

Article

Distinct Roles of Forest Stand Types in Regulating Soil Organic Carbon Stability Across Depths

Jiaxi Zhao ¹, Liming Lai ¹, Ye Mei ¹, Yanming Zhao ¹, Zimo Li ¹, Yanxing Dou ^{1,2,*} , Lin Hou ^{1,2}, Qinghong Geng ^{1,2} and Shuoxin Zhang ^{1,2}

¹ College of Forestry, Northwest A&F University, Yangling 712100, China; zhaojiaxi@nwafu.edu.cn (J.Z.); 2021011389@nwafu.edu.cn (L.L.); meiyee@nwafu.edu.cn (Y.M.); zymzym@nwafu.edu.cn (Y.Z.); lizimolxy@nwafu.edu.cn (Z.L.); houlin_1969@nwsuaf.edu.cn (L.H.); gengqh0529@nwafu.edu.cn (Q.G.); sxzhang@nwsuaf.edu.cn (S.Z.)

² Qinling National Forest Ecosystem Research Station, Yangling 712100, China

* Correspondence: douyanxing@nwafu.edu.cn

Abstract

Soil organic carbon (SOC) is the largest reservoir of terrestrial organic carbon and plays a pivotal role in regulating global climate dynamics. And there are some differences in SOC stocks under different forest stand types. But it is unclear whether this phenomenon is related to SOC stability, especially stable components of SOC. Therefore, coniferous (*Pinus tabulaeformis*), broad-leaved (*Quercus aliena*), and mixed forests were selected to explore the distributions and chemical structures of SOC components, as well as SOC stabilization mechanisms. Higher SOC contents but lower stability were observed under *Quercus aliena* forests. Contents of SOC and its components were lowest under *Pinus tabulaeformis* forests. Yet the highest relative abundances of alkyl and aromatic carbon in mineral-associated organic carbon (MAOC) were found at 10–40 cm soil layers, with the highest MAOC/SOC. In contrast, MAOC/SOC was highest under mixed forests at 0–10 cm layer. Total nitrogen (TN), lignin, and silt contents were identified as key drivers of SOC stability. These findings indicated that mixed forest contributes more to enhancing SOC stability in topsoil, whereas coniferous forest promotes greater stability in subsurface layers. These results suggested that the functional complementarity among forest stand types may enhance carbon sequestration and promote the sustainability of forest management.

Keywords: particulate organic carbon; mineral-associated organic carbon; chemical structure; forestland; Qinling mountains



Academic Editor: Xingkai Xu

Received: 2 September 2025

Revised: 4 October 2025

Accepted: 13 October 2025

Published: 15 October 2025

Citation: Zhao, J.; Lai, L.; Mei, Y.; Zhao, Y.; Li, Z.; Dou, Y.; Hou, L.; Geng, Q.; Zhang, S. Distinct Roles of Forest Stand Types in Regulating Soil Organic Carbon Stability Across Depths. *Forests* **2025**, *16*, 1585. <https://doi.org/10.3390/f16101585>

Copyright: © 2025 by the authors. Licensee MDPI, Basel, Switzerland. This article is an open access article distributed under the terms and conditions of the Creative Commons Attribution (CC BY) license (<https://creativecommons.org/licenses/by/4.0/>).

1. Introduction

Soil, as the largest terrestrial carbon pool on earth, holds approximately 2.3 to 2.5 times carbon more than the atmosphere [1]. In this context, soil organic carbon (SOC) can act as a carbon sink, mitigating climate change through long-term carbon sequestration. But if soil was disturbed, it may also release substantial amounts of CO₂, thereby accelerating climate deterioration [2–4]. Forest ecosystems are the major contributors to terrestrial carbon storage, containing approximately 52% of the global soil carbon pool in the topsoil [5,6]. And SOC stocks are related to its stability. Therefore, understanding the mechanisms governing SOC formation and stabilization in forest soils is essential for assessing and enhancing the functionality of terrestrial carbon sinks [7]. Particulate organic carbon (POC) and mineral-associated organic carbon (MAOC) are physical components of SOC [4,7]. This

classification based on physical accessibility provides a more accurate assessment of SOC persistence [2]. POC is considered an active organic carbon fraction and primarily consists of structurally complex plant residues that rely on biochemical recalcitrance and aggregate formation for protection. Due to its high physical accessibility, microorganisms can readily colonize POC, resulting in rapid turnover and a short residence time in soil [5]. In contrast, MAOC is stabilized mainly through chemical bonds or pore sorption to soil mineral surfaces and occlusion in aggregates [2], making it more difficult for microorganisms and enzymes to utilize. Hence, the accumulation of MAOC is beneficial for enhancing SOC stability [2,8]. Furthermore, the chemical structure of SOC is also an important indicator of its stability [9,10]. Aromatic carbon derived from lignin and alkyl carbon derived from lipids, waxes, and aliphatic components of plant represent the easily recalcitrant carbon difficultly utilized by microorganisms [11]. In contrast, alkoxy carbon is mainly derived from carbohydrates, which exhibit higher degradability [12]. Therefore, the accumulation of aromatic carbon and alkyl carbon is more conducive to improving SOC stability [9]. MAOC represents the recalcitrant component of SOC, implying that relative abundances of chemical functional groups in MAOC are strongly associated with the long-term storage and stability of SOC [13]. While current research primarily assesses SOC stability through the lens of SOC chemical structural resistance [11], limited studies have specifically focused on the chemical structural stability of MAOC itself.

Variations in composition of tree species, with distinct sources of litter, root exudates, mycorrhizal fungal, hyphal exudates, and microbial composition [3,14,15], lead to the different accumulation and chemical structure of POC and MAOC, which further affects SOC stability under different stand types [11,16]. Just as Xu et al. (2024) [17] have found that the relative abundance of alkyl carbon was the highest under mixed forests, increased litter diversity may enhance stability of SOC due to increased metabolic cost of microbial decomposition and diversified bond strength between soil organic matter and minerals. Conversely, some studies have shown that relative abundance of aromatic carbon and the value of (alkyl carbon)/(alkoxy carbon) under coniferous forests were higher [11]. In coniferous forests dominated by ectomycorrhizal (ECM) fungi, the widespread mycorrhizal symbionts form a reciprocal relationship with their host trees [18]: ECM fungi acquire photosynthetic carbon from their host plants while facilitating the uptake of water and soil-derived nutrients for the plants [19]. A portion of this assimilated carbon is utilized by the fungi for biosynthesis of their own biomass, which ultimately converted into microbial residues enriched in recalcitrant compounds, including chitin and melanin, which serve as persistent precursors for the formation of MAOC [18]. The remaining carbon is released into the rhizosphere as mycelial exudates, including organic acids and extracellular enzymes [20]. These exudates play a critical role in decomposing organic matter and weathering mineral particles to mobilize limited nutrients such as nitrogen. This efficient nutrient acquisition strategy supports robust growth of ECM fungi, thereby indirectly enhancing the accumulation of fungal residues and promoting MAOC formation [21]. Moreover, the dense mycelial network and its secreted adhesives (extracellular polysaccharides and glycoproteins) promote soil aggregate formation and stability via a hybrid mechanism of physical entanglement and chemical binding [14,18]. However, we still have little knowledge on whether the chemical structures of MAOC could also affect SOC stability under different stand types [16].

Serving as a crucial dividing line between the northern and southern climate and a key ecological barrier, the Qinling Mountains also play a significant role in the carbon cycle of terrestrial ecosystems both nationally and globally [3]. While numerous studies of forest soil in this region have focused on the spatial variation of SOC storage and mineralization [22,23], the mechanism of SOC stabilization remains poorly understood with

respect to chemical structures of SOC fractions, particularly POC and MAOC. Furthermore, forest stand type is widely recognized as a major driving factor affecting the stability of SOC [24]. The Huoditang forest region in the Qinling Mountains, which features long-term monitoring plots across diverse forest stand types and is characterized by a substantial capacity for carbon sequestration [1,25], provides an ideal setting to investigate the effects of stand types on SOC stability [3].

Hence this research aimed to 1. quantify SOC components and semi-quantify relative abundances of functional groups in MAOC chemical structure at different depths and in three stand types. 2. Identify the soil and litter properties that drive the regulation of SOC stabilization. 3. Assess how different stand types contribute to SOC stability in the topsoil and subsurface soil layers. These results will provide a theoretical foundation and data support for studying the carbon sink function of forest ecosystems and sustainable forest management. And this is of great significance for optimizing carbon sequestration and achieving the goals of carbon peaking and carbon neutrality in the Qinling Mountains.

