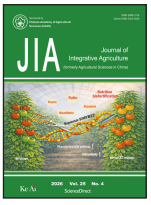
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RESEARCH ARTICLE

Straw tissue quality influence the formation pathways of soil organic carbon *via* living microbes or microbial necromass in a Mollisols, Northeast China

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Highlights

- The phospholipid fatty acid (PLFA) concentration of bacteria and fungi exhibited a continuous decrease throughout the incubation period, while necromass remained in-fluctuating until showing a notable increase in the later stage.
- Straw leaves generated higher quantities of straw-derived particulate organic carbon (POC) and mineral-associated OC (MAOC) compared to straw stems and sheaths.
- The POC dynamics were associated with straw chemical characteristics, while MAOC showed associations with both microbial necromass traits and straw chemical properties.

Abstract

Soil organic carbon (SOC), representing the largest terrestrial organic carbon pool, significantly influences soil quality. The incorporation of residues is widely recognized as a method to regulate SOC sequestration. A 365-day incubation experiment was conducted to evaluate the contribution of straw-derived carbon (SDC) of varying quality to SOC fractions (free-floating particulate organic carbon (fPOC), occluded POC (oPOC) and mineral-associated OC (MAOC)), and examine the relationships between microorganisms and SOC fractions by incorporating ^{13}C-labelled maize stem straw (ST), leave straw (LE), sheath straw (SH) (1%) in Chinese Mollisols. Results indicated that compared to control (CK), ST, LE and SH treatments enhanced SOC, fPOC and MAOC by 4.8–19.5, 35.7–49.5 and 1.6–3.9%, respectively. The SDC-SOC and MAOC content of LE were 29.1–38.1% and 17.5–44.5% higher than ST and SH, respectively. The SDC-oPOC content of SH was 3.1% higher than LE. The PLFA concentration decreased steadily throughout the incubation period, while necromass remained in-fluctuating until an obvious increasing trend observed at later stage. Furthermore, structural equation model (SEM) revealed that lignin to nitrogen ratio (LigN) of ST exhibited negative association with SDC-fPOC, and bacterial diversity in SH showed negative correlation with LigN and positive correlation with SDC-oPOC, while demonstrating positive correlation between microbial necromass and SDC-MAOC in LE. These findings indicated that POC dynamics correlated with straw chemical traits, while MAOC showed links to both microbial necromass traits and straw chemical characteristics. These findings advance our understanding of how straw residue quality influences SOC turnover and stabilization through microbial community interactions, contributing to the development of policies to improve soil fertility, and promote the rational and efficient utilization of straw.

Keywords: soil organic carbon, straw quality, microbial necromass, living microbial, particulate organic carbon, mineral-associated organic carbon

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1. Introduction

Soil organic carbon (SOC) contains more C than plant biomass and the atmosphere combined; therefore, even minor changes in soil C can significantly impact soil functioning and ecosystem services (Ridgeway *et al.* 2022; Fu *et al.* 2023). Land-use change and intensive use of arable land have resulted in substantial depletion of SOC and adverse effects on soil functions (Amelung *et al.* 2020), necessitating appropriate management practices to increase C input, prevent these losses, and rebuild C stocks (Beck *et al.* 1995; Maynard *et al.* 2017). Straw incorporation into farmland has emerged as a promising and environmentally sustainable management practice for new SOC formation, offering the additional benefit of carbon sequestration for improved management and ecosystem services (Tinoco *et al.* 2004; Yin *et al.* 2024). While some research has found neutral (Pan *et al.* 2010) or negative (van Kessel *et al.* 2013; Bai *et al.* 2023) impacts on SOC contents following straw return, previous studies have demonstrated increased SOC contents with straw incorporation (Wu *et al.* 2023). Both biotic and abiotic factors influence the mineralization of native SOC, reflected in SOC storage, which demonstrates a dynamic equilibrium between exogenous C inputs and outputs (Zhang J *et al.* 2024). Although the effects of residue quality on stabilization and SOC fractions remain debatable, residue quality still plays an significant role in residue C dynamics, subsequently influencing soil C sequestration. Recent concepts suggest high-quality crop residues, characterized by rapid decomposition rates, low C/N ratios, and low ligin/N ratio, should facilitate more efficient SOC accumulation compared to low-quality plant litters with slow decomposition rates, high C/N ratios, and high ligin/N ratio (Cotrufo *et al.* 2013). Bai *et al.* (2024) observed that the addition of *Quercus wutaishanica* (high-quality litter) resulted in higher SOC content compared to *Populus davidiana* with low quality. Contrasting results have been reported, as Lyu *et al.* (2023) found that low-quality litter produces twice the amount of new SOC compared to high-quality litter. Mwafulirwa *et al.* (2019) demonstrated that low-quality root residues enhance soil C storage more effectively than shoot residues. While current studies primarily address how varied quality of residues, determined by plant species and root-shoot differences, impacts SOC accumulation, analyses of how different straw tissues of aboveground residues contribute to SOC stability and distribution remain limited. Understanding the role of crop residue quality management in SOC formation and stabilization is essential for better predicting responses of C cycling and storage after crop residues return to the soil.

Research suggests that total SOC may not serve as the most sensitive indicator for understanding SOC accrual mechanisms or estimating SOC stock changes (Heckman *et al.* 2022). Contemporary frameworks propose that soil carbon accumulation can be more precisely characterized by dividing SOC into particulate organic carbon (POC) and mineral-associated organic carbon (MAOC) pools, given their distinct physical and chemical properties, varying mean residence times, and differential responses to plant litter inputs (Cotrufo *et al.* 2019, 2022). The POC fraction, dominated by partially decomposed plant-derived C, represents a labile C pool readily decomposed by microorganisms (Lehmann and Kleber 2015). MAOC consists primarily of low molecular weight compounds through two pathways: direct leaching from residues and association with the mineral phase, or generation *via* the "*in vivo* microbial turnover pathway" producing necromass that incorporates into MAOC (Liang *et al.* 2017). Residue quality significantly influences contributions to various SOC pools. Although increased carbon inputs enhance both MAOC and POC content, empirical studies reveal contrasting patterns: Zhang *et al.* (2022) noted greater effects for MAOC compared to POC, while Hu *et al.* (2023) found stronger POC responses under similar conditions. High-quality exogenous C (corn straw) predominantly enhanced MAOC accumulation, whereas low-quality exogenous C (miscanthus or grass) mainly contributed to POC accrual (Cheng *et al.* 2023). Additionally, structurally complex root tissues generated less MAOC than leaf and shoot tissues (Ridgeway *et al.* 2022). Kaštovská *et al.* (2024) determined that root tissues produced more MAOC than shoot tissues through direct binding of depolymerized root-C to mineral surfaces without microbial transformation. These inconsistent findings suggest the research is needed to assess POC and MAOC formation by straw aboveground tissues with varying qualities, as they demonstrate greater sensitivity to modifications.

Numerous previous studies on the impacts of agricultural practices (e.g., crop residue return) have concentrated solely on the role of the microbial community in controlling the turnover of organic compounds (Song *et al.* 2017; Cui *et al.* 2018; Xu *et al.* 2022), despite soil living microbial biomass C comprising less than 5% of SOC. The classical concepts suggested that bacteria generally prefer to utilize labile substrates and exhibit rapid growth, while fungi excel at metabolizing resistant substrates with slower growth rates (Zhang F T *et al.* 2024). Research has established that straw incorporation influences microbial community composition and diversity (Chen *et al.* 2022; Chen *et al.* 2024), with high-quality exogenous C tends to favor bacterial rather than fungal growth, and *vice versa* for low-quality exogenous C (Hicks *et al.* 2021). The shifts in fungal/bacterial ratios further affect their respective necromass contributions to SOC sequestration due to specific nutrient requirements and environmental adaptations (Wang B R *et al.* 2021). Furthermore, microbial necromass derived from the accumulative legacy of anabolic products may contribute to more than 50% of SOC in cropland (Liang *et al.* 2019), with a greater contribution to the formation of MAOC (Cotrufo *et al.* 2019). Evidence indicates that microbial necromass exhibits particular susceptibility to soil protection through association with silt and clay minerals, serving as indicators of long-term effects of agricultural management (Craig *et al.* 2022; Xu *et al.* 2022). Therefore, studies on microbial necromass production and accumulation patterns could be used to assess how crop residue incorporation affects SOC sequestration.

The balance between microbial necromass formation and decomposition significantly influences SOC accumulation (Wang B R *et al.* 2021). Ding *et al.* (2013) demonstrated that long-term straw application increased total amino

sugar concentrations (4.4–8.4%) compared to the control, while Liu *et al.* (2019) reported that maize straw mulching enhanced microbial necromass accumulation in SOC and increased its contribution to SOC sequestration compared to maize residue removal, particularly facilitating fungal over bacterial necromass accumulation (Liu *et al.* 2019). Both biotic and abiotic factors, including crop straw quality, regulate microbial necromass accumulation. Studies have shown that larger amounts of amino sugars were formed at ahigher rate with increasing plant residue quality (Bai *et al.* 2013). Cotrufo *et al.* (2015) and Xu *et al.* (2022) found that high-quality straw addition generated more microbial necromass than low-quality straw, whereas Lyu *et al.* (2023) presented contrasting evidence suggesting recalcitrant compounds are important sources of microbial necromass. Related research revealed that plant roots exert stronger influences on microbial necromass production and stabilization than above-ground C sources (Jia *et al.* 2022). Furthermore, bacterial and fungal necromass exhibited different responses to straw return, with bacterial necromass affected by both residue quantity and quality, while fungal necromass storage remained unaffected (Zhang *et al.* 2023). Current evidence remains insufficient to determine microbial necromass contribution to increased SOC storage and residue quality impacts on fungal and bacterial necromass carbon. A quantitative synthesis is necessary to further differentiate bacterial and fungal necromass in MAOC and POC across varying residue qualities.

