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Litter chemical traits, microbial and soil stoichiometry regulate organic carbon accrual of particulate and mineral-associated organic matter

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Abstract

Plant litter quality considerably affects C accrual in soil organic matter (SOM). However, the chemical traits of litter that influence C distribution in SOM fractions, such as particulate organic matter (POM) and mineral-associated organic matter (MAOM), are not fully understood. Thus, we conducted a 150-day incubation experiment with litter addition (poplar leaves, roots, grasses grown under the canopy, and a mixture of these three litter types). We analyzed the organic C concentration in the POM and MAOM fractions and the stoichiometric ratios (C:N:P) of the soil and microbial biomass 50, 100, and 150 days after the initial litter addition. Microbial residue C (amino sugar biomarkers) in SOM fractions was registered at the end of decomposition. High-quality litter (i.e., leaf) increased MAOM-C accrual, and low-quality litter (i.e., root and grass) contributed more to POM-C accrual. The mixed litter addition accumulated more C in the SOM via high POM-C levels compared to single litter input, likely resulting from an antagonistic effect caused by different litter trait dissimilarity. Moreover, POM-C dynamics were dominated by litter chemical traits during litter decomposition, and MAOM-C was controlled mainly by microbial and soil stoichiometry. Furthermore, the contribution of microbial residue C to SOM (especially POM-C) was lower in the mixed litter than in the single litter. These findings highlight the direct or indirect impacts of litter types on the C dynamics of POM and MAOM, and demonstrate that litter diversity is conducive to C accumulation in SOM.

Keywords Soil organic matter · Particulate organic matter · Mineral-associated organic matter · Microbial residue · Organic carbon accumulation

Introduction

Soil organic matter (SOM) forms the largest C pool in terrestrial ecosystems and plays a crucial role in regulating atmospheric CO_2 concentrations (Jackson et al. 2017). SOM consists of distinct fractions, separating into particulate organic matter (POM) and mineral-associated organic matter (MAOM) fractions have been suggested as a useful approach for better understanding SOM formation and stabilization (Lavallee et al. 2020). POM mainly consists of partially decomposed plant litter that is easily broken down by soil microbes (Haddix et al. 2020; Cotrufo et al. 2022). In contrast, MAOM primarily consists of single molecules or microscopic fragments of organic material formed via microbial transformation and/or direct mineral surface sorption from plant litter, and are considered to be more stable than POM (Cotrufo et al. 2015; Kopittke et al. 2020). Elucidating the factors that affect the formation of POM and MAOM from the decomposition of plant material is crucial for gaining an insight into SOM dynamics and stabilization.

Plant litter input is the primary source of SOM in forest ecosystems. Numerous studies have shown that formation, turnover, and stabilization of SOM rely on the quality (e.g., structural components and nutrients) of plant litter (Cotrufo et al. 2015; Börger et al. 2022). In forest ecosystems, plant litter consists of various materials (e.g., leaves and roots) with distinct chemical traits that affect SOM formation and accumulation (Almeida et al. 2021). Previous studies have shown that high-quality (with high

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N concentration and low ligin:N and C:N ratios) leaf litter decomposes faster and contributes more to C accrual in MAOM than low-quality root litter (Bonanomi et al. 2021; Almeida et al. 2021). Additionally, litter diversity enhances the litter decomposition rate compared to that of single litter at early stages of decomposition (Kou et al. 2020). Numerous studies have reported variations in the decomposition rates of single and mixed litter (more than two species) in different ecosystems (Porre et al. 2020). However, additional research is required to determine the amount of litter that is transformed into different SOM fractions (i.e., POM and MAOM), influence of various factors on the transformation process, and effects of litter diversity on the dynamics of POM and MAOM fractions (Prescott and Vesterdal 2021).

Elemental stoichiometry (C:N:P ratios) is widely considered to regulate the linkage between plant litter, soil microbes, and SOM (Zechmeister-Boltenstern et al. 2015; Cheng et al. 2022). Soil microbial processing alters the stoichiometric element ratios during litter decomposition and SOM formation (Mooshammer et al. 2014). The nutrient requirements of decomposers communities are based on microbial stoichiometry, and a stoichiometric imbalance between resources availability and microbial biomass may possibly restrict microbial activity, thereby controlling ecosystem C and nutrient flows (Zechmeister-Boltenstern et al. 2015). Although microbes are considered to consistently maintain homeostasis, microbial stoichiometric flexibility has been found in different biome and soil types (Asada et al. 2022). Moreover, microbial C:N:P ratios depend on the substrate quality (Khan and Joergensen 2019), which is regulated by plant litter traits (Mooshammer et al. 2014). The C:N:P stoichiometry of microbial biomass and soil nutrients have been widely reported in different ecosystems (Asada et al. 2022). However, research on litter type that induces shifts in microbial and soil C:N:P ratios how to influence the dynamics of SOM fractions is lacking.

Although living microbial biomass C constitutes < 3% of soil organic C (SOC) in soil (Gao et al. 2022), accumulating evidence has shown that microbial residue C derived from the accrual of anabolic products is the main source of stable soil C pools (Miltner et al. 2012; Liang 2020). Several studies have demonstrated that the effects of plant litter type (e.g., aboveground and aboveground components) on microbial residue C accrual depend on land-use type (Almeida et al. 2021; Jia et al. 2022). Additionally, previous studies have mainly focused on the contribution of microbial residue C to MAOM owing to its high stability (Cotrufo et al. 2019; Sokol and Bradford 2019; Craig et al. 2022), whereas the contribution of microbial residue C to POM remains largely unknown. Understanding the connection between plant litter, microbial and soil stoichiometry, and microbial contribution to the POM and MAOM fractions is important for determining the potential mechanism of C accrual and stability in SOM.

In this study, we aimed to explore the influence of different litter types (e.g., leaf, root, grass, and a mixture of these) and their induced microbial and soil stoichiometry on organic C accrual in POM and MAOM. We hypothesized that (1) organic C accrual would increase in MAOM (MAOM-C) and decrease in POM (POM-C) with increasing litter quality (e.g., decreasing ligin:N or ligin:P ratio); (2) litter chemical traits and microbial and soil stoichiometry would jointly affect the dynamics of POM-C and MAOM-C; and (3) high-quality litter would form more microbial residue C in MAOM-C and less microbial residue C in POM-C at the end of decomposition.

Materials and methods

Plant and soil material collection

Plant materials were collected from a 12-year-old poplar (*Populus deltoides*) plantation at Dongtai Forest Farm (32°38′–32°45′ N, 120°53′–120°57′ E), in the Jiangsu Province, China. The poplar plantation is located on coastal reclaimed land (reclaimed in 1995), and the trees have an average height of 18.4 ± 2.7 m and diameter at breast height of 21.6 ± 2.2 cm. Leaves and roots of poplars and grasses growing under the poplar canopy were collected in September 2019. Mature leaves were collected from the intermediate and upper parts of the tree crown. Fine roots ($\emptyset < 2$ mm) of poplar trees were collected from the 0–20 cm soil layer using a soil auger ($\emptyset = 8$ cm). The live fine roots were identified based on their vitality, elasticity, and flexibility (Bennett et al. 2002). The aboveground parts of the grasses (dominated by *Pennisetum alopecuroides* and *Arthraxon hispidus*) were harvested. All samples were oven dried at 60 °C for 48 h, ground, and then sieved through a 1-mm mesh to facilitate easier and faster decomposition via microorganisms.

