



Tansley insight

Root effects on soil organic carbon: a double-edged sword

Author for correspondence:

Feike A. Dijkstra

Email: feike.dijkstra@sydney.edu.au

Received: 19 August 2020

Accepted: 19 October 2020

Feike A. Dijkstra¹ , Biao Zhu² and Weixin Cheng³

¹Sydney Institute of Agriculture, School of Life and Environmental Sciences, The University of Sydney, Camden, NSW 2570, Australia;

²Institute of Ecology, College of Urban and Environmental Sciences, Key Laboratory for Earth Surface Processes of the Ministry of Education, Peking University, Beijing 100871, China; ³Environmental Studies Department, University of California, Santa Cruz, CA 95064, USA

Contents

Summary	60	V. Conclusions	64
I. Introduction	60	Acknowledgements	64
II. Root-driven SOC stabilization	61	References	64
III. Root-driven SOC destabilization	61		
IV. The Rhizo-Engine framework	63		

New Phytologist (2021) **230**: 60–65

doi: 10.1111/nph.17082

Key words: microbial turnover, nutrient and water uptake, mineral associated organic carbon, rhizodeposition, rhizosphere priming effect, soil aggregation.

Summary

From recent developments on how roots affect soil organic carbon (SOC) an apparent paradox has emerged where roots drive SOC stabilization causing SOC accrual, but also SOC destabilization causing SOC loss. We synthesize current results and propose the new Rhizo-Engine framework consisting of two linked components: microbial turnover and the soil physicochemical matrix. The Rhizo-Engine is driven by rhizodeposition, root turnover, and plant uptake of nutrients and water, thereby accelerating SOC turnover through both stabilization and destabilization mechanisms. This Rhizo-Engine framework emphasizes the need for a more holistic approach to study root-driven SOC dynamics. This framework would provide better understanding of plant root effects on soil carbon sequestration and the sensitivity of SOC stocks to climate and land-use changes.

I. Introduction

The interplay between plant roots and the soil in which plant roots grow, often referred to as rhizosphere processes, has been a main research focus within the disciplines of plant and soil sciences. Ever since the concept rhizosphere was coined more than a hundred years ago (Hiltner, 1904), the definition of the *rhizosphere* (Box 1) has been constantly evolving and expanding and often been tailored to suit the context of individual studies (Luster *et al.*, 2009). For example, the spatial extent of the rhizosphere in some working definitions may range from a few millimeters of the root surface and, depending on root density, to as large as the entire rooting zone of all vegetated ecosystems on earth, harboring pivotal functions in the earth system. For instance, some estimates suggest that

rhizosphere processes at the global scale may release 3–10 times more CO₂ than fossil fuel burning by human activities (Hopkins *et al.*, 2013), or *c.* 30–60% of global primary production on land (Friedlingstein *et al.*, 2019), and fundamentally regulate many aspects of biogeochemical cycles (Finzi *et al.*, 2015). Given the recognized functional importance of the rhizosphere, understanding of how plant roots and associated rhizosphere processes may regulate the soil carbon (C) cycle, particularly in relation to climate change, has increasingly gained attention.

The root–soil organic carbon paradox

In general plant roots control and influence soil organic carbon (SOC) dynamics by providing organic C to the soil primarily in the

forms of root litter and rhizodeposition (Box 1). This C input results in SOC gain, particularly when plant roots promote SOC stabilization (Box 1). However, roots can also promote SOC destabilization (Box 1), exposing previously protected C to microbial decomposition causing SOC loss. In most cases, the role of plant roots contributing to SOC stabilization has been studied in isolation from their role in contributing to destabilization. As a consequence, there exists an apparent paradox (Fig. 1): results from studies on SOC stabilization by plant roots convincingly suggest that roots stabilize or increase SOC, and reduce SOC loss (Schmidt *et al.*, 2011; Slessarev *et al.*, 2020); whereas, an emerging body of results from other studies shows that plant roots destabilize SOC and accelerate SOC decomposition (Hartley *et al.*, 2012; Cheng *et al.*, 2014). In this Tansley insight we summarize key recent developments for both sides of this apparent paradox and provide a new framework integrating current knowledge about root effects on SOC dynamics.

II. Root-driven SOC stabilization

It has become increasingly clear that organic matter inputs from roots tend to contribute to SOC stabilization significantly more than aboveground plant inputs (Rasse *et al.*, 2005; Jackson *et al.*, 2017). The scope and fundamental mechanisms of root-driven SOC stabilization has been recently reviewed (Poirier *et al.*, 2018) and deliberated in terms of the three widely known SOC stabilization pathways, i.e. biochemical recalcitrance, mineral adsorption, and physical inaccessibility (or disconnect) (Sollins *et al.*, 1996; Schmidt *et al.*, 2011), and here we only highlight recent advances.