2. Materials and Methods

2.1. Study Area

This study took Huoditang Teaching Experimental Forestry Station in Ningshan County, Shaanxi Province, as the study area, which covers a total area of 2037 ha, with a forest coverage of 91.8%. The station is situated in the Qinling Mountains, a transition zone between northern subtropical and warm temperate, characterized by a humid warm temperate mountainous climate. The annual precipitation averages 1023 mm, with the majority occurring in July and August. The average annual temperature is 12 °C, with an annual sunshine duration of 1327.5 h and a growing season of six months. The soil is classified as mountain-brown soil (Luvisol in the World Reference Base for Soil Resources), with approximately 60 cm in thickness. The mountain-brown soil is usually slightly acidic and sticky. The predominant tree species include *Pinus tabuliformis*, *Quercus aliena*, *Pinus armandii*, *Abies fabri*, *Picea asperata*, and *Betula albosinensis*, etc. [3,25].

2.2. Experimental Design

At the end of July 2023, three stand types were selected in the study area: broad-leaved forests (*Quercus aliena*), coniferous forests (*Pinus tabuliformis*), coniferous and broad-leaved mixed forests (*Pinus tabuliformis* and *Quercus aliena*). Three plots measuring 20 m × 20 m were randomly established for each stand type. Within each plot, five shrub quadrants (2 m × 2 m) were positioned at each of the four corners and the center of plot. Additionally, within each shrub quadrant, five herb quadrants (1 m × 1 m) were set up. A vegetation survey was conducted first, followed by the collection of soil and litter samples. The basic information of sample plots is shown in Table S1.

2.3. Soil Sample Collection and Processing

Collection and processing of soil samples: Soil samples were collected separately from 0 to 10 cm, 10 to 20 cm, and 20 to 40 cm soil layers using an auger (length of 1 m) according to the “S-type” method, and the samples from the same layer were mixed together. A total of 27 soil samples were obtained, representing three stand types with three replicate plots per type, and three samples collected from each plot. The soil samples were thoroughly mixed in sterile plastic containers and transferred into sterile self-sealing bags. Upon transport to the laboratory, visible debris and plant roots were removed from the soil samples. All soil samples were sieved through a 2 mm sieve. A portion of the samples was further air-dried naturally and sieved through a 2 mm and 0.15 mm sieve for the analysis of SOC and its components, the chemical structure of MAOC, as well as soil physicochemical

properties. Additionally, soil samples were collected with a cutting ring from 0 to 10 cm, 10 to 20 cm, and 20 to 40 cm soil layers, respectively, to dry for the determination of soil bulk density (BD).

Collection and processing of litter samples: Litter was collected from a quarter of 1 m × 1 m herb quadrant's area, and litter from the same plot was mixed together and placed into preservation bags separately. These samples were then dried at 65 °C until a constant weight was reached and subsequently smashed by a pulverizer to pass through a 0.15 mm sieve. The prepared samples were then placed into self-sealing sterile bags for analysis of cellulose, hemicellulose, and lignin contents.

2.4. Soil Samples Determinations

Determination of POC and MAOC: POC and MAOC were separated by the sodium hexametaphosphate dispersion method [9,15]. A total of 20 g of air-dried soil samples was passed through a 2 mm sieve and placed into a 100 mL plastic bottle. Next, 60 mL of sodium hexametaphosphate (mass/volume = 5%) was added, and the mixture was manually stirred before being placed on a shaking table for 18 h. The resulting turbid liquid was then filtered through a 53 µm sieve and rinsed repeatedly with deionized water until the effluent ran clear. The coarse material retained on the sieve was POC (>53 µm), while the fine material that passed through was classified as MAOC (<53 µm). Both components were collected using a 500 mL beaker, dried at 60 °C, weighed, and recorded, which allowed for the calculation of ratios of the upper and lower components to total soil mass. The dried soil in the beaker was then ground through a 0.15 mm sieve, and SOC content was determined using the potassium dichromate external heating method [26]. Additionally, to analyze chemical structures of MAOC, 1 g of desiccated soil was taken from the beaker.

Determination of MAOC chemical structure: The infrared spectra of soil were determined using a Fourier transform infrared spectrometer (FTIR) (Nicolet iS5, Thermo Fisher Scientific, Waltham, MA, USA). The mineral-bonded soil sample (<53 µm) weighing 0.005 g was combined with dried, spectral-grade potassium bromide (KBr) at a ratio of 1:100. Subsequently, these samples were uniformly pulverized using an infrared lamp, compressed into semi-transparent flakes, and then analyzed with the spectrometer. The spectral determination range was 4000–400 cm^{−1} [27]. The infrared data were processed using OMNIC 9.2 to quantify characteristic peak areas and relative abundances of different functional groups. A semi-quantitative analysis of changing characteristics of the chemical structure of MAOC was performed, with (alkyl carbon)/(alkoxy carbon) reflecting the stability of MAOC [9].

Determination of soil physicochemical properties: Soil water content and BD were measured by oven-drying and weighing method [28]. Total nitrogen (TN) content was assessed using the semi-micro Kjeldahl method [29], while total phosphorus (TP) content was determined through the potassium hydroxide alkali fusion molybdenum–antimony anti-colorimetric method [28]. The sedimentation and hydrometer methods were used to classify soil texture, with the corresponding particle size distributions calculated according to classification for sand (0.02–2 mm), silt (0.02–0.002 mm), and clay (<0.002 mm) [28].

Determination of cellulose, hemicellulose, and lignin in litter: The acid-detergent method was used to quantify contents of these components [30].

The chemical properties of litter in each sampled site are presented in Table 1, and the physicochemical properties of soil are detailed in Table S2.

Table 1. Chemical properties of the litter under different stand types. Different capital letters indicate the significant differences in cellulose, hemicellulose, and lignin contents between different stand types ($p < 0.05$) ($n = 3$).

Litter Types	Chemical Properties of the Litter		
	Cellulose/%	Hemicellulose/%	Lignin/%
<i>Quercus aliena</i> forests litter	8.07 ± 0.41 A	5.87 ± 1.93 A	40.12 ± 4.15 A
<i>Pinus tabuliformis</i> forests litter	10.74 ± 2.25 A	5.65 ± 0.43 A	46.11 ± 7.31 A
Mixed forests litter	8.55 ± 0.74 A	4.92 ± 0.29 A	36.89 ± 3.06 A

2.5. Data Analysis

Excel 2021 was used to perform preliminary statistical analyses on the original data, and Duncan's method within one-way ANOVA in SPSS 27.0 was used to compare significant differences in contents of SOC, POC, MAOC, and values of the (alkyl carbon)/(alkoxy carbon) between different stand types and soil layers ($p < 0.05$). Origin 2023 was used to generate visualizations of these changes. The relationships among soil physicochemical properties, litter chemical properties, SOC, POC, MAOC contents, and MAOC chemical structure were analyzed by Spearman's correlation ($p < 0.05$). The “ggplot” package in R 4.3.0 (<https://cran.r-project.org/>, accessed on 15 March 2024) was used to generate the correlation heatmap ($p < 0.05$). The “vegan” and the “rdacca.hp” package were employed to perform redundancy analysis (RDA) and hierarchical partitioning analysis [31], as well as to visualize these results, in order to explore the correlations among them.

3. Results

3.1. Distribution of SOC, POC, and MAOC Under Different Stand Types

In the 0–10 cm soil layer, the contents of SOC, MAOC, and POC followed the order of *Quercus aliena* forests > mixed forests > *Pinus tabuliformis* forests. In the 10–20 cm layer, the trend shifted to mixed forests > *Quercus aliena* forests > *Pinus tabuliformis* forests. At 0–40 cm soil layers, contents of SOC, POC, and MAOC were lowest under *Pinus tabuliformis* forests. *Quercus aliena* forests promoted the accumulation of SOC and its components at 0–10 cm and 20–40 cm soil layers, while higher levels of these components were found under the mixed forests at the 10–20 cm soil layer (Figure 1). As the soil layer deepened, SOC, POC, and MAOC contents decreased by 17.89%–48.84%, 27.58%–55.54%, and 0.59%–29.75% under three stand types, respectively (Figure 1), which represented that variations in MAOC content were more stable with the increasing of soil layers. The POC content exceeded that of MAOC in 0–40 cm soil layers under three stand types (Figure 1b,c).

