

COMMENTARY

Closing in on the last frontier: C allocation in the rhizosphere

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Tree processes belowground are as intricate and complex as aboveground processes. In fact, they are more complex, probably since the soil, being a solid medium, is denser and richer than the atmosphere, which is a gas medium. Around 2000 billion tons of organic C are stored in the soil, which is more than the combined C pools of the atmosphere and vegetation. As trees assimilate C and allocate it to their roots, they are crucial in belowground processes. Trees can store C in the roots, allocate C for root growth, release C as root exudation, and finally deposit C as litter (Klein & Hoch, 2015). Soil microorganisms, including bacteria, archaea, fungi, protozoa, and viruses are an important part of the belowground C sink of trees. They regulate the organic C stored in the soil and released back to the atmosphere, depending on soil chemistry, temperature and moisture. The place where tree roots interact with soil microorganisms, called the rhizosphere, is the center of belowground C processes. Rhizosphere processes account for up to one-third of total C and N mineralized in soils of temperate forests. To quantify the involvement of soil microorganisms in the C cycle, we first need to quantify the amount of C allocated belowground, by assessing whole tree C fluxes. A powerful tool in studying ecosystem fluxes is stable C isotope labeling. C allocation is traced with a high temporal resolution by measuring discrete fluxes. C labeling includes enrichment or depletion of $\delta^{13}\text{C}_2\text{CO}_2$ gas, however, labeling can become expensive, especially on a canopy scale. Hence the method of choice usually uses mildly depleted $\delta^{13}\text{C}_2\text{CO}_2$ gas. Another way of assessing C allocation in trees is using a carbon mass balance approach (Klein & Hoch, 2015):

$$A = R + Gr + L + Ex + S - C \quad (1)$$

where the C source is assimilation (A), and C sinks are respiration (R), growth (Gr), litter production (L), root exudation (Ex), and the balance between C storage (S) and reserve consumption (C).

In this issue, Hikino et al. (2022) combine a rain exclusion experiment and a ^{13}C labeling experiment performed on mature trees in the

field, representing a new achievement in tree eco-physiology research. Furthermore, this experimental approach, applied at a large scale, facilitated the characterization of novel mechanisms in tree eco-physiology, such that belowground allocation of current photoassimilates covers only half of the C used for fine-root growth. Another enlightening example from the same research regards the sustained C allocation to root exudation, despite drought (Brunn et al., 2022). This finding corroborates observations from a more drought-exposed forest (Jakoby et al., 2020). Further, Hikino et al. (2022) show that 90% of C allocated to root exudation came from new photoassimilates after drought release, compared with 65% under control conditions. An increase in belowground C allocation, as Hikino et al. (2022) presented, might potentially increase soil C sequestration, leading to a net removal of atmospheric CO_2 .

Soil organic C (SOC) is primarily formed by (1) aboveground litter, (2) root litter, and (3) net rhizodeposition (organic C that remains after microbial utilization and decomposition in the rhizosphere; Villarino et al., 2021; Figure 1). Mycorrhizal fungi are among the highest contributors of organic C to the soil and might play a significant role in adding exudates and necromass to the net rhizodeposition. SOC can be divided into particulate (POC), and mineral-associated (MAOC) forms, where POC is more vulnerable to microbial decomposition and MAOC displays higher persistence. Rhizodeposition has the highest MAOC formation efficiency and root biomass input has the highest POC formation efficiency (Villarino et al., 2021). This finding is confirmed by a recent study revealing that residues from saprotrophic and mycorrhizal fungi contribute more to MAOC than plant residues (Klink et al., 2022). Despite the “priming effect” of root exudates (increased microbial activity leading to destabilization of already existing C pools), Panchal et al. (2022) suggest that the rhizosphere environment of forests can help to stabilize root exudates due to the accumulation of microbial biomass residues, leading to long-term sequestration.