The black soils of China's frigid northeastern region, classified as Mollisols by the United States Department of Agriculture, possess high SOC content and represent typical high-yielding soils predominantly found in Heilongjiang and Jilin provinces (Mei *et al.* 2021). Over the last few decades, these black soils have faced challenges of "quantity reduction and quality decline" due to long-term irrational farming and intensive exploitation, directly impacting regional grain yield stability. Crop residue return to fields represents a crucial strategy for mitigating or preventing this decline (Zhang *et al.* 2023; Cai *et al.* 2024; Gao *et al.* 2024). Although evidence exists for residue return improving SOC formation in aggregates (Dai *et al.* 2014), limited knowledge exists regarding aboveground crop residue incorporation into different SOC fractions with varied stabilities, such as POC and MAOC in China Mollisols. Consequently, a 365-day incubation experiment was conducted to analyze straw derived-^{13}C content and distribution in SOC to trace C flow from decomposing residues into different SOC fractions, alongside coupling microbial community distributions and microbial necromass content following ^{13}C-labeled aboveground straw tissue (corn straw stem, leaves and sheath) addition into a Mollisol. This study examined two hypotheses: (1) Aboveground residues exhibit variations in tissue quality, affecting residue-derived C distribution between POC and MAOC; (2) high-quality residues contribute more microbial necromass C to MAOC than POC. The study objectives were to: (1) quantify straw-derived C accumulation and distribution in SOC, free-floating particulate organic carbon (fPOC), occluded POC (oPOC) and mineral-associated organic carbon (MAOC) over time and demonstrate specific stabilization patterns regarding residue quality; (2) distinguish the influences of straw stem, leaves and sheath on the dynamics of bacterial and fungal necromas, as well as microbial community distributions; (3) determine how microbial community distributions and necromass affect straw-derived C accrual in POC and MAOC, and identify key indicators for bacterial and fungal necromass accumulation.

2. Materials and methods

2.1. Soil sampling and analysis

Soil samples were collected from the Mollisol region of China, specifically from the 0–20 cm topsoil, at the Northeast Institute of Geography and Agroecology (43°59′51′′N, 125°24′5′′E), Chinese Academy of Sciences in Jilin Province, China. Five individual cores were collected randomly in the permanent maize (*Zea mays* L.) field using a 5 cm diameter stainless-steel auger. Each core was handled as an individual subsample: visible roots and organic debris were manually removed. All five subsamples were combined into one composite sample, homogenized, and passed through a 2 mm stainless-steel sieve. The processed samples were immediately stored at 4°C prior to the incubation experiments. Other soil samples had plant residues and stones removed before being pulverized to pass through a 2 mm sieve for soil chemical analysis. The sampling site had been used for continuous maize (*Zea mays* L.) cultivation for approximately eight years. This location experiences a typical middle-latitude monsoon climate, with an average annual temperature of 4.4°C and 520 mm of precipitation. Mollisol soil type was confirmed in the field (Mei *et al.* 2021).

2.2. Incubation experiment and sampling

Prior to storage at 4°C for the incubation experiment, all visible plant litter in the soils was removed. To activate soil microbial activity, soil samples (<2 mm) were pre-incubated for one week at 25°C and 45% water-holding capacity in dark conditions. Subsequently, 100 g of these pre-incubated soils (dry weight) were placed into 500 mL Mason jars with 1 g straw tissues. This setup established four treatments for straw tissue addition: straw stem (ST), leaves (LE), sheath (SH) and control (CK). Throughout the 365-day incubation period, soil samples were incubated at 25°C and kept at 65% of their water-holding capacity through frequent weighing and addition ofdeionized water. The incubation duration was sufficient to ensure input C protection in the soil.

Eighty-four jars were prepared to ensure three replicates at each soil sampling point. Soils were sampled on days 5, 10, 20, 40, 80, 120 and 365 to measure SOC, fPOC, oPOC MAOC, phospholipid fatty acid (PLFA) and amino sugars content.

Physical fractionation and subsequent analyses The soil was separated into three distinct OC fractions using a combined density and particle size fractionation scheme (Mueller and Koegel-Knabner 2009; Witzgall *et al.* 2021). Air-dried soil (18–20 g) was gently capillary-saturated with 100 mL 1.8 g cm^{-3} NaI and after 12 h, fPOC was extracted using a vacuum pump. oPOC was released from aggregated soil structures *via* ultrasonic dispersion (F-100S, Shenzhen

Fuyang Technology Group Co., Ltd., China) allowing its separation from heavier minerals. Both fPOC and oPOC fractions were washed several times using deionized water. While sand and coarse silt fractions were separated by wet sieving, mineral fractions<20 μm were separated *via* sedimentation, and later combined as one MAOC fraction. The carbon and ^{13}C contents for milled OM fractions (fPOC, oPOC and MAOC), as well as milled bulk soil (SOC), were determined *via* dry combustion with an isotope ratio mass spectrometer (Delta V Advantage, Thermo Fisher, Dreieich, Germany) coupled with an elemental analyzer (Euro EA, Eurovector, Milano, Italy).

PLFA analysis The PLFA analysis was employed to identify microbes and analyze community structure, as described by Bossio and Scow (1998). The soil microbial community composition was analyzed according to the procedures of Frostegard and Baath (1996) and Marshall *et al.* (2011).

Microbial community types were classified based on nonspecific bacteria, gram-positive bacteria (G^+), gram-negative bacteria (G^-), actinobacteria, and fungi, which constituted the total soil microbial biomass. The nonadecanoic acid methyl ester (19:0) served as an endogenous control. The identified PLFAs were categorized into specific microbiota: bacteria (i15:0, a15:0, 15:0, i16:0, 16:1 ω 5, 16:1 ω 9, i17:0, 17:0, a17:0, cy17:0, and cy19:0), fungi (18:2 ω 6c and 18:3 ω 6c), actinomycetes (16:1 ω 7c, 17:1 ω 8c, and 18:1 ω 7c), G^+ bacteria (i14:0, a15:0, i15:0, i16:0, a17:0, and i17:0), and G^- bacteria (16:1 ω 7c, 16:1 ω 9c, cy17:0, 17:1 ω 8c, 18:1 ω 7c, and cy19:0) (Sun *et al.* 2023).

The concentration of the target PLFAs in the sample was calculated as follows:

$$C_{PLFA}=(F_{PLFA}/F_{IS})\times(C_{IS}/M_{PLFA})\times(V/m)$$

where C_{PLFA} represents the concentration of the target PLFA (nmol g^{-1}), F_{PLFA} denotes the peak area for the PLFAs, F_{IS} indicates the area of the internal standard peak, C_{IS} signifies the internal standard concentration (25 ng μL^{-1}), M_{PLFA} represents the molecular weight of the target PLFA, V denotes the sample dissolution volume (120 μL^{-1}), and m indicates the soil weight (4 g).

Amino sugars To estimate microbial necromass derived from bacteria and fungi in all soils at each sampling time, amino sugars were analyzed according to the classic method described by Zhang and Amelung (1996). Specifically, 0.5–1.0 g soil samples underwent hydrolysis with 10 mL 6 mom L^{-1} HCl at 105°C for 8 h. An internal standard solution containing 100 μL myoinositol was then added, followed by filtration through filter paper (<0.45 μm). The filtrate underwent vacuum drying at 65°C and was re-dissolved in 5 mL MilliQ water. The solution was adjusted to a pH of 6.6 to 6.8 by adding 3–5 mL of 0.4 mol L^{-1} KOH to remove iron and aluminium residues before centrifugation at 1,000×g for 10 min. The supernatant underwent vacuum drying, and amino sugars were extracted with methanol before recovery by centrifugation at 1,000×g for 10 min. The extracted amino sugars were transformed into aldo-nonitrile derivatives with hydroxylamine hydrochloride, 4-dimethylamine pyridine, and acetic anhydride, then extracted with dichloromethane. Before the final quantification, the amino sugar derivatives were dissolved in a hexane and ethyl acetate solvent (1:1 by volume) after being removed from dichloromethane under a stream of N_2. Before derivatization, N-methylglucamine served as an amino sugar recovery standard. The extracted amino sugars, including glucosamine (GlcN), galactosamine (GalN), and muramic acid (MurA), were identified through comparison with standard peaks and quantified using an internal standard.

Fungal necromass carbon (FNC) and bacterial necromass carbon (BNC) were calculated according to Liang *et al.* (2019). The total microbial necromass carbon (MNC) was considered to be the sum of FNC and BNC. The ratios FNC/SOC, BNC/SOC, and MNC/SOC represented the contributions of FNC, BNC, and MNC to SOC, respectively.

Microbial necromass carbon concentration was estimated based on three amino sugars (glucosamine, GluN; galactosamine, GalN; and muramic acid, MurN):

$$FNC\ (mg\ kg^{-1})=(GlcN/179–2\times MurN/251.2)\times 179\times 9$$

$$BNC\ (mg\ kg^{-1})=MurN\times 45$$

$$MNC\ (mg\ kg^{-1})=BNC+FNC$$

2.3. Statistical methods

One-way ANOVA was performed using IBM SPSS Statistics 25 (SPSS, Chicago, Illinois USA) software for Windows to determine the effects of straw stem, leaves and sheath addition on SOC, POC, MAOC, PLFA and microbial necromass (bacterial necromass and fungal necromass) content across sampling periods. Statistical significance was established at $P<0.05$. Additionally, linear regression was used to evaluate the relationship between bacterial, and fungal necromass content and carbon fraction content. A correlation-based principal component analysis (PCA) determined the physicochemical variations among straw tissues. Redundancy analysis (RDA) established relationships between SOC fractions and microbial community composition using the 'vegan' package in R 4.2.1. Spearman correlation analysis and the linkET package examined correlations between SOC fractions and PLFA, bacterial necromass, and fungal necromass. The Sobol global sensitivity analysis, conducted using the sensitivity package, generated two key indices: the first-order effect index (S_i), representing individual parameter contributions, and the total-effect index (T_i), encompassing all interactions.