Soil was collected from the 0–20 cm layer of the tideland of the coastal wetland, which represents the initial soil conditions before wetland reclamation. Few plants grow on the tideland. The soil in the tideland, derived from sediment accumulation from the Yangtze River, is classified as sandy loam (Gleyic Salic Fluvisol, World Reference Base 2015), with high salinity and poor nutrient levels (Xing et al. 2020). A portion of each soil sample was stored at 4 °C and used to determine soil microbial biomass. The remainder was used to determine the soil physical and chemical properties (Table S1) and for an incubation experiment.

Incubation experiment

This experiment included five treatments: soil amended with leaf, root, or grass litter (hereafter denoted as "leaf," "root," and "grass"), soil amended with a mixture of litter types (leaf:root:grass = 1:1:1, hereafter denoted as "mixture"), and soil used as a control. Sixty jars (five treatments × four replicates × three harvest times) were incubated together. For each 800-mL plastic jar, 200 g of soil and 2 g of ground litter were added and mixed thoroughly. The amount of litter added was determined by the annual litter fall input (0.8 t ha^{-1}) and was similar to that in previous studies (Lavallee et al. 2018; Almeida et al. 2021). All jars were incubated at 25 ± 0.5 °C in the dark, and the moisture content was maintained at 70–80% water-holding capacity by adding deionized water every 4 days. Soil samples were collected after 50, 100, and 150 days (representing early, intermediate, and late stages of decomposition, respectively) and stored at 4 °C for further processing within 2–3 weeks.

Plant and soil sample measurement

The concentrations of C and N in the initial leaf, root, and grass litter were measured via dry combustion using an elemental analyzer (Vario EL III; Elementar, Germany), and P concentration in these litters was determined using molybdenum blue colorimetry (Pansu and Gautheyrou 2006). Concentrations of cellulose, hemicellulose, and lignin in the initial litter samples were determined according to the procedure described by Van Soest et al. (1991). Briefly, 1 g of air-dried and ground litter samples was boiled with 100 mL of neutral detergent solution (Na-lauryl sulfate, EDTA, pH =7.0) for 1 h, filtered, washed with hot water to pH 7.0, dried, and weighed to record W0. The residue was boiled at 100 °C for 50 min with 70 ml HCl (2 mol L^{-1}), filtered, washed with hot water to pH 7.0, dried, and weighed to record W1. Finally, the residue was treated with a 72% H$_2$SO$_4$ solution for 3 h, dried, and weighed to record W2. The residue was then incinerated in an electric muffle furnace at 600 °C for 4 h. The weight of the ash samples was recorded as W3. The lignocellulosic content was calculated as hemicellulose (W0– W1), cellulose (W1–W2), lignin (W2–W3), and ash (W3). The chemical traits for the different litter types are shown in Table 1.

The SOC and total N (SN) concentrations in the soil samples before the incubation experiment were measured using an elemental analyzer. The soil pH was measured using a glass electrode potentiometer (soil:water = 1:2.5, PHS-3C, Leici Instruments, Shanghai, China) and the soil electrical conductivity was measured using a DDS-307A instrument (Leici Instruments, Shanghai, China). The sand (> 0.02 mm), silt (0.002–0.02 mm), and clay (< 0.002 mm) contents of the soil were determined using a Mastersizer 2000 Particle Analyzer (Malvern, UK). The concentrations of dissolved organic C (DOC), dissolved organic N (DON), and available P (AP) in the soil were measured after 50, 100, and 150 days of incubation. Subsequently, DOC and DON were extracted from fresh soil using 0.5 mol L^{-1} K$_2$SO$_4$, and the filtrate was analyzed using Multi N/C3100 TOC/ TN Instruments (Analytik Jena AG, Jena, Germany). Total P (TP) and AP from soil were measured using Na$_2$CO$_3$-fusion and the Olsen method, respectively (Pansu and Gautheyrou 2006). Briefly, for TP, 1 g of air-dried soil was mixed with 5 g of Na$_2$CO$_3$, gradually heated (900 °C), and then cooled. Next, 30 mL of 5 mol (½H$_2$SO$_4$ L^{-1}) acid was added to the mixture until it was completely dissolved, and then it was filtered. For AP, 1 g of air-dried soil was placed in a 50-mL centrifugation tube, 20 mL of 0.5 mol L^{-1} Na$_2$CO$_3$ solution (pH 8.5) was added, the mixture was shaken for 30 min at 25 °C, and then centrifuged and filtered. Additionally, TP

Table 1 Chemical traits of leaves, roots, grasses, and their mixture for the incubation experiment. Data are presented as the mean ± SD, $n = 4$

Variable	Leaf	Root	Grass	Mixture*
C concentration (g kg^{-1})	454.44 ± 10.03a	436.93 ± 6.83b	433.57 ± 6.39b	441.65 ± 3.82b
N concentration (g kg^{-1})	23.26 ± 0.19a	3.66 ± 0.10d	5.81 ± 0.08c	10.91 ± 0.06b
P concentration (g kg^{-1})	2.00 ± 0.03a	0.27 ± 0.01d	0.57 ± 0.04c	0.95 ± 0.01b
Hemicellulose concentration (g kg^{-1})	233.48 ± 11.87c	221.00 ± 9.94c	325.25 ± 2.90a	259.91 ± 6.07b
Cellulose concentration (g kg^{-1})	248.78 ± 12.53a	254.28 ± 7.93a	169.27 ± 10.87c	224.11 ± 4.9b
Lignin concentration (g kg^{-1})	107.52 ± 4.26c	140.89 ± 0.25a	143.09 ± 4.34a	130.50 ± 2.50b
Lignin:N ratio	4.62 ± 0.21d	38.46 ± 1.13a	24.58 ± 0.50b	11.95 ± 0.29c
Lignin:P ratio	53.61 ± 1.50d	524.63 ± 29.70a	248.54 ± 13.37c	137.30 ± 1.44c
C:N ratio	19.52 ± 0.40d	119.32 ± 5.17a	74.52 ± 1.89b	40.47 ± 0.25c
C:P ratio	226.75 ± 7.81d	1627.67 ± 110.06a	753.27 ± 41.00b	464.72 ± 7.44c
N:P ratio	11.57 ± 0.25b	13.65 ± 0.90a	10.10 ± 0.62c	11.47 ± 0.20b

* The values of litter mixture were the average value of leaf, root, and grass

Different lowercase letters indicate significant differences among the litter types for the same chemical trait at the 0.05 level

and AP in the soil were colorimetrically measured at 880 nm using the molybdenum blue method.

The chloroform fumigation-extraction method was used to determine the soil microbial biomass C (MBC, Vance et al. 1987), N (MBN, Brookes et al. 1985), and P (MBP, Brookes et al. 1982). Briefly, fresh soil was fumigated with alcohol-free chloroform, and then both the fumigated and non-fumigated soil were extracted with 0.5 mol L^{-1} K$_2$SO$_4$ for MBC and MBN, and 0.5 mol L^{-1} NaHCO$_3$ solution for MBP. We measured MBC and MBN using a Multi N/C3100 TOC/TN analyzer, and MBP was measured using a UV-1100 spectrophotometer (Meipuda Instruments, Shanghai, China) at 882 nm. The conversion coefficients for MBC, MBN, and MBP are 0.45, 0.54, and 0.40, respectively (Wu et al. 1990; Brookes et al. 1982, 1985).

