Panchal, Poonam; Preece, Catherine; Peñuelas, Josep; [et al.]. «Soil carbon sequestration by root exudates». Trends in Plant Science, Vol. 27, issue 8 (August 2022), p. 749-757. DOI 10.1016/j.tplants.2022.04.009

Soil carbon sequestration by root exudates

Poonam Panchal[1], Catherine Preece[2,3], Josep Peñuelas[3,4] and Jitender Giri[1]*

1. National Institute of Plant Genome Research, Aruna Asaf Ali Marg, New Delhi 110067, India

2. Plants and Ecosystems (PLECO), Biology Department, University of Antwerp, BE-2610 Wilrijk, Belgium

3. CREAF, Cerdanyola del Vallès 08193, Catalonia, Spain

4. CSIC, Global Ecology Unit CREAF-CSIC-UAB, Bellaterra 08193, Catalonia, Spain

***Correspondence:** jitender@nipgr.ac.in

Keywords: Root exudates, soil organic carbon, labile, ecosystems, microorganisms, rhizosphere

Abstract

Root exudates are well-known "labile" sources of soil carbon that can prime microbial activity. Recent investigations suggest that stability of labile carbon inputs in soil mostly depends upon the physical, chemical and biological properties of the surroundings. Here, we propose that in some ecosystems such as forests and grasslands, root exudates can function as a source of soil carbon that can be stabilized through various mechanisms leading to long-term sequestration. Increasing soil carbon sequestration is important for capturing atmospheric CO_2 and combating climate change issues. Thus, there is an urgent need to preserve the existing ecosystems to adopt strategies like afforestation, reforestation and establishment of artificial grasslands to foster carbon sequestration through higher root exudate inputs in the soil.

Greenhouse gas emissions-a global concern

The annual United Nations climate change conference- **COP**26 (Conference of Parties) (See glossary) recently took place in Glasgow, UK (2-11 November, 2021) (https://ukcop26.org). One of its prime goals was to work towards the strict compliance of the Paris agreement-COP21, which was signed by more than 170 countries. These countries are required to work towards the reduction of greenhouse gas (GHG) emissions in such a way that global warming can be limited to less than 2 ^{0}C compared to the pre-industrial temperature level. Following this policy, an international initiative was launched on 1st December 2015 and it was termed as the "**4 per 1000 initiative**". This initiative aims to increase soil carbon assets by 0.4% annually, within the top 30-40 cm layer of soil of agricultural fields, grassland and forests (https://www.4p1000.org) [1,2]. Some of the joint statements and declarations during COP26 were actually launched for the purpose of practically working towards increasing carbon sequestration (https://ukcop26.org). Soil contains around 2500 gigatons (Gt) of carbon which is far more abundant than that in the atmosphere [3]. The addition of more organic carbon in the soil should result in net removal/reduction of carbon dioxide (CO_2), a common GHG, from the environment. A crude calculation by Kell, (2012) indicates that around 10% additional CO_2 sequestered in soil may result in up to 20% removal of CO_2 from the atmosphere [4]. Thus, increasing organic carbon content in soil is an important process to mitigate climate changes due to CO_2 emission from various natural and **anthropogenic activities**.

A number of artificial and natural routes can lead to the sequestration of atmospheric carbon into the soil. Common artificial processes are many, and include **afforestation**, **reforestation**, **natural regeneration**, **reduced impact logging** (RIL), minimum or no tillage, mulch farming, growing perennial crops, judicious nutrient management and manuring, cover residue management, cover cropping, rotational grazing and judicious application of irrigation water [5–7]. Natural processes include plant litter deposition, accumulation of soil microorganism biomass, plant root debris accumulation and root exudation [8,9]. Earlier studies have shown that the belowground carbon inputs are much more important sources of stable soil organic carbon (**SOC**), compared to aboveground inputs [9–11]. However, the contribution of carbon-rich **root exudates** in **soil carbon sequestration** has not been the focus of much research, perhaps due to the counter effects of microbial processes and the "priming effect". The priming effect counters the net stability of root exudates in the soil making them a transient or "labile" source of SOC. In this opinion article, we compare the utility of root exudates in enhancing soil carbon content in three ecosystems: agricultural lands (croplands), forests and grasslands. We further highlight the potential of forests and grasslands in increasing soil carbon pools by root exudation of organic carbon compounds. We argue that various properties of the soil and the plant root exudates help to stabilize these compounds within the soil, thus, helping to increase the pool of SOC in the soil of these ecosystems. Therefore, preserving and protecting these ecosystems might significantly add to the SOC content via deposition and stabilization of plant root exudates.

The paradox of soil carbon sequestration by root exudates

A significant amount of soil carbon input comes from below-ground plant processes [9,10,12] (Figure 1A-C). Photosynthetically fixed carbon is deposited within the **rhizosphere** primarily as root biomass, exudates and microbial biomass as soil organic matter (SOM). It has recently been pointed out that there is a "paradox" between stabilization and destabilization of SOC due to plant root-associated processes, including the process of root exudation [13]. A number of studies have categorized root exudates as a "labile" form of SOC [14–18]. Here, it is important to define the term labile in the context of plant root exudates, which indicates that they are easily broken down by soil microorganisms. Freshly added root exudates, can increase SOC utilization by increasing microbial activities in the rhizosphere, leading to a significant amount of CO_2 release in the atmosphere. These freshly added carbon compounds can thus lead to the destabilization of already existing carbon pools in the soil, a phenomenon known as the "priming effect" [19]. Interestingly, a few other studies state that despite the visible priming effect, freshly added carbon can still contribute to higher net SOC [20,21]. Multiple factors influence the effect of root exudates on SOC stabilization or SOC replenishment. These include soil texture, species richness, microbial composition (numbers and diversity), C:N ratio of added compounds, relative ratio of rhizosphere and **bulk soil**, nutrient availability, climate and already existing C pools in the soil [9,10,20,22–24]. Thus, the extent to which root exudates can cause "positive" or "negative" priming effects in the rhizosphere predominantly determines their role in soil carbon liberation or sequestration, respectively [25].