Structural equation modeling evaluated the impact of straw chemical traits, PLFA content, microbial necromass, and microbial community composition on straw-derived SOC using R software 4.0.2 (http://www.r-project.org/). A priori model was constructed based on current understanding of their interactions and correlation analysis. The R library 'lavaan' tested model fit using root mean square error of approximation (RMSEA) and Goodness of Fit Index (GFI). The PCA axis 1 score served as a proxy for bacterial community composition.

3. Results

3.1. SOC, POC and MAOC content

The SOC, straw-derived SOC and soil-derived SOC were affected by the aforementioned straw tissues (ST, LE, and

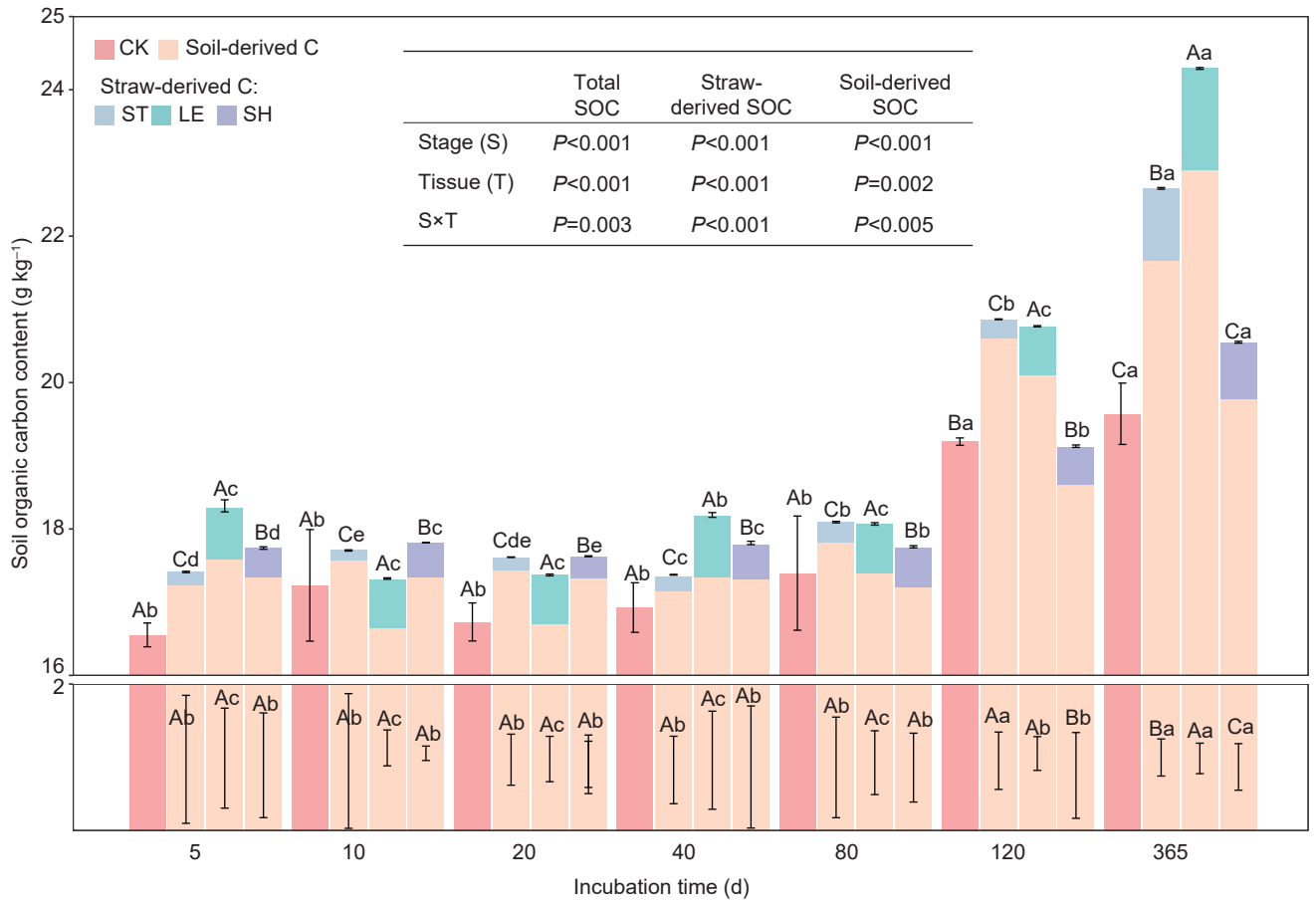


Fig. 1 Effect of the straw stem (ST), straw leaf (LE) and straw sheath (SH) incorporation into the soil on soil organic carbon content at different sampling days. Data are mean±SD (n=3). Lowercase represents the significant difference between sampling times, the uppercase represents the significant difference between straw tissues.

Table 1 The properties of straw stem, leaves and sheath tissue[1)]

	Straw stem	Leaf	Sheath tissue
Total carbon content (%)	43.6±0.2 a	43.2±0.7 ab	42.5±0.1 b
Total nitrogen content (%)	1.7±0.01 b	2.3±0.1 a	1.1±0.01 c
Cellulose content (%)	8.5±0.4 b	13.4±0.4 a	14.6±0.9 a
Lignin content (%)	28.8±0.6 a	20.6±0.5 c	24.0±0.6 b
Soluble sugar content (%)	6.0±0.2 b	9.2±0.8 a	9.5±0.6 a
Hemicellulose (%)	6.2±0.4 c	6.8±0.1 b	7.6±0.2 a
Ether extract (%)	4.2±0.1 b	5.5±0.6 a	4.9±0.1 ab
Crude protein (g kg^{-1})	108.2±0.5 b	141.4±6.4 a	66.9±0.4 c
C/N	25.2±0.2 b	19.1±1.2 c	39.7±0.2 a
LigN	4.9±0.2 b	6.0±0.4 b	13.6±0.9 a

[1)] The C/N indicated that the carbon to nitrogen ratio of straw stem, leaves and sheath, the LigN indicated that the lignin to nitrogen ratio of straw stem, leaves and sheath.
All data are expressed as the mean±standard error (n=3). Different lowercase letters indicated significant differences between different treatments under 0.05 level.

SH), sampling stage and tissue-stage interaction (P<0.05; Fig. 1). After one year of straw incorporation, SOC content ranged from 16.6 to 24.3 g kg^{-1} across treatments, with LE exhibiting the highest values. Compared to CK treatment, ST, LE, and SH treatments significantly increased SOC content by 14.3, 21.9 and 7.9% (P<0.05), respectively. The straw-derived SOC content in ST, LE and SH treatments increased with incubation time (P<0.05). At the early stage of incubation, LE had the highest straw-derived SOC content, followed by SH and ST. After 120 days, straw-derived SOC content ranked as LE>ST>SH (Fig. 1).

Fig. 2 illustrates the contribution of OC derived from straw stem, leaves and sheath to distinct stabilized OC pools *via* soil fractionation according to density and size. The fPOC, oPOC, and MAOC content of total straw-derived and soil-derived, and straw-derived MAOC content, were influenced by straw tissues, sampling stage and their interaction (P<0.05). Total fPOC content in LE and SH treatments increased by 32.7 and 30.7% with incubation time, while oPOC content decreased (P<0.05). Straw-derived fPOC and oPOC contents increased with incubation time across treatments (P<0.05). Initially, straw-derived fPOC content ranked LE>ST>SH, shifting to LE>SH>ST after 40 days (Fig. 2). Throughout incubation, straw-derived oPOC content was consistently LE>SH>ST. During the first 120 days, straw-derived MAOC content in ST, LE, and SH treatments increased by 71.9, 80.3 and 70.2%, respectively, followed by a reverse trend after 120 days.