SOM fractionation

Bulk soils were separated into POM and MAOM fractions using the wet sieving method to quantify their contributions to organic C (OC) accumulation (Xu et al. 2021). Briefly, air-dried soil (20 g) was placed in a 50-mL plastic bottle and dispersed with 5% sodium hexametaphosphate solution. These bottles were shaken on a reciprocal shaker (18 h), and then the soil homogenates were placed onto a 53-µm sieve and washed with continuous distilled water. The fractions that remained on the sieve (POM, ≥ 53 µm) and passed through the sieve (MAOM, < 53 µm) were collected, dried at 60 °C, and weighed separately. The OC concentrations in POM (POM-C) and MAOM (MAOM-C) were measured using an elemental analyzer.

Amino sugar measurement

The soil amino sugars were determined using the method proposed by Zhang and Amelung (1996). Briefly, air-dried soil samples were ground and hydrolyzed with 6 mol L^{-1} HCl (8 h, 105 °C). The cooled sample was added to 0.1 mL (6 mol L^{-1}) of myoinositol as a surrogate standard, filtered, and dried completely using a rotary evaporator at 40 °C under vacuum. The residue was then dissolved in 20 mL of water and the pH was adjusted to 6.6–6.8. The precipitates were discarded after centrifugation (2000 × g, 10 min) and the supernatant was freeze-dried. Amino sugars were dissolved in 3 mL CH$_4$O and separated from the salts by centrifugation (2000 × g, 10 min). The amino sugar fractions were transformed into aldononitrile derivatives by heating in 0.3 mL of a derivatization reagent containing 32 mg mL^{-1} of hydroxylamine hydrochloride and 40 mg mL^{-1} of 4-(dimethylamino) pyridine in a pyridine and methanol mixture (4:1) at 75 °C for 30 min. The derivatives were further acetylated with 1 mL of acetic anhydride at 75–80 °C for 20 min and mixed with 1.5 mL of dichloromethane after cooling. Excess derivatization reagents were removed by extraction with HCl (1 mol L^{-1}) and MilliQ water, while the dichloromethane phase containing amino sugar derivatives was dried under nitrogen before quantification.

The amino sugars in the residue were measured using gas chromatography (Agilent 6890A, Agilent Technologies, Wilmington, DE, USA) equipped with a flame ionization detector and an HP-5 capillary column (25 m × 0.25 mm × 0.25 µm). The temperature was initially held at 120 °C for 1 min, and then increased to 250 °C at a rate of 10 °C min^{-1} for 2.5 min with a final isothermal hold at 270 °C for 5 min. Amino sugars were identified by comparing their retention times with those of authentic standards. Quantification was performed relative to the internal standard myoinositol, which was added to the samples before purification, and the recovery standard methylglucamine, which was added before derivatization. Four amino sugars were quantified: glucosamine (GlcN), galactosamine (GalN), muramic acid (MurA), and mannosamine (ManN), and their sum was considered the total amino sugar concentration. GlcN and MurA are derived from fungal and bacterial residue (Zhang and Amelung 1996; Guggenberger et al. 1999). GalN and ManN were not used to estimate microbial residue C because their origin was uncertain (Joergensen 2018). Therefore, fungal and bacterial residue C was estimated using the following equations (Engelking et al. 2007; Appuhn and Joergensen 2006):

$$\text{Fungal residue C} = (\text{GlcN}/179.17 - 2 \times \text{MurA}/251.23) \times 179.17 \times 9 \quad (1)$$

$$\text{Bacterial residue C} = \text{MurA} \times 45 \quad (2)$$

The total microbial residue C in soil is the sum of the fungal and bacterial residue C.

Statistical analyses

Microbial C use efficiency (CUE) was estimated using a biogeochemical equilibrium model (Sinsabaugh and Follstad Shah 2012) based on the following equations:

$$\text{CUE} = \text{CUE}_{max} \times \left\{ (H_{C:N} \times H_{C:P}) / [(K_{C:N} + H_{C:N}) \times (K_{C:P} + H_{C:P})] \right\}^{0.5} \quad (3)$$

$$H_{C:N} = M_{C:N}/L_{C:N} \times 1/E_{C:N} \quad (4)$$

$$H_{C:P} = M_{C:P}/L_{C:P} \times E_{C:P} \quad (5)$$

where $H_{C:N}$ and $H_{C:P}$ are the scalars for the relative N and P availability, respectively; $K_{C:N}$ and $K_{C:P}$ are the half-saturation constants for CUE according to the C, N, and P availability, respectively; $M_{C:P}$ and $M_{C:N}$ are microbial biomass C:P and C:N ratios, respectively; and $L_{C:P}$ and $L_{C:N}$ are the ratios of soil labile substrate availability for C (DOC), N

(DON), and P (AP). $K_{C:N}$ and $K_{C:P}$ were 0.5, and CUE_{max} was 0.6 according to the results of Sinsabaugh and Follstad Shah (2012).

The effects of different litter additions on SOM fractions, elemental concentrations, stoichiometry of different soil components, and microbial residue C were estimated using a linear mixed-effects model. The litter type was treated as a fixed factor and the replicates were treated as random factors. The differences among the different litter treatments were further tested using Tukey's honest significant difference test ($P < 0.05$). Normality (Shapiro–Wilk test; $\alpha = 0.05$) and homogeneity of residues were examined for all models (Bartlett test; $\alpha = 0.05$), and data were log- or square-root-transformed when required before fitting the linear mixed-effect model. The linear mixed-effects model was fitted using the R package 'lmerTest' (v 3.0-1, Kuznetsova et al. 2017).

Variation partitioning analysis was performed to assess the relative importance of soil and microbial traits when explaining the variability of SOM fractions using the 'rdacca.hp' package (v 1.0-8, Lai et al. 2022). To reduce collinearity and the number of variables (Sanaei et al. 2021), we conducted principal component analysis for litter chemical traits, bulk soil nutrient stoichiometry, and microbial biomass stoichiometry. The first axis (PC1, accounting for 79–96% of the variance for these variables) was used to represent these variables in the variation partitioning analysis. Pearson correlation analysis was used to test the correlations between litter, soil and microbial traits, and microbial residue C using the package 'corrplot' (v. 0.84, Wei and Simko 2017). All statistical analyses were performed using the R software (R Core Team, v.4.0.2 2020).

Results

Soil C concentration in the SOM fractions

Litter addition increased the C concentration of SOM (SOM-C) and its fractions (POM-C and MAOM-C) compared to that of the control soil during the experiment (Fig. 1). The SOM-C concentrations were higher in the root and grass treatments compared to other treatments during the early and intermediate stages of decomposition and were highest in the mixture treatments at the end of decomposition. The POM-C concentrations in the leaf, root, grass, and mixture treatments increased by 6.6, 8.9, 9.9, and 7.1 times, respectively, compared to those in the control soil during the early stages of decomposition. The pattern was similar during the intermediate decomposition stage. Mixture treatments presented the highest POM-C concentrations, followed by those of the root and grass treatments, and the POM-C concentration was not significantly different between the leaf and control treatments at the end of decomposition. In comparison, the MAOM-C concentrations in the leaf, root, and grass treatments increased with incubation time, they increased by 1.9, 1.5, 1.5, and 1.4 times, respectively, compared to those of the control soil at the end of decomposition.