Recently, Lavalley *et al.* (2020) recommended to separate soil organic matter (SOM) into particulate organic matter (POM, Box 1) and mineral-associated organic matter (MAOM, Box 1). Root litter tends to be more recalcitrant than leaf litter (e.g. Xia *et al.*, 2015) and may therefore contribute more to POM, which could particularly accumulate in soil environments with low oxygen and temperature (e.g. arctic and alpine ecosystems), or once it is thermally altered by fire. However, SOM has usually a longer residence time once organic matter is stabilized through adsorption onto minerals forming MAOM (Lavalley *et al.*, 2020).

There is now mounting evidence that labile C inputs are particularly efficient in stabilizing C. In their Microbial Efficiency-

Matrix Stabilization (MEMS) framework Cotrufo *et al.* (2013) argued that MAOM is predominantly formed from microbial products. Because labile or 'high quality' plant C inputs are more efficiently transformed into microbial products than 'low quality' plant litter, more of the high-quality plant C inputs remain in the soil and ultimately are stabilized through sorption onto soil minerals. This has also been referred to as the microbial necromass 'entombing effect' (Liang *et al.*, 2017), and further suggests that SOC stabilization rates relate to microbial turnover rates. Recently, it was suggested that microbial products derived from rhizodeposition are more efficiently transformed into MAOM compared to microbial products derived from root and shoot litter (Sokol & Bradford, 2019; Sokol *et al.*, 2019). This entombing effect on stabilizing SOC from rhizodeposition may therefore be more prominent in ecosystems where there is greater production of labile C (or high energy yielding substrates) in the rhizosphere, such as in ecosystems with fast growing acquisitive plant species (Henneron *et al.*, 2020), and in ecosystems dominated by trees associated with arbuscular mycorrhizas than trees associated with ectomycorrhizas (Craig *et al.*, 2018).

Roots can contribute to SOC stabilization by forming soil aggregates thereby making SOC less accessible to microbial decomposition, but can also contribute to SOC destabilization through aggregate destruction, discussed later in section III. Root growth and death can further engineer the soil by altering the distribution of soil pores thereby affecting micro-environments for microbes to grow and influence both SOC stabilization and destabilization. For instance, using a combination of X-ray microtomography and micro-scale enzyme mapping it was shown that more diverse plant communities stimulated development of pores with 30–150 µm radii that had the largest enzyme activity, and it was suggested that those pores were particularly important for the production of microbially processed C and stabilization of soil C (Kravchenko *et al.*, 2019).

III. Root-driven SOC destabilization

While root-driven SOC stabilization is increasingly recognized, paradoxically SOC destabilization by plant roots has also emerged as a crucial aspect of soil C dynamics. The majority of published reports demonstrating SOC destabilization by plant roots is related

Box 1 Glossary

Mineral associated organic matter (MAOM): Organic matter adsorbed to soil minerals and thereby protected from further microbial decomposition.
Particulate organic matter (POM): Organic matter of partly undecomposed or charred plant litter and decomposed microbial products that are not adsorbed to soil minerals.

Rhizodeposition: organic material released from plant roots including exudates, sloughed cells and mucilage. It can also include mycorrhizal biomass depending on how it is measured (e.g. it is often included in carbon isotope-based methods).

Rhizosphere: the region of soil that is directly influenced by rhizodeposition, root growth and death, and nutrient and water uptake.

Rhizosphere priming effect (RPE): the stimulation (or occasionally suppression) of soil organic matter (SOM) decomposition by live roots and associated rhizosphere organisms when compared to SOM decomposition from rootless soils under the same environmental conditions.

Soil organic carbon (SOC) stabilization: any process that makes SOC persist longer and decompose at a much slower rate than the unstabilized SOC.
SOC destabilization: any process that activates stabilized SOC.