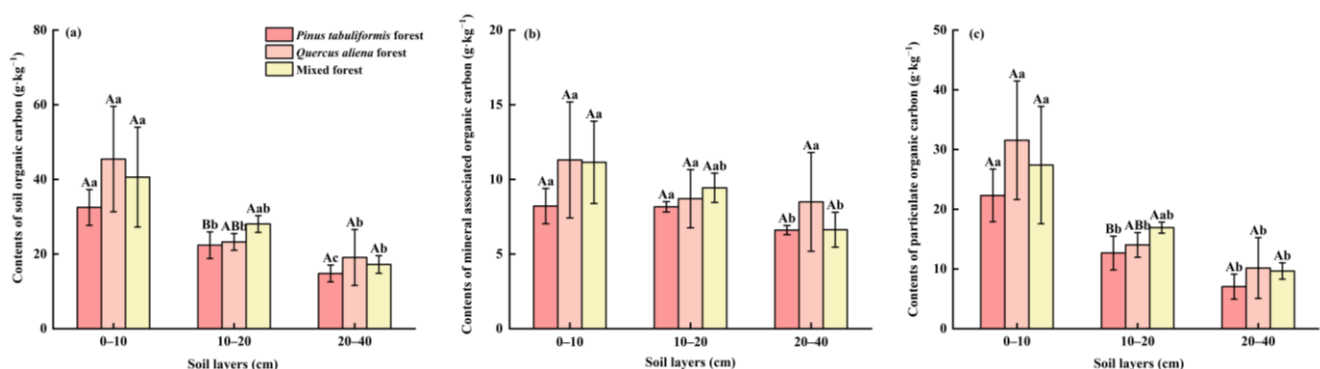


Figure 1. Distributed characterization of SOC (a), MAOC (b), and POC (c) contents under different stand types. Different capital letters indicate significant differences in SOC, POC, and MAOC contents under different stand types at the same soil layer, and different lowercase letters indicate significant differences in SOC, POC, and MAOC contents at different soil layers under the same stand type.

Under different stand types, POC/SOC was higher than MAOC/SOC at the same soil layer. As soil layers deepened, POC/SOC decreased, while MAOC/SOC increased significantly ($p < 0.05$) (Figure 2). This trend might imply an increase in SOC stability with the increase in soil layer under three stand types. At 0–10 cm soil layer, values of MAOC/SOC represented mixed forests (27.9%) > *Pinus tabuliformis* forests > *Quercus aliena* forests (24.8%) (Figure 2b), while values of POC/SOC exhibited the trend of *Quercus aliena* forests > *Pinus tabuliformis* forests > mixed forests (Figure 2a). At the same time, the highest MAOC/SOC was observed under *Quercus aliena* forests (37.4% and 46.4%, respectively) at 10–20 cm and 20–40 cm soil layers, while the lowest MAOC/SOC was found under mixed forests (33.6% and 38.4%, respectively) (Figure 2b). Conversely, POC/SOC exhibited the opposite trend to MAOC/SOC at 10–20 cm and 20–40 cm soil layers (Figure 2a). These results suggested that the mixed forest enhanced SOC stability in topsoil, while pure coniferous forest and broad-leaved forest resulted in an increase in SOC stability in subsurface layers.

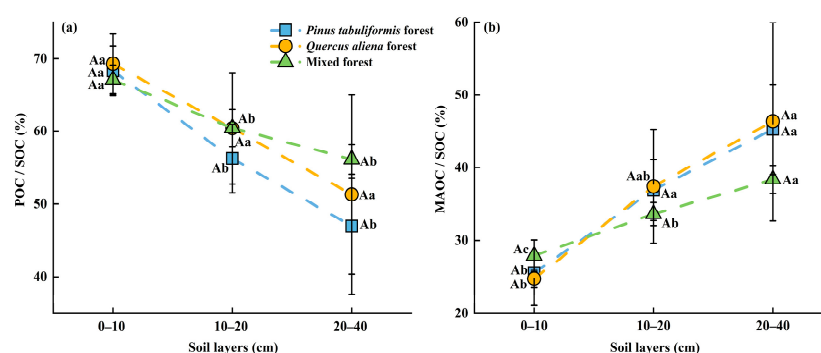


Figure 2. Ratios of POC to SOC (a) and MAOC to SOC (b) under different stand types. Different capital letters indicate significant differences in SOC, POC, and MAOC contents under different stand types at the same soil layer, and different lowercase letters indicate significant differences in SOC, POC, and MAOC contents at different soil layers under the same stand type.

3.2. Characteristics of the Chemical Structure of MAOC Under Different Stand Types

Shapes of FTIR spectra and wavenumbers of absorption peaks of MAOC chemical structure were generally similar at different soil layers under three stand types, and seven primary absorption peaks corresponding to five main functional groups were observed: 1032 cm^{-1} (C-O in alcohols and carbohydrates), 1425 cm^{-1} (C-H in alkyl), 1542 cm^{-1} and 1649 cm^{-1} (C=C in aromatics), 2932 cm^{-1} (C-H in aliphatic methyl and methylene groups), 3363 cm^{-1} and 3452 cm^{-1} (O-H in alcohols, phenols, and carboxyl groups) (Figure 3).

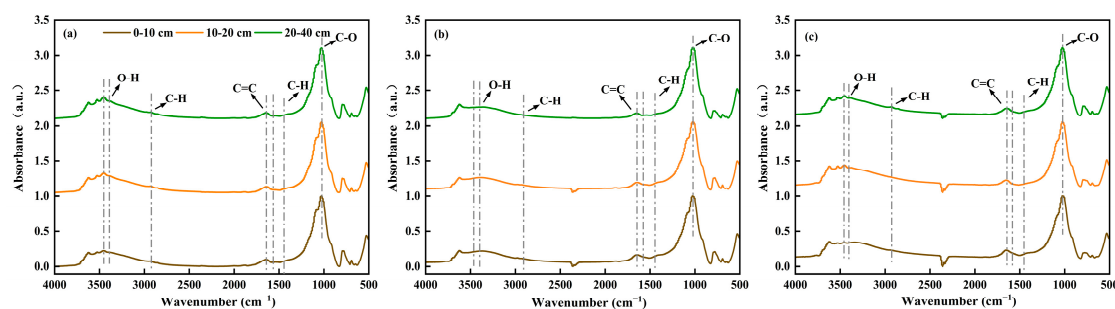


Figure 3. FTIR spectra of MAOC under different stand types. (a) FTIR spectra of MAOC under mixed forests; (b) FTIR spectra of MAOC under *Quercus aliena* forests; (c) FTIR spectra of MAOC under *Pinus tabuliformis* forests.

Among three stand types, it was observed that relative abundances of five functional groups in MAOC showed: alkoxy carbon > phenolic alcohol components carbon > aliphatic carbon > aromatic carbon > alkyl carbon (Figure 4), indicating that MAOC was primarily dominated by easily decomposed substances (such as alkoxy carbon). With increasing soil depth, relative abundances of alkyl carbon and aromatic carbon in MAOC decreased under both *Quercus aliena* forests and the mixed forests (Figure 4d–i), while those of *Pinus tabuliformis* forests increased first but still showed an decreasing trend overall (Figure 4a–c), suggesting that chemical structural stability of MAOC did decrease with the deepening of soil layers.

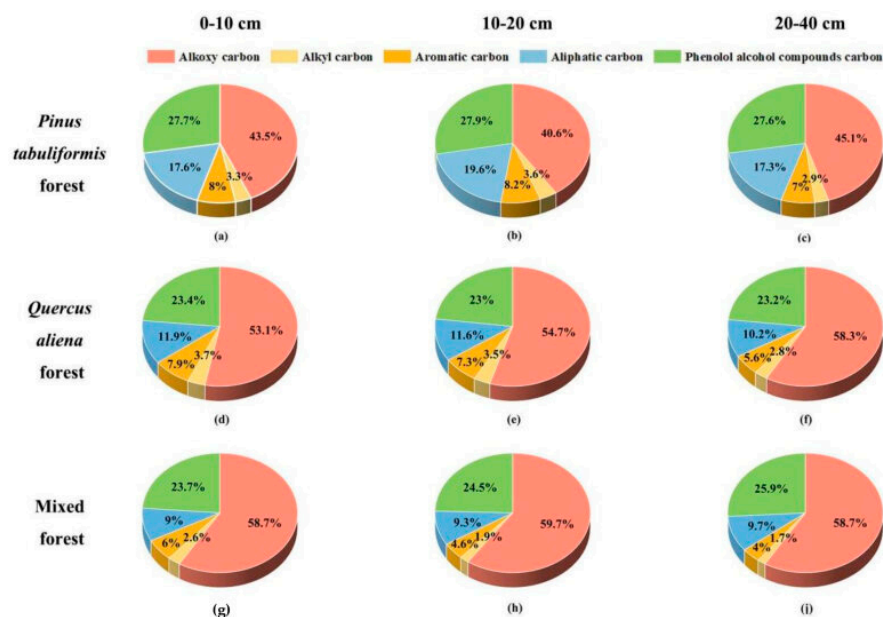


Figure 4. Relative abundances of chemical functional groups of MAOC under different stand types. (a–c) Relative abundances of MAOC functional groups under *Pinus tabuliformis* forest across three soil layers; (d–f) Relative abundances of MAOC functional groups under *Quercus aliena* forest across three soil layers; (g–i) Relative abundances of MAOC functional groups under mixed forest across three soil layers.