As demonstrated well in Hikino et al. (2022), it is crucial to consider tree C allocation to predict C sequestration in the soil. Abiotic

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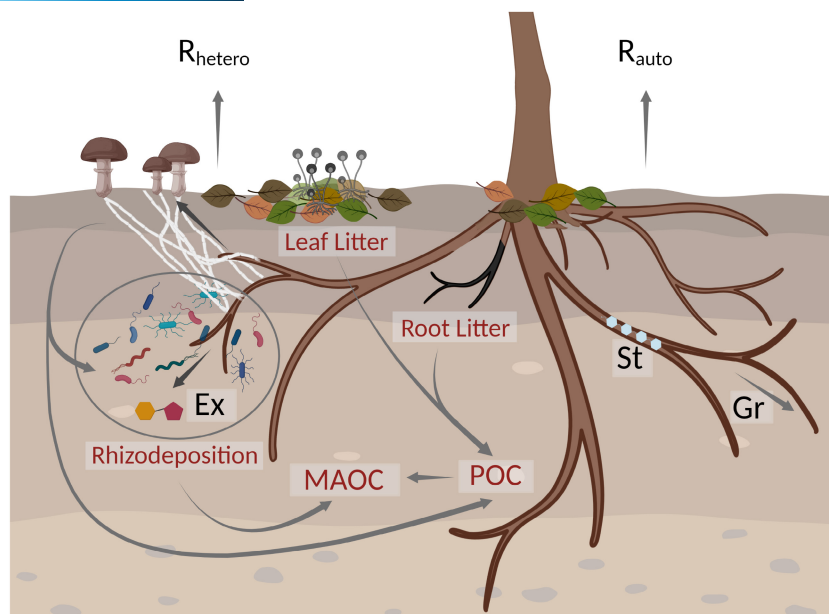


FIGURE 1 The fate of carbon belowground. A tree transfers C belowground in root growth (Gr), C storage (St), root exudation (Ex), and leaf and root litter. Microorganisms such as bacteria, mycorrhizal fungi, and saprophytic fungi use available C, from Ex and leaf and root litter. CO_2 is being emitted due to respiration (R) by these microorganisms (R_{hetero} = heterotrophic respiration) and also by root respiration (R_{auto} = autotrophic respiration). SOC (soil organic C) is formed in the soil as POC (particulate organic C) and MAOC (mineral-associated organic C). POC is primarily formed by litter residues, and MAOC is primarily formed by rhizodepositions. Created with BioRender (<https://biorender.com/>).

factors such as intensified drought, elevated atmospheric CO_2 ($e\text{CO}_2$) and warming are already influencing tree C fluxes. Jakoby et al. (2020) found an increase in the exudation rate during seasonal drought in a Mediterranean mixed forest. Similarly, oak trees in a greenhouse study showed an increased root exudation rate under drought treatment (Preece et al., 2018). Under $e\text{CO}_2$, enhanced C assimilation of pines increased root exudation (Dror & Klein, 2021). In a long-term soil warming experiment in a hardwood forest, different phases of C losses were found over 26 years due to warming. The study estimated that three-quarters of the total C loss occurred during the first 9 years due to high microbial activity (Melillo et al., 2017). After 6 years of microbial community reorganization (without increased C loss in warmed plots), soil respiration increased again until reaching another plateau. Overall, SOC dynamics are complex due to its sensitivity to warming and dynamic soil microbial communities.

After drought release in the combined rain exclusion- ^{13}C labeling experiment, fine root growth increased; however, no change in root exudation or ectomycorrhizae was found (Hikino et al., 2022). Because the more vulnerable POC might be formed first (Figure 1), the increase in root biomass might not contribute to a more stable belowground C pool. Even though rhizosphere processes are crucial for stable SOC formation, studies about root exudation and their role in the formation and stabilization of SOC are scarce. There is a severe lack of in situ studies on root exudation, partly because of the technical challenges of root exudation collection in natural ecosystems. In addition, studies on rhizosphere processes under global change scenarios are rare. In this matter, Hikino et al. (2022) lead the way forward. Still, research must be accelerated, considering the unknown

effects of global change on C allocation in the rhizosphere. Finally, the soil is not the ultimate last frontier. A large portion of tree roots can be found in the rock layer, where roots access additional mineral and water resources. Hence, future research should consider rhizosphere processes for C sequestration not only in the soil but also in the rock layer, which is even more challenging to access and study in natural environments.

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CONFLICT OF INTEREST

The authors declare no conflict of interests in preparation of this manuscript.

DATA AVAILABILITY STATEMENT

No data were used for this commentary.

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