Variation in soil nutrient stoichiometry

The concentrations of soil DOC and DON increased in the litter addition treatments compared with the control soil, and a significant increase was observed in the leaf litter treatment ($P < 0.05$; Fig. 2). The AP concentration did not differ

Fig. 1 C concentration of the particulate organic matter (POM) and mineral-associated organic matter (MAOM) fractions for the different treatments after 50, 100, and 150 days of incubation. Different uppercase letters represent significant differences in C concentration among the treatments ($P < 0.05$). Different lowercase letters represent significant differences in C concentration of the POM or MAOM fractions among treatments ($P < 0.05$)
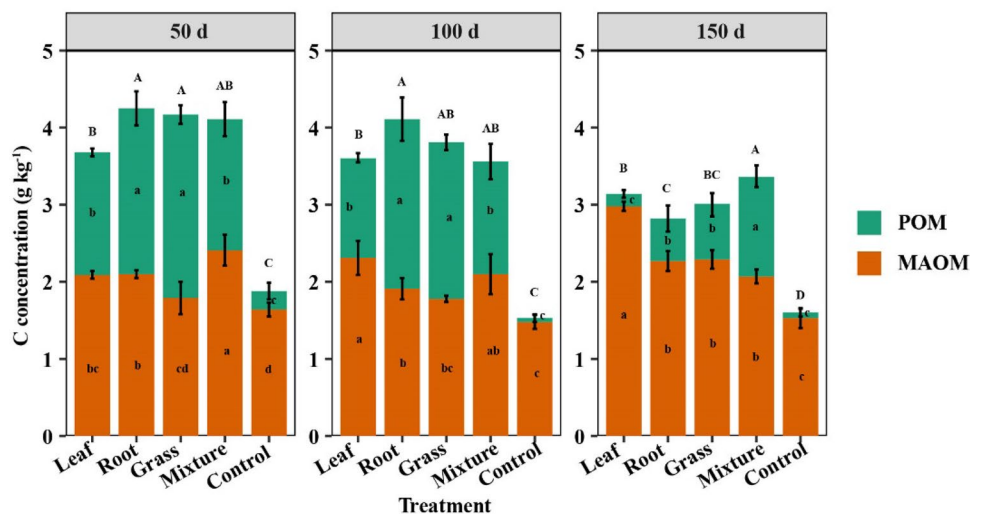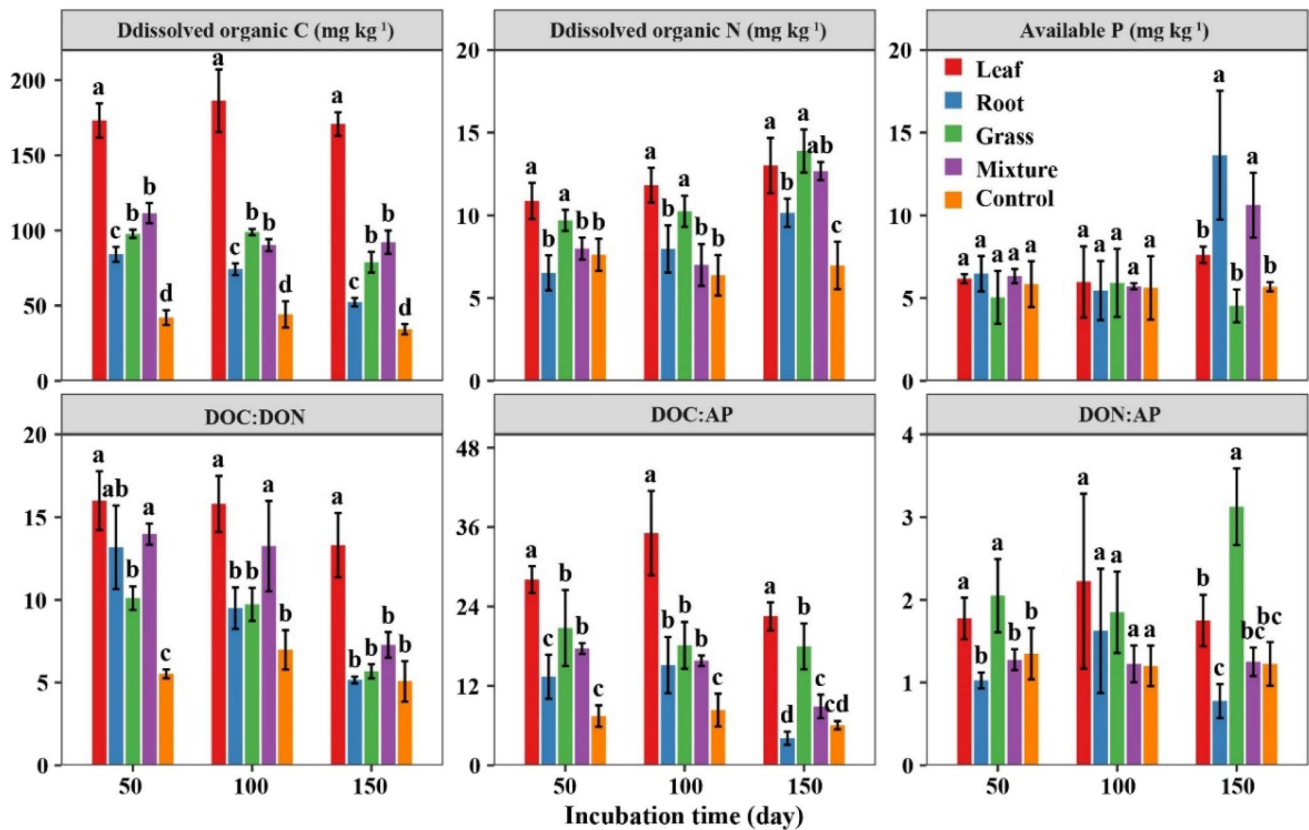
Fig. 2 Concentration and stoichiometry of soil dissolved organic C (DOC), dissolved organic N (DON), and available P (AP) in the different treatments after 50, 100, and 150 days of incubation. Different lowercase letters represent significant differences in the concentration of DOC, DON, AP, and their ratios (DOC:DON, DOC:AP, and DON:AP) among treatments ($P < 0.05$)

among the five treatments during the early and intermediate stages of decomposition but was significantly higher in the root and mixture treatments than in the control soil at the end of decomposition ($P < 0.05$). Compared to that in the control soil, the DOC:DON ratios in all litter addition treatments increased significantly during the early stage of decomposition ($P < 0.05$) and increased in the leaf and mixture treatments during the intermediate and late stages of decomposition. The DOC:AP ratios in all litter addition treatments increased significantly during the early and intermediate stages of decomposition ($P < 0.05$) and increased in the leaf and grass treatments at the end of decomposition. The DON:AP ratio was higher in the leaf and grass treatments than in the control soil during the early and late stages of decomposition.

Variations in soil microbial biomass stoichiometry and CUE

Litter addition increased the soil MBC, MBN, and MBP compared to those in the control soil during the experiment, and higher increases were observed in the leaf and grass treatments (Fig. 3). The MBC:MBN ratio varied little among the treatments

during the early and intermediate stages of decomposition, and it increased significantly in all litter addition treatments (~4.3 times) compared to that in the control soil at the end of decomposition ($P < 0.05$). The MBC:MBP ratio, compared to that in the control soil, increased significantly in the leaf and grass treatments during the early stage of decomposition and increased in all litter addition treatments at the end of decomposition. The MBN:MBP ratio, compared to that in the control soil, increased in the leaf and mixture treatments during the intermediate stage of decomposition and decreased in the root and grass treatments at the end of decomposition.

Microbial CUE decreased in most litter addition treatments during the early and intermediate stages of decomposition, increasing significantly for all the litter addition treatments compared to that in the control soil, especially for the root litter treatment ($P < 0.05$), at the late stage of decomposition (Fig. 4).

