The Vertical Distribution Pattern of Microbial- and Plant-Derived Carbon in the Rhizosphere in Alpine Coniferous Forests

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Abstract

Background and aims

While the quantitative assessment of plant- and microbial-derived carbon (C) in the soil organic C (SOC) chemical composition in soil profiles has been initially explored, the vertical distribution pattern of these two C sources and their dominant role in SOC formation based on the insights related to the rhizosphere are still lacking.

Methods

We quantified the divergent accumulation of microbial-derived C (i.e., microbial residues), plant-derived C (i.e., lipids and lignin phenols) and SOC in the rhizosphere at various depths (0-10 cm, 10-20 cm and 20-30 cm) in the upper mineral soil and analyzed its control factors in an alpine coniferous forest (*Picea asperata*. Mast). We further revealed the relative contribution of plant- or microbial-derived C to rhizosphere SOC in the soil profile.

Results

The contents of microbial- and plant-derived C and SOC in the rhizosphere decreased with soil depth and were mainly regulated by root and microbial biomass. Moreover, the contribution of microbial-derived C dominated by fungal residues to rhizosphere SOC at each soil depth (more than 62%) was much higher than that of plant-derived C (less than 6%), implying that the soil microbial C pump was intensely stimulated in the rhizosphere.

Conclusions

These results indicated that microbial-derived C was the main contributor of rhizosphere SOC at various depths in the upper mineral soil. Our findings provide direct experimental evidence for assessing the dominant contribution of microbial- or plant-derived C to SOC in the soil profile from the perspective of the rhizosphere.

Introduction

Global soil carbon (C) stocks exceed global vegetation and atmospheric C storage combined and play a significant role in mitigating climate change, regulating the global C cycle and improving human well-being (Lehmann and Kleber, 2015; Li et al., 2018). However, given that the understanding of the major genesis and controls of soil organic C (SOC) remains limited thus far, the dynamics of SOC and its response to environmental change may be predicted inaccurately (Zhu et al., 2020a). Historically, it has been assumed that plant-derived compounds (lipids and compounds containing aromatic ring structures) are dominant contributors to the slow-cycling SOC pool due to their chemical recalcitrance (Cotrufo et al., 2015; Kögel-Knabner, 2017). However, increasing evidence has shown that the products (microbial residues) from microbial anabolism (i.e., the soil microbial carbon pump (MCP), Liang et al., 2017) are

likely to play a more important role than plant-derived compounds in the slow-cycling SOC pool (Liang et al., 2017; Ma et al., 2018; Yuan et al., 2021). In particular, in some microbial hotspots with higher microbial abundance and activity, such as the rhizosphere, plant-derived C inputs may be easily metabolized by microorganisms, resulting in intense turnover of microbial biomass and accumulation of necromass (Kuzyakov and Blagodatskaya, 2015; Angst et al., 2021). However, the dominant role of plant- and microbial-derived C in rhizosphere SOC formation is still an open question, especially considering root extension in the soil profile and vertical variation in the magnitudes and directions of root-soil interaction, which further aggravates the complexity for the assessment of the major genesis of rhizosphere SOC.

The vertical variation in physicochemical and biological traits in the rhizosphere on the soil profile has a profound effect on soil C dynamics (Hinsinger et al., 2005; Herold et al., 2014; Delgado- Baquerizo et al., 2016; Dijkstra et al., 2020). Previous studies indicated that root exudates, as the most direct labile C input into the rhizosphere, showed an obvious decreasing trend with soil depth, which significantly affected the metabolic activity of rhizosphere microbes (Goberna et al., 2005; Fierer et al., 2003) and mediated the soil C cycle (Tückmantel et al., 2017). Accordingly, the change in microbial activity not only regulates the vertical distribution of plant-derived C in the rhizosphere through catabolism for rhizodeposition and litter but also affects the divergent accumulation of microbial residues at different soil depths through anabolism processes (Liang et al., 2017; Zhu et al., 2020a). Although some empirical studies and meta-analyses have suggested that the contribution of microbial-derived C to SOC increases with soil depth (Ni et al., 2020a, 2020b), the contribution of plant-derived C to SOC decreases (Feng and Simpson, 2007; Angst et al., 2016). However, almost all existing studies have ignored how vertical changes in root activity with soil depth shape the vertical differentiation pattern of rhizosphere SOC formation. Therefore, the vertical heterogeneity of rhizosphere SOC formation is an important part of underground C dynamics that have still not received enough attention.