Compared to pure coniferous forests and broad-leaved forests, relative abundances of alkyl carbon and aromatic carbon in MAOC were lower under the mixed forests, while alkoxy carbon reached a higher level (Figure 4). Conversely, *Pinus tabuliformis* forests contributed more to the improvement of relative abundance of alkyl carbon (with the exception of 10–20 cm soil layer) and aromatic carbon, whereas relative abundance of alkoxy carbon was the lowest (Figure 4). These results showed that coniferous forest exhibited the strongest stability in chemical structure of MAOC at 0–40 cm soil layers, while the mixed forest demonstrated the weakest one.

(Alkyl carbon)/(alkoxy carbon) can indicate the humification level of SOC. The larger the ratio, the greater stability of SOC. Values of (alkyl carbon)/(alkoxy carbon) at 0–40 cm soil layers were as follows: *Pinus tabuliformis* forests > *Quercus aliena* forests > mixed forests (Figure 5), indicating that coniferous forests were conducive to promoting MAOC stability.

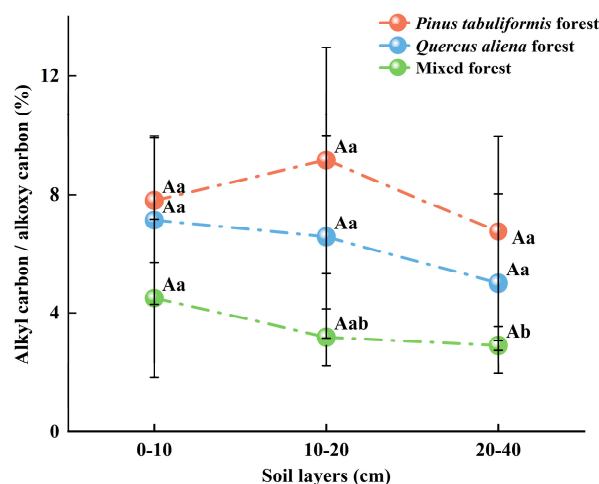


Figure 5. The chemical structural stability of MAOC under different stand types. Different capital letters indicate significant differences in SOC, POC, and MAOC contents under different stand types at the same soil layer, and different lowercase letters indicate significant differences in SOC, POC, and MAOC contents at different soil layers under the same stand type.

3.3. Correlation of SOC, POC, MAOC, and the Chemical Structure of MAOC with Properties of Soil and Litter

Under *Pinus tabuliformis* forests, SOC, POC, and POC/SOC were significantly positively correlated with TN, whereas MAOC/SOC showed a negative correlation with TN ($p < 0.05$). Furthermore, alkoxy carbon exhibited a significantly positive relationship with silt, but negatively correlated with sand. There was also a positive correlation between alkyl carbon and silt ($p < 0.05$). At the same time, significant positive correlations were observed between TN, TP, WRC, and silt with MAOC, alkyl carbon, aromatic carbon, and (alkyl carbon)/(alkoxy carbon) under *Quercus aliena* forests, whereas these properties showed negative correlations with alkyl carbon ($p < 0.05$). Additionally, MAOC/SOC was positively correlated with pH ($p < 0.05$). Under the mixed forests, alkyl carbon, aromatic carbon, (alkyl carbon)/(alkoxy carbon), SOC and its components were significantly positively correlated with TN ($p < 0.05$), while MAOC/SOC showed an opposite relationship with TN. Moreover, alkoxy carbon was positively correlated with silt, but exhibited a negative correlation with pH. Significant positive correlations were also observed between alkyl carbon and (alkyl carbon)/(alkoxy carbon) with TP ($p < 0.05$) (Figure 6).

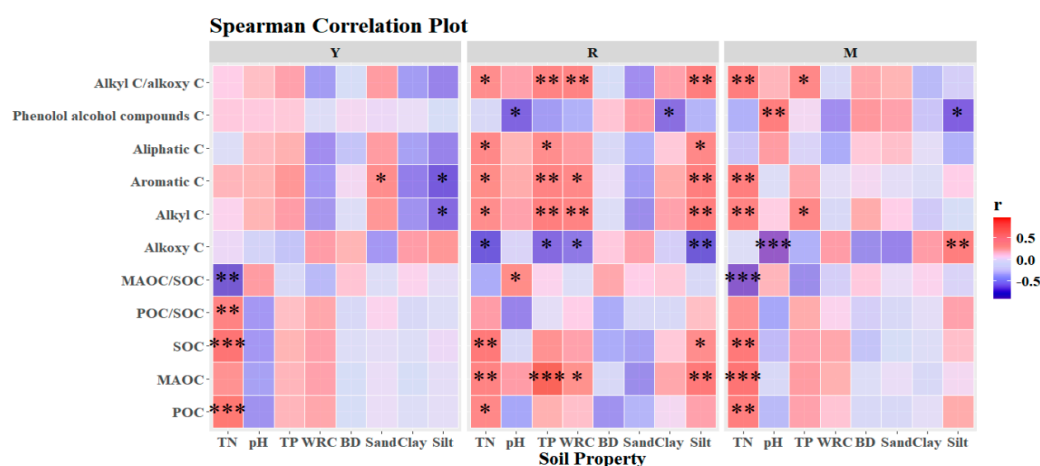


Figure 6. Spearman correlation analysis of SOC, POC, MAOC contents, and the chemical structure of MAOC with soil properties under three stand types. Correlation coefficients are marked with asterisks:

*** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$. The “carbon” in the name of the chemical structure functional group is replaced with a capital letter “C”. BD: Soil bulk density; WRC: Soil water relative content; TP: Total phosphorus; TN: Total nitrogen; Y: *Pinus tabuliformis* forests; R: *Quercus aliena* forests; M: Mixed forests (*Pinus tabuliformis* and *Quercus aliena*), the same below.

RDA showed that soil and litter properties explained 82.38% of variations in distributions of SOC, POC, MAOC, and the chemical structure of MAOC. TN, lignin, and silt contents accounted for 45.09%, 13.54%, and 8.8% of the total variables, respectively (Figure 7b).

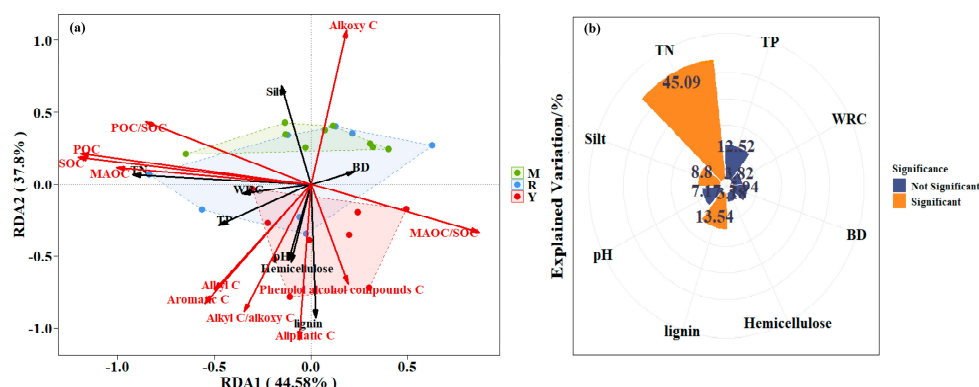


Figure 7. Redundancy analysis of SOC, POC, MAOC contents, and the chemical structure of MAOC with soil and litter properties (a,b).