Straw stems, leaves and sheath addition significantly

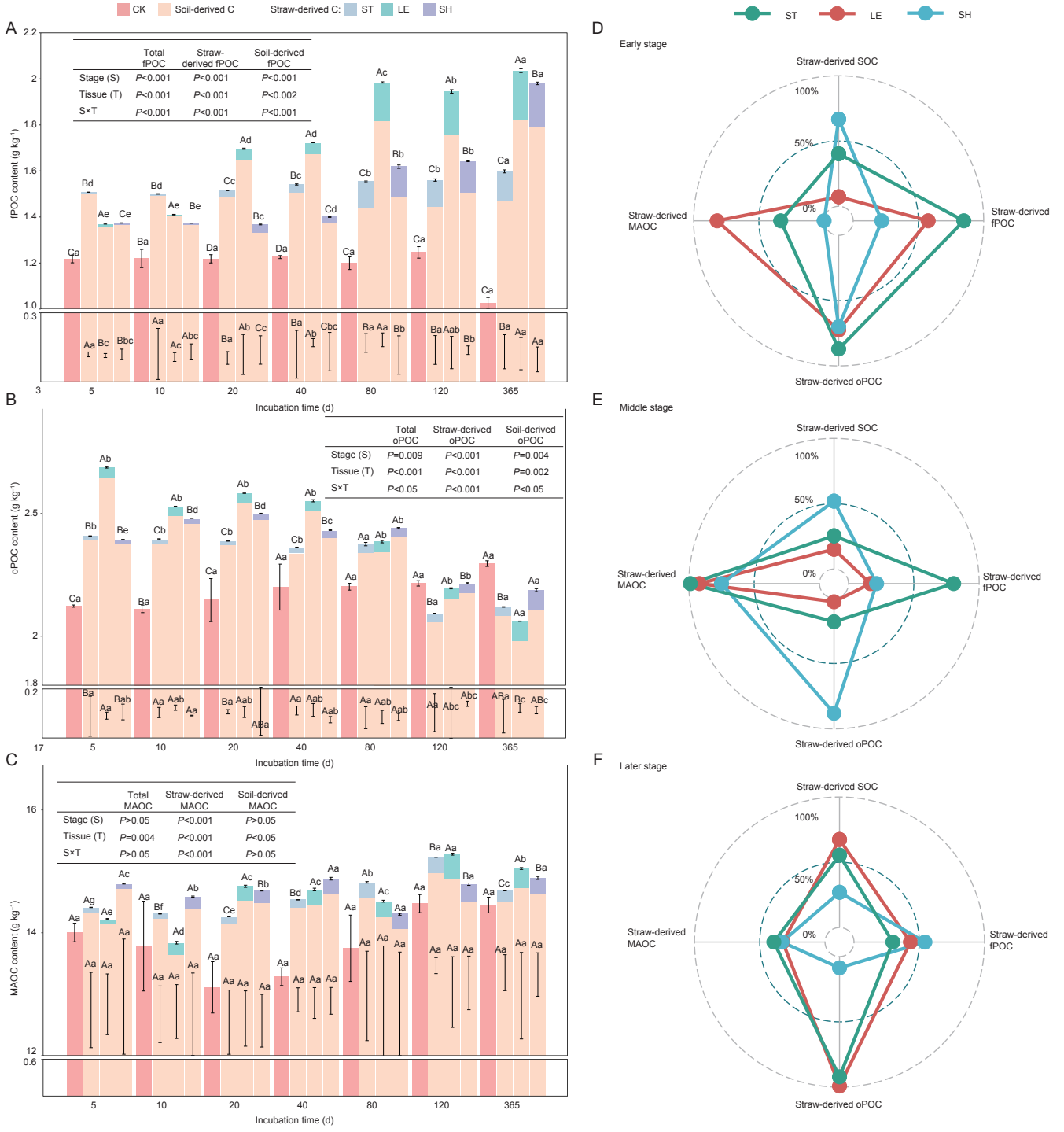


Fig. 2 Effect of incorporating straw stem (ST), straw leaf (LE) and straw sheath (SH) into soil on soil organic carbon fractions (A–C) across sampling periods and carbon dynamics during decomposition stages (D–F). fPOC, free-floating particulate organic carbon; oPOC, occluded particulate organic carbon; MAOC, mineral-associated organic carbon. Data expressed as mean±standard deviation (n=3). Lowercase letters indicate temporal variations (P<0.05); uppercase letters denote inter-tissue differences (P<0.05).

increased straw-derived fPOC, oPOC and MAOC during early, middle and later stages (P<0.05; Fig. 2-D–F). In early incubation, LE enhanced straw-derived MAOC, while ST and SH generally boosted straw-derived fPOC and oPOC. In the middle incubation, ST, LE and SH enhanced straw-derived MAOC but increased straw-derived oPOC in later stages.

3.2. PLFA

Fig. 3 illustrates the PLFA content for total, bacteria, fungi, actinobacteria, G^+, and G^- in CK, ST, LE and SH treatments at different sampling stages, with increases of 4.3–46.5, 2.7–29.6, 14.8–46.3, 3.1–26.1, 7.6–29.2, and 6.5–29.5%, respectively, in ST, LE and SH treatments compared to CK. The PLFA content for total, fungi, actinobacteria, G^+, and G^-

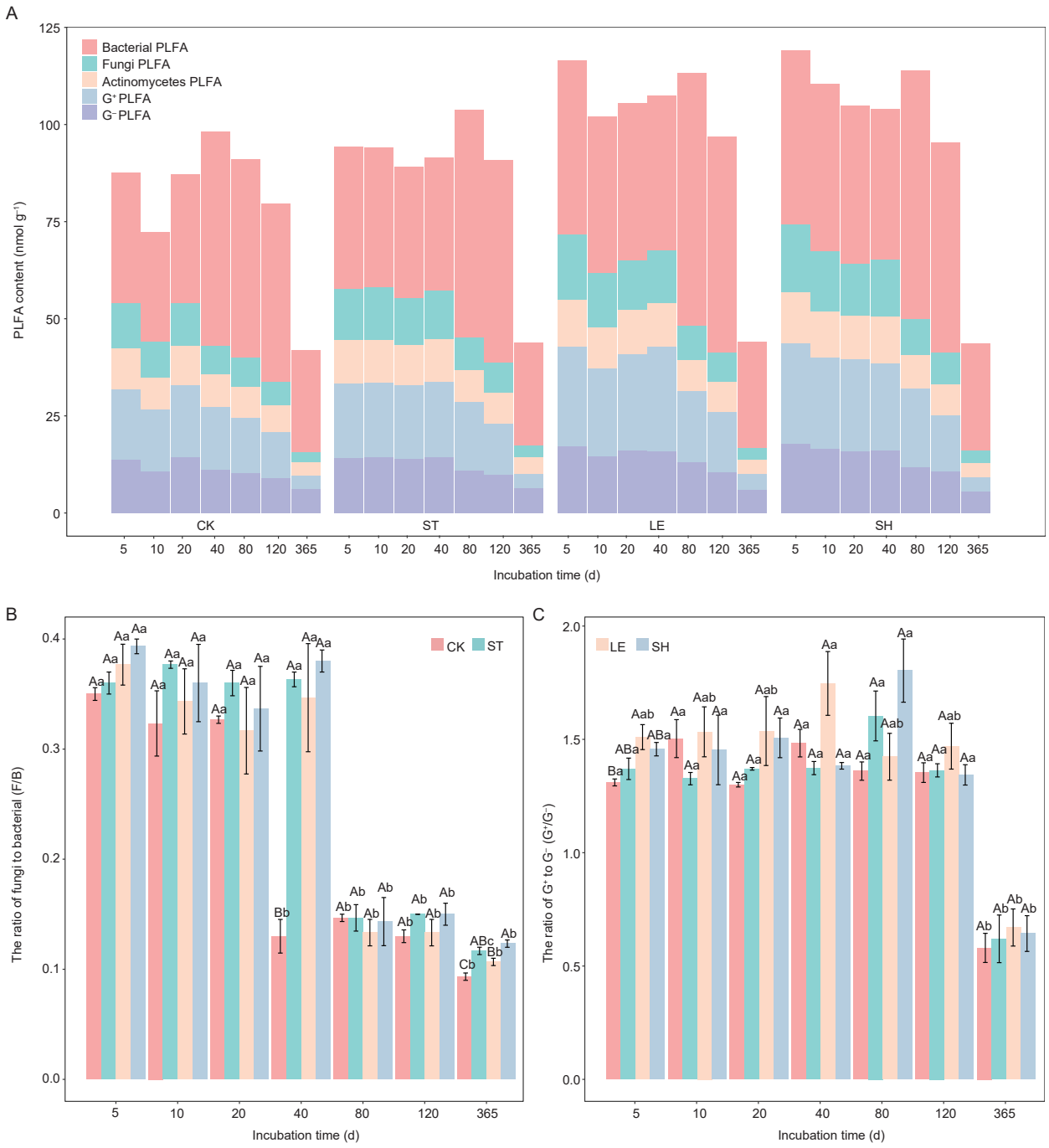


Fig. 3 Effect of straw stem (ST), straw leaf (LE) and straw sheath (SH) incorporation into the soil on the phospholipid fatty acids (PLFA) content (A), the ratio of fungi to bacterial (B), and the G^+ to G^- ratio (C) under different sampling times. CK, the treatment without straw tissue addition. Data are mean±SD (n=3). Lowercase represents the significant difference between sampling times, the uppercase represents the significant difference between straw tissues.

in CK, ST, LE and SH treatments decreased with incubation time (P<0.05). The highest bacterial PLFA content in CK occurred between days 40 and 80 of incubation, ranging from 51.2–55.2 nmol g^{-1}. The ST, LE, and SH treatments exhibited peak bacterial PLFA content between 80 and 120 days, with values of 52.3–58.6, 55.7–65.2, 54.0–64.1 nmol g^{-1}, respectively. The F/B ratios of CK, ST, LE and SH treatments decreased by 74.3, 67.6, 71.7 and 68.7% during incubation (P<0.05). The G^+/G^- ratios of the CK, ST, LE and SH treatments fluctuated within the first 120 days of incubation, ranging from 1.3–1.5, 1.3–1.6, 1.4–1.8, and 1.3–1.8. By the end of incubation, the G^+/G^- decreased by 55.7, 54.7, 55.6, and 55.8% for the CK, ST, LE and SH treatments, respectively (P<0.05).

3.3. Microbial necromass content

Fig. 4 presents the bacterial, fungi and microbial necromass content, along with the proportion of organic carbon. The ST,