The accumulation of plant- and microbial-derived C components in the stable SOC pool is co-controlled by biotic and abiotic factors. According to the theoretical framework proposed by Cotrufo et al. (2013), the input of labile substrates in mineral soils can improve the microbial C utilization efficiency and then promote the accumulation of microbial residues. Many models and laboratory incubation also indicated that high-quality substrates could enhance the accumulation of microbial-derived C compared with low-quality substrates (Castellano et al., 2015; Córdova et al., 2018; Shao et al., 2019). Moreover, the stabilization of microbial-derived C is highly dependent on the physical protection of soil aggregates and the chemical adsorption of mineral surfaces (Totsche et al., 2018; Olivelli et al., 2020). The accumulation of plant-derived C components is not only affected by the plant traits (Waldrop and Firestone, 2004), climate (Otto and Simpson 2006; Dai et al. 2018), and physicochemical properties of soil (Feng et al. 2005; Angst et al. 2017) but also determined by the balance between microbial catabolism and physicochemical protection (Liang et al., 2017). If plant materials enter an area with low-density microbes, they may be attacked and transformed by extracellular enzymes, resulting in the deposition of plant-derived C that is not readily assimilated by microorganisms. In contrast, if plant materials enter an area with high-density microbes (e.g., rhizosphere), they may be easily metabolized by microbes, leading

to a large loss of plant-derived C (Angst et al., 2021). However, although the controlling factors of the accumulation of microbial- and plant-derived C components in bulk soil have been well reported, knowledge of the rhizosphere remains limited.

The forest SOC pool is the most important and the largest soil C pool in terrestrial ecosystems (Jandl et al., 2007). Previous studies on microbial- and plant-derived C have mainly focused on temperate agriculture, grassland, and forest ecosystems (Ma et al., 2018; Liang et al., 2019; Wang et al., 2020), subtropical and tropical forest ecosystems (Shao et al., 2017; Ma et al., 2020; Yuan et al., 2021) while ignoring in-depth studies on SOC formation in alpine forests. Alpine coniferous forest is a typical representative of boreal forests, and its soil C stock accounts for approximately 18% of the total C stock in terrestrial ecosystems (Carvalhais et al., 2014) and is extremely sensitive to global changes (Xu et al., 2010; Yin et al., 2013). Thus, understanding and identifying the dominant role of plant- and microbial-derived C components in rhizosphere SOC formation in alpine forests will provide new insights into soil C sequestration. In this study, therefore, rhizosphere soils from different soil depths (0-10 cm, 10-20 cm and 20-30 cm) in the upper mineral soil in a ca. 75-year-old spruce plantation in Southwest China were collected separately. The contents of microbial- and plant-derived C were determined using two groups of widely accepted biomarkers (amino sugars, plant-derived lipids and lignin phenols), and then the proportion contributions of these two C resources to rhizosphere SOC at different soil depths were estimated. Simultaneously, the controls of vertical distribution pattern of microbial- and plant-derived C in rhizosphere were analyzed by integrating the soil and root properties. Given that the root-derived organic matter and labile C inputs gradually decreased with soil depth (Tückmantel et al., 2017), we hypothesized that the contents of microbial- and plant-derived C components would show a vertical decreasing pattern in the soil profile.