Root exudates encompass the majority of non-volatile rhizodeposits and include an abundance of soluble organic compounds like sugars, amino acids and organic acids [26]. Both low molecular weight root exudates and mucilages can be used as a carbon source for the microbial community [26]. A number of studies have investigated the role of important root exudate compounds in SOC stabilization. For instance, Landi *et al*. used exogenous application of glucose and oxalic acid, compounds frequently present in root exudates, to study the CO_2 emission induced by the forest soil microbial community. Their analysis suggested that the addition of oxalic acid caused a more pronounced **positive priming effect** compared to glucose [27]. Keiluweit *et al*. used ^{13}C-labelled artificial exudates along with an artificial root system to mimic natural soil conditions. Despite having slight differences in the methods used, their study also indicated that oxalic acid causes higher respiration compared to glucose [28]. Similarly, Luo *et al*. tested the respiration rates in soil samples of various biotopes, amended with glucose, citric acid and oxalic acid, however, they obtained conflicting results [29]. The highest respiration rate was obtained for glucose amendments, while oxalic acid amendments did not cause a positive priming effect among the various biotopes used. Here, the question arises of why the same components show contrasting results in terms of SOC stabilization? Recently, some groups have argued that the stability of organic carbon added to the soil is largely influenced by the nature and properties of the soil and the below ground ecosystem, and is less dependent upon the chemistry of the added compounds [8,30,31]. For instance, organic acids like oxalic acid can form stable SOC components by binding to aluminium and iron oxides [17,32], while in contrast they can also demineralize existing SOC pools [28]. Thus, it may depend upon the aluminium/iron oxide content and the other properties of the soil in the particular ecosystem.

The involvement of soil microorganisms is also important in terms of the SOC stability. Root exudates are well-known for attracting soil microorganisms within the rhizosphere [33]. The accumulation of microorganisms may either lead to SOC destabilization through increased respiration or SOC stabilization due to accumulation of microbial biomass residues (necromass) [24,34,35]. Under this scenario, it is worth doing a comparative study on the role of root exudates in SOC formation and stabilization, between the major ecosystems on Earth. While anthropogenic activities in agricultural land can directly or indirectly affect net SOC gain or stabilization, grasslands and forests can be habitats where net soil carbon sequestration by root exudates is feasible [7,36–39].

SOC sequestration in agricultural lands is highly affected by anthropogenic activities

One of the major sources of GHG emission is agricultural land, contributing up to 10.3% of total GHG (https://ourworldindata.org/emissions-by-sector). While the current COVID19 pandemic situation has led to a temporary decrease in worldwide GHG emission by sectors like power, industry, surface transport and aviation, there are still no signs of reduction in the emissions by the agricultural and forestry sector [40,41]. Agricultural soils can accumulate a significant amount of organic carbon, while at the same time fulfilling the ever-increasing global food demands [42]. The total SOC content of agricultural land and managed areas is around 160.2 Gt [43] . However, many agricultural practices such as soil tillage, removal of crop litter, and deep ploughing lead to increased mineralization of labile SOC [42]. Indeed, there is recent experimental evidence showing SOC stabilization following “no tillage” adoption [44]. Also, the flooding associated with rice cultivation usually results in higher GHG emission from soils [45]. There is evidence that the conversion of natural ecosystems to cultivated ones has significantly reduced earth’s soil carbon pools [3,8]. Pausch *et al*. showed that annual crop species allocate a lower amount of belowground carbon compared to grass and tree species (Figure 1A) [46]. The SOC accumulation in the form of fungal and bacterial biomass is also smaller than in forests and grasslands (Table S2). Moreover, the intense application of chemical fertilizers might lead to higher GHG emissions and eutrophication which can revert the overall effect of SOC sequestration by root exudation or any other natural modes of carbon sequestration (plant litter and microbial necromass deposition) [47]. Thus, despite having a very high carbon sink capacity due to its relatively high productivity, agricultural land is often a poor candidate for soil carbon sequestration. This could explain the decrease in soil organic matter on intensely farmed agricultural land since the ‘green revolution’ in the middle of the last century [48].