4. Discussion

4.1. Characteristics of SOC Stability Under Different Stand Types

4.1.1. Contents and Proportions of SOC Components

At 0–40 cm soil layers, it was found that SOC, POC, and MAOC contents were lowest under *Pinus tabuliformis* forests, indicating that broad-leaved forest and mixed forest were more conducive to the accumulation of SOC than coniferous forest, which aligns with the previous study [24]. This may be attributed to the variations in quantity and quality of organic matter input from different vegetation, producing distinct litter types, which result in different accumulation of SOC [7,15]. The carbon-to-nitrogen ratio of coniferous litter is high, which limits microbial activity due to nitrogen scarcity [32]. To mitigate this constraint, microorganisms employ a “high-cost, high-consumption” strategy for nitrogen acquisition [14,18]. As a substantial portion of nitrogen is sequestered in lignin–protein complexes, the activities of lignin-degrading enzymes, such as lignin peroxidase, manganese peroxidase, and laccase, are upregulated [33]. However, the synthesis and secretion of these enzymes demand considerable energy. Concurrently, microbial carbon use efficiency (CUE) declines significantly during the decomposition of such low-quality, nitrogen-poor substrates [34]. This implies that during energy acquisition, a greater proportion of assimilated carbon is respired as CO₂ rather than allocated to microbial biomass synthesis, thereby reducing the accumulation of microbial residues. As a result, the potential for MAOC formation is diminished [21,34]. Therefore, the overall efficiency of converting litter into stable MAOC is limited, ultimately leading to a lower SOC content under coniferous forests. Conversely, under broad-leaved and mixed forests, litters contain relatively high contents of high-quality compounds that allow for easier decomposition and utilization by soil microorganisms, thereby accelerating the breakdown rate of plant residues and increasing inputs of organic carbon sources into soil [6]. Under these conditions, the input of new carbon may exceed the loss from SOC decomposition induced by priming effects [14], resulting in a net enhancement of SOC accumulation [35].

MAOC/SOC is an indicator of the stability of SOC, and a high MAOC/SOC value suggests relatively greater SOC stability [2,4]. In this study, MAOC/SOC increased with soil

depth under three stand types, implying that SOC stability was enhanced with the increase in soil layer, consistent with results of existing studies [8]. With the deepening of soil layers, soil nutrient contents gradually decrease, which limits the availability of carbon and nitrogen sources for soil microorganisms to grow and reproduce. Extracellular enzymes are typically produced by microorganisms to degrade recalcitrant organic substrates such as lignin and cellulose, particularly when labile carbon is depleted; this process facilitates the breakdown of complex polymers into usable forms, while the incomplete decomposition of these resistant compounds contributes to the relative accumulation of refractory carbon [2]. Moreover, subsurface layers lead to lower soil temperature and permeability, which inhibit respiratory intensity and decomposition rate of microorganisms, resulting in increased accumulation of microbial residue carbon and refractory carbon [15], which is more likely to combine with minerals to form MAOC. At the same time, an increase in soil depth more strongly inhibits the decomposition of MAOC, as total mineral surface area is the primary limiting factor for MAOC formation [4]. The greater carbon saturation deficit in subsurface soil layers enhances MAOC stability and promotes the transfer efficiency of POC to MAOC, thereby enhancing the stability of SOC [36].

In topsoil, mixed forests demonstrated relatively stronger SOC stability but *Quercus aliena* forests showed the weakest one, which is similar to the findings of Qin et al. [24]. Enhanced stability of SOC under the mixed forest may be attributed to the accumulation of MAOC, which is facilitated by improved soil nutrient availability. In contrast, the litter contains a higher content of easily decomposed hemicellulose with a larger leaf area under *Quercus aliena* forest, making it more susceptible to being decomposed by contact with microorganisms [37]. This process can result in the increased formation of POC and a corresponding decrease in SOC stability. At the same time, we found that *Pinus tabuliformis* forests contributed more to enhancing SOC stability in subsurface layers, whereas the stability under mixed forests was weaker, contrasting with the findings of Yu et al. [23]. This discrepancy may be due to the high carbon-to-nitrogen ratio of litter under coniferous forest, coupled with the predominant role of fungi among soil microorganisms under *Pinus tabuliformis* forest [38], leading to an increased production of fungal residue carbon. Compared to coniferous forest, the higher quality litter provides more available sources of carbon and nitrogen for soil bacteria under the mixed forest, facilitating the accumulation of bacterial residue carbon [24]. At the same time, hyphae and extracellular enzymes produced by fungi can serve as cementing agents that promote the formation of micro-aggregates more effectively, thereby improving physical protection for SOC [21]. Consequently, the increased accumulation of fungal residue carbon is more beneficial for enhancing the stability of SOC. Moreover, the close connection between the mycelial network in coniferous forests and soil minerals helps to combine exogenous mycelial residues with strong anti-decomposition ability and root secretions with complex chemical structures [20], thereby promoting the formation of MAOC.

4.1.2. Chemical Structure of MAOC

The FTIR spectra of chemical structures of MAOC were similar under different stand types. Specifically, the relative abundance of alkoxy carbon was the highest, while relative abundances of alkyl carbon and aromatic carbon were lower, which is consistent with previous studies [9,12,16]. According to the “initial litter” theory, differences in initial properties of the litter may have a lasting impact on decomposition and accumulation of organic matter. Forest litter with a higher carbohydrate content is one of the primary sources of SOC, thus it can promote the enrichment of alkoxy carbon in MAOC [9,39]. In addition, hemicellulose and cellulose are regarded as easily decomposed compounds in plant residues and litters, which can rapidly disappear during the decomposition process

and be utilized by soil microorganisms to form alkoxy carbon, thereby resulting in higher alkoxy carbon levels [40]. At the 20–40 cm soil layer, relative abundances of alkyl carbon, aromatic carbon, and (alkyl carbon)/(alkoxy carbon) in MAOC were the lowest under different stand types, suggesting that the chemical structural stability of MAOC in subsurface layer is weaker. This is different from the findings of Chen et al. [41], which is probably due to the fact that soil microorganisms are severely limited by nutrients and energy in the subsurface layer. As a result, some relatively stable organic matter is decomposed to support the growth and reproduction of microorganisms [42], leading to the reduction in MAOC stability at the 20–40 cm soil layer.

Variations in the chemical structure of SOC exist among different vegetation types [12], with the research indicating a significantly higher alkyl carbon content under coniferous forest than that of the two other forests [43]. It was observed that at 0–40 cm soil layers, *Pinus tabuliformis* forests could inhibit the accumulation of alkoxy carbon in MAOC but was conducive to promoting relative abundances of alkyl carbon, aromatic carbon, and (alkyl carbon)/(alkoxy carbon), while mixed forests exhibited the totally contrary functions, suggesting a higher chemical structural stability of MAOC under *Pinus tabuliformis* forests and a lower stability under mixed forests [9]. The reason could be that, compared to broad-leaved forest, the litter of coniferous forest contains higher keratin and lignin contents along with lower hemicellulose contents [27]. Consequently, the litter inputs more lignin-derived carbon into soil, which leads to easier integration with minerals following decomposition by fungi, contributing to the accumulation of alkyl carbon and aromatic carbon in MAOC, thereby enhancing its chemical structural stability [37]. Elevated litter levels under mixed forest could enhance the biomass and activity of soil microorganisms, which release additional extracellular enzymes that can break down lignin and cellulose, thereby decreasing the relative abundance of aromatic carbon in MAOC [44]. In addition, the formation of larger aggregates could be improved due to increased inputs of organic matter under the mixed forest, which could protect alkoxy carbon through physical barriers and consequently diminish its interactions with soil microorganisms [27]. This results in a higher accumulation of alkoxy carbon and lower stability of MAOC.

4.2. Main Influencing Factors of SOC Stability Under Different Stand Types

Existing studies have shown that SOC, POC, and MAOC contents were significantly positively correlated with TN contents ($p < 0.001$) [45], and our study demonstrates similar result under different stand types ($p < 0.05$). In addition, there was a significant positive correlation between TN and POC/SOC, and a significant negative correlation with MAOC/SOC ($p < 0.05$), which contrasts with the findings of Xu et al. [46]. Firstly, nitrogen serves not only as the substrate for synthesizing organic matter in plant growth, but also as a primary component of microbial cells. Therefore, the increase in soil TN can enhance litter input, improve biomass and activity of microorganisms, and accelerate the decomposition of plant residues, thereby promoting POC synthesis [47,48]. Secondly, contents of MAOC and SOC decreased with the decrease in TN, but reduction in MAOC is less pronounced compared to that of SOC, leading to an increase in MAOC/SOC as TN decreases. In addition, as MAOC and POC are primary components of SOC, a significant positive correlation between POC/SOC and TN, along with a significant negative correlation between MAOC/SOC and TN ($p < 0.05$), further supports these results.

