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A Conceptual Framework on the Fate of Rhizodeposits in Forming Mineral-Associated Organic Matter or Encapsulating Into Microaggreagtes

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ABSTRACT: Rhizodeposition, as transported from photosynthates and exudated in soils via fine roots, is the pivot linking above- and belowground carbon (C) cycling pathways. Meanwhile, rhizodeposit C serves as "currency" for plant nutrient acquisition because of its critical roles in priming soil microorganisms, maintaining plant-mycorrhizal symbionts, and elongating plant roots. Therefore, a conceptual framework integrating knowledge on the biogeochemical fate of rhizodeposit C can help understand plant nutrient economics and soil C sink function. However, it still remains a great challenge to efficiently delineate the dynamics of rhizodeposit C in soils. In the framework, we present the possible stabilization pathways of rhizodeposit C via formation of mineral-associated organic matter (MAOM) or encapsulation by microaggregates. We further propose that continuous and pulse $^{13}CO_2$ labeling are powerful techniques to track the fate of rhizodeposit C and to quantify how much C could eventually be sequestrated in soils as the component of MAOM or microaggregates. This framework would provide future research possibilities to better optimize plant C allocation and productivity and preserve soil C stocks.

KEYWORDS: Rhizodeposition, carbon allocation, mineral-associated organic matter, soil aggregate, stable isotope, mycorrhizal symbiont

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Introduction

Plant-soil microbial carbon (C) "trade" at root and soil interface (i.e. rhizosphere) is incrementally receiving research attention within the disciplines of plant and soil sciences (Prescott et al., 2020; Wang et al., 2022). Reasons for this emerging hot topic lie in the fact that C allocation to rhizosphere is considered as the "currency" of trading for other resources but comes at the expense of reducing C for shoot growth (Hartmann et al., 2020). For instance, some estimates suggest that plants allocate nearly one-third of photosynthetic assimilates belowground with the proportion varying substantially among plant species and experimental/environmental conditions (Pausch & Kuzyakov, 2018). Therefore, rhizospheric C trading is a fundamental ecological process for plants optimizing belowground nutrient acquisition versus aboveground biomass yield, which is usually interpreted at the angles of plant C-nutrient economics or tradeoffs in C allocation between above- and belowground components (Kong & Fridley, 2019; Ledo et al., 2018).

Specifically, the traded C is mainly used to elongate plant roots, prime soil microorganisms, and maintain symbiosis between plants and soil mycorrhizas (Wang et al., 2022). Therefore, rhizosphere C-nutrient exchanges are plant strategies to upregulate nutrient-acquisition efficiencies, thereafter, adapting to nutrient-poor or resource-fluctuating environments (Raven et al., 2018). Rhizodeposit C, as an integral part of rhizospheric C trading, is mainly exudated in soils via fine roots after transporting photosynthates downwards (Villarino et al., 2021). Rhizodeposits fuel soil microbial turnover to destabilize soil organic matter and at the same time accelerate nutrient release for plant growth (Dijkstra et al., 2021). This underlies the current consensus of regarding rhizodeposit C as a pivot linking above- and belowground C cycling pathways. A substantial proportion of belowground allocated C (over 30%) is mineralized into CO_2 during short periods of time via pathways of root respiration, rhizodeposit decomposition, and mycorrhizal fungal respiration (Han et al., 2021; Pausch & Kuzyakov, 2018; Wang, Bicharanloo, et al., 2021). The rest of C remains in the ecosystem in relatively longer terms in the form of root biomass, rhizodeposits, and fungal biomass or necromass (Wang, Cavagnaro, et al., 2021). The above-mentioned rhizodeposit cycling processes are largely sketched in greenhouse studies with most of them being precisely controlled and viable for the collection and measurement of rhizodeposits (Hao et al., 2022; Semchenko et al., 2021; Wang, Bicharanloo, et al., 2021; Wang, Cavagnaro, et al., 2021). However, challenges are still formidable in upscaling the results from laboratory studies to ecosystems (Chen et al., 2023). Nevertheless, it remains largely elusive for both laboratory and field studies in terms of how newly incorporated soil C from rhizodeposits would be stabilized in the soil.

A Conceptual Framework of Rhizodeposit C Stabilization

In this review, we proposed a conceptual framework synthesizing the current knowledge to anticipate the possible stabilizing pathways of the belowground allocated C as rhizodeposits (Figure 1). Mounting evidence has proved that treating soil organic matter as a single and uniform entity would impede