Materials And Methods

Study sites

Our experiment was performed at the Miyaluo Alpine Forest Ecology Research Site, which is located on the eastern Tibetan Plateau (31°35'N; 102°35'E; 3150 m a.s.l.). Monoculture *Picea asperata* plantations were established after natural spruce-fir forests were deforested in the 1950s. The regional climate is continental with a mean annual air temperature of 8.9°C, and the mean annual precipitation ranges from 600 to 1100 mm. The understory of the plantation is dominated by several *Festuca ovina*, *Deyeuxia arundinacea*, and *Carex capilliformis* (Zhang et al., 2017). The soil type and properties of this experimental region have been well reported by previous studies (Yuan et al., 2018; Zhang et al., 2018).

Experimental design and sampling

Soil and root samples were collected in situ in July and October 2019, respectively. We set five 30 m-long sampling lines in spruce plantations that were spaced more than 20 m apart. We then set 15 sampling points on each sampling line 2 m apart. After removing the litter and organic layer above each sampling point, a complete soil core (10 cm in diameter) at a 0-30 cm depth of the upper mineral soil was collected.

The whole soil core was then divided into three sections (0-10, 10-20, and 20-30 cm) from top to bottom, and the roots (diameter < 2 mm) were collected. The soil adjacent to roots (range less than 2 mm) was carefully collected. Roots were also collected synchronously. After the soil collection was completed, the rhizosphere soil of each sampling line and each soil layer was mixed into a composite soil sample, which was stored at low temperature and transported back to the laboratory.

Laboratory analysis

Soil pH was measured at a 1:2.5 soil:water suspension using a pH electrode (Star A 420C-01A, Thermo Orion, United States). The SOC content was determined using the $K_2Cr_2O_7$ oxidation method (Walkley and Black, 1934). The nitrogen (N) content was determined using the micro-Kjeldahl method (Lu, 2000). The Fe (Fe-MOC) and Al (Al-MOC) ions bound in the metal-organic complexes were extracted using the method described by Keiluweit et al. (2015), and their contents were determined by an inductively coupled plasma optical emission spectrometer (ICP-OES, Optima 8300, Perkin Elmer, USA). The activities of three extracellular enzymes (β -glucosidase, BG; β -xylosidase, BX; cellobiohydrolase, CBH; polyphenol oxidase, PPO) related to soil C transformation were measured using microplate fluorometric and spectrophotometric assays (Saiya-Cork et al., 2002, Zhu et al., 2020b). Soil microbial biomass carbon (MBC) was evaluated using the chloroform fumigation extraction method and conversion coefficient (0.45) (Vance et al., 1987).

Root samples were washed with deionized water, and their root length (RL) was determined by WinRHIZO (Régent Instruments, Québec, Canada). Subsequently, root mass (RB) was measured after oven-drying at 60 °C for 48 h to a constant mass. Then, specific root length (SRL) were calculated.

Lipids and lignin phenol monomers were used to indicate the plant-derived C components (Hedges and Mann, 1979; Feng et al., 2007). Solvent-extractable free lipids, hydrolyzable bound lipids, and lignin-derived phenols were separated by solvent extraction, base hydrolysis, and CuO oxidation, respectively (Otto and Simpson, 2007; Tamura et al., 2017). The lipids and lignin phenol components extracted from each soil sample were analyzed by gas chromatography-mass spectrometry (GCMS-QP2020 NX, Shimadzu, Kyoto, Japan). The identified compounds were quantified based on external standards of known concentrations. Details regarding the extraction procedures can be found in Text S1. In this study, lipids extracted included: long-chain fatty acids (LFA: > C_{24} alkanes, > C_{22} n-alkanoic acids and alkanols); cutin (Cutin: C_{14} - C_{18} hydroxyalkanoic acids, C_{16} -di-hydroxyalkanoic acids, ω -hydroxy- and ω -hydroxy-epoxy alkanoic acids (C_{16} - C_{18})); Suberin (suberin: α,ω -dicarboxylic acids (C_{16} - C_{24}) and ω -hydroxyalkanoic acids (C_{20} - C_{30})). Lignin phenol monomers included vanillyl (vanillin, acetovanillone, and vanillic acid), syringyl (syringaldehyde, acetosyringone, and syringic acid), and cinnamyl (p-coumaric acid and ferulic acid), which were summarized to represent lignin in the soil (Kögel, 1986; Bahri et al., 2008).