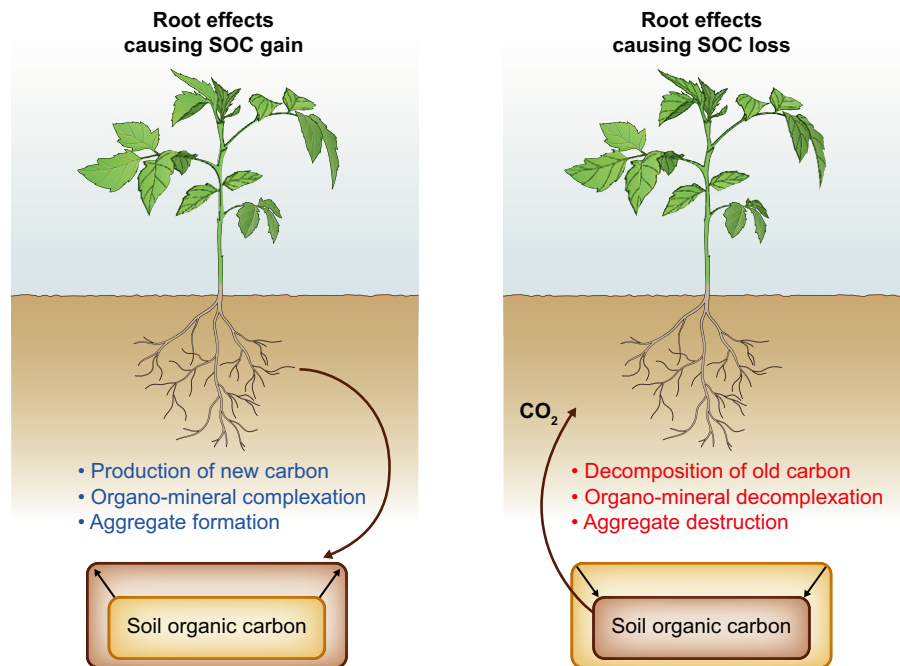


Fig. 1 The root–soil organic carbon (SOC) paradox. Roots can cause SOC stabilization (resulting in SOC gain) through formation of new carbon (C), and promotion of organo-mineral complexation and aggregate formation, but can also cause SOC destabilization (resulting in SOC loss) through enhancing old C decomposition, and promoting organo-mineral decomplexation and aggregate destruction.

to the phenomenon called rhizosphere priming effect (RPE, Box 1). While there are several hypotheses explaining the RPE, rhizodeposition is considered as one of the main factors, where it is used as a substrate by a specific set of microbes, thereby enhancing SOC decomposition by other microbes (Cheng *et al.*, 2014; Huo *et al.*, 2017). Similar to the entombing effect described earlier, the magnitude of the RPE is to a large degree controlled by rhizodeposition effects on microbial turnover (Yin *et al.*, 2019). The magnitude of SOC destabilization by plant roots as gauged by the RPE may range widely from 380% enhancement to 50% reduction as compared to the decomposition rates from root-free soils (Zhu & Cheng, 2011; Cheng *et al.*, 2014). In a study combining empirical values of the RPE, root morphology and distribution with a numerical model, it was suggested that root-driven SOC destabilization may account for one-third of the total SOC mineralization in temperate forest soils (Finzi *et al.*, 2015).

Besides these direct effects on microbial activity, rhizodeposition can also indirectly enhance the RPE by chemically liberating C and exposing fresh C to microbial decomposition. For instance, organic acids released by plants can break up bonds or 'bridges' between organic structures formed by polyvalent metals (iron (Fe), aluminum (Al) and calcium (Ca)) thereby destabilizing SOC and exposing smaller fragments to microbial decomposition (Clarholm *et al.*, 2015). Moreover, these organic acids produced by roots can destabilize MAOM, where organic acids liberate organic matter from mineral surfaces and increase their microbial access and decomposition (Keiluweit *et al.*, 2015).

As mentioned earlier, roots can form and destroy aggregates thereby exposing previously protected C to microbial decomposition (Six *et al.*, 2000). For instance, roots produce extracellular

polymeric substances that can enhance soil aggregation (Sher *et al.*, 2020), or take up water thereby intensifying drying–rewetting cycles in soils, which can result in breakage of existing aggregates and formation of new ones, particularly in more heavy-textured soils. In recent studies less aggregates were observed in soil grown with plants after a period of time, and where the net destruction in aggregates resulted in a RPE (Lu *et al.*, 2019; Wang *et al.*, 2020). However, a limitation with this approach is that roots not only destroy aggregates, but also form new aggregates, often in combination with mycorrhizal hyphae. While destruction of aggregates can result in enhanced decomposition of previously exposed SOC, formation of aggregates can incorporate and protect existing SOC as well as C from rhizodeposition. Therefore, net changes in soil aggregation induced by root growth underestimate the real contribution of aggregate turnover to SOC loss and SOC gain. Recently, rare earth oxides (REOs) were used to assess the turnover of aggregates in soil (Peng *et al.*, 2017). When combined with C isotope methods that can assess C sources and transformations, the REO tracing method would be a powerful method to link root-induced aggregate turnover to RPEs.

