Enhanced microbial respiration due to carbon sequestration in pruning litter incorporated soil reduced the net carbon dioxide flux from atmosphere to tea ecosystem. J. Sci. Food Agric. 100, 295–300.

Ridgeway, J.R., Morrissey, E.M., Brzostek, E.R., 2022. Plant litter traits control microbial decomposition and drive soil carbon stabilization. Soil Biol. Biochem. 175, 108857.

Rocci, K.S., Lavallee, J.M., Stewart, C.E., Cotrufo, M.F., 2021. Soil organic carbon response to global environmental change depends on its distribution between mineral-associated and particulate organic matter: a meta-analysis. Sci. Total Environ. 793, 148569.

de la Rosa, J.M., Rosado, M., Paneque, M., Miller, A.Z., Knicker, H., 2018. Effects of aging under field conditions on biochar structure and composition: implications for biochar stability in soils. Sci. Total Environ. 613, 969–976.

Sarker, T.C., Incerti, G., Spaccini, R., Piccolo, A., Mazzoleni, S., Bonanomi, G., 2018. Linking organic matter chemistry with soil aggregate stability: insight from ^{13}C NMR spectroscopy. Soil Biol. Biochem. 175–184.

Sjöberg, G., Nilsson, S.I., Persson, T., Karlsson, P., 2004. Degradation of hemicellulose, cellulose and lignin in decomposing spruce needle litter in relation to N. Soil Biol. Biochem. 36, 1761–1768.

Sokol, N.W., Sanderman, J., Bradford, M.A., 2019. Pathways of mineral-associated soil organic matter formation: integrating the role of plant carbon source, chemistry, and point of entry. Glob. Change Biol. 25, 12–24.

Song, Y.Z., Li, Y.F., Cai, Y.J., Fu, S.L., Luo, Y., Wang, H.L., Liang, C.F., Lin, Z.W., Hu, S.D., Li, Y.C., Chang, S.X., 2019. Biochar decreases soil N_2O emissions in Moso bamboo plantations through decreasing labile N concentrations, N-cycling enzyme activities and nitrification/denitrification rates. Geoderma 348, 135–145.

Soong, J.L., Fuchslueger, L., Marañon-Jimenez, S., Torn, M.S., Janssens, I.A., Penuelas, J., Richter, A., 2020. Microbial carbon limitation: the need for integrating microorganisms into our understanding of ecosystem carbon cycling. Glob. Change Biol. 26, 1953–1961.

Tang, H.M., Li, C., Xu, Y.L., Cheng, K.K., Shi, L.H., Wen, L., Li, W.Y., Xiao, X.P., 2021. Effects of fertilizer practice on fungal and actinobacterial cellulolytic community with different humified particle-size fractions in double-cropping field. Sci. Rep. 11, 18441.

Team, R.C., 2013. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna.

Wang, W., Chen, D., Sun, X., Zhang, Q., Koide, R.T., Insam, H., Zhang, S., 2019. Impacts of mixed litter on the structure and functional pathway of microbial community in litter decomposition. Appl. Soil Ecol. 144, 72–82.

Wang, J., Fu, X., Sainju, U.M., Zhao, F.Z., 2018. Soil carbon fractions in response to straw mulching in the Loess Plateau of China. Biol. Fertil. Soils 54, 423–436.

Wang, F.W., Gao, Y., Li, X., Luan, M.D., Wang, X.Y., Zhao, Y.W., Zhou, X.H., Du, G.Z., Wang, P., Ye, C.L., Guo, H., 2024. Changes in microbial composition explain the contrasting responses of glucose and lignin decomposition to soil acidification in an alpine grassland. Sci. Total Environ. 930, 172671.

Wang, W., Lai, D.Y.F., Wang, C., Pan, T., Zeng, C., 2015. Effects of rice straw incorporation on active soil organic carbon pools in a subtropical paddy field. Soil Tillage Res 152, 8–16.

Wang, D., Wu, B.S., Li, F., Li, X.Q., Wang, Z., Hou, J.F., Cao, R., Yang, W., 2023. Soil organic carbon stock in China's tea plantations and their great potential of carbon sequestration. J. Clean. Prod. 421, 138485.

Wang, J., Xiong, Z.Q., Kuzyakov, Y., 2016. Biochar stability in soil: meta-analysis of decomposition and priming effects. GCB Bioenergy 8, 512–523.

Wei, L., Razavi, B.S., Wang, W.Q., Zhu, Z.K., Liu, S.L., Wu, J.S., Kuzyakov, Y., Ge, T., 2019. Labile carbon matters more than temperature for enzyme activity in paddy soil. Soil Biol. Biochem. 135, 134–143.