Amino sugars are critical components of microbial cell walls (Joergensen, 2018) and mainly include glucosamine (GluN), galactosamine (GalN), and muramic acid (MurA). Among them, MurA exclusively exists in bacteria, GluN exists in both fungi and bacteria (Amelung et al., 2001), and GalN generally exists

in bacteria and the cell walls of some rare archaeal species (Joergensen, 2018). These three amino sugars were quantified according to the method described by Indorf et al. (2011) with minor modifications (Mou et al., 2020). The chromatograms of standard solutions containing mixed amino sugars were applied to identify and quantify each amino sugar. The concentrations of individual and total amino sugars were expressed in $\mu\text{g/g}$ dry soil and converted to microbial residue C by the following equation:

$$\text{Bacterial residual C } (\mu\text{g/g}) = \text{MurA} \times 45 \quad \text{Eqn. 1}$$

$$\text{Fungal residue C } (\mu\text{g/g}) = (\text{GluN}/179.2 - 2 \times \text{MurA}/251.2) \times 179.2 \times 9 \quad \text{Eqn. 2}$$

$$\text{Microbial residual C } (\mu\text{g/g}) = \text{Bacterial residual C} + \text{Fungal residue C} \quad \text{Eqn. 3}$$

where 45 is the conversion factor of MurA to bacterial residue C (Appuhn and Joergensen, 2006). Fungal residue C was calculated by subtracting bacterial GluN from total GluN, assuming that MurA and GluN on average occur at a 1 to 2 molar ratio in bacterial cells (Engelking et al., 2007). 179.2 and 251.2 are the molecular weights of GluN and MurA, respectively, and 9 is the conversion factor of fungal GluN to fungal residue C (Shao et al., 2017). Microbial residue C was approximated as the sum of fungal and bacterial residue C (Joergensen, 2018; Liang et al., 2019).

Statistical analysis

One-way ANOVA was used to examine differences in the content of SOC, microbial-derived C (microbial residue C) and plant-derived C (lipids and lignin phenols) among the three soil depths. Data were checked for normality and the homogeneity of variances and log-transformed to correct deviations from these assumptions if necessary. The single and interactive effects of sampling depth and/or sampling time on all measured variables across two sampling time were assessed by repeated measures ANOVA. All statistical analyses were performed using SPSS 26.0 (SPSS Inc., Chicago, Illinois, USA) for Windows, and differences were considered significant at the $P < 0.05$ level. Redundancy analysis (RDA, CANOCO 5.0) was performed to determine which biotic or abiotic environmental variables were related to the contents of microbial- and plant-derived C in the soil profile. Partial least squares path modeling (PLS-PM) was performed to further identify the direct and indirect effects of soil and root traits and microbial- and plant-derived C on SOC by using Smart-PLS software. The SRMR (< 0.08) or NFI (> 0.9) index was met to ensure that the model was valid.

Results

SOC content with soil depths

The contents of rhizosphere SOC were $31.40 \sim 34.40$, $21.88 \sim 24.44$ and $17.50 \sim 17.73$ mg/g soil in the 0-10, 10-20, and 20-30 cm soil depths, respectively (Fig. 1). The SOC content decreased significantly with increasing soil depth (Fig. 1, $P < 0.05$). Compared to the 0-10 cm soil layer, the content of rhizosphere SOC

decreased by 28.95 ~ 30.31% in the 10-20 cm soil layer and 43.52 ~ 49.12% in the 20-30 cm soil layer (Fig. 1).