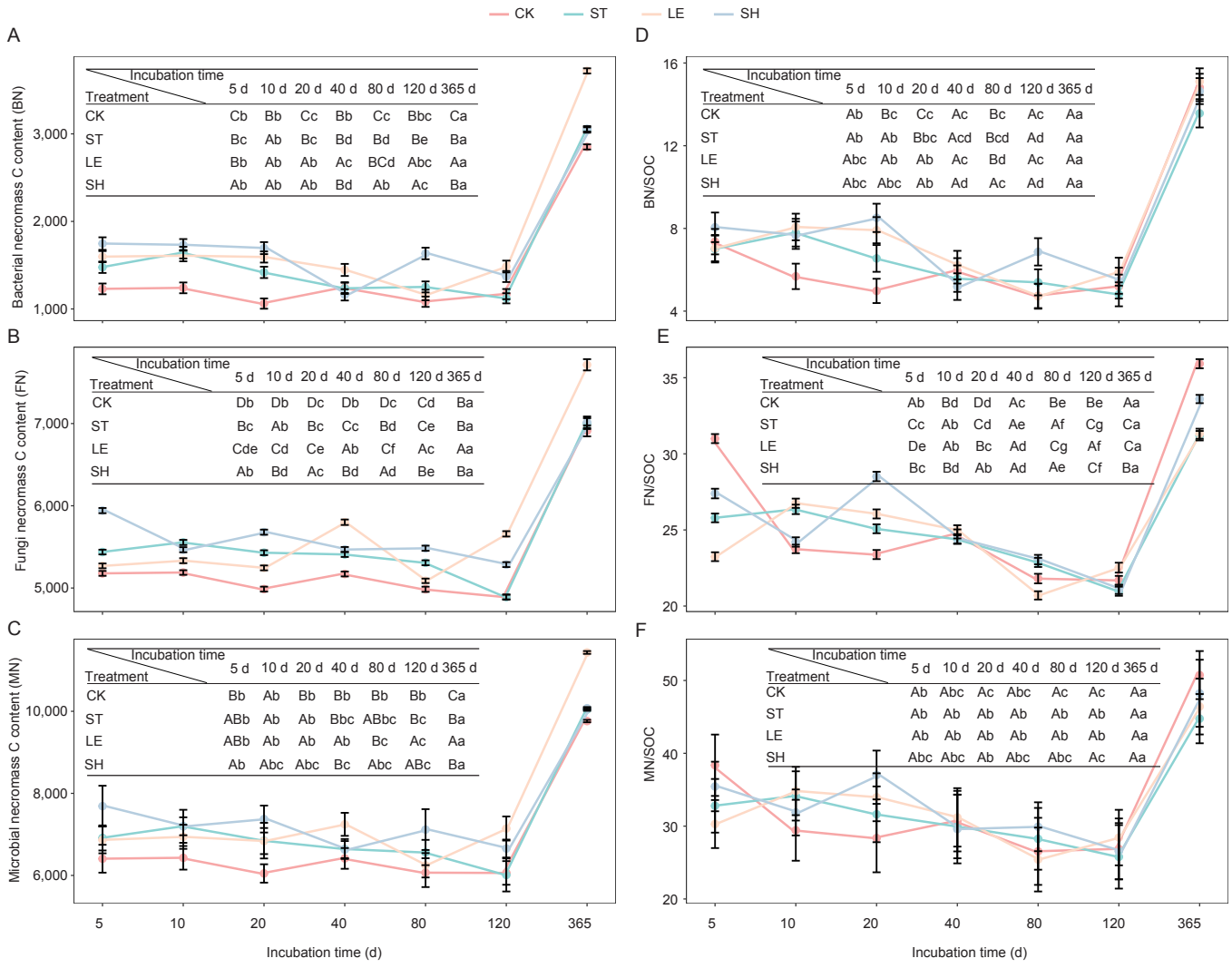


Fig. 4 The effect of straw stem (ST), straw leaf (LE) and straw sheath (SH) incorporation into the soil on bacterial, fungal, and microbial necromass content (A–C) and the proportion of organic carbon (D–F) at different sampling times. CK, the treatment without straw tissue addition. Data are mean±SD (n=3). Lowercase represents the significant difference between sampling times, the uppercase represents the significant difference between straw tissues.

LE, and SH treatments exhibited higher bacterial, fungal, and microbial necromass content compared to the CK treatment. During the first 120 days of incubation, there was a fluctuation in the BNC, FNC and MNC content, as well as the ratios of BNC/SOC, FNC/SOC, and MN/SOC in the four treatments. Following incubation, the BNC, FNC and MNC content, along with the BNC/SOC, FNC/SOC, and MN/SOC ratios, increased by 42.9–57.1, 15.3–31.7, 23.7–39.9, 45.0–53.3, 13.7–25.8, and 24.4–34.8%, respectively (P<0.05).

3.4. The relationship between SOC fractions and microbial traits

Fig. 5 presents the Spearman correlation analysis of straw-derived SOC fractions and PLFA, microbial necromass. The Mantel test correlation analysis revealed a significant positive relationship between straw-derived fPOC, oPOC, MAOC and SOC in the ST, LE and SH treatments. Furthermore, straw-derived MAOC showed a significant positive correlation with FN in the LE treatment. Conversely, straw-derived fPOC, oPOC and MAOC exhibited a significant negative correlation with fungi, actinomycetes PLFA, and F/B ratios in the ST, LE and SH treatments.

The fPOC, oPOC and MAOC content exhibited negative correlations with PLFA traits, including bacterial PLFA, Actinomycetes PLFA, G^+ PLFA, G^- PLFA and F/B ratios (P<0.01; Fig. 6). The fPOC and oPOC content showed negative correlation with the G^+/G^- ratio (P<0.001; Fig. 6). Additionally, the fPOC and oPOC content showed positive correlation with bacterial, fungal, and total microbial necromass content (P<0.001; Fig. 6). The fPOC and oPOC contents were negatively associated with the FN/BN ratio (P<0.01; Fig. 6).

Random forest analysis revealed that straw chemical traits were related to the variation in POC accrual, accounting for 65.5% of the variance (Fig. 7-A). Microbial necromass traits explained 55.0% of MAOC variance, while straw chemical traits accounted for 32.3% of MAOC variance (Fig. 7-B). Specifically, the lignin and TC content of straw tissues

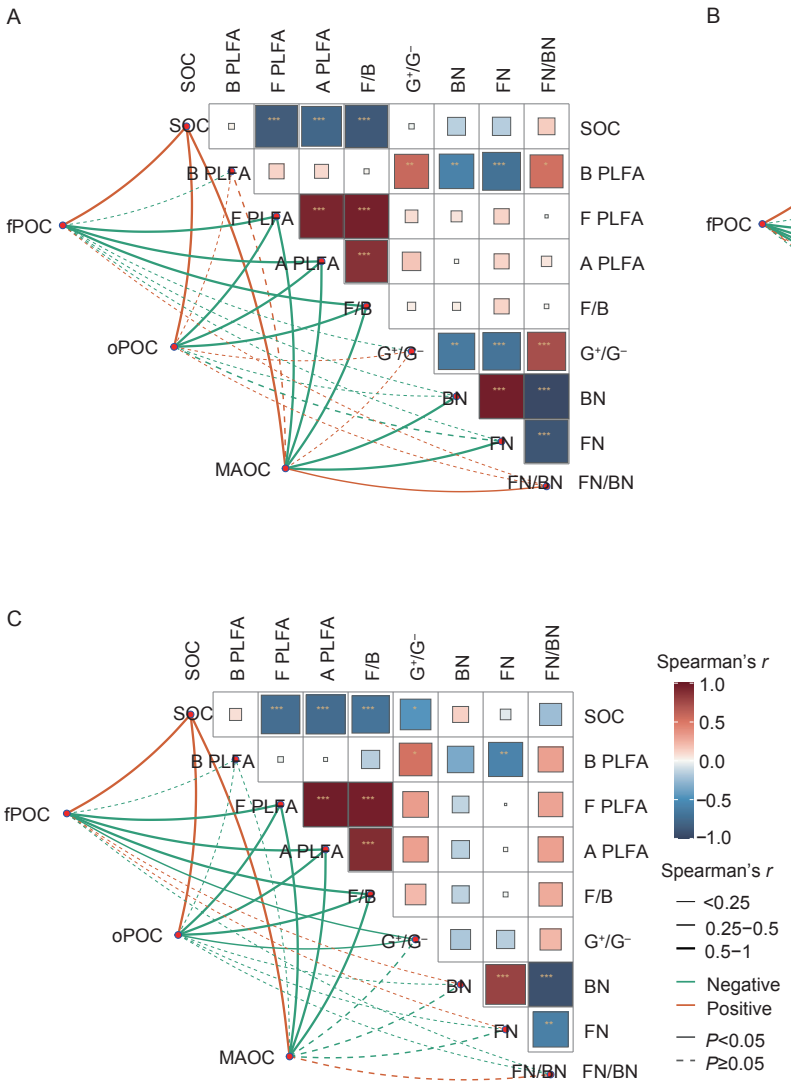


Fig. 5 Results of correlation and Mantel analyses between straw-derived soil organic carbon (SOC) fractions, phospholipid fatty acids (PLFA), and microbial necromass fractions in straw stem (A), leaf (B), and sheath (C) treatments. The color gradient denotes Spearman's correlation coefficients. Edge width corresponds to Mantel's *r* statistic for the corresponding distance correlations. The edge colour denotes the statistical significance of Mantel's *P*-value based on 9,999 permutations. fPOC, free-floating particulate organic carbon; oPOC, occluded particulate organic carbon; MAOC, mineral-associated organic carbon. B PLFA, bacterial PLFA content; F PLFA, fungal PLFA content; A PLFA, actinomycete PLFA content; F/B ratio, the relative abundance of fungi to bacteria PLFA content; G^+/G^- ratio, the proportion of Gram-positive (G^+) to Gram-negative (G^-) bacteria PLFA content; BN, bacterial necromass carbon content; FN, fungal necromass carbon content; FN/BN, the ratio of fungal necromass carbon content to bacterial necromass carbon content.

influenced POC accrual, whereas both fungal necromass content and microbial necromass content significantly influenced MAOC accrual (Appendix A).

RDA examined the relationship between straw-derived SOC fractions and microbial phyla abundance (Appendix B). In early stages, straw-derived MAOC enhanced the relative abundance of Firmicutes, Acidobacteriota and Ascomycota. Both straw-derived SOC and oPOC had a notable positive impact on Actinobacteriota and Chloroflexi abundance. In later stages, Firmicutes and Acidobacteriota abundance showed the highest variability in straw-derived SOC fractions, followed by Gemmatimonadota and Actinobacteriota. These findings indicate these microorganisms' involvement in converting straw-derived C to SOC fractions.

Structural equation modeling assessed whether changes in microbial community composition, microbial necromass and PLFA mediated by straw tissue application influenced straw-derived SOC (Fig. 8). In the ST treatment, the Lignin/N ratio of stem showed negative correlation, while microbial necromass, straw-derived fPOC and bacterial diversity exhibited positive correlations with straw-derived SOC. The LE treatment revealed positive correlations between straw-derived MAOC, oPOC and fungi/bacterial ratio, and straw-derived SOC. Conversely, the Lignin/N ratio of leaf negatively correlated with straw-derived SOC, affecting straw-derived MAOC. In the SH treatment, the Lignin/N ratio of sheath negatively correlated with straw-derived SOC, influencing bacterial diversity, while straw-derived oPOC and bacterial composition and diversity showed positive correlations with straw-derived SOC.