At the same time, this study demonstrated that MAOC/SOC was significantly positively correlated with pH ($p < 0.05$), which was different from the results of some studies [7]. This may be attributed to higher soil bacterial biomass under acidic conditions, leading to an accelerated decomposition rate of litter and the generation of bacterial residue carbon with lower stability. Conversely, the increase in pH facilitates fungal proliferation, resulting

in greater formation of fungal residue carbon, which is relatively stable and more likely to combine with minerals to form MAOC, thus promoting the accumulation of MAOC [10,49].

The relative abundances of alkyl carbon and aromatic carbon also exhibited significant positive correlations with TN ($p < 0.05$), which is consistent with previous research [16]. The underlying mechanism could be attributed to two aspects. Firstly, an increase in soil nitrogen levels leads to a decrease in the level of lignin-degrading enzymes secreted by white-rot fungi, which in turn reduces decomposition of lignin, consequently promoting the accumulation of lignin-derived aromatic carbon. Secondly, nitrogen can conjugate with aromatic carbon and form a more recalcitrant complex, thereby enhancing the decomposition resistance of the complex [27]. Meanwhile, alkoxy carbon exhibited significant negative correlations with TP ($p < 0.05$). Elevated TP mainly promotes accumulation of chemically stable substances such as lignin and keratin by enhancing the input of plant biomass and litter carbon, thereby increasing the relative abundance of alkoxy carbon [41].

Soil particles of varying sizes exhibit distinct surface areas and chemical characteristics, and the stability of organic matter combined with soil minerals is also significantly different [12]. In our study, alkoxy carbon was positively correlated with silt and clay contents, while negatively correlated with sand content ($p < 0.001$). Nonetheless, different correlations between relative abundances of functional groups with soil particle size were observed among three stand types. Under *Quercus aliena* forests, alkyl carbon and aromatic carbon were significantly positively related to silt content, aligning with the study of Mao et al. [50], which demonstrated that higher contents of silt could improve the stability of SOC. This is probably because the silt tends to form a granular structure, which can physically protect SOC from decomposition by preventing it from direct contact with soil microorganisms [4]. Conversely, alkyl carbon and aromatic carbon exhibited a negative correlation with silt under *Pinus tabulaeformis* forests. A possible explanation is that silt content was considerably lower than those of the other two stand types, but higher lignin and keratin contents in its litter entered soil through microbial decomposition, contributing to the accumulation of stable chemical components such as alkyl carbon. Furthermore, mycorrhizal fungi exhibit a high infection rate under coniferous forest [51], which possess a strong ability to generate binding agents and a lower secretion of soil enzymes responsible for decomposition aggregates [52]. Consequently, new organic matter (such as organic matter with a high relative abundance of alkyl carbon) tends to adhere to existing organic mineral clusters, creating bigger aggregates instead of merging with minerals to create micro-aggregates [14]. The phenomenon of “organic-organic interactions” might be prevalent in study area, causing deviations in the relationship between alkyl carbon, aromatic carbon, and soil texture from previous results [50].

Furthermore, aromatic carbon, alkyl carbon, and (alkyl carbon)/(alkoxy carbon) showed significant positive correlations with lignin ($p < 0.05$), which differs from previous findings [53]. This could be due to elevated lignin content in litter restricting the extracellular enzymatic decomposition of cell wall polysaccharides, leading to decreased litter decomposition rates and transformation efficiency [14,33]. Under this nutrient-deficient condition, lignin may directly participate in the formation of MAOC, thereby enhancing the stability of its chemical structure [53]. Conversely, high-quality litter primarily fosters the formation of MAOC through microbial metabolism and the subsequent accumulation of microbial residues [14]. But aromatic and alkyl carbon in MAOC are predominantly derived from direct plant residues, such as lignin and waxes [11,12]. Consequently, lower relative abundances of these stable chemical functional groups were observed under forests with low-lignin litter.

In conclusion, this study demonstrates that mixed forests are more effective in stabilizing SOC compared to monospecific stands, primarily due to the combined influence of

litter quality diversity, soil texture heterogeneity, and nitrogen availability. Notably, the MAOC/SOC in mixed forests remains higher, with reduced decomposition risks, underscoring their potential as a key strategy for long-term carbon sequestration and climate change mitigation. These findings suggest that integrating mixed forest management into ecological restoration and carbon policy frameworks could optimize SOC stability under variable environmental conditions by leveraging the interplay between aboveground litter diversity and subsurface mineral–microbe interactions. Given the critical role of SOC in global carbon cycling and climate regulation [54], such management strategies may contribute to climate change mitigation by enhancing long-term carbon sequestration in forest ecosystems worldwide.

5. Conclusions

Mixed forests can promote the relative accumulation of mineral-associated organic carbon in topsoil, potentially reflecting that mixed forests could enhanced soil organic carbon stability. Conversely, in subsurface layers, *Pinus tabuliformis* forests could increase the relative content of mineral-associated organic carbon and relative abundances of recalcitrant chemical functional groups in mineral-associated organic carbon, suggesting greater soil organic carbon stability in deeper layers under coniferous forests. These differences were primarily driven by nitrogen availability, litter quality (especially lignin content), and soil texture. These findings are important to soil carbon sink management of forest ecosystems and provide practical insights for designing management strategies that enhance carbon sequestration and long-term soil resilience in temperate mountain ecosystems. Maybe future research can refine this relatively single method for assessing SOC stability and extend it to deeper soil profiles and species combinations of different microbial, as well as the analysis of root secretions, rhizosphere microorganisms, and mycorrhizal secretions.

Supplementary Materials: The following supporting information can be downloaded at: <https://www.mdpi.com/article/10.3390/f16101585/s1>, Table S1: Basic information of Plots; Table S2: Soil physicochemical properties under different stand types.

Author Contributions: Conceptualization, Y.D. and J.Z.; methodology, Z.L.; software, Y.Z.; validation, Y.M.; formal analysis, Y.Z.; investigation, Z.L.; resources, Y.D.; data curation, L.L.; writing—original draft preparation, J.Z.; writing—review and editing, L.H., Q.G., and S.Z.; visualization, J.Z.; supervision, Y.M.; project administration, L.L.; funding acquisition, Y.D. All authors have read and agreed to the published version of the manuscript.

Funding: This research was funded by Science and Technology Department of Shaanxi Province, grant number (2025-JC-YBQN-235, 2023-JC-QN-0228).

Data Availability Statement: The original contributions presented in this study are included in the article and Supplementary Materials. Further inquiries can be directed to the corresponding author.

Conflicts of Interest: The authors declare no conflicts of interest.

Abbreviations

The following abbreviations are used in this manuscript:

SOC	Soil organic carbon
MAOC	Mineral-associated organic carbon
POC	Particulate organic carbon
BD	Bulk density
FTIR	Fourier transform infrared