Microbial-derived C content with soil depths

The contents of total microbial, fungal and bacterial residue C consistently decreased with increasing soil depth (Fig. 2, $P < 0.05$). Compared to the 0-10 cm soil layer, the content of microbial residue C was reduced by an average of 36.15% in the 10-20 cm soil layer and 44.94% in the 20-30 cm soil layer (Fig. 2a); the content of fungal residue C was reduced by an average of 38.56% in the 10-20 cm soil layer and 46.24% in the 20-30 cm soil layer (Fig. 2b); and the content of bacterial residue C was reduced by an average of 17.67% in the 10-20 cm soil layer and 35.00% in the 20-30 cm soil layer (Fig. 2c). Moreover, fungal residue C was the dominant fraction of total microbial residue C in the rhizosphere in each soil layer (Fig. 2). The content of fungal residue C was 8.01, 5.73 and 6.35 times greater than the content of bacterial residue C at the 0-10 cm, 10-20 cm and 20-30 cm soil layers, respectively (Fig. 2).

Plant-derived C content with soil depths

The contents of long-chain fatty acids, cutin, suberin and CSV lignin consistently decreased with increasing soil depth (Fig. 3, $P < 0.05$). Compared to the 0-10 cm soil layer, the contents of long-chain fatty acids, cutin, suberin and CSV lignin were reduced by an average of 35.75%, 37.12%, 38.06% and 46.73% in the 10-20 cm soil layer and 62.59%, 61.50%, 65.13% and 81.64% in the 20-30 cm soil, respectively (Fig. 3). In addition, suberin was the major component in plant-derived C (accounting for 57.59 ~ 63.27%), followed by long-chain fatty acids (accounting for 17.14 ~ 24.66%), and finally lignin phenol monomers (accounting for 4.74 ~ 13.55) and cutin (accounting for 9.80 ~ 11.40%) in each soil layer (Fig. 3).

Control factors of microbial- and plant-derived C content with soil depth

RDA of microbial-derived C and biotic/abiotic factors suggested that the first two axes explained 94.02% of the variation in fungal, bacterial and microbial residue C content (93.71% by axis 1 and 0.31% by axis 2; Fig. 4a). There was a positive relationship of fungal, bacterial and total microbial residue C content with microbial biomass C, enzyme activity, root biomass, Fe-MOC/Al-MOC content, and soil C/N and a negative relationship with soil pH and specific root length (Fig. 4a). In addition, the RDA of plant-derived C and biotic/abiotic factors indicated that the first two axes explained 97.99% of the variation in plant-derived C content (97.88% by axis 1 and 0.11% by axis 2; Fig. 4b). Similarly, the microbial biomass C, enzyme activity, root biomass, Fe-MOC/Al-MOC content, and soil C/N positively affected the change in plant-derived C content with soil depth, while soil pH and specific root length had negative effects (Fig. 4b).

Partial least square path modeling (PLS-PM) was used to further explore the effects of soil and root traits on microbial- and plant-derived C as well as rhizosphere SOC content (Fig. 5). PLS-PM analysis suggested that microbial biomass C (0.88), root biomass (0.73) and soil pH (0.50) had direct and

significant effects on microbial-derived C (Fig. 5). Microbial biomass C (0.49) and root biomass (0.33) had direct and significant effects on plant-derived C, and the total effect of root biomass (0.92) on plant-derived C was much higher than that of microbial biomass C (0.58) (Fig. 5). In addition, the effect of microbial-derived C (0.64) on SOC was greater than that of plant-derived C (0.38) (Fig. 5).

Contribution of microbial- and plant-derived C to rhizosphere SOC

The contribution of microbial-derived C to rhizosphere SOC was more than 62% in each soil layer, while the contribution of plant-derived C to rhizosphere SOC was less than 6% (Fig. 6). Specifically, the contributions of microbial-derived C were 14.23, 15.10 and 23.86 times greater than those of plant-derived C in the 0-10 cm, 10-20 cm and 20-30 cm soil layers, respectively (Fig. 6). Furthermore, the contribution of fungal residue C to rhizosphere SOC reached averages of 62.82%, 54.65% and 62.79% and was 14.23-, 15.10- and 23.86-fold higher than that of bacterial residue C in the 0-10 cm, 10-20 cm and 20-30 cm soil layers, respectively (Table S2). In addition, the contribution of suberin to rhizosphere SOC was significantly greater than that of other components, accounting for approximately 60% of the total contribution of plant-derived C, followed by long-chain fatty acids, lignin phenol monomers and cutin (Table. S2).