Uptake of nitrogen (N) by plant roots can further destabilize SOC by increasing microbial demand for N so that microbes use rhizodeposition to mine for N contained in SOM that is relatively rich in N (Craine *et al.*, 2007; Dijkstra *et al.*, 2013; Boilard *et al.*, 2019). Microbial mining for N causing enhanced SOC decomposition would particularly occur under conditions when available soil N (N that can be directly taken up by microbes) is low, although the opposite may also occur, where under low available N conditions competition for N between plants and microbes becomes more severe thereby reducing microbial activity and

SOC decomposition (Dijkstra *et al.*, 2013). Mining for N could potentially be more efficient with destabilization of MAOM, given that it is richer in N and has lower activation energies compared to POM (Lavalley *et al.*, 2020). Preference for root N uptake as ammonium cation (NH_4^+) over nitrate (NO_3^-) and exudation of organic acids that result in rhizosphere acidification, could further inhibit the RPE (Wang *et al.*, 2016; Wang & Tang, 2018).

IV. The Rhizo-Engine framework

From the earlier-mentioned, a picture emerges showing that plant roots strongly accelerate both SOC stabilization (resulting in SOC gain) and destabilization (resulting in SOC loss), illustrating the relevance of biological, chemical and physical mechanisms in the rhizosphere due to the action of rhizodeposition, root turnover, and uptake of nutrients and water (Hinsinger *et al.*, 2009). To better understand SOC dynamics in terrestrial ecosystems, we therefore argue that both SOC stabilization and destabilization mechanisms causing accelerated SOC turnover by plant roots need to be considered. Here we describe a new framework: the Rhizo-Engine framework (Fig. 2).

The Rhizo-Engine is driven by the three modes of plant action: rhizodeposition, root turnover, and uptake of nutrients and water. The 'Engine' has two key components or 'gears' that affect the rate of SOC stabilization and destabilization: the microbial turnover component, which includes microbial growth, death, and mycorrhizal interactions, and the physicochemical matrix component, which includes mechanisms related to organo-mineral complexation and soil structural and aggregate dynamics (but excludes biochemical recalcitrance mechanisms of SOC stabilization). The two components are linked together, where the microbial turnover is responsible for C decomposition and production of microbial necromass and other decomposition products, while the physicochemical matrix is directly responsible for SOC stabilization and destabilization. The microbial turnover is fueled by C from plant litter and rhizodeposition, but also gets its C from unprotected organic matter (i.e. POM not in aggregates including recycled microbial necromass), and protected organic matter (C in MAOM and aggregates) supplied by the physicochemical matrix. Some of the decomposition products from microbial turnover flows back into the unprotected SOC, but some of the C fuels the physicochemical matrix to stabilize and destabilize SOC.

Using this framework, we envision several potential scenarios (Fig. 3). In the first scenario, rhizodeposition and root action modes can accelerate the microbial turnover to increase decomposition and production of microbial products, but without affecting the physicochemical matrix. This scenario would occur where there is no potential to stabilize SOC into MOAM or aggregates, such as in sandy soils. Only unprotected SOC is affected by roots, and because C flowing in and out of this pool can be large, we refer to this as the *Susceptible* scenario (Fig. 3a). A second scenario, the *Destabilizing* scenario is where plant roots accelerate the microbial turnover and production of unprotected SOC, and accelerate SOC destabilization by the physicochemical matrix and subsequent decomposition by the microbial turnover component (Fig. 3b). This replacement of protected SOC with unprotected SOC could occur in soils that