WRC	Water relative content
TP	Total phosphorus
TN	Total nitrogen

References

- Pan, Y.; Birdsey, R.A.; Fang, J.; Houghton, R.; Kauppi, P.E.; Kurz, W.A.; Phillips, O.L.; Shvidenko, A.; Lewis, S.L.; Canadell, J.G.; et al. A large and persistent carbon sink in the world's forests. *Science* **2011**, *333*, 988–993. [\[CrossRef\]](#) [\[PubMed\]](#)
- Liu, M.; Zheng, S.; Pendall, E.; Smith, P.; Liu, J.; Li, J.; Fang, C.; Li, B.; Nie, M. Unprotected carbon dominates decadal soil carbon increase. *Nat. Commun.* **2025**, *16*, 2008. [\[CrossRef\]](#)
- Sun, W.L.; Liu, X.H.; Tian, Z.X.; Shao, X.M. Analysis on Characteristics of Vegetation and Soil Bacterial Community under 20 Years' Restoration of Different Tree Species: A Case Study of the Qinling Mountains. *Forests* **2021**, *12*, 562. [\[CrossRef\]](#)
- Zhou, Z.; Ren, C.; Wang, C.; Delgado-Baquerizo, M.; Luo, Y.; Luo, Z.; Du, Z.; Zhu, B.; Yang, Y.; Jiao, S.; et al. Global turnover of soil mineral-associated and particulate organic carbon. *Nat. Commun.* **2024**, *15*, 5329. [\[CrossRef\]](#) [\[PubMed\]](#)
- Ren, S.; Wang, H.; Zhou, T.; Wang, C.; Zhou, Z.; Liu, S. Storage Potential of Soil Functional Carbon Fractions in the World's Largest Plantations. *Adv. Sci.* **2025**, e04995. [\[CrossRef\]](#)
- Schmidt, M.W.; Torn, M.S.; Abiven, S.; Dittmar, T.; Guggenberger, G.; Janssens, I.A.; Kleber, M.; Kögel-Knabner, I.; Lehmann, J.; Manning, D.A.; et al. Persistence of soil organic matter as an ecosystem property. *Nature* **2011**, *478*, 49–56. [\[CrossRef\]](#) [\[PubMed\]](#)
- Angst, G.; Mueller, K.E.; Eissenstat, D.M.; Trumbore, S.; Freeman, K.H.; Hobbie, S.E.; Chorover, J.; Oleksyn, J.; Reich, P.B.; Mueller, C.W. Soil organic carbon stability in forests: Distinct effects of tree species identity and traits. *Glob. Change Biol.* **2019**, *25*, 1529–1546. [\[CrossRef\]](#)
- Yang, E.; Wang, B.R.; Yao, H.J.; Huang, Y.M.; An, S.S. Dynamics of particulate and mineral-associated organic carbon during the development of biological soil crusts in the Loess Plateau. *Res. Soil Water Conserv.* **2023**, *30*, 25–33+40. [\[CrossRef\]](#)
- Deng, J.J.; Zhu, W.X.; Zhou, Y.B.; Yin, Y. Soil Organic Carbon Chemical Functional Groups under Different Revegetation Types Are Coupled with Changes in the Microbial Community Composition and the Functional Genes. *Forests* **2019**, *10*, 240. [\[CrossRef\]](#)
- Yang, Y.; Wang, B.R.; Dou, Y.X.; Xue, Z.J.; Sun, H.; Wang, Y.Q.; Liang, C.; An, S.S. Advances in the research of transformation and stabilization of soil organic carbon from plant and microbe. *J. Appl. Ecol.* **2024**, *35*, 111–123. [\[CrossRef\]](#)
- Wang, H.; Ding, Y.; Zhang, Y.G.; Wang, J.X.; Freedman, Z.B.; Liu, P.C.; Cong, W.; Wang, J.; Zang, R.G.; Liu, S.R. Evenness of soil organic carbon chemical components changes with tree species richness, composition and functional diversity across forests in China. *Glob. Change Biol.* **2023**, *29*, 2852–2864. [\[CrossRef\]](#) [\[PubMed\]](#)
- Li, N.; Sheng, M.; You, M.Y.; han, X.Z. Advancement in research on application of ¹³C NMR techniques to exploration of chemical structure of soil organic matter. *Acta Pedol. Sin.* **2019**, *56*, 796–812. [\[CrossRef\]](#)
- Si, Q.; Chen, K.L.; Wei, B.; Zhang, Y.W.; Sun, X.; Liang, J.Y. Dissolved carbon flow to particulate organic carbon enhances soil carbon sequestration. *Soil* **2024**, *10*, 441–450. [\[CrossRef\]](#)
- Guo, X.W.; Zhang, Y.X.; You, Y.M.; Sun, J.X. Research advance in the effects of litter input on forest soil organic carbon transformation and stability. *Chin. J. Appl. Ecol. Yingyong Shengtai Xuebao* **2024**, *35*, 2352–2361. [\[CrossRef\]](#)
- Lai, L.M.; Zhao, J.X.; Dou, Y.X. Fungal necromass carbon contributes more to POC and MAOC under different forest types of Qinling Mountains. *Plant Soil* **2025**, *512*, 603–618. [\[CrossRef\]](#)
- Pei, Z.F.; Hong, M.; Wu, Z.D.; Lu, J.Y.; Zhang, Y.X.; Shen, Q.G. Responses of Soil Organic Carbon Content and Its Chemical Structure of Different Components to Long-term Nitrogen Input in Meadow Steppe. *Soils* **2022**, *54*, 481–489. [\[CrossRef\]](#)
- Xu, S.; Yang, Y.; Sun, G.; Zhang, Q.; Wang, Y.; Zeng, H.; Simpson, M.J.; Wang, J. Aridity affects soil organic carbon concentration and chemical stability by different forest types and soil processes across Chinese natural forests. *Sci. Total Environ.* **2024**, *944*, 174002. [\[CrossRef\]](#)
- Guan, X.; Jiang, J.; Classen, A.T.; Ullah, S.; Wang, G. Disentangling the contribution of mycorrhizal fungi to soil organic carbon storage. *Soil Biol. Biochem.* **2025**, *209*, 109900. [\[CrossRef\]](#)
- Leifheit, E.F.; Verbruggen, E.; Rillig, M.C. Arbuscular mycorrhizal fungi reduce decomposition of woody plant litter while increasing soil aggregation. *Soil Biol. Biochem.* **2015**, *81*, 323–328. [\[CrossRef\]](#)
- Chen, X.; Mou, Z.; Zhang, J.; Li, Y.; Wu, W.; Wang, T.; Zhu, X.; Wu, D.; Petticord, D.F.; Hui, D.; et al. Roots Dominate Over Extraradical Hyphae in Driving Soil Organic Carbon Accumulation During Tropical Forest Succession. *Glob. Change Biol.* **2025**, *31*, e70499. [\[CrossRef\]](#)
- Deng, F.B.; Liang, C. Revisiting the quantitative contribution of microbial necromass to soil carbon pool: Stoichiometric control by microbes and soil. *Soil Biol. Biochem.* **2022**, *165*, 108486. [\[CrossRef\]](#)
- Lu, M.Z.; He, G.; Fan, L.; Liu, G.H.; Wu, J.J.; Liu, W.Z.; Ma, L. Temperature sensitivity of aerobic and anaerobic organic carbon mineralization varies with climate and soil depth in riparian zones. *Soil Biol. Biochem.* **2024**, *195*, 109455. [\[CrossRef\]](#)
- Yu, Z.J.; Wang, K.B.; Li, J.W.; Shangguan, Z.P.; Deng, L. Mixed plantations have more soil carbon sequestration benefits than pure plantations in China. *For. Ecol. Manag.* **2023**, *529*, 120654. [\[CrossRef\]](#)