Discussion

An in-depth understanding of the vertical heterogeneity of the genesis of rhizosphere SOC is a key link for the complete assessment of soil C stocks and dynamics and for the accurate prediction of its responses to future climate change. In this study, we used specific biomarkers to analyze the vertical distribution pattern of plant- and microbial-derived C contents in the rhizosphere and further revealed their dominant contribution to rhizosphere SOC accrual in the soil profile. We found that microbial- and plant-derived C contents in the rhizosphere showed consistent vertical decreasing trends with soil depth, which were mainly controlled by microbial and root biomass. The contribution of microbial-derived C to rhizosphere SOC at each soil depth (more than 62%) was higher than that of plant-derived C (less than 6%). These results indicate that the chemical composition and sources of rhizosphere SOC have obvious vertical differentiation patterns, and microbial-derived C is the main contributor to rhizosphere SOC accumulation.

The vertical variation and controls of microbial- and plant-derived C in the rhizosphere

Our results showed that microbial- and plant-derived C contents in the rhizosphere displayed consistent vertical decreasing patterns with increasing soil depth, which supported our hypothesis. This vertical variation trend of microbial-derived C was consistent with previous studies in bulk soil at the global scale (Ni et al., 2020a, 2020b). The vertical variation pattern may be mainly attributed to the vertical decrease of the quantity and quality of root C inputs and its mediated microbial processes in the rhizosphere (Tückmantel et al., 2017). Moreover, the vertical difference in the physicochemical protection of plant- and microbial-derived C may also be an important reason for this variation, given that the two main chemical components of SOC are easily protected by soil aggregates or adsorbed on the mineral surface (Cotrufo et al., 2013; Clemente et al., 2011).

Root-derived input and microbial activity significantly controlled the vertical decreasing pattern of microbial- and plant-derived C, but that of microbial-derived C was also regulated by soil pH. Previous studies have also found that microbial biomass positively drives the accumulation of microbial residues in bulk soil in the soil profile (Wang et al., 2020; Ni et al., 2020b). Soil pH had a negative effect on the vertical distribution of microbial-derived C in the rhizosphere, resulting in most fungi being more likely to survive and accumulate in topsoil (Rousk et al., 2010); subsequently, fungal residues showed a vertical decreasing trend (Fig. 2b). In addition, with increasing soil depth, the root biomass gradually decreased (Table S3), which directly affected the accumulation and long-term retention of stable plant-derived C components after decomposition of root litter (Feng et al., 2010). Meanwhile, the higher microbial biomass C and extracellular enzyme activities in topsoil (Table S3) also accelerated the microbial decomposition process of root litter. Accordingly, suberin, as the major product of root decomposition (Kögel-Knabner, 2002) and the major contributor to plant-derived C accumulation in different soil layers, showed a vertical declining trend (Fig. 3c). Furthermore, the metal-organic complex had a positive effect on the vertical distribution of microbial- and plant-derived C rhizosphere (Fig. 4), indicating that microbial residues and plant-derived lipids and lignin phenols in rhizosphere in the topsoil may be more protected by minerals, thus leading to a large amount of accumulation.