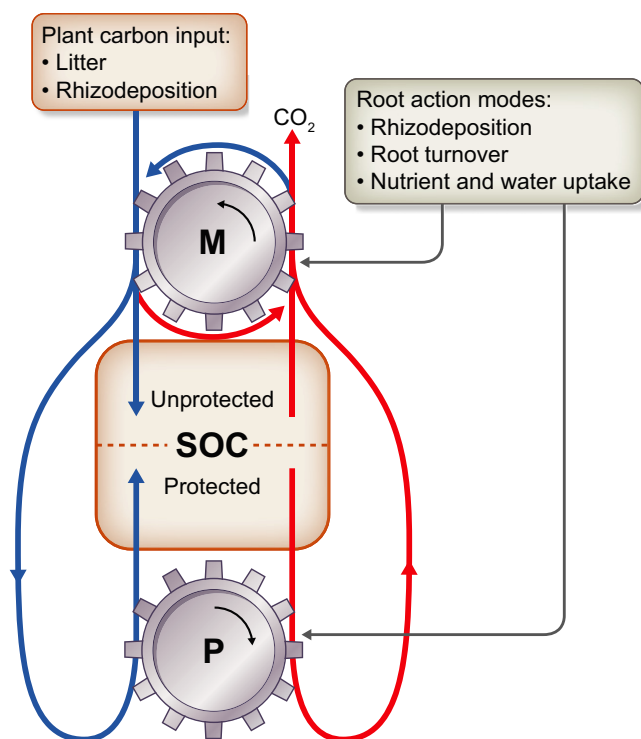


Fig. 2 The Rhizo-Engine framework. The Rhizo-Engine has two key components driving soil organic carbon (SOC) stabilization and destabilization: microbial turnover (M) and the physicochemical matrix (P), represented by the gray gears. The microbial turnover is fueled with carbon (C) from plant litter and rhizodeposition, but also from unprotected SOC (or C in particulate organic matter not protected in aggregates, including recycled microbial necromass) and protected SOC (C in mineral-associated organic matter and aggregates). The microbial turnover releases CO_2 , but also produces microbial necromass, which then flows into unprotected SOC pool or becomes a C source for the physicochemical matrix. The physicochemical matrix is directly responsible for stabilization of microbial necromass into protected SOC and destabilization of protected SOC. Destabilized SOC then fuels the microbial turnover. Both the microbial turnover and the physicochemical matrix are further affected by root action modes (gray arrows), including physical and chemical liberation of C in protected SOC by rhizodeposition, formation and destruction of aggregates by root turnover and water uptake, and acceleration or deceleration of microbial activity by nutrient uptake. Blue arrows represent C flows resulting in SOC gain; red arrows represent C flows resulting in C loss.

are C saturated, i.e. in soils where the maximum protective capacity through physicochemical pathways has been reached (Six *et al.*, 2002). By contrast, a third scenario, in soils where this maximum has not been reached yet, the *Stabilizing* scenario could occur, where plant roots accelerate stabilization of SOC, but at the same time can accelerate decomposition of unprotected SOC (Fig. 3c). A fourth scenario is where soils are C saturated, where plant roots continuously destabilize SOC, but at the same time replace the destabilized C with stabilization of new microbial products from microbial turnover. Because this scenario involves stabilization and destabilization of protected SOC only, we refer to this as the *Resistant* scenario (Fig. 3d).

We emphasize that potentially large changes in SOC stabilization and destabilization may be concealed by relatively smaller net changes in soil C pools, for instance, in response to climate and