Microbial residue C in the SOM fractions

The concentration of fungal residue C in the POM at the end of decomposition increased significantly in the root and grass treatments, compared to that in the control soil,
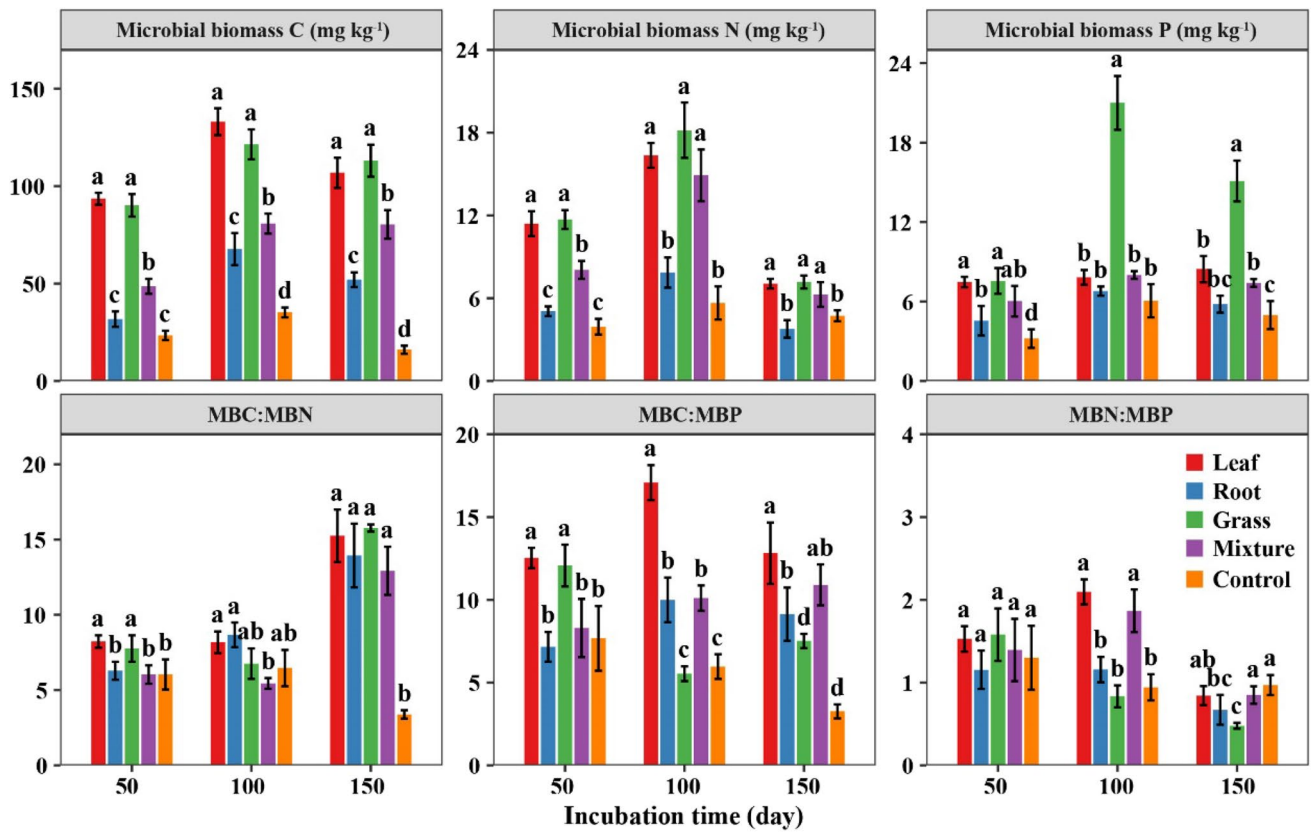
Fig. 3 Concentration and stoichiometry of soil microbial biomass C (MBC), N (MBN), and P (MBP) in the different treatments after 50, 100, and 150 days of incubation. Different lowercase letters represent significant differences in the concentrations of MBC, MBN, MBP, and their ratios (MBC:MBN, MBC:MBP, and MBN:MBP) among treatments ($P < 0.05$)
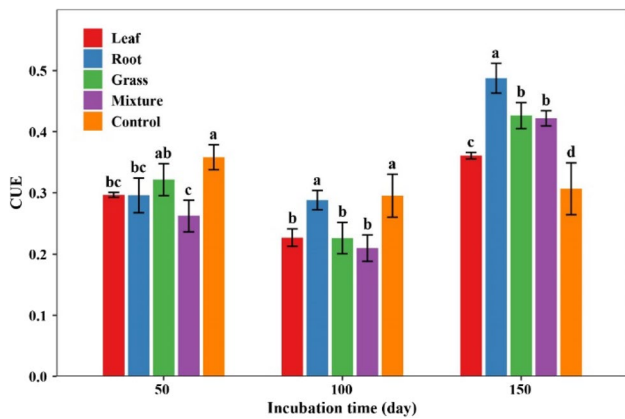

Fig. 4 Microbial C use efficiency (CUE) in the different treatments after 50, 100, and 150 days of incubation. Different lowercase letters represent significant differences in CUE among treatments ($P < 0.05$)

and increased significantly in MAOM for all litter addition treatments ($P < 0.05$; Fig. 5). The concentration of bacterial residue C in POM increased significantly in the leaf, grass, and mixture treatments when compared to that in the control soil, whereas the bacterial residue C in MAOM only increased significantly in the root treatment ($P < 0.05$). The total microbial residue C in the POM and MAOM fractions in the leaf, root, grass, and mixture treatments increased by 72%, 86%, 84% and 37%, respectively, compared to that in the control soil. The ratio of fungal residue C:bacterial residue C in POM increased significantly only in the root treatments compared to that in the control soil ($P < 0.05$), it increased in the grass treatments and decreased in the mixture treatment compared to that in the control soil in MAOM ($P < 0.05$). The proportion of microbial residue C to POM-C decreased significantly in the litter addition treatments compared to that in the control soil ($P < 0.05$), especially in the mixture treatment. The proportion of microbial residue C to MAOM-C did not differ among treatments. The proportion of microbial residue C to SOM-C decreased significantly in the leaf and mixed litter treatments compared to that in the control soil ($P < 0.05$).