24. Qin, Z.K.; Liu, R.H.; He, P.; Wang, C.; Nie, Y.X.; Shen, W.J. Effects of mixed broadleaved tree species with pure *Pinus massoniana* plantation on soil microbial necromass carbon and organic carbon fractions. *Chin. J. Appl. Ecol. Yingyong Shengtai Xuebao* **2024**, *35*, 141–152. [\[CrossRef\]](#)
25. Yang, H.; Song, Y.H.; Pang, Y.; Kang, H.B.; Xue, Y.; Wang, D.X. Driving Factors of Chinese Pine Population Distribution in the Ridge Habitats of the Southern Slope of the Mid-Qinling Mountains, China. *Forests* **2023**, *14*, 2252. [\[CrossRef\]](#)
26. Deng, W.B.; Wang, X.; Hu, H.B.; Zhu, M.D.; Chen, J.Y.; Zhang, S.; Cheng, C.; Zhu, Z.Y.; Wu, C.M.; Zhu, L. Variation Characteristics of Soil Organic Carbon Storage and Fractions with Stand Age in North Subtropical *Quercus acutissima* Carruth. *Forest in China. Forests* **2022**, *13*, 1649. [\[CrossRef\]](#)
27. Li, Z.; Zhao, B.; Wang, Q.; Cao, X.; Zhang, J. Differences in chemical composition of soil organic carbon resulting from long-term fertilization strategies. *PLoS ONE* **2015**, *10*, e0124359. [\[CrossRef\]](#)
28. Bao, S.D. *Soil Agricultural Chemistry Analysis*, 3rd ed.; China Agriculture Press: Beijing, China, 2000.
29. Yang, C.; Chen, Y.; Sun, W.; Zhang, Q.; Diao, M.; Sun, J. Extreme soil salinity reduces N and P metabolism and related microbial network complexity and community immigration rate. *Environ. Res.* **2025**, *264*, 120361. [\[CrossRef\]](#) [\[PubMed\]](#)
30. Yue, K.; Wu, F.Z.; Yang, W.Q.; Zhang, C.; Peng, Y.; Tan, B.; Xu, Z.F.; Huang, C.P. Cellulose Dynamics during Foliar Litter Decomposition in an Alpine Forest Meta-Ecosystem. *Forests* **2016**, *7*, 176. [\[CrossRef\]](#)
31. Lai, J.; Zou, Y.; Zhang, J.; Peres-Neto, P. Generalizing hierarchical and variation partitioning in multiple regression and canonical analyses using the rdacca.hp R package. *Methods Ecol. Evol.* **2022**, *13*, 782–788. [\[CrossRef\]](#)
32. Lu, S.; He, Y.H.; Chen, Y.Q.; Chen, L.J.; Wang, Z.Y.; Yuan, J.; Wu, L.C. Co-analysis of rhizosphere metabolomics and bacterial community structures to unfold soil ecosystem health in *Camellia oleifera* land under long-term cultivation. *Appl. Soil Ecol.* **2022**, *171*, 104336. [\[CrossRef\]](#)
33. Hall, S.J.; Huang, W.; Timokhin, V.I.; Hammel, K.E. Lignin lags, leads, or limits the decomposition of litter and soil organic carbon. *Ecology* **2020**, *101*, e03113. [\[CrossRef\]](#)
34. Cotrufo, M.F.; Wallenstein, M.D.; Boot, C.M.; Deneff, K.; Paul, E. The Microbial Efficiency-Matrix Stabilization (MEMS) framework integrates plant litter decomposition with soil organic matter stabilization: Do labile plant inputs form stable soil organic matter? *Glob. Change Biol.* **2013**, *19*, 988–995. [\[CrossRef\]](#) [\[PubMed\]](#)
35. Huang, J.; Gao, Y.; Peng, Y.; Chang, P.; Wu, Y.; Guo, L.; Luo, J.; Liu, L. Influences of plant functional traits on soil organic carbon stocks: The roles of carbon input quality and diversity. *Ecology* **2025**, *106*, e70148. [\[CrossRef\]](#) [\[PubMed\]](#)
36. Liang, C.; Schimel, J.P.; Jastrow, J.D. The importance of anabolism in microbial control over soil carbon storage. *Nat. Microbiol.* **2017**, *2*, 17105. [\[CrossRef\]](#)
37. Thiessen, S.; Gleixner, G.; Wutzler, T.; Reichstein, M. Both priming and temperature sensitivity of soil organic matter decomposition depend on microbial biomass—An incubation study. *Soil Biol. Biochem.* **2013**, *57*, 739–748. [\[CrossRef\]](#)
38. Templer, P.H.; Findlay, S.; Lovett, G. Soil microbial biomass and nitrogen transformations among five tree species of the Catskill Mountains, New York, USA. *Soil Biol. Biochem.* **2003**, *35*, 607–613. [\[CrossRef\]](#)
39. Zhang, Y.X.; Tang, Z.X.; You, Y.M.; Guo, X.W.; Wu, C.J.; Liu, S.R.; Sun, O.J. Differential effects of forest-floor litter and roots on soil organic carbon formation in a temperate oak forest. *Soil Biol. Biochem.* **2023**, *180*, 109017. [\[CrossRef\]](#)
40. Mathers, N.J.; Xu, Z.H. Solid-state ¹³C NMR spectroscopy: Characterization of soil organic matter under two contrasting residue management regimes in a 2-year-old pine plantation of subtropical Australia. *Geoderma* **2003**, *114*, 19–31. [\[CrossRef\]](#)
41. Chen, C.Y.; Chen, F.S.; Zheng, Z.Y.; Peng, Y.T.; Liu, Q.; Wang, S.N.; Wang, F.C. Effects of litter management on chemical structure and thermal stability of soil organic carbon in a Chinese fir forest. *Shengtaixue Zazhi* **2024**, *43*, 2641–2649. [\[CrossRef\]](#)
42. Lehmann, J.; Kleber, M. The contentious nature of soil organic matter. *Nature* **2015**, *528*, 60–68. [\[CrossRef\]](#)
43. Wang, H.; Liu, S.R.; Song, Z.C.; Yang, Y.J.; Wang, J.X.; You, Y.M.; Zhang, X.; Shi, Z.M.; Nong, Y.; Ming, A.G.; et al. Introducing nitrogen-fixing tree species and mixing with *Pinus massoniana* alters and evenly distributes various chemical compositions of soil organic carbon in a planted forest in southern China. *For. Ecol. Manag.* **2019**, *449*, 117477. [\[CrossRef\]](#)
44. Liu, R.; Zhang, Y.; Hu, X.F.; Wan, S.Z.; Wang, H.M.; Liang, C.; Chen, F.S. Litter manipulation effects on microbial communities and enzymatic activities vary with soil depth in a subtropical Chinese fir plantation. *For. Ecol. Manag.* **2021**, *480*, 118641. [\[CrossRef\]](#)
45. Zhang, X.; Li, X.; Ji, X.D.; Zhang, Z.Q.; Zhang, H.S.; Zha, T.G.; Jiang, L. Elevation and total nitrogen are the critical factors that control the spatial distribution of soil organic carbon content in the shrubland on the Bashang Plateau, China. *Catena* **2021**, *204*, 105415. [\[CrossRef\]](#)
46. Xu, J.H.; Sun, Y.; Gao, L.; Cui, X.Y. A review of the factors influencing soil organic carbon stability. *Chin. J. Eco-Agric.* **2018**, *26*, 222–230. [\[CrossRef\]](#)
47. Chang, Y.; Sokol, N.W.; Groenigen, K.J.; Bradford, M.A.; Ji, D.; Crowther, T.W.; Liang, C.; Luo, Y.; Kuzyakov, Y.; Wang, J.; et al. A stoichiometric approach to estimate sources of mineral-associated soil organic matter. *Glob. Change Biol.* **2024**, *30*, e17092. [\[CrossRef\]](#) [\[PubMed\]](#)

48. Morrissey, E.M.; Kane, J.; Tripathi, B.M.; Rion, M.S.I.; Hungate, B.A.; Franklin, R.; Walter, C.; Sulman, B.; Brzostek, E. Carbon acquisition ecological strategies to connect soil microbial biodiversity and carbon cycling. *Soil Biol. Biochem.* **2023**, *177*, 108893. [\[CrossRef\]](#)
49. Malik, A.A.; Puissant, J.; Buckeridge, K.M.; Goodall, T.; Jehmlich, N.; Chowdhury, S.; Gweon, H.S.; Peyton, J.M.; Mason, K.E.; van Agtmaal, M.; et al. Land use driven change in soil pH affects microbial carbon cycling processes. *Nat. Commun.* **2018**, *9*, 3591. [\[CrossRef\]](#)
50. Mao, H.R.; Cotrufo, M.F.; Hart, S.C.; Sullivan, B.W.; Zhu, X.F.; Zhang, J.C.; Liang, C.; Zhu, M.Q. Dual role of silt and clay in the formation and accrual of stabilized soil organic carbon. *Soil Biol. Biochem.* **2024**, *192*, 109390. [\[CrossRef\]](#)
51. Lazarevic, J.; Menkis, A. Exploring Fungal Communities in the Needles of Marginal Conifer Tree Populations. *Forests* **2025**, *16*, 968. [\[CrossRef\]](#)
52. Philippot, L.; Chenu, C.; Kappler, A.; Rillig, M.C.; Fierer, N. The interplay between microbial communities and soil properties. *Nat. Rev. Microbiol.* **2024**, *22*, 226–239. [\[CrossRef\]](#) [\[PubMed\]](#)
53. Guo, X.; Luo, Z.; Sun, O.J. Long-term litter type treatments alter soil carbon composition but not microbial carbon utilization in a mixed pine-oak forest. *Biogeochemistry* **2021**, *152*, 1–17. [\[CrossRef\]](#)
54. Goldstein, A.; Turner, W.R.; Spawn, S.A.; Anderson-Teixeira, K.J.; Cook-Patton, S.; Fargione, J.; Gibbs, H.K.; Griscom, B.; Hewson, J.H.; Howard, J.F.; et al. Protecting irrecoverable carbon in Earth’s ecosystems. *Nat. Clim. Change* **2020**, *10*, 287–295. [\[CrossRef\]](#)

Disclaimer/Publisher’s Note: The statements, opinions and data contained in all publications are solely those of the individual author(s) and contributor(s) and not of MDPI and/or the editor(s). MDPI and/or the editor(s) disclaim responsibility for any injury to people or property resulting from any ideas, methods, instructions or products referred to in the content.