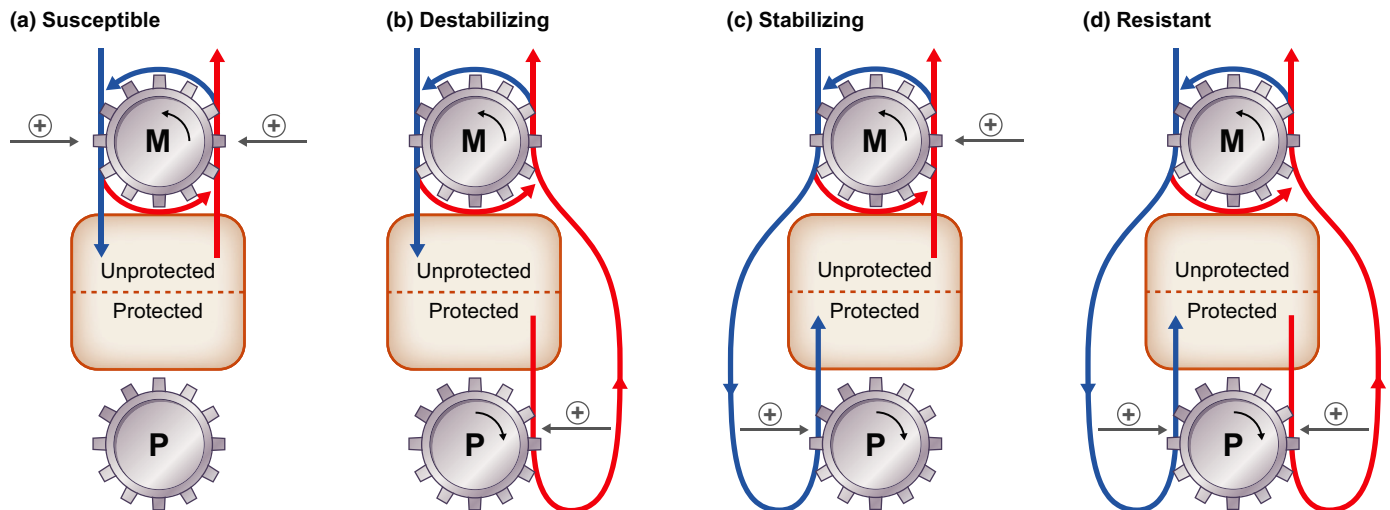


Fig. 3 Potential scenarios of root-driven soil organic carbon (SOC) dynamics. (a) *Susceptible* scenario: plant roots accelerate formation of unprotected SOC, for instance due to increased production of microbial necromass derived from rhizodeposition, and where plant roots also accelerate decomposition of unprotected SOC, for instance when rhizodeposition is used to increase SOC decomposition. Root-induced changes in formation and decomposition rates could be large, potentially resulting in a large net change in unprotected SOC. (b) *Destabilizing* scenario: plant roots accelerate formation of unprotected SOC as in the *Susceptible* scenario, and accelerate decomposition of protected SOC, for instance due to increased physical liberation of carbon (C) in organo-mineral complexes and enhanced aggregate destruction. In this scenario protected C is replaced by unprotected C. (c) *Stabilizing* scenario: plant roots accelerate formation of protected SOC, for instance due to an enhanced microbial necromass entombing effect in organo-mineral complexes and aggregates, and accelerate decomposition of unprotected SOC as in the *Susceptible* scenario. In this scenario unprotected C is replaced by protected C. (d) *Resistant* scenario: plant roots accelerate formation of protected SOC as in the *Stabilizing* scenario, and accelerate decomposition of protected SOC as in the *Destabilizing* scenario. Although root-induced changes in formation and decomposition of SOC could be small compared to the *Susceptible* scenario, this does not mean that the SOC pool in this scenario is inert. M, microbial turnover; P, physicochemical matrix. Blue arrows represent C flows resulting in SOC gain; red arrows represent C flows resulting in C loss; gray arrows are root action modes affecting the microbial turnover and physicochemical matrix.

land-use changes. Indeed, climate and land-use changes may have the potential to tip the balance between root-driven SOC stabilization and destabilization resulting in either long-term SOC accrual or depletion (Luo & Weng, 2011), where root-driven SOC stabilization should dominate in most aggrading ecosystems, while destabilization would dominate in degrading ecosystems. Furthermore, while plant roots may only cause small or no net changes in SOC pools, root-induced changes in SOC stabilization and destabilization may have important consequences for nutrient cycling. For instance, in the *Destabilizing* scenario plant roots could enhance net N mineralization and consequently plant N uptake, where decomposition of organic matter liberated by roots from MOAM relatively rich in N, could result in N mineralization rates larger than N immobilization caused by formation of relatively N-poor POM (Lavallee *et al.*, 2020). By contrast, root effects on SOC dynamics could disadvantage plants in terms of N uptake in the *Stabilizing* scenario by causing net N immobilization.

V. Conclusions

With our Rhizo-Engine framework, we highlight the double-edged sword effect that roots have on SOC dynamics, causing both stabilization or gain and destabilization or loss in SOC. Our framework does not specifically address how the balance between SOC stabilization and destabilization depends on factors such as plant economic traits (Henneron *et al.*, 2020), symbiotic relationships between plants and microbes (e.g. differences between arbuscular mycorrhizal and ectomycorrhizal plants (Craig *et al.*,

2018)), or environmental factors (Cheng *et al.*, 2014), which remain key areas for future research. However, we believe there is much need for understanding the relative importance of the different modes of action by which roots affect the magnitude of SOC stabilization and destabilization. Considering both stabilization and destabilization mechanisms will provide better understanding of how the Rhizo-Engine functions may aid actions for soil C sequestration, and new opportunities for understanding the sensitivity of SOC pools to climate and land-use changes.

VI. Acknowledgements

FAD and WC acknowledge the support from the Sydney Institute of Agriculture, University of Sydney, in the form of the Nancy Roma Paech Visiting Professorship in Agriculture. BZ acknowledges the support from the National Natural Science Foundation of China (31988102).