Linkage between litter quality, microbial traits, and SOM fractions

In the early stage of decomposition, POM-C was positively correlated with the litter chemical traits (i.e., C:N,
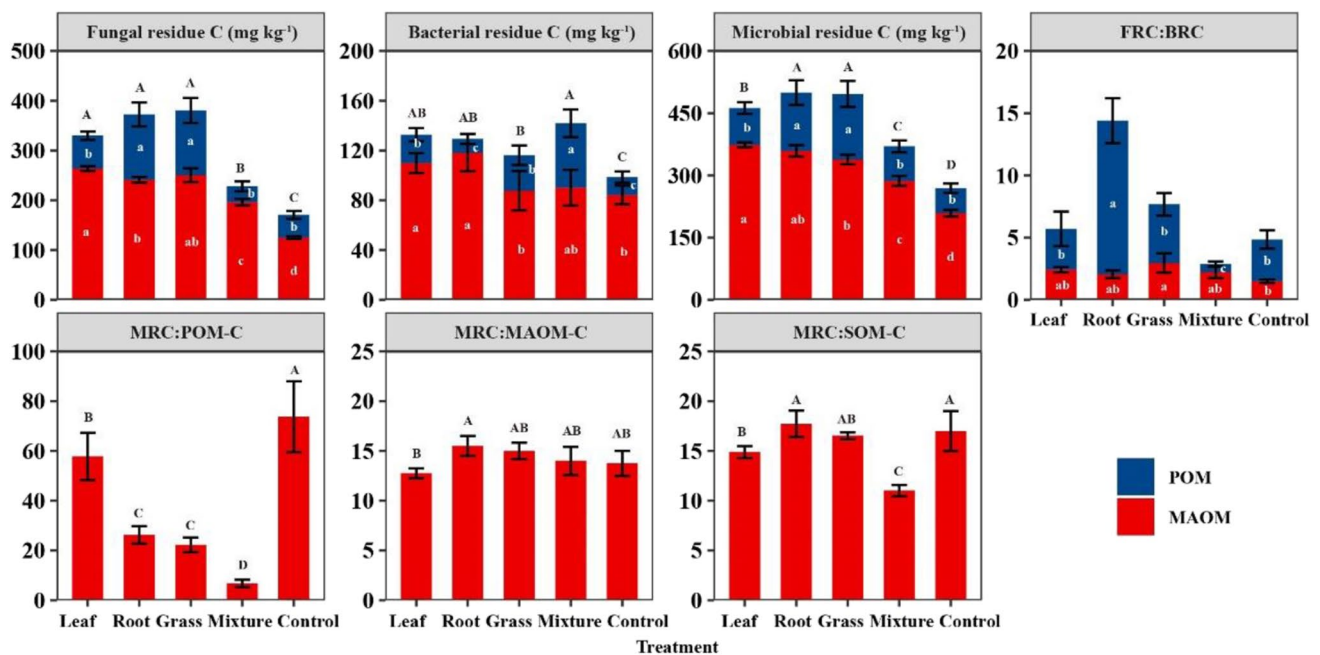
Fig. 5 Production of microbial residue C in particulate organic matter (POM-C) and mineral-associated organic matter (MAOM-C) and their contributions to the different treatments after 150 days of incubation. (**a**): Fungal residue C (glucosamine); (**b**): bacterial residue C (muramic acid); (**c**): microbial residue C (glucosamine + muramic acid); (**d**): fungal residue C to bacterial residue C ratio; (**e**): proportion of microbial residue C to POM-C; (**f**): proportion of microbial residue C to MAOM-C; and (**g**): proportion of microbial residue C to C in the soil organic matter. Different uppercase letters (**a–c**) represent significant differences in C concentration of the microbial residue groups in the SOM among treatments ($P < 0.05$). Different lowercase letters (**a–d**) represent significant differences in C concentrations of the microbial residue groups in the POM or MAOM fractions among treatments ($P < 0.05$). Different uppercase letters (**e–g**) represent significant differences in the ratios of the microbial residue C to SOM fractions among the treatments ($P < 0.05$)

lignin:N, and lignin:P ratios) and DOC:DON ratio ($P < 0.05$), MAOM-C was positively correlated with the DOC:DON and DOC:DOP ratios ($P < 0.05$), and both the POM-C and MAOM-C were negatively correlated with microbial CUE ($P < 0.05$; Fig. 6a). During the intermediate stage of decomposition, the litter chemical traits were positively correlated with POM-C ($P < 0.05$) and negatively correlated with MAOM-C ($P < 0.05$), while MAOM-C was positively correlated with the MBC:MBP, MBN:MBP, DOC:DON, and DOC:DOP ratios ($P < 0.05$), and both POM-C and MAOM-C were negatively correlated with microbial CUE ($P < 0.05$; Fig. 6b). At the end of decomposition, POM-C was only significantly and positively correlated with CUE ($P < 0.05$), and MAOM-C was negatively correlated with litter chemical traits and positively correlated with soil and microbial stoichiometry ($P < 0.05$; Fig. 6c).

Variation partitioning analysis showed that litter chemical traits dominated the variation in POM-C during the litter decomposition process, and bulk soil stoichiometry also exerted an important effect on POM-C at the end of decomposition (Fig. 7). Microbial biomass stoichiometry accounted for most of the MAOM-C variation during the early and intermediate decomposition stages. In the late

decomposition stage, bulk soil stoichiometry played an important role in MAOM-C.

Correlation analysis showed that the fungal residue C, microbial residue C, and fungal to bacterial residue C ratio in POM-C were negatively correlated with the C, N, and P concentrations in the litter and positively correlated with litter stoichiometry ($P < 0.05$; Fig. 8). Moreover, the fungal residue C and microbial residue C were negatively correlated with the MBC:MBP and MBN:MBP ratios ($P < 0.05$). The microbial residue C in MAOM-C was weakly correlated with most of the litter chemical traits and soil and microbial traits. Additionally, the ratio of microbial residue C to MAOM-C was negatively correlated with C, N, and P concentrations in the litter and positively correlated with litter stoichiometry and CUE ($P < 0.05$).