Root exudates can help to sequester carbon in forests

Forest soils sequester more soil carbon when compared to cropland soils [4]. The SOC content in forests is around 702 Gt for soil layers up to 100 cm, which is further divided into the topsoils, 0-30 cm (342.6) and subsoils, 30-100 cm (359.5) [43]. Forests can be sub-divided into five major biomes- boreal, polar, temperate, subtropical and tropical. Among these five biomes, tropical forests cover 45% of total forested land [49]. The quantitative data on SOC content in the top 100 cm soil of tropical, temperate and boreal forest suggests that tropical forests contain around 214–435 Gt of SOC, while temperate and boreal forest soils contain up to 153–195 Gt and 338 Gt, respectively [50]. However, there exists a very high uncertainty regarding the SOC content below 100 cm depth in these biomes [50]. Emissions of CO_2 due to the positive priming effect were found to be lower in soils of tropical forests than in other ecosystems such as drylands and croplands [31]. The **negative priming effect** in the soil of tropical forests seems to be a function of their higher initial SOC content. When a **labile carbon** source is added to these soils, the **apparent priming effect** rarely shows up due to the lower microbial turnover activity. Interestingly, these results were obtained by comparing the various factors affecting the priming, such as climate, soil properties and microbial composition of tropical forests, which seem to be favorable for SOC stabilization [31]. Another study suggests that while a single addition of labile carbon may induce a positive priming effect, the continuous addition of root exudates leads to net SOC retention in tropical forest soils [51]. Very few studies have analyzed root exudate composition from tree species probably because of the difficulties in the sampling of exudates from their roots. However, the quantity of carbon added to the soil by trees in the form of root exudates is more than that of crops and grasses (Figure 1A-C, Table S1). Microorganisms such as fungi contribute to stable SOC formation using labile carbon sources [52]. Interestingly, soils of boreal, tropical and temperate forests carry high fungal biomass compared to grasslands and croplands [31,53,54]. Soils of boreal and temperate forests are abundant in slow-decomposing ectomycorrhizal fungi, helping to stabilize recalcitrant SOC, while the tropical and sub-tropical forest soils are rich in arbuscular mycorrhizal fungi biomass that are involved in fast SOC turnover [55]. However, the experimental addition of root exudates in the arbuscular mycorrhizal fungi-dominant forests caused lower priming compared to ectomycorrhizal fungi-dominant forests due to higher physical protection of SOC [56]. Thus, the combination of a lower positive priming effect and higher SOC formation by the fungal population using carbon sources provided by root exudates could lead to accumulation of SOC from root exudates in these forest ecosystems.

SOC is often subdivided into two types- Particulate Organic Carbon (**POC**) and Mineral Associated Organic Carbon (**MAOC**) [57]. While the POC fraction of SOC is much more vulnerable to microbial decomposition, the MAOC displays higher persistence due to protection by mineral association [58]. Root exudates are important in the formation of MAOC stock building in soil with high nitrogen content [21,59] (Figure 1D). The abundant stocks of nitrogen in tropical soils can efficiently support MAOC formation in these soils [60]. Macroaggregate formation is well-known to facilitate carbon retention in soil [61]. Root exudates can instigate macroaggregate formation in tropical forest soils with the help of their high clay composition [62–64] (Figure 1D). Polysaccharides including sugar molecules like rhamnose, galactose, arabinose, xylose, mannose and glucose are the "sticky" components found in extracts of mucilages, that help in the stabilization of soil aggregates (Table S1) [65–67]. This phenomenon of SOC formation through high quality labile root litter, termed the "soil centered" approach, leads to long term stabilization (>10 years) compared with stabilization through the recalcitrant "litter-centered" approach (1-10 years) [68]. In this way, root exudates can both increase and stabilize the forest SOC content using the surrounding soil properties.

Role of root exudates in carbon sequestration in grasslands

Just like forests, grasslands also represent a natural reserve of SOC. Grasslands contain around 439 Gt of SOC [44]. Grasses exude a plethora of organic compounds with organic acids and amino acids as relatively abundant forms [69]. A positive correlation between root exudation and SOC accumulation was shown in an experiment that manipulated grassland biodiversity. The grasslands with higher species richness showed higher SOC accumulation [24]. The study also indicated that since root exudates drive SOC accumulation by attracting micro-organisms, the carbon storage in soil was mostly due to accumulation of microbial residues [24].

The soil microbial content in grasslands shows a higher range of variation as compared to forests and croplands. While one study found a higher proportion of bacterial biomass, and so lower proportion of fungal biomass, in grasslands compared with forests and croplands [53], another study showed that grasslands carry intermediate proportions of bacterial biomass (Table S2) [54]. However, the fungal and bacterial biomass is appreciably high in **pasture lands** [54]. It is hypothesized that the belowground biomass of dead roots and microbial necromass carrying the recalcitrant sources of SOC are stabilized by the processes of aggregation and chemical bonding to the mineral soil matrix. This process is known as the microbial efficiency-matrix stabilization (MEMS) framework, which requires the involvement of labile carbon sources such as root exudates [22,70,71]. The high water holding capacity of mucilages further helps in this aggregation process [72]. SOC formation from dead roots is much more efficient in the deeper soils of grasslands, as compared to forests [73]. The possible reason could be the higher age and rigidity of tree roots compared to the roots of grasses. Though the tree roots are a more recalcitrant reservoir of C, they are mostly accumulated in the top layers of soil and the top layers are more prone to decomposition. The grass roots, on the other hand, form a dense network of fine roots in deeper soils which leads to slower decomposition [74]. Further, the recalcitrance of tree roots usually leads to short term stabilization, while the fine roots of grasses increase SOC stabilization in the longer term through the reaction of microbial products with mineral surfaces in the rhizosphere (for more details please see [68]). Also, The dense vegetation in grasslands with higher species richness also results in lower evaporation rates, thus mitigating the climate effect on SOC decomposition [24].

Another study showed that following the pattern of tropical forest, grassland soils also displayed a net negative priming effect after the addition of fresh carbon sources [31]. The reason for the SOC stabilization could be high iron and aluminium oxide content in grassland soils (like Savannahs and Tibetan Alpine grasslands), which leads to mineral protection of labile SOC [75,76]. A significant amount of carbon may be added by root exudates to the grasslands during grazing. There is considerable evidence which suggests that grazing stimulates fine root exudation from C4 grasses and adds to the SOC [77–80]. Overall, the top 0-20 cm layer soil of grazing grasslands, which is closely associated with the roots, carries a high SOC density [81] and the higher SOC content is positively related to the higher total nitrogen content in grasslands [82].