ORCID

Weixin Cheng <https://orcid.org/0000-0003-2964-2376>
Feike A. Dijkstra <https://orcid.org/0000-0002-6191-6018>
Biao Zhu <https://orcid.org/0000-0001-9858-7943>

References

- Boilard G, Bradley RL, Paterson E, Sim A, Brown LK, George TS, Bainard L, Carubba A. 2019. Interaction between root hairs and soil phosphorus on

- rhizosphere priming of soil organic matter. *Soil Biology and Biochemistry* 135: 264–266.
- Cheng W, Parton WJ, Gonzalez-Meler MA, Phillips R, Asao S, McNickle GG, Brzostek E, Jastrow JD. 2014. Synthesis and modeling perspectives of rhizosphere priming. *New Phytologist* 201: 31–44.
- Clarholm M, Skjellberg U, Rosling A. 2015. Organic acid induced release of nutrients from metal-stabilized soil organic matter – the unbutton model. *Soil Biology and Biochemistry* 84: 168–176.
- Cotrufo MF, Wallenstein MD, Boot CM, Denef K, Paul E. 2013. 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? *Global Change Biology* 19: 988–995.
- Craig ME, Turner BL, Liang C, Clay K, Johnson DJ, Phillips RP. 2018. Tree mycorrhizal type predicts within-site variability in the storage and distribution of soil organic matter. *Global Change Biology* 24: 3317–3330.
- Craine JM, Morrow C, Fierer N. 2007. Microbial nitrogen limitation increases decomposition. *Ecology* 88: 2105–2113.
- Dijkstra FA, Carrillo Y, Pendall E, Morgan JA. 2013. Rhizosphere priming: a nutrient perspective. *Frontiers in Microbiology* 4: 216.
- Finzi AC, Abramoff RZ, Spiller KS, Brzostek ER, Darby BA, Kramer MA, Phillips RP. 2015. Rhizosphere processes are quantitatively important components of terrestrial carbon and nutrient cycles. *Global Change Biology* 21: 2082–2094.
- Friedlingstein P, Jones MW, O'Sullivan M, Andrew RM, Hauck J, Peters GP, Peters W, Pongratz J, Sitch S, Le Quéré C *et al.* 2019. Global carbon budget 2019. *Earth System Science Data* 11: 1783–1838.
- Hartley IP, Garnett MH, Sommerkorn M, Hopkins DW, Fletcher BJ, Sloan VL, Phoenix GK, Wookey PA. 2012. A potential loss of carbon associated with greater plant growth in the European Arctic. *Nature Climate Change* 2: 875–879.
- Henneron L, Cros C, Picon-Cochard C, Rahimian V, Fontaine S. 2020. Plant economic strategies of grassland species control soil carbon dynamics through rhizodeposition. *Journal of Ecology* 108: 528–545.
- Hiltner L. 1904. Über neuere Erfahrungen und Probleme auf dem Gebiete der Bodenbakteriologie unter besonderer Berücksichtigung der Gründüngung und Brache. *Arbeiten der Deutschen Landwirtschaftlichen Gesellschaft* 98: 59–78.
- Hinsinger P, Bengough AG, Vetterlein D, Young IM. 2009. Rhizosphere: biophysics, biogeochemistry and ecological relevance. *Plant and Soil* 321: 117–152.
- Hopkins F, Gonzalez-Meler MA, Flower CE, Lynch DJ, Czimczik C, Tang J, Subke JA. 2013. Ecosystem-level controls on root-rhizosphere respiration. *New Phytologist* 199: 339–351.
- Huo C, Luo Y, Cheng W. 2017. Rhizosphere priming effect: a meta-analysis. *Soil Biology and Biochemistry* 111: 78–84.
- Jackson RB, Lajtha K, Crow SE, Hugelius G, Kramer MG, Piñeiro G. 2017. The ecology of soil carbon: pools, vulnerabilities, and biotic and abiotic controls. *Annual Review of Ecology, Evolution, and Systematics* 48: 419–445.
- Keiluweit M, Bougoure JJ, Nico PS, Pett-Ridge J, Weber PK, Kleber M. 2015. Mineral protection of soil carbon counteracted by root exudates. *Nature Climate Change* 5: 588–595.
- Kravchenko AN, Guber AK, Razavi BS, Koestel J, Quigley MY, Robertson GP, Kuzyakov Y. 2019. Microbial spatial footprint as a driver of soil carbon stabilization. *Nature Communications* 10: 3121.
- Lavallee JM, Soong JL, Cotrufo MF. 2020. Conceptualizing soil organic matter into particulate and mineral-associated forms to address global change in the 21st century. *Global Change Biology* 26: 261–273.
- Liang C, Schimel JP, Jastrow JD. 2017. The importance of anabolism in microbial control over soil carbon storage. *Nature Microbiology* 2: 17105.