The dominant contribution of microbial-derived C to rhizosphere SOC

Our results showed that the contribution of microbial-derived C to rhizosphere SOC was more than 62% in each soil layer, while the contribution of plant-derived C was less than 6% (Fig. 6). This finding is highly consistent with the emerging view that microbial-derived C is the dominant contributor to SOC formation (Cotrufo et al., 2013; Kallenbach et al., 2016; Zhu et al., 2020a). However, the latest meta-analysis at the global scale indicated that the contribution of microbial-derived C to total SOC in bulk soil was less than 50% at depths above 50 cm in forest mineral soil (Liang et al., 2019; Ni et al., 2020b). In contrast, the rhizosphere drives higher soil microbial C pump (MCP) efficacy (i.e., the contribution of microbial residues to SOC; Zhu et al., 2020) in the topsoil of forest mineral soil. Previous studies have demonstrated that soil microbial residues are closely related to soil microbial biomass (Ni et al., 2020a; Yuan et al., 2020). The rhizosphere is considered a microbial hotspot with high microbial abundance and activity due to the higher input of labile substrates (Hinsinger et al., 2005; Walker et al., 2003). Accordingly, plant-derived organic matter in the rhizosphere can be easily and quickly metabolized by microorganisms, resulting in the loss of plant-derived C components via catabolism or the formation of microbial-derived C components via anabolism (Liang et al., 2017; Angst et al., 2021). To some extent, this process accelerates the transformation of plant-derived organic matter to microbial-derived C through an *in vivo* microbial turnover pathway (Liang et al., 2017). Hence, the rhizosphere intensely stimulated the operation of soil MCP and promoted microbial-derived C to become the dominant contributor of SOC.

Conclusion

In this study, the vertical variation in microbial residues, plant-derived lipids and lignin phenols in the rhizosphere in a soil profile was quantitatively analyzed to reveal the dominant contribution of plant- or

microbial-derived C to rhizosphere SOC. Our results suggest that the contents of plant- and microbial-derived C in the rhizosphere decreased with increasing soil depth, and the vertical decreasing trend were mainly controlled by root biomass and microbial biomass. Microbial-derived C plays a dominant role in the accumulation of rhizosphere SOC in the 0-30 cm range in the upper layer of mineral soil, implying that the soil microbial C pump was intensely stimulated in the rhizosphere. Nevertheless, we fully recognized the limitations regarding our study design, which was based on a single typical coniferous plantation in an alpine forest. However, our findings provide a significant reference and direct experimental evidence for assessing the dominant contribution of microbial- and plant-derived C to SOC in the soil profile from the perspective of the rhizosphere.

Declarations

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Figures

Figure 1

Contents of SOC in the rhizosphere at different soil depths. Values are means with SE. Different lowercase letters above the bars indicate significant differences among the three different soil depths at each sampling time ($P < 0.05$).

Figure 2

Contents of microbial-derived C components in the rhizosphere at different soil depths. Values are means with SE. Different lowercase letters above the bars indicate significant differences among the three different soil depths at each sampling time ($P < 0.05$).

Figure 3

Contents of plant-derived C components in the rhizosphere at different soil depths. Values are means with SE. Different lowercase letters above the bars indicate significant differences among the three different soil depths at each sampling time ($P < 0.05$).

Figure 4

Two-dimensional biplot of redundancy analysis (RDA) for the relationship between microbial-derived C (a) or plant-derived C (b) and environmental variables. Green circles, yellow stars, and red squares represent samples collected from 0-10 cm, 10-20 cm, and 20-30 cm soil, respectively. The predictor variables included soil microbial biomass carbon (MBC), enzyme activity (EA), root biomass (RB), specific root length (SRL), soil carbon to nitrogen ratio (C/N), soil pH (pH), iron ion content (Fe), and aluminum ion content (Al). BRC, bacterial residue carbon; FRC, fungal residue carbon; MRC, microbial residue carbon; LFA, long-chain fatty acids; C, cutin; S, suberin; LP, lignin phenols; PC, plant-derived C.

Figure 5

Partial least square path modeling (PLS-PM) was used to determine the cascading relationships of microbial- and plant-derived C to SOC via soil and plant root variables. Red solid, black solid and black dashed lines indicate significant negative, positive and insignificant correlations with the corresponding factors, respectively. Numbers on lines indicate standardized path coefficients and are proportional to the arrow width. R^2 indicates the variance of factors explained by the model.

Figure 6

Contributions of microbial- and plant-derived C to SOC in the rhizosphere at different soil depths. Values are means with SE. Different capital letters and lowercase letters above the bars represent significant differences ($P < 0.05$) in plant- and microbial-derived C among the three different soil depths at each sampling time, respectively.

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