Recently, a decade long experimental set up was used to test the utility of **biochar** amendment in increasing the stability of exudates in ferralsols, a common soil type in the grasslands of tropical and sub-tropical regions. They found that biochar can stabilize labile carbon from freshly-added ryegrass root exudates, by enhancing organo-mineral interactions [83]. Further, biochar can increase both POC and MAOC content in ferralsols. The narrow rhizosphere to bulk soil ratio

(~1/4) in the top soil of the grasslands is the key to the stable MAOC formation by the root exudates compared to ecosystems where rhizosphere to bulk soil ratio widens (>1/10), owing to higher root exudates inputs in the rhizosphere [9]. A few other studies have also supported the effectiveness of biochar in stabilizing SOC built-up by root exudates due to negative priming in the long term [84,85]. Natural biochar can comprise up to 40% of grassland and boreal forest SOM content [30]. Additional inputs of "naturally generated" biochar along with natural exudation processes are efficacious processes in SOC sequestration in tropical and sub-tropical grasslands and pasture lands (Figure 1D).

Concluding remarks and future perspectives

Root exudates are highly rich in organic compounds. However, studies into their potential roles in SOC formation and stabilization largely remain elusive. While human interference has led to disturbances to the SOC pools of agricultural lands, forests and grasslands appear to be much more promising in terms of achieving high soil carbon sequestration [7,36–39] . Most terrestrial soils are far from carbon saturation, and in many places, roots can reach up to several meters in the soil with exudates able to penetrate even further, and so can function in increasing SOC pools [4]. Thus, restoring and preserving degraded tropical forests and grasslands, identifying and sowing seeds of rich root biomass species that can secrete abundant amounts of carbon compounds, addition of naturally generated biochar, and establishment of pasture lands are some of the important practices to enhance SOC sequestration via root exudates in these ecosystems.

It is also important to consider the technical issues for the study of root exudates in soil carbon sequestration in natural ecosystems. There is a severe lack of *in situ* studies of root exudates [86,87]. These in *situ* experiments may give a more realistic picture of how root exudates add to

SOC pools in forests and grasslands. While the analysis of exudates from short-term experiments in controlled conditions is comparatively simple, the sampling and analysis of exudates from older plants in their native conditions is a technically demanding process which has resulted in a dearth of data regarding the actual composition of root exudates in soil [88–91]. Most exudate studies are based on samples collected in hydroponics and more research is needed to identify the composition of root exudates in real soil [92]. The use of stable ^{13}C tracer techniques, to measure root exudates derived from SOC is a better approach compared to the use of artificial exudates within artificial experimental setups, as it can measure net accumulation of root exudates in the rhizosphere and is not biased towards any specific components [91,93–96]. Many studies have used breeding and genetically modified plants for the past two decades to increase their resistance towards multiple stress conditions through increased root exudation [33,97–99]. Similar approaches could be tested for native plant species of forests and grasslands to increase SOC in these ecosystems through root exudate deposition. In this way, the goals of dealing with climate change, in addition to increasing food security, might be achieved with the help of cultivars with higher root exudation **(See outstanding question)**.

Glossary

4 per 1000 initiative- An initiative started by the French government at the COP21, Paris climate summit in 2015 with the purpose of increasing soil carbon by 0.4% each year to deal with climate change and increase food security.

Afforestation- It is the establishment of a forest or stand of trees (forestation) in an area where there was no previous tree cover.

Anthropogenic activities- Human activities.

Apparent priming effect- The change in emission of CO_2 due to microbial decomposition/respiration after addition of labile carbon compounds in the soil.

Biochar- Charcoal-like substance produced from burnt plant matter.

Bulk soil- Soil other than the rhizosphere.

COP- Conference of parties is the decision-making body responsible for monitoring and reviewing the implementation of the United Nations Framework Convention on Climate Change.

Labile carbon pools- The fraction of soil organic carbon which can be broken down very quickly (e.g. during respiration of microorganisms) as compared to the other stable part of SOC

MAOC-Mineral associated organic carbon. Organic carbon that is associated with soil minerals. These associations help to stabilize organic carbon.

Natural regeneration- Renewal of forest trees by self-sown seeds, coppice or root suckers

Negative priming effect- Addition of labile carbon compounds leads to decrease in soil organic matter mineralization

Pasture lands-Grasslands used for grazing by domesticated animals

POC- Particulate Organic Carbon. A part of organic carbon which is made up of small particles and is partially undecomposed. It is not associated with minerals.

Positive priming effect- Addition of labile carbon compounds leads to increase in soil organic matter mineralization.

Reduced impact logging (RIL)- Careful planning of timber harvest, which results in lower impact on environment as compared to conventional logging methods.

Reforestation- The process of replanting trees in areas that have been affected by natural disturbances like wildfires, drought, and insect and disease infestations — and unnatural ones like logging, mining, agricultural clearing, and development.

Rhizosphere- Soil closely associated with the plant roots.

Root exudates- Root exudates refer to a suite of substances in the rhizosphere that are secreted by the roots of living plants and microbially modified products of these substances. They consist of low- and high-molecular-weight organic compounds that are passively and actively released.

Soil carbon sequestration- The addition of atmospheric carbon into the soil, resulting in net decrease in carbon dioxide in atmosphere.

SOC- Soil organic carbon. The measurable part of soil organic matter. Soil organic carbon comes actively or passively from plants, animals and microorganisms

Acknowledgments

PP acknowledges the research fellowship from UGC, India, and Newton Bhabha PhD placement fellowship from DBT, India, and the British Council, UK. JG acknowledges Swarna Jayanti Fellowship (DST/SJF/LSA-02/2018–19) from DST, India. CP acknowledges the research fellowship of the Research Foundation – Flanders (FWO), CP and JP acknowledge Spanish Government grant PID2019-110521GB-I00, Catalan Government grant SGR 2017-1005, and Fundación Ramón Areces grant CIVP20A6621.