Fig. 6 Relationship between C in the particulate organic matter ▶ (POM) and mineral-associated organic matter (MAOM) fractions and litter, soil, and microbial traits after 50 (**a**), 100 (**b**), and 150 (**c**) days of incubation. LC:LN, leaf C: N; lignin:P, lignin:leaf P; DOC:DON, dissolved organic C:N; DOC:AP, dissolved organic C:available P; MBC: MBN, microbial biomass C:N; MBC:MBP, microbial biomass C:P
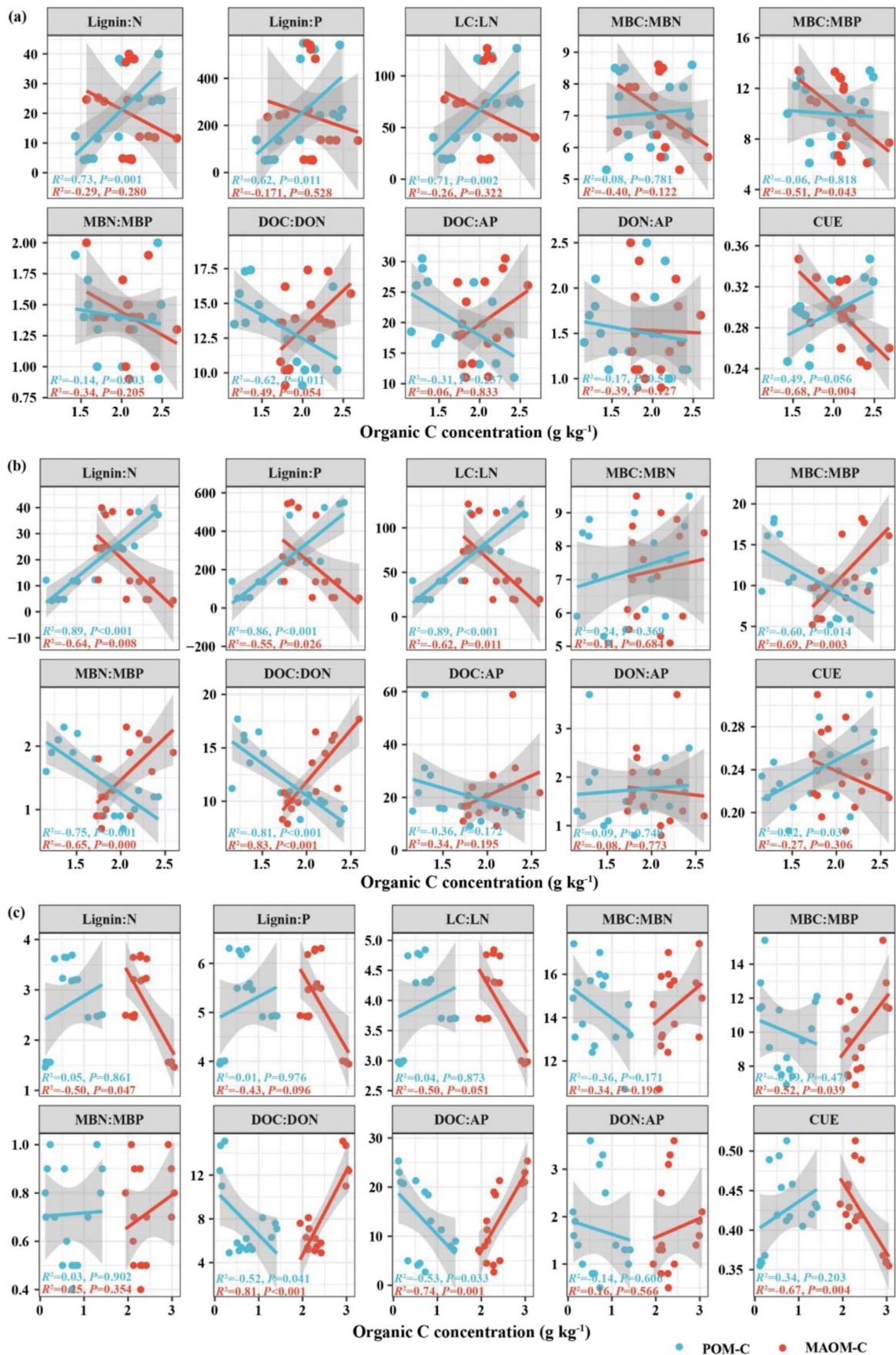
Fig. 7 Relative contributions of litter, soil, and microbial traits to POM and MAOM based on variation partitioning analysis. The litter chemical traits include C, N, P, lignin, hemicellulose, cellulose, and their stoichiometry ratios; bulk soil stoichiometry includes DOC:DON:AP ratios; microbial stoichiometry includes MBC:MBN:MBP ratios. The values on the outer ring represent the relative contributions of litter, soil, and microbial traits to the variance of POM or MAOM, and the values on the inner ring represent the proportion of variance that can be explained by the predictor variables
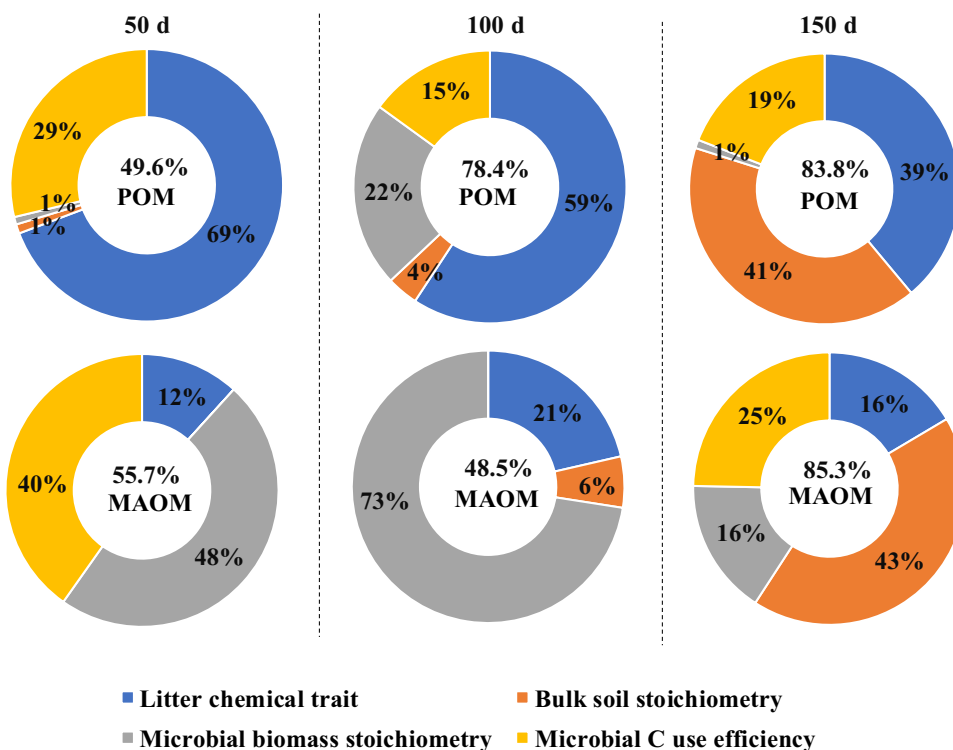
Discussion

Effect of litter quality on OC in the POM and MAOM fractions

In this study, litter chemical traits strongly affected the dynamics of POM-C and MAOM-C with increasing incubation time. Specifically, high-quality leaf litter had a rapid decomposition rate due to its high N concentration and low recalcitrant components (e.g., lignin), leading to a significant decrease in POM-C and increased MAOM-C accumulation. In contrast, root and grass litter with high C:N and lignin:N ratios caused more C to remain in the POM and reduced MAOM-C accumulation. The higher MAOM-C in leaf litter than in root and grass litter at the end of decomposition was attributed to the fact that leaves with more labile parts are readily decomposed by microbes and were more rapidly transferred into MAOM via microbial transformation (e.g., microbial products of metabolism) and/or direct mineral surface sorption (Cotrufo et al. 2015; McFarland et al.
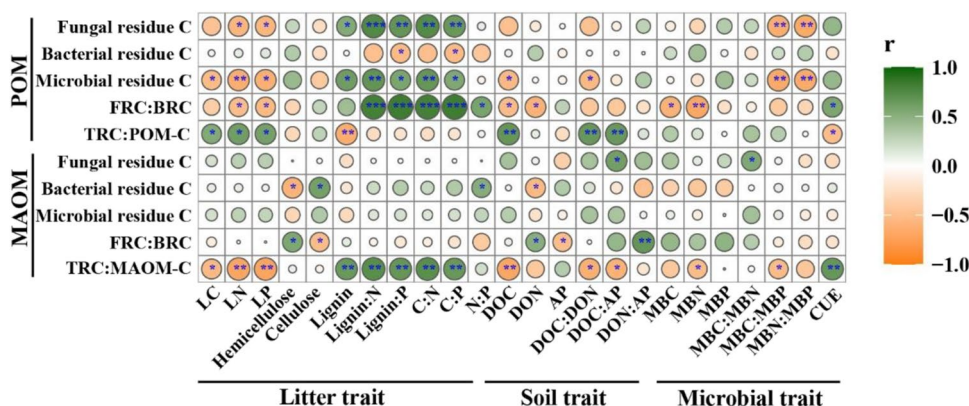

Fig. 8 Correlation analysis between the concentration and contribution of microbial residue C and the traits of litter, soil, and microbes after 150 days of incubation. LC, leaf C; LN, leaf N; LP, leaf P; DOC, dissolved organic C; DON, dissolved organic N; AP, available P; MBC, microbial biomass C; MBN, microbial biomass N; MBP, microbial biomass P; FRC, fungal residue C; BRC, bacterial residue C; MRC, microbial residue C; POM, particulate organic matter; MAOM, mineral-associated organic matter