4. Discussion

4.1. Dynamics of SOC, POC and MAOC content

The estimation based on ^{13}C probing revealed that SOC content increased with the addition of straw stems, leaves and sheaths, despite concurrent increases in the priming effect (Zhang Q L *et al.* 2024b), suggesting that SOC formation through exogenous carbon inputs can offset SOC loss due to the priming effect, as shown in limited studies (Zhang *et al.* 2018; Wu *et al.* 2020). These results align with previous research showing increased SOC content following crop straw addition (Xu *et al.* 2021; Feng *et al.* 2022; Zhang J *et al.* 2024). Berhane *et al.* (2020) found that straw return enhanced soil microbial growth, accelerating SOC sequestration. Soil microorganisms degrade straw tissues,

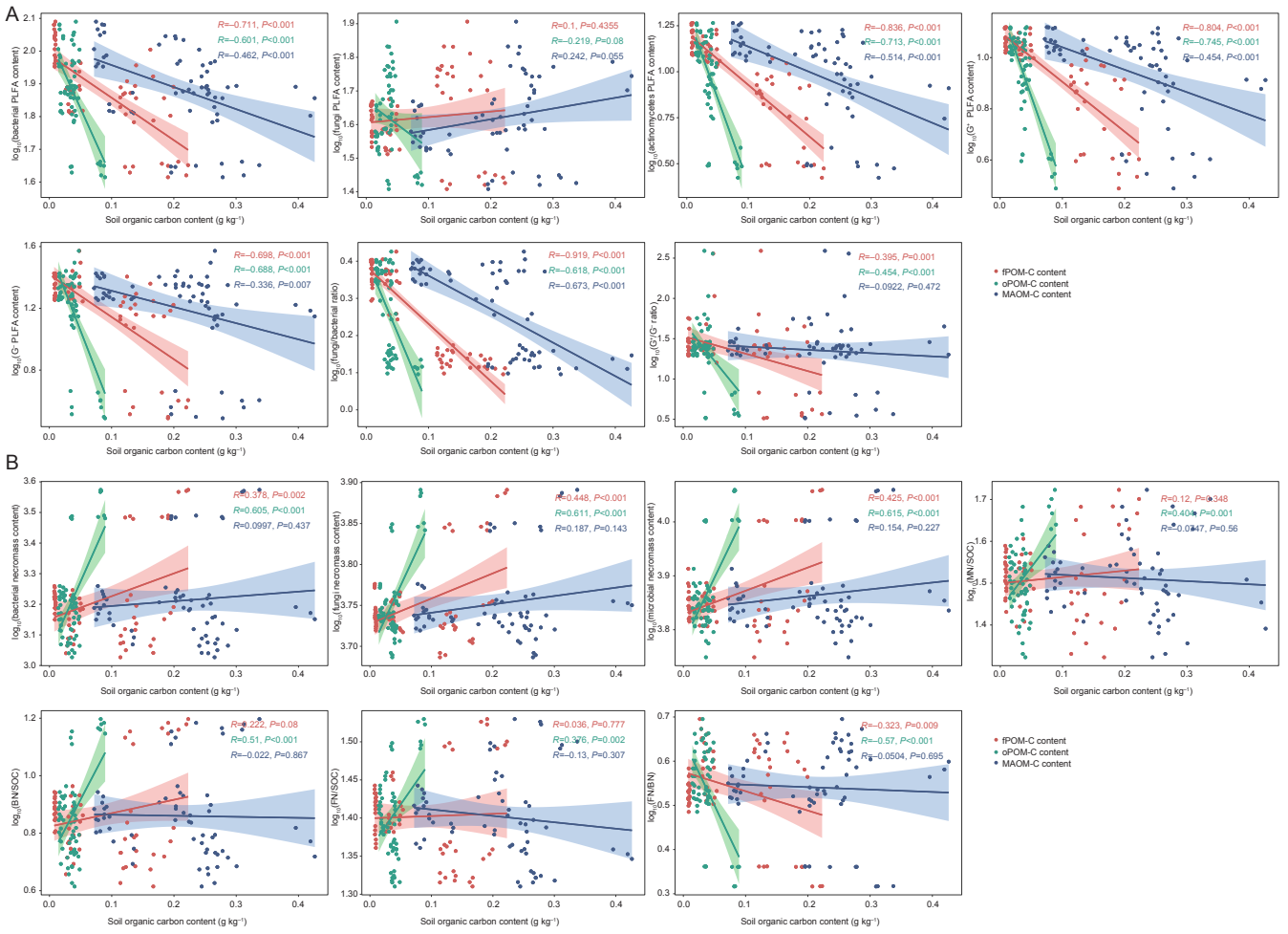


Fig. 6 Relationship between C in the particulate organic carbon (POC) and mineral-associated organic carbon (MAOC) fractions and phospholipid fatty acids (PLFA), microbial necromass traits. MN, BN and FN stands for microbial, bacterial and fungal necromass content.

maintaining or increasing SOC by converting straw material into SOC (Lavallee *et al.* 2020; Yang C Q *et al*. 2024). Our results further indicated that higher straw-derived SOC content in leaves-amended treatments compared to stem- and sheath-amended treatments, which is consistent with other investigations (Ridgeway *et al.* 2022; Peng *et al.* 2023). This finding suggests that high-quality residues with low C/N ratios, such as leaves, convert most efficiently to stable SOC, as described by the Microbial Efficiency-Matrix Stabilization framework and subsequent models (Cotrufo *et al.* 2013). This could be because the decomposition of high-quality residues promotes microbial growth efficiency, resulting in increased stabilization of microbial-derived SOC namely microbial necromass (Cotrufo *et al.* 2015). However, Lyu *et al.* (2023) reported contrasting findings, indicating that high-quality litter initially contributes more C to SOC relative to low-quality litter, low-quality litter generates nearly twice as much new SOC over extended periods. This discrepancy may be attributed to variations in ecosystem conditions, climate, duration, and litter mixing patterns. Additionally, the Mollisol soil in this study contains higher clay content, which provides better protection for SOC against microbial decomposition compared to the silty clay loams examined by Lyu *et al.* (2023). Soil pH also plays a pivotal role in modulating SOC dynamics by influencing microbial communities (Shen *et al.* 2024). For instance, fungi that decompose more resistant substrates predominate in yellow red soil, while bacteria preferring easily degradable labile substrates become more prevalent in Mollisols. Therefore, practices such as retaining more leaf residues and implementing no-till or reduced tillage may enhance SOC accumulation in Mollisol.

This study quantified the differences among aboveground tissues in their contribution of straw-derived carbon to SOC pools. The results demonstrated that the distribution of straw-derived C in aboveground straw tissues varied significantly between POC and MAOC pools. Specifically, leaf tissues generated more MAOC than stem and sheath tissues, while sheath tissues contributed more C to the POC pool than leaf tissues (Fig. 2). These findings align with Abiven *et al.* (2008) and Ridgeway *et al.* (2022), who observed that high-quality leaf litter forms more MAOC than low-quality litter, such as roots and stems. Several factors may explain these results: (1) Leaf tissues with high N concentration and low recalcitrant components (e.g., lignin)

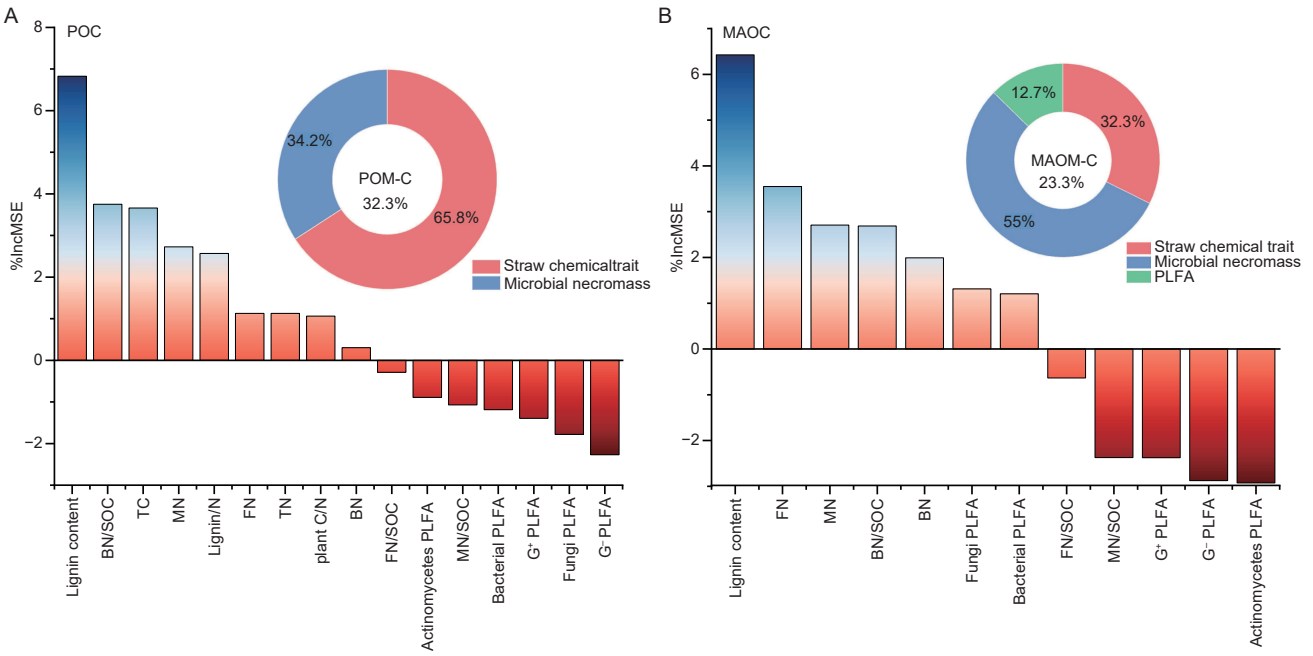


Fig. 7 Random Forest mean predictor importance of straw chemical trait, microbial necromass, and phospholipid fatty acids (PLFA) content as drivers of particulate organic carbon (POC; A) and mineral-associated organic carbon (MAOC; B) content. Straw chemical traits include the following indicators: the total carbon (TC), total nitrogen (TN), lignin content, carbon-to-nitrogen ratio (C/N), and lignin-to-nitrogen ratio (lignin/N); microbial necromass include bacteria, fungi, and microbial necromass content and their contributions to SOC; PLFA include bacteria, fungi, Actinomycetes, G^+ and G^- PLFA content. The values on the outer ring represent the relative contributions of straw chemical trait, microbial necromass, and PLFA content traits to the variance of POC or MAOC, whereas the values on the inner ring represent the proportion of variance that can be explained by the predictor variables.