References

1. Nath, A.J. et al. (2018) Managing India’s small landholder farms for food security and achieving the “4 per Thousand” target. Sci. Total Environ. 634, 1024–1033
2. Rumpel, C. et al. (2018) Boost soil carbon for food and climate. Nature 553, 27

3. Lal, R. (2004) Soil carbon sequestration impacts on global climate change and food security. Science 304, 1623–1627
4. Kell, D.B. (2012) Large-scale sequestration of atmospheric carbon via plant roots in natural and agricultural ecosystems: Why and how. Philos. Trans. R. Soc. B Biol. Sci. 367, 1589–1597
5. Abdullahi, A.C. et al. (2018) Carbon Sequestration in Soils: The Opportunities and Challenges. Carbon Capture, Util. Sequestration 1, 3–16
6. Haddaway, N.R. et al. (2017) How does tillage intensity affect soil organic carbon ? A systematic review. Environ. Evid. 6, 1-48
7. Lal, R. (2004) Soil carbon sequestration to mitigate climate change. Geoderma 123, 1–22
8. Navarro-Pedreño, J. et al. (2021) The Increase of Soil Organic Matter Reduces Global Warming, Myth or Reality? Sci 3, 18
9. Sokol, N.W. and Bradford, M.A. (2018) Microbial formation of stable soil carbon is more efficient from belowground than aboveground input. Nat. Geosci. 12, 46–53
10. Sokol, N.W. et al. (2019) Evidence for the primacy of living root inputs, not root or shoot litter, in forming soil organic carbon. New Phytol. 221, 233–246
11. Chen, S. et al. (2018) Plant diversity enhances productivity and soil carbon storage. Proc. Natl. Acad. Sci. U. S. A. 115, 4027–4032
12. Rasse, D.P. et al. (2005) Is soil carbon mostly root carbon? Mechanisms for a specific stabilisation. Plant Soil 269, 341–356
13. Dijkstra, F.A. et al. (2021) Root effects on soil organic carbon: a double-edged sword. New Phytol. 230, 60–65
14. Girkin, N.T. et al. (2018) Root exudate analogues accelerate CO_2 and CH_4 production in tropical peat. Soil Biol. Biochem. 117, 48–55
15. Girkin, N.T. et al. (2018) Composition and concentration of root exudate analogues regulate greenhouse gas fluxes from tropical peat. Soil Biol. Biochem. 127, 280–285
16. Shahzad, T. et al. (2015) Contribution of exudates, arbuscular mycorrhizal fungi and litter depositions to the rhizosphere priming effect induced by grassland species. Soil Biol. Biochem. 80, 146–155
17. Merino, C. et al. (2015) Soil carbon controlled by plant, microorganism and mineralogy interactions. J. Soil Sci. Plant Nutr. 15, 321–332

18. Cheng, W. et al. (2014) Synthesis and modeling perspectives of rhizosphere priming. New Phytol. 201, 31–44
19. Zhou, J. et al. (2021) Strong priming of soil organic matter induced by frequent input of labile carbon. Soil Biol. Biochem. 152, 108069
20. Liang, J. et al. (2018) More replenishment than priming loss of soil organic carbon with additional carbon input. Nat. Commun. 9, 1–9
21. Villarino, S.H. et al. (2021) Plant rhizodeposition: A key factor for soil organic matter formation in stable fractions. Sci. Adv. 7, 1–14
22. Cotrufo, M.F. et al. (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? Glob. Chang. Biol. 19, 988–995
23. Liang, C. et al. (2017) The importance of anabolism in microbial control over soil carbon storage. Nat. Microbiol. 2, 1–6
24. Lange, M. et al. (2015) Plant diversity increases soil microbial activity and soil carbon storage. Nat. Commun. 6, 6707
25. Hamer, U. and Marschner, B. (2005) Priming effects in different soil types induced by fructose, alanine, oxalic acid and catechol additions. Soil Biol. Biochem. 37, 445–454
26. Dennis, P.G. et al. (2010) Are root exudatesmore important than other sources of rhizodeposits in structuring rhizosphere bacterial communities? FEMS Microbiol. Ecol. 72, 313-27
27. Landi, L. et al. (2006) Root exudate effects on the bacterial communities, CO2 evolution, nitrogen transformations and ATP content of rhizosphere and bulk soils. Soil Biol. Biochem. 38, 509–516
28. Keiluweit, M. et al. (2015) Mineral protection of soil carbon counteracted by root exudates. Nat. Clim. Chang. 5, 588–595
29. Luo, Y.Q. et al. (2014) Artificial root exudates and soil organic carbon mineralization in a degraded sandy grassland in northern China. J. Arid Land 6, 423–431
30. Schmidt, M.W.I. et al. (2011) Persistence of soil organic matter as an ecosystem property. Nature 478, 49–56
31. Bastida, F. et al. (2019) Global ecological predictors of the soil priming effect. Nat. Commun. 10, 1–9