Wei, C.C., Ren, S.M., Yang, P.L., Wang, Y., He, X., Xu, Z.A., Wei, R., Wang, S.J., Chi, Y.B., Zhang, M.T., 2021. Effects of irrigation methods and salinity on CO_2 emissions from farmland soil during growth and fallow periods. Sci. Total Environ. 752, 141639.

Whitman, T., Pepe-Ranney, C., Enders, A., Koechli, C., Campbell, A., Buckley, D.H., Lehmann, J., 2016. Dynamics of microbial community composition and soil organic carbon mineralization in soil following addition of pyrogenic and fresh organic matter. ISME J. 10, 2918–2930.

Wu, L., Zhang, W., Wei, W., He, Z., Kuzyakov, Y., Bol, R., Hu, R., 2019. Soil organic matter priming and carbon balance after straw addition is regulated by long-term fertilization. Soil Biol. Biochem. 135, 383–391.

Xie, S., Yang, F., Feng, H., Yu, Z., Liu, C., Wei, C., Liang, T., 2021. Organic fertilizer reduced carbon and nitrogen in runoff and buffered soil acidification in tea plantations: evidence in nutrient contents and isotope fractionations. Sci. Total Environ. 762, 143059.

Yan, P., Wu, L.Q., Wang, D.H., Fu, J.Y., Shen, C., Li, X., Zhang, L.P., Zhang, L., Fan, L.C., Han, W.Y., 2020. Soil acidification in Chinese tea plantations. Sci. Total Environ. 715, 136963.

Yang, X., Ni, K., Ma, L., Shi, Y., Yi, X., Ji, L., Ruan, J., 2022. ^{13}C labelling of litter added to tea (*Camellia sinensis* L.) plantation soil reveals a significant positive priming effect that leads to less soil organic carbon accumulation. Agronomy 12, 293.

Yu, Q., Hu, X., Ma, J., Ye, J., Sun, W., Wang, Q., Lin, H., 2020. Effects of long-term organic material applications on soil carbon and nitrogen fractions in paddy fields. Soil Tillage Res. 196, 104483.

Zhang, M., Chen, Y.G., Fan, D.M., Zhu, Q., Pan, Z.Q., Fan, K., Wang, X.C., 2017. Temporal evolution of carbon storage in Chinese tea plantations from 1950 to 2010. Pedosphere 27, 121–128.

Zhang, S.B., Fang, Y.Y., Kawasaki, A., Tavakkoli, E., Cai, Y.J., Wang, H.L., Ge, T.D., Zhou, J.S., Yu, B., Li, Y.F., 2023. Biochar significantly reduced nutrient-induced positive priming in a subtropical forest soil. Biol. Fertil. Soils 59, 589–607.

Zhang, S.B., Fang, Y.Y., Luo, Y., Li, Y.C., Ge, T.D., Wang, Y.X., Wang, H.L., Yu, B., Song, X.Z., Chen, J.H., Zhou, J.S., Li, Y.F., Chang, S.X., 2021. Linking soil carbon availability, microbial community composition and enzyme activities to organic carbon mineralization of a bamboo forest soil amended with pyrogenic and fresh organic matter. Sci. Total Environ. 801, 149717.

Zhang, Q., Liang, G., Guo, T., He, P., Wang, X., Zhou, W., 2017. Evident variations of fungal and actinobacterial cellulolytic communities associated with different humified particle-size fractions in a long-term fertilizer experiment. Soil Biol. Biochem. 113, 1–13.

Zhou, J., Jiang, X., Zhou, B.K., Zhao, B.S., Ma, M.C., Guan, D.W., Li, J., Chen, S.F., Cao, F.M., Shen, D.L., Qin, J., 2016. Thirty four years of nitrogen fertilization decreases fungal diversity and alters fungal community composition in black soil in northeast China. Soil Biol. Biochem. 95, 135–143.

Zhou, J., Zang, H., Loeppmann, S., Gube, M., Kuzyakov, Y., Pausch, J., 2020. Arbuscular mycorrhiza enhances rhizodeposition and reduces the rhizosphere priming effect on the decomposition of soil organic matter. Soil Biol. Biochem. 140, 107641.

Zhou, J.S., Zhang, S.B., Hui, D.F., Vancov, T., Fang, Y.Y., Tang, C.X., Jiang, Z.H., Ge, T.D., Cai, Y.J., Yu, B., White, J.C., Li, Y.F., 2024. Pyrogenic organic matter decreases while fresh organic matter increases soil heterotrophic respiration through modifying microbial activity in a subtropical forest. Biol. Fertil. Soils 60, 509–524.

Zimmerman, A.R., Gao, B., Ahn, M.Y., 2011. Positive and negative carbon mineralization priming effects among a variety of biochar-amended soils. Soil Biol. Biochem. 43, 1169–1179.