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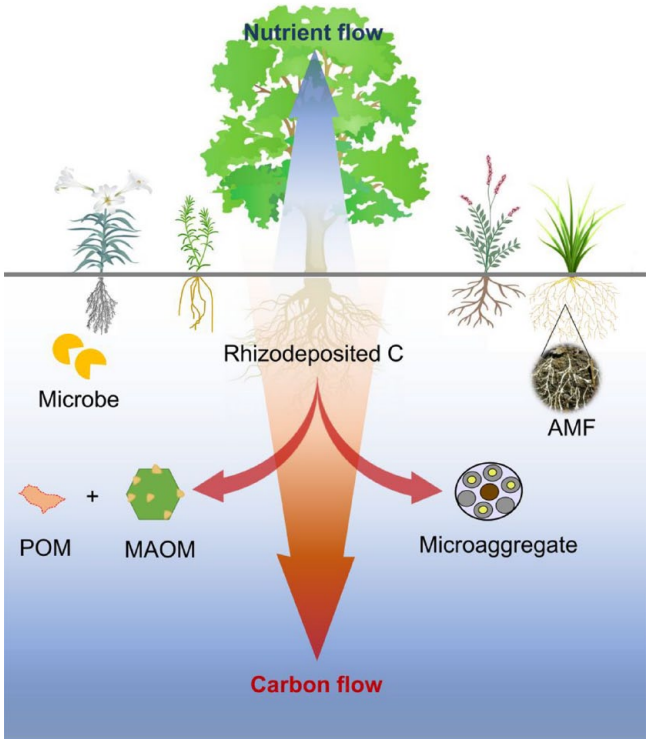

Figure 1. Rhizodeposited carbon (C) is an essential plant investment strategy for taking up soil nutrients, because it can be used to prime soil microorganism, maintain plant-mycorrhizal symbionts, and elongate plant roots. Some of the rhizodeposited C can also remain in the soil in a short term via forming particulate organic matter (POM) and in a long term as mineral-associated organic matter (MAOM) or encapsulated in microaggregates. Vertical arrow represents the direction of carbon (downward and red) and nutrient flow (upward and blue).
Note. AMF = arbuscular mycorrhizal fungi.

our broader scope and deeper understanding in C stabilization mechanisms (Lavallee et al., 2020). Therefore, this framework mostly emphasized key processes of C incorporation and stabilization in two fundamentally and differently conceptualized soil fractions, that is, formation of mineral-associated organic matter (MAOM) and C integration into microaggreagtes.

As a complex of soil inorganics and organic matter, MAOM is resistant to microbial attack due to the strong chemical bond between organic matter and minerals or occlusion within micropores (Lavallee et al., 2020). Given the fact that MAOM averagely shows a lower C:nitrogen (N) ratio, it is primarily considered as an organic matter fraction of microbial origin from ex vivo modification and in vivo transformation of plant- and microbial-derived C (Bai & Cotrufo, 2022). Moreover, it is pervasively evidenced that rhizodeposits exhibit a high MAOM formation efficiency (46%, Villarino et al., 2021). This is because low-molecular-weight C compounds from rhizodeposition, such as sugars and amino acids, are more accessible to microbial in vivo transformations as compared to structural compounds from plant litter (Villarino et al., 2021). Currently, if the transformation efficiency of rhizodeposits is greater than that of plant residues still lacks a holistic evaluation across different ecosystem types with various environmental conditions.

Soil microaggregates are widely known to physically protect organic matter via limiting microbial proliferation and activity (Wang et al., 2020). Indeed, microaggregates are proved to possess smaller pore sizes and lower rates of water and oxygen diffusion (Totsche et al., 2018). Consequently, microbial activity and organic C turnover rates are strongly restricted in microaggregates. In this context, tracking the processes of photosynthetic C to be adsorbed by soil minerals and to be encapsulated within microaggregates are crucial for understanding the C flow from plant photosynthesis to soils and therefore evaluating soil potential of C sequestration. However, studies on this C flow from rhizodeposition to soil aggregates are conducted sporadically and thereby give a limited view of the C dynamics in soil microsites.

Exploring the Fate of Rhizodeposits With ^{13}C Tracing Techniques

Stable carbon isotope (namely ^{13}C) is a powerful tracer to depict the fate of photosynthates in plant and soil components (Chomel et al., 2022). Both continuous and pulse labeling using $^{13}CO_2$ are sensitive, precise, and practical approaches to achieve this C-tracing goal but in different ways (Figure 2; Liu et al., 2019). Continuous $^{13}CO_2$ labeling approach is capable of labeling plant materials homogenously by exposing plants in a $^{13}CO_2$-enriched condition for a long time from days to years (Pang et al., 2021). This approach can determine rhizodeposition rates approximately by quantifying how much photosynthetic C allocated to soils and respired as CO_2 during a given period (Pausch & Kuzyakov, 2018). However, pulse labeling feeds plants with $^{13}CO_2$ from minutes to hours via injecting the tracer gas in an air-tight chamber (Figure 2; Pang et al., 2021). This technique can only deliver the information of plant C allocation patterns, such as the proportions of photosynthates translocated to roots and soils or mineralized into CO_2 via root and soil respiration (Wang, Bicharanloo, et al., 2021). Therefore, studies using pulse labeling approach treated CO_2 efflux from rhizodeposition decomposition as a proxy for rhizodeposition rates (Bicharanloo et al., 2022; Wang, Bicharanloo, et al., 2021). Of course, this assumes that rhizodeposition rate is linearly proportional to its decomposition rates. Irrespective of labeling techniques, the way to separate different C sources is constrained to two-source isotopic mixing models. Moreover, the use of these quantifying methods requires to implement the measurements in a relatively short time scale from days to weeks. This principle is set to avoid any significant plant C inputs through root turnover or aboveground biomass abscission and decomposition (Wang, Cavagnaro, et al., 2021). Nevertheless, to outline the essential pathway of plant C flowing into soils via rhizodeposition, isotopic techniques of ^{13}C tracing, either continuous or pulse labeling, as followed by the calculations with isotopic