32. Jeewani, P.H. et al. (2020) Rusty sink of rhizodeposits and associated keystone microbiomes. Soil Biol. Biochem. 147, 107840
33. Panchal, P. et al. (2021) Organic acids: versatile stress-response roles in plants. J. Exp. Bot.72, 4038-4052
34. Miltner, A. et al. (2011) SOM genesis: microbial biomass as a significant source. Biogeochemistry 111, 41–45
35. Hu, Y. et al. (2020) Direct measurement of the in situ decomposition of microbial-derived soil organic matter. Soil Biol. Biochem. 141, 107660
36. Lal, R. (2001) World cropland soils as a source or sink for atmospheric carbon. Adv. Agron. 71, 145–191
37. Morais, T.G. et al. (2019) Detailed global modelling of soil organic carbon in cropland, grassland and forest soils. PLoS One 14, 1–27
38. Davidson, E.A. and Ackerman, I.L. (1993) Changes in soil carbon inventories following cultivation of previously untilled soils. Biogeochemistry 20, 161–193
39. Delgado-Baquerizo, M. et al. (2017) Climate legacies drive global soil carbon stocks in terrestrial ecosystems. Sci. Adv. 4, 1–8
40. Forster, P.M. et al. (2020) Current and future global climate impacts resulting from COVID-19. Nat. Clim. Chang. 10, 913–919
41. Le Quéré, C. et al. (2020) Temporary reduction in daily global CO2 emissions during the COVID-19 forced confinement. Nat. Clim. Chang. 10, 647–653
42. Lal, R. (2009) Sequestering atmospheric carbon dioxide. CRC. Crit. Rev. Plant Sci. 28, 90–96
43. Montanarella, L. et al. eds (2015) Status of the world's soil resources: main report. Embrapa Solos-Livro científico (ALICE). FAO.
44. Cooper, H. V. et al. Long- term zero- tillage enhances the protection of soil carbon in tropical agriculture. Eur. J. Soil Sci. 72, 2477-2492
45. Weller, S. et al. (2015) Methane and nitrous oxide emissions from rice and maize production in diversified rice cropping systems. Nutr. Cycl. Agroecosystems 101, 37–53
46. Pausch, J. and Kuzyakov, Y. (2018) Carbon input by roots into the soil: Quantification of rhizodeposition from root to ecosystem scale. Glob. Chang. Biol. 24, 1–12
47. Chai, R. et al. (2019) Greenhouse gas emissions from synthetic nitrogen manufacture and

fertilization for main upland crops in China. Carbon Balance Manag. 14,1-10

48. Rumpel, C. and Chabbi, A. (2021) Managing Soil Organic Carbon for Mitigating Climate Change and Increasing Food Security. Agron. 11, 1553
49. FAO. 2020. Global Forest Resources Assessment 2020: Main report. Rome. FAO.
50. Lorenz, K., and Lal, R. (2009). Carbon sequestration in forest ecosystems. Springer Science & Business Media.
51. Qiao, N. et al. (2014) Labile carbon retention compensates for CO_2 released by priming in forest soils. Glob. Chang. Biol. 20, 1943–1954
52. Kallenbach, C.M. et al. (2016) Direct evidence for microbial-derived soil organic matter formation and its ecophysiological controls. Nat. Commun. 7, 1-10
53. Smith, L.C. et al. (2021) Large- scale drivers of relationships between soil microbial properties and organic carbon across Europe. Glob. Ecol. Biogeogr.10, 2070–2083
54. He, L. et al. (2020) Global biogeography of fungal and bacterial biomass carbon in topsoil. Soil Biol. Biochem. 151, 108024
55. Crowther, T.W. et al. (2019) The global soil community and its influence on biogeochemistry. Science 365, eaav0550
56. Sulman, B.N. et al. (2017) Feedbacks between plant N demand and rhizosphere priming depend on type of mycorrhizal association. Ecol. Lett. 20, 1043–1053
57. Lavallee, J.M. et al. (2020) Conceptualizing soil organic matter into particulate and mineral-associated forms to address global change in the 21st century. Glob. Chang. Biol. 26, 261–273
58. Cotrufo, M.F. et al. (2019) Soil carbon storage informed by particulate and mineral-associated organic matter. Nat. Geosci. 12, 989–994
59. Lehmann, J. and Kleber, M. The contentious nature of soil organic matter. Nature, 528, 60-68
60. Lu, X. et al. (2021) Nitrogen deposition accelerates soil carbon sequestration in tropical forests. Proc. Natl. Acad. Sci. U. S. A. 118, 1–7
61. Six, J. et al. (2000) Soil macroaggregate turnover and microaggregate formation: A mechanism for C sequestration under no-tillage agriculture. Soil Biol. Biochem. 32, 2099–2103
62. Baumert, V.L. et al. (2018) Root exudates induce soil macroaggregation facilitated by

fungi in subsoil. Front. Environ. Sci. 6, 1–17

63. Chhabra, A. et al. (2003) Soil organic carbon pool in Indian forests. For. Ecol. Manage. 173, 187–199
64. Baumert, V. et al. (2018) Artificial rhizospheres: Exudate effects on soil organic carbon content, aggregation and microbial community composition in topsoil vs. subsoil. In EGU General Assembly Conference Abstracts (p. 8612).
65. Clifford, S.C. et al. (2002) Mucilages and polysaccharides in Ziziphus species (Rhamnaceae): Localization, composition and physiological roles during drought-stress. J. Exp. Bot. 53, 131–138
66. Mizuta, K. et al. (2015) Soil aggregate formation and stability induced by starch and cellulose. Soil Biol. Biochem. 87, 90–96
67. Oades, J.M. (1984) Soil organic matter and structural stability: mechanisms and implications for management. Plant Soil 76, 319–337
68. Poirier, V. et al. (2018) The root of the matter: Linking root traits and soil organic matter stabilization processes. Soil Biol. Biochem. 120, 246–259
69. Dietz, S. et al. (2020) Root exudate composition of grass and forb species in natural grasslands. Sci. Rep. 10, 1–15
70. Cagnarini, C. et al. (2019) Zones of influence for soil organic matter dynamics: A conceptual framework for data and models. Glob. Chang. Biol. 25, 3996–4007
71. Liang, C. et al. (2019) Quantitative assessment of microbial necromass contribution to soil organic matter. Glob. Chang. Biol. 25, 3578–3590
72. Vetterlein, D. et al. (2020) Rhizosphere Spatiotemporal Organization–A Key to Rhizosphere Functions. Front. Agron. 2, 1–22
73. Yang, Y. et al. (2019) Soil carbon sequestration accelerated by restoration of grassland biodiversity. Nat. Commun. 10, 1–7
74. Guo, L.B. and Gifford, R.M. (2002) Soil carbon stocks and land use change: A meta analysis. Glob. Chang. Biol. 8, 345–360
75. Fang, K. et al. (2019) Al/Fe Mineral Controls on Soil Organic Carbon Stock Across Tibetan Alpine Grasslands. J. Geophys. Res. Biogeosciences 124, 247–259
76. Chen, L. et al. (2019) Regulation of priming effect by soil organic matter stability over a broad geographic scale. Nat. Commun. 10, 1–10