2019; Craig et al. 2022). We also found that litter chemical traits (e.g., lignin:N ratio) were negatively correlated with MAOM-C (Fig. 6). The value of mixed litter chemical traits was between that of leaf and root litter and did not show an additive effect for POM-C and MAOM-C accrual. At the end of decomposition, compared to the impact of single litter input, the addition of mixed litter significantly increased C in SOM, mainly due to the high POM-C level, indicating that the litter mixture decreased the litter decomposition rate and retained more C in POM. Previous studies have shown that litter mixture decomposition generally enhanced litter mass loss and N release compared to the impact of single litter, and this synergistic effect was pronounced at the early stage of decomposition (Kou et al. 2020). Litter diversity has recently been shown to enhance labile C (e.g., soluble compounds and cellulose) but slow recalcitrant C (e.g., lignin) decomposition in a 3.5-year field experiment in an alpine forest (Wang et al. 2022). We also found that MAOM-C was higher in the mixed litter treatment than in the single source litter treatments at the early stage of decomposition. This outcome may be due to the dissimilarity in the labile fractions among the different litter types, which favors the leaching of water-soluble compounds (Talbot and Treseder 2012; Wang et al. 2022) and consequently enhances available substrate decomposition and microbial turnover, improving MAOM formation. However, with the depletion of the labile fraction at the end stage of decomposition, the interaction of lignin and N in the litter mixture treatment may reduce litter decomposition as lignin chemically or physically protects N from hydrolysis or microbial attack (Boerjan et al. 2003; Talbot et al. 2012; Wang et al. 2022), thereby slowing the decomposition of recalcitrant components and leading to a relatively higher POM concentration. Another possible explanation is the antagonistic effect caused by litter trait (e.g., N and lignin concentration) dissimilarity (Wang et al. 2022); however, the underlying mechanisms of this antagonistic effect and its relationship to litter dissimilarity are still unclear. Nevertheless, our analysis of the effects of litter quality partially supports our first hypothesis that high-quality litter increases MAOM-C accumulation and decreases POM-C accumulation over the incubation time. Furthermore, we determined that the pattern of POM-C and MAOM-C accumulation differed between mixed litter and single source litter treatments.

Previous studies have shown that litter chemical traits affect the formation of SOM pools (Córdova et al. 2018; Almeida et al. 2021; Ridgeway et al. 2022). Similarly, we found that the variation in POM-C was mainly controlled by litter chemical traits during litter decomposition (Fig. 7); thus, it was not surprising that POM primarily consisted of undecomposed litter fragments or partially decomposed litter (Witzgall et al. 2021). We also found that microbial and soil stoichiometry primarily controlled the dynamics of MAOM-C, and litter chemical traits played a minor role (Fig. 7).

These findings were consistent with our second hypothesis that the dynamics of POM-C and MAOM-C were controlled jointly by initial litter chemical traits and microbial and soil stoichiometry. Furthermore, we found that litter addition greatly increased the availability of C and nutrients in the soil (Fig. 2), which resulted in a shift in microbial biomass stoichiometry via changes in microbial community composition and function (Mooshammer et al. 2014). Moreover, an increase in the microbial C:N:P ratio implies increased C availability, which is conducive to microbial growth. Under these conditions, soil microorganisms tend to utilize more C for anabolism, thereby increasing MBC, which enhances the formation of MAOM because a higher MBC can produce more microbial residue C. During the later stages of decomposition, soil stoichiometry (C:N:P ratios) dominated the variation in MAOM-C (Fig. 7). Substrate availability in the soil is considered a crucial factor influencing microbial activity and turnover (Mooshammer et al. 2014). With the depletion of labile compounds from the substrate, microbial CUE increased in this study (Fig. 4), suggesting that soil microbial growth is limited by substrate availability. Thus, soil nutrient stoichiometry influenced litter decomposition by regulating microbial activity and played an important role in the formation of MAOM-C at the end of decomposition.

Microbial residue C accrual in the POM and MAOM fractions

Plant litter inputs supply more available substrates and promote microbial biomass growth and turnover, which can increase the accumulation of microbial residue (Liang et al. 2017). In this study, input of leaf litter produced more microbial residue C in MAOM-C than input of root and grass litters, and a contrasting pattern was observed in the production of POM-C. The amount of microbial residue C in SOM-C (including POM-C and MAOM-C) was lower in the mixed litter than in the single litter (except for POM-C in leaf litter treatment) (Fig. 5), implying that the litter mixture resulted in low microbial residue C production. These results were partly consistent with our third proposed hypothesis. The leaf litter contained more easily decomposable components than the root and grass litters, which effectively promoted microbial growth, leading to greater residue production and a higher microbial residue C content in MAOM-C (Cotrufo et al. 2015). In comparison, the high microbial residue C level in POM-C in the root and grass litter treatments was due to the high fungal residue C production. Fungi are commonly considered to use more recalcitrant components (e.g., lignin) as energy sources than bacteria (Bahram et al. 2018; Zhang et al. 2019). Therefore, root and grass litters contributed more fungal residue C and microbial residue C to POM-C. The difference in microbial residue C production between mixed litter and single litters absent direct experimental evidence other

than litter treatment effects, we propose that the low microbial residue C production in the mixed litter treatment was caused by an antagonistic effect induced by slow microbial utilization of recalcitrant C at the end of decomposition due to litter trait dissimilarity. We also found that the ratio of fungal residue C to bacterial residue C was greatly reduced in the mixed litter treatment, indicating a decrease in fungal metabolic capacity (Fig. 5). Additionally, previous studies have shown that substrate quality may alter microbial community composition and competition in resource acquisition (Liang 2020; Bai et al. 2021), thus affecting the production of microbial residue C.

In this study, the average contribution of microbial residue C to SOM-C among the litter treatments varied from 11 to 18%, which was lower than the average value (~35%) in global forest soils (Wang et al. 2021). This discrepancy may be attributed to the soil properties in the study area, which are characterized by high pH (8.8) and high electrical conductivity (16.6 µS m^{-1}), poor nutrient levels, and coarse texture (Table 1). Thus, the microbial activities could be constrained, leading to low microbial residue production (Wichern et al. 2006; Khan et al. 2016; Chen et al. 2021). Taken together, these findings highlight that litter type substantially affects the production and contribution of microbial residue C to the POM and MAOM fractions.

Study limitations

We must acknowledge that the study results were derived from incubation experiments conducted in a lab rather than in situ field experiments. The quality and quantity of plant litter in forest ecosystems generally vary with climate and vegetation composition (Sun et al. 2019). Transformation of plant materials into SOM fractions is influenced by many abiotic and biotic factors, including litter, soil, and microbial traits as well as soil fauna (Sokol and Bradford 2019). Moreover, inputs of litter at different times and in different amounts change environmental factors, such as temperature and moisture, which have direct and indirect effects on the physiology and metabolism of microorganisms (Manzoni et al. 2012; Schimel and Schaeffer 2012). Finally, plant litter inputs may stimulate native SOM decomposition (i.e., the priming effect), which was not measured during the experiment. This phenomenon might affect the C distribution in SOM fractions; thus, more research is needed to evaluate the dynamics of SOM fractions and the factors that control them in the field.

Conclusions

In this study, the chemical traits of different litter types and their induced microbial and soil stoichiometry were found to greatly affect C distribution in SOM fractions.

Low-quality litter increased POM-C, mainly regulated by litter chemical traits during litter decomposition; high-quality litter was prone to form MAOM-C, controlled mainly by microbial and soil stoichiometry. The litter mixture treatment considerably increased C accrual in the SOM compared to that under the single source litter treatment, and this effect resulted from high POM-C. Moreover, the litter mixture treatment had a lower production and contribution of microbial residue C to SOM compared to those of the single source litter treatment. Furthermore, the study results provide direct evidence that litter-driven C, rather than microbial assimilation products, dominated SOM-C accumulation in coastal coarse-textured soils. Overall, these results highlight that the microbial and soil stoichiometry induced by different litter types strongly control the dynamic of MAOM-C accrual. Furthermore, the study findings enhance the understanding of the relationship between litter input and C distribution in SOM fractions.

Declarations

Competing interests The authors declare no competing interests.

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