- Lu J, Dijkstra FA, Wang P, Cheng W. 2019. Roots of non-woody perennials accelerated long-term soil organic matter decomposition through biological and physical mechanisms. *Soil Biology and Biochemistry* 134: 42–53.
- Luo Y, Weng E. 2011. Dynamic disequilibrium of the terrestrial carbon cycle under global change. *Trends in Ecology and Evolution* 26: 96–104.
- Luster J, Göttlein A, Nowack B, Sarret G. 2009. Sampling, defining, characterising and modeling the rhizosphere – the soil science tool box. *Plant and Soil* 321: 457–482.
- Peng X, Zhu Q, Zhang Z, Hallett PD. 2017. Combined turnover of carbon and soil aggregates using rare earth oxides and isotopically labelled carbon as tracers. *Soil Biology and Biochemistry* 109: 81–94.
- Poirier V, Roumet C, Munson AD. 2018. The root of the matter: linking root traits and soil organic matter stabilization processes. *Soil Biology and Biochemistry* 120: 246–259.
- Rasse DP, Rumpel C, Dignac MF. 2005. Is soil carbon mostly root carbon? Mechanisms for a specific stabilisation. *Plant and Soil* 269: 341–356.
- Schmidt MWI, Torn MS, Abiven S, Dittmar T, Guggenberger G, Janssens IA, Kleber M, Kogel-Knabner I, Lehmann J, Manning DAC *et al.* 2011. Persistence of soil organic matter as an ecosystem property. *Nature* 478: 49–56.
- Sher Y, Baker NR, Herman D, Fossum C, Hale L, Zhang X, Nuccio E, Saha M, Zhou J, Pett-Ridge J *et al.* 2020. Microbial extracellular polysaccharide production and aggregate stability controlled by switchgrass (*Panicum virgatum*) root biomass and soil water potential. *Soil Biology and Biochemistry* 143: 107742.
- Six J, Conant RT, Paul EA, Paustian K. 2002. Stabilization mechanisms of soil organic matter: implications for C-saturation of soils. *Plant and Soil* 241: 155–176.
- Six J, Elliott ET, Paustian K. 2000. Soil macroaggregate turnover and microaggregate formation: a mechanism for C sequestration under no-tillage agriculture. *Soil Biology and Biochemistry* 32: 2099–2103.
- Slessarev EW, Nuccio EE, McFarlane KJ, Ramon CE, Saha M, Firestone MK, Pett-Ridge J. 2020. Quantifying the effects of switchgrass (*Panicum virgatum*) on deep organic C stocks using natural abundance ¹⁴C in three marginal soils. *GCB – Bioenergy* 12: 834–847.
- Sokol NW, Bradford MA. 2019. Microbial formation of stable soil carbon is more efficient from belowground than aboveground input. *Nature Geoscience* 12: 46–53.
- Sokol NW, Kuebbing SE, Karlsen-Ayala E, Bradford MA. 2019. Evidence for the primacy of living root inputs, not root or shoot litter, in forming soil organic carbon. *New Phytologist* 221: 233–246.
- Sollins P, Homann P, Caldwell BA. 1996. Stabilization and destabilization of soil organic matter: mechanisms and controls. *Geoderma* 74: 65–105.
- Wang X, Dijkstra FA, Yin L, Sun D, Cheng W. 2020. Rhizosphere priming effects in soil aggregates with different size classes. *Ecosphere* 11: e03027.
- Wang X, Tang C. 2018. The role of rhizosphere pH in regulating the rhizosphere priming effect and implications for the availability of soil-derived nitrogen to plants. *Annals of Botany* 121: 143–151.
- Wang X, Tang C, Severi J, Butterly CR, Baldock JA. 2016. Rhizosphere priming effect on soil organic carbon decomposition under plant species differing in soil acidification and root exudation. *New Phytologist* 211: 864–873.
- Xia M, Talhelm AF, Pregitzer KS. 2015. Fine roots are the dominant source of recalcitrant plant litter in sugar maple-dominated northern hardwood forests. *New Phytologist* 208: 715–726.
- Yin L, Corneo PE, Richter A, Wang P, Cheng W, Dijkstra FA. 2019. Variation in rhizosphere priming and microbial growth and carbon use efficiency caused by wheat genotypes and temperatures. *Soil Biology and Biochemistry* 134: 54–61.
- Zhu B, Cheng W. 2011. Rhizosphere priming effect increases the temperature sensitivity of soil organic matter decomposition. *Global Change Biology* 17: 2172–2183.