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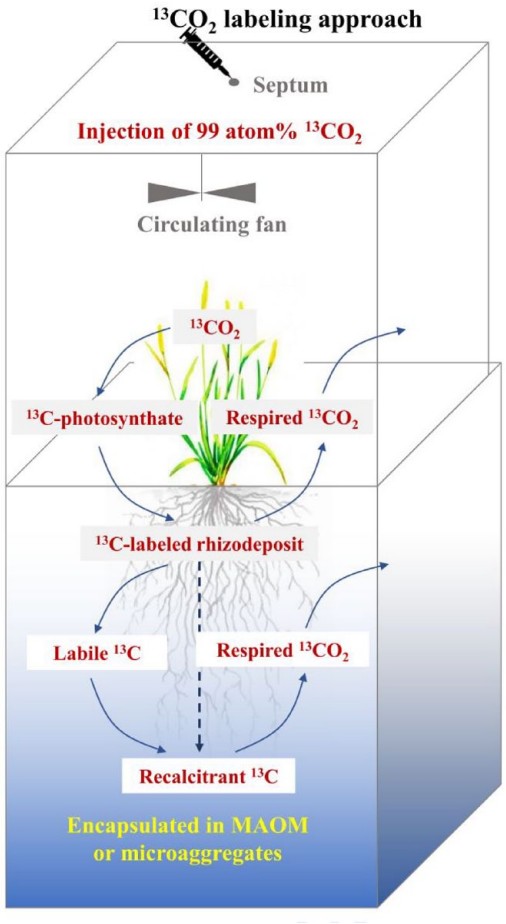

Figure 2. Continuous or pulse $^{13}CO_2$ labeling of plants in an air-tight chamber (i.e. the box at the top). Plants photosynthesize $^{13}CO_2$ and allocate ^{13}C-labeled carbohydrates belowground to roots (i.e. the box at the bottom). Respired rhizodeposit C can be roughly used to represent rhizodeposition rate. However, residual rhizodeposit C in the soil would form labile (e.g. particulate organic C) and recalcitrant C fractions, for example, encapsulated in mineral-associated organic matter (MAOM) or microaggreagtes.

two-source mixing models (see Wang, Bicharanloo, et al., 2021) are vastly needed.

After ^{13}C-labeled photosynthate deposited into the soil, separation of MAOM from particulate organic matter and consecutive ^{13}C measurements could help delineate the C flow and stabilization from plants to soils (Dijkstra et al., 2021). Similarly, quantifying the ^{13}C recovery across aggregate size classes with isotopic mass balance equations (see Wang, Cavagnaro, et al., 2021) can illustrate integration of photosynthate C among soil particles with different capability of physical C protection (Wang et al., 2020). According to the soil aggregate hierarchy hypothesis (Totsche et al., 2018), the absolute amount and proportion of ^{13}C distributed in microaggreagtes somewhat show the degree of physical protection of newly secreted C from roots. Particle size fractionation of the ^{13}C-labeled soils can simply follow the widely-used standard protocols, which are fractionation by size (53 μm) after full soil dispersion for POM versus MAOM (sensu Cotrufo et al., 2019) and wet sieving for soil aggregates (Six et al., 2000). Overall, quantification of ^{13}C allocation in MOAM and microaggregates are undoubtedly the central key to unlock how much C from this shoot-root-soil flow pathway will be stabilized.

Conclusion

Considerable efforts and progresses have already made toward understanding the role of rhizodeposit carbon in promoting plant nutrient acquisition. Currently, a major challenge is to probe the stabilization mechanisms of rhizodeposits in order to formulating management practices for sequestering and preserving plant-derived carbon in soils. By systematically synthesizing current knowns and unknowns, we proposed a conceptual framework on the fate of rhizodeposits in forming mineral-associated organic matter or encapsulating into microaggregates. We also underscored continuous or pulse $^{13}CO_2$ labeling techniques to be powerful approaches to tackle the unknowns in terms of the fate of rhizodeposits.

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Author Contribution

RW wrote the manuscript. BG and RW both contributed to manuscript revision.

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Declaration of Conflicting Interests

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Ethical Approval and Consent to Participate

Not applicable.

Consent for Publication

The authors read and approved the final manuscript.

Availability of Data and Material

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