leading to a higher degree of decomposition (Zhang Q L *et al.* 2024a), increasing more MAOC accumulation through microbial anabolism products (e.g., microbial necromass) (Cotrufo *et al.* 2015), and this study confirmed that straw tissues chemical traits (e.g., lignin content) negatively correlated with MAOC content (Appendix C); (2) leaf tissues with lower C/N ratios enhanced microbial carbon use efficiency, thereby increasing microbial biomass and total C inputs into the MAOC (Von Haden *et al.* 2019); our microbial biomass findings (PLFAs) partially support this, as leaf addition resulted in higher PLFA levels than stem and sheath addition; (3) straw sheath tissues with higher C/N ratios exhibit chemical characteristics associated with recalcitrance and POC formation, including the presence of a casparian strip and higher lignin contents (Geldner *et al.* 2013). However, other studies suggest that low-quality residues form MAOC more efficiently than high-quality residues (Castellano *et al.* 2015; Kaštovská *et al.* 2024). These contradictory results lie in differences in soil texture and soil C saturation level. Research indicates that residue quality affects SOC storage primarily when there is a saturation deficit (Castellano *et al.* 2015). The eroded soils in Castellano *et al.* (2015) had a large carbon saturation deficit, enabling partially degraded, lower-quality crop residue-derived carbon to adsorb directly on mineral surfaces without undergoing the *in vivo* microbial conversion pathway. Conversely, the Mollisol used in our study has carbon saturation, so MAOC formation primarily occurs through microbial necromass conversion of high-quality straw leaf tissue. This study supports our hypothesis regarding distinct pathways of POC and MAOC formation from different straw components, emphasizing the importance of representing these independent formation pathways.

4.2. Dynamics of PLFA and microbial necromass content

The incorporation of straw stems, leaves, and sheaths into the soil increased total PLFA content (Fig. 3), with peak values occurring on the fifth day, except for bacterial PLFA. Previous research demonstrates that soil microbial biomass peaks after 7 days of residue addition (Arcand *et al.* 2016; Bai *et al.* 2016), attributed to the rapid availability of enriched labile components derived from additional residue during initial decomposition. Furthermore, straw tissue addition altered soil microbial community structure due to temporal changes in chemical composition of straw over time, i.e., increase of the recalcitrant components percentage (Abiven *et al.* 2005). The results indicate bacterial dominance in microbial communities, with a slight increase in fungal abundance following straw addition (Fig. 3). Fungal dominance typically promotes SOC accumulation while decreasing SOC turnover rate by forming fungal hyphae networks that make SOC less accessible to microbial decomposition (Liu *et al.* 2022). These discrepancies arise from differences in ecosystems, soil types, initial soil pH, and exogenous substrate quality. The study also revealed that adding straw stems, leaves and sheaths increased bacterial and fungal biomass (Fig. 3), which was consistent with previous findings (Zhou *et al.*

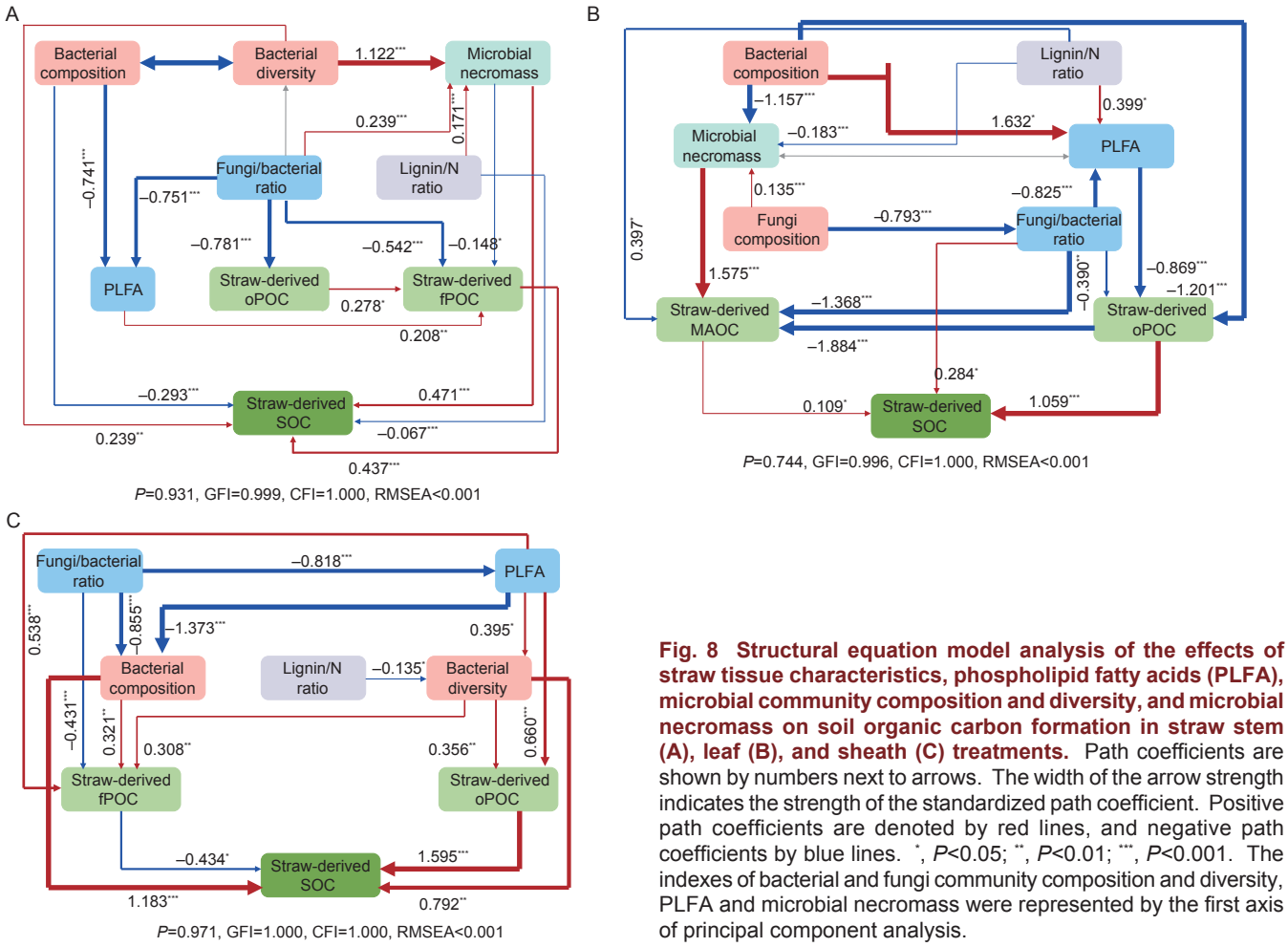


Fig. 8 Structural equation model analysis of the effects of straw tissue characteristics, phospholipid fatty acids (PLFA), microbial community composition and diversity, and microbial necromass on soil organic carbon formation in straw stem (A), leaf (B), and sheath (C) treatments. Path coefficients are shown by numbers next to arrows. The width of the arrow strength indicates the strength of the standardized path coefficient. Positive path coefficients are denoted by red lines, and negative path coefficients by blue lines. *, $P<0.05$; **, $P<0.01$; ***, $P<0.001$. The indexes of bacterial and fungi community composition and diversity, PLFA and microbial necromass were represented by the first axis of principal component analysis.

2020; Liu *et al.* 2022; Ren *et al.* 2023). Research has produced varying results: some studies found that high-quality substrates C favored fungal dominance (Rousk and Frey 2015), others suggested enhanced fungal growth in low-quality stem-amended soil (Habtewold *et al.* 2020), and Hicks *et al.* (2021) observed increased growth in both fungi and bacteria with higher C quality.

It is well recognized that microbial necromass formation is determined by living microbial biomass production and cell residue degradation (Chen *et al.* 2020). Studies indicate that straw incorporation may enhance microbial necromass accumulation by providing additional available substrates, thus stimulating microbial biomass growth and turnover (Liang *et al.* 2017). Our results demonstrated that bacteria and fungi PLFA content declined continuously with incubation time, while their necromass remained fluctuating until an obvious increasing trend was observed at the end of the experiment (Fig. 4). This pattern suggests that microbial necromass maintained a dynamic equilibrium between accumulation and decomposition over the first 120 days of incubation, attributed to its ongoing utilization as a carbon source during accumulation. While sheath-amended treatment enhanced microbial necromass accumulation in the first 120 days, the leaves-amended treatment ultimately yielded higher necromass content by the end of experiment, demonstrating that microbial necromass dynamics correlate strongly with substrate quality changes during crop residue decomposition. In contrast, Xu *et al.* (2022) observed that root residue treatments produced greater microbial necromass accumulation compared to shoot treatments by the end of the experiment. This phenomenon is attributed to the higher concentration of resistant components in root residues (Shahbaz *et al.* 2017), which become the primary C source for microbial metabolism as readily decomposable components diminish, thereby promoting microbial reproduction and rapid necromass accumulation. These results emphasize the significant influence of straw tissue quality on microbial necromass buildup. This validates our earlier idea that aboveground residues vary in the development and distribution of microbial necromass Cin SOC.