77. Augustine, D.J. et al. (2011) Rhizosphere interactions , carbon allocation , and nitrogen acquisition of two perennial North American grasses in response to defoliation and elevated atmospheric CO_2. Oecologia 165, 755-770
78. Henry, Ã. and Vesterga, M. (2008) Evidence for a transient increase of rhizodeposition within one and a half day after a severe defoliation of Plantago arenaria grown in soil. Soil Biol.Biochem. 40, 1264–1267
79. Hamilton, E.W. and Frank, D.A. (2001) Can plants stimulate soil microbes and their own nutrient supply? Evidence from a grazing tolerant grass. Ecology 82, 2397–2402
80. Wilson, C.H. et al. (2018) Grazing enhances belowground carbon allocation, microbial biomass, and soil carbon in a subtropical grassland. Glob. Chang. Biol. 24, 2997-3009
81. An, S. et al. (2010) Soil organic carbon density and land restoration: Example of southern mountain area of Ningxia Province, Northwest China. Commun. Soil Sci. Plant Anal. 41, 181–189
82. Xue, Z. and An, S. (2018) Changes in soil organic carbon and total nitrogen at a small watershed scale as the result of land use conversion on the Loess Plateau. Sustain. 10, 4757
83. Han Weng, Z. et al. (2017) Biochar built soil carbon over a decade by stabilizing rhizodeposits. Nat. Clim. Chang. 7, 371–376
84. Weng, Z.H. et al. (2015) Plant-biochar interactions drive the negative priming of soil organic carbon in an annual ryegrass field system. Soil Biol. Biochem. 90, 111–121
85. Maestrini, B. et al. (2015) A meta-analysis on pyrogenic organic matter induced priming effect. GCB Bioenergy 7, 577–590
86. Tückmantel, T. et al. (2017) Root exudation patterns in a beech forest: Dependence on soil depth, root morphology, and environment. Soil Biol. Biochem. 107, 188–197
87. Akatsuki, M. and Makita, N. (2020) Influence of fine root traits on in situ exudation rates in four conifers from different mycorrhizal associations. Tree Physiol. 40, 1071–1079
88. Jaitz, L. et al. (2011) LC-MS analysis of low molecular weight organic acids derived from root exudation. Anal. Bioanal. Chem. 400, 2587–2596
89. Herz, K. et al. (2018) Linking root exudates to functional plant traits. PLoS One 13, 1–14
90. Shi, S. et al. (2013) Challenges in Assessing Links Between Root Exudates and the Structure and Function of Soil Microbial Communities. Mol. Microb. Ecol. Rhizosph. 1,

125–135

91. Kuzyakov, Y. and Domanski, G. (2000) Carbon input by plants into the soil. Review. J. Plant Nutr. Soil Sci. 163, 421–431
92. Oburger, E. and Jones, D.L. (2018) Sampling root exudates – Mission impossible? Rhizosphere 6, 116–133
93. Meharg, A.A. (1994) A critical review of labelling techniques used to quantify rhizosphere carbon-flow. Plant Soil 166, 55–62
94. Werth, M. and Kuzyakov, Y. (2008) Root-derived carbon in soil respiration and microbial biomass determined by ^{14}C and ^{13}C. Soil Biol. Biochem. 40, 625–637
95. Paterson, E. et al. (2009) Through the eye of the needle: A review of isotope approaches to quantify microbial processes mediating soil carbon balance. New Phytol. 184, 19–33
96. Wang, R. et al. (2021) A novel ^{13}C pulse-labelling method to quantify the contribution of rhizodeposits to soil respiration in a grassland exposed to drought and nitrogen addition. New Phytol. 230, 857–866
97. López-Bucio, J. et al. (2000) Enhanced phosphorus uptake in transgenic tobacco plants that overproduce citrate. Nat. Biotechnol. 18, 450–453
98. Delhaize, E. et al. (2004) Engineering high-level aluminum tolerance in barley with the ALMT1 gene. Proc. Natl. Acad. Sci. U. S. A. 101, 15249–15254
99. Zhao, J. et al. (2004) Characterization of root architecture in an applied core collection for phosphorus efficiency of soybean germplasm. Chinese Sci. Bull. 49, 1611–1620
100. Falge, E. et al. (2002) Seasonality of ecosystem respiration and gross primary production as derived from FLUXNET measurements. Agric. For. Meteorol. 113, 53-74.
101. Riederer, M. et al. (2015) Partitioning NEE for absolute C input into various ecosystem pools by combining results from eddy-covariance, atmospheric flux partitioning and $^{13}CO_2$ pulse labeling. Plant Soil 390, 61-76