4.3. The relationship between SOC formation and microbial traits

Our findings suggest that aboveground stem, leaves and sheath contribute to distinct pathways of SOC formation at different stages. During the initial incubation stage, straw leaves tissues predominantly contributed to MAOC formation rather than fPOC and oPOC (Fig. 2). This phenomenon is attributed to the fact that labile components of straw leaves being more readily assimilated by microorganisms, facilitating an *in vivo* turnover of labile C *via* cell uptake-biosynthesis

growth-death process, resulting in microbial necromass accumulation and eventually forming MAOC. This finding aligns with Liang *et al*. (2017), who demonstrated that labile components of plant litter could form mineral-stabilized soil organic matter. Our findings further revealed that straw-derived MAOC content from leaves was significantly higher compared to stem and sheath treatments (Fig. 2). Our results indicated that microbial necromass, particularly fungal necromass, is the primary source of MAOC. Fungal necromass exhibited more pronounced changes than bacterial necromass, consistent with previous studies showing fungal necromass had higher responses than bacterial necromass to the changes in straw inputs (Jia *et al.* 2022). The reasons include: (1) fungal hyphae expansion and interactions with mineral particles (Witzgall *et al.* 2021), along with direct adsorption of fungal-derived metabolites onto mineral surfaces; (2) fungal cell walls, enriched with recalcitrant macromolecules, exhibit slower decomposition rates and greater propensity to form stable associations withmineral surfaces (Qian *et al.* 2023). In contrast, bacterial necromass undergoes rapid microbial degradation due to its labile chemical nature (Xue *et al.* 2024); (3) fungi secrete extracellular oxidative enzymes that decompose aromatic macromolecules, generating polyphenolic and aliphatic compounds with high affinity for Fe/Al (hydr)oxides (Klink *et al.* 2022). Additionally, Wu *et al.* (2025) found significant correlation between lignin-degrading genes (e.g., *abfA*, *xylA*, *lig* and *mnp*) and fungi, indicating that fungi encoded lignin-degrading genes to degrade refractory C such as lignin. Bacterial metabolic byproducts, including labile polysaccharides and amino acids, display weaker sorption capacities. This corresponds with the finding that MAOC was linked to microbial necromass traits and straw chemical characteristics (Fig. 7). Similarly, Dai *et al.* (2025) found that leaf treatments showed the highest MAOC content compared to branch and straw treatments, likely because leaves contain more non-structural compounds readily adsorbed by soil minerals. Additionally, these soluble compounds were easily assimilated by microbes, with subsequent microbial necromass formation further contributing to MAOC. These results suggest a synergistic interaction between microbial necromass traits and straw chemical characteristics during MAOC formation. Conversely, our results showed that straw stems and sheaths with higher C/N ratios preferentially remain in POC as undecomposed or partially decomposed litter fragments. This pattern aligns with previous findings indicating greater POC formation occurs in tissues with higher C/N ratios (Lavallee *et al.* 2018). This consistency highlights differences in the chemical composition and structure of various tissues. Tissues with higher C/N ratios exhibit chemical characteristics associated with recalcitrance and POC formation (Geldner *et al.* 2013). In later stages, POC formation occurs when labile C components are gradually consumed and structural components are not easily utilized by microorganisms, consistent with earlier studies (Cheng *et al.* 2023; Bai *et al.* 2024). The reasons for increased straw-derived POC in the later stage include: (1) Straw-derived POC enriched with structural C compounds persists in soil through inherent biochemical recalcitrance, physical protection in aggregates and/or microbial inhibition (Cotrufo *et al.* 2019; Witzgall *et al.* 2021), not easily utilized by microorganisms, as indicated by lower PLFA content (Fig. 3); (2) additionally, some microbial amino sugars become immobilized into POC (Almeida *et al*. 2021) as POC can accumulate without apparent upper limits (Ridgeway *et al*. 2022), verified by the positive relationship between microbial necromass content and fPOC and oPOC content (Fig. 6); (3) in resource-limited environments, fungi increase their biomass by preferentially using bacterial necromass rather than recalcitrant plant material (Ma *et al.* 2022). Our results support the hypothesis that structural components contribute to POC formation, evidenced by the positive relationship between POC and microbial relative abundance, especially Proteobacteria, Firmicutes, Ascomycota and Basidiomycota (Appendix D). An important reason for this phenomenon is that Proteobacteria and Firmicutes utilize labile and recalcitrant carbon fractions (e.g., lignin), while Ascomycota and Bacteroidetes specialize in degrading recalcitrant compounds like lignin and cellulose (Li *et al.* 2024). For example, Proteobacteria was the main microbial group involved in both carbon degradation and fixation processes, and it has beendemonstrated that Proteobacteria is the most dominant bacterial phyla carrying carbon fixation genes under straw return treatments (Li *et al.* 2025). Firmicutes possessed versatile life strategies to use various C substrates, which are involved in the decomposition of unstable organic matter and also degraded lignocellulose and recalcitrant C sources, including chitin, cellulose, and lignin (Yang F K *et al.* 2024; Zhang Q L *et al.* 2024a). Soil fungi perform soil nutrient transformation and plant nutrient acquisition by decomposing organic matter (especially recalcitrant materials). In Zhang F T *et al.* (2024), Ascomycota and Basidiomycota were dominant at the fungal phylum level, converting complex organic matter into available components and closely associated with C turnover and storage in soil (Zhang T T *et al.* 2024). Compared with Basidiomycota, Ascomycota may decompose diverse organic matter including simple sugars, while Basidiomycota has unique ability to decompose lignin and lignocellulose complexes (Wang Q *et al.* 2021). Therefore, these microbes played important roles in C cycling. This finding corroborates the recent concept that fungi and bacteria, as primary consumers of complex substrates, play crucial roles in SOC stabilization (Lopez-Mondejar *et al.* 2020). A previous study confirmed that bacteria could produce CAZyme to access C from cellulose, hemicellulose and chitin (Eichorst and Kuske 2012). Furthermore, incorporating straw increased the abundance of CAZymes involved in lignin degradation, likely due to the relatively high lignin content in the straw (Cui et al. 2022; Zhou et al. 2025). The positive relationship between straw-derived POC content and microbial necromass content suggests that microbial necromass persists in the POC pool as MAOC approaches saturation, because the surfaces of particulate organic matter can serve as hotspots for microbial turnover, driving the formation of necromass in the later stage (Witzgall et al. 2021).

4.4. Sensitivity analysis and limitations

Amino sugars have been widely used to estimate fungal and bacterial necromass carbon levels using conversion

coefficients (45 and 9), based on an assumed fixed ratio of G^+ to G^- bacteria (Appuhn and Joergensen 2006; Liang *et al*. 2019). However, bacterial community structures exhibit significant variability across different ecosystems, thereby challenging the validity of this assumption (Cao *et al.* 2023). A sensitivity analysis of microbial necromass content was conducted by adjusting the conversion factor according to the G^+ to G^- bacteria ratio (Appendix E). The results indicate strong robustness regarding the influence of conversion factors on both bacterial and fungal necromass carbon content. This suggests these conversion factors have minimal impact on microbial necromass quantification, further validating the robustness of our findings. Nevertheless, novel methodologies should be explored to enhance the precision and applicability of microbial necromass assessments.

This study focused solely on measuring living microbial biomass without employing high-throughput sequencing techniques, such as metagenomics and enzymatic assays. The absence of metagenomics or enzymatic data limited our ability to further understanding of validation of the roles of varying straw carbon inputs in SOC formation pathways. Moreover, metagenomics and enzymatic enable the molecular-level elucidation of microbial mediation mechanisms in straw-derived soil organic carbon formation pathways. Previous studies have demonstrated that bacteria produce CAZyme to access C from cellulose, hemicellulose and chitin, while fungi encode lignin-degrading genes (e.g., *abfA*, *xylA*, *lig* and *mnp*) to degrade refractory C such as lignin (Cui *et al.* 2022; Cao *et al.* 2023; Zhou *et al.* 2025). PLFA analysis reflects only live microbial biomass and broad structural shifts (Orwin *et al.* 2018; Yang *et al.* 2023), without resolving microbial functional traits or and validating biochemical pathways. Therefore, combining phospholipid fatty acids with molecular techniques alongside stoichiometric calculations or isotopic methods would better validate the formation pathway of straw carbon conversion to soil organic carbon.

5. Conclusion

This study demonstrated that the addition of aboveground straw tissues of varying quality, along with induced living microbial and microbial necromass, significantly influenced straw-derived C distribution in SOC fractions including POC and MAOC. Low-quality straw tissues, specifically stem and sheath, enhanced POC formation, primarily regulated by Proteobacteria, Firmicutes, Ascomycota and Basidiomycota; high-quality straw tissues, particularly leaves, facilitated MAOC formation, predominantly controlled by fungal necromass. Furthermore, straw leaves generate more straw-derived POC and MAOC than stems and sheaths. These findings provide crucial insights for interpreting soil C dynamics in response to straw tissue inputs, offering novel understanding of how different aboveground straw tissues influence SOC accumulation pathways. However, as these results derive from laboratory incubation experiments rather than *in situ* field studies, further research is necessary to examine the distributions and stability of SOC fractions affected by aboveground straw quality across broader ranges of SOC content and moisture gradients in Mollisols.

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Declaration of competing interest

The authors declare that they have no conflicts of interest

Declaration of generative AI and AI-assisted technologies in the writing process

The authors declare that they did not use AI in the preparation and writing of this manuscript.

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