Supplemental references

S1. Grayston, S.J. et al. (1997) Rhizosphere carbon flow in trees, in comparison with annual plants: The importance of root exudation and its impact on microbial activity and nutrient availability. Appl. Soil Ecol. 5, 29–56

S2. Uren, N.C. (2005) Types, Amounts, and Possible Functions of Compounds Released into the Rhizosphere by Soil-Grown Plants. In The rhizosphere: biochemistry and organic substances at the soil-plant interface (R Pinton, Z Varanini, P Nannipieri. eds), pp 1-21 CRC Press

S3. Dakora, F.D. and Phillips, D.A. (2002) Root exudates as mediators of mineral acquisition in low-nutrient environments. Plant Soil 245, 35–47

Figure

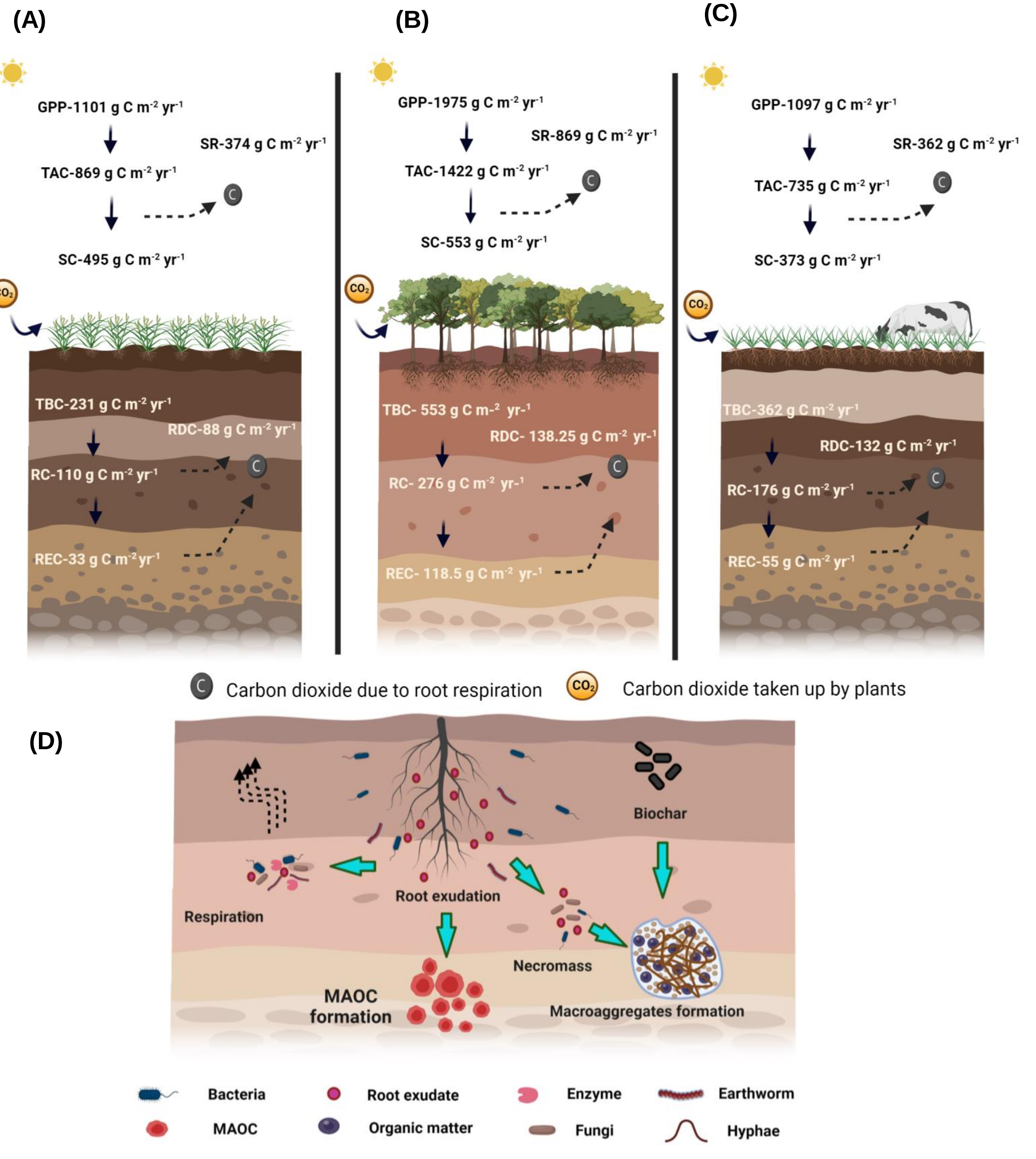

Figure 1. Soil carbon sequestration by root exudates The belowground soil carbon sequestration patterns in three ecosystems (A) agricultural lands (B) forests (C) grasslands. Carbon allocation patterns of crops, trees and grasses represent agriculture, forests and grasslands, respectively. Data for carbon allocation patterns was taken from [46], which is a compilation of 281 datasets. The carbon partitioning is depicted in terms of absolute values with the unit, grams carbon per meter square per year (g C m^{-2} yr^{-1}) GPP- Gross Primary Production; TAC-Total Aboveground Carbon; SC-Shoot Carbon; SR-Shoot Respiration; TBC-Total belowground carbon; RC-Root Carbon; REC-Root exudates carbon; RDC-Root Derived Carbon dioxide (released by root respiration). GPP values for crops were taken from [100] and for grasslands from [101], while GPP values for forests were calculated by taking averages of GPP of tropical, temperate and boreal forest ecosystems from [50] (D) Root exudates can act as a carbon source in soil and are also stabilized by processes such as MAOC formation and macro-aggregates formation. Root exudates also help in incorporation of plant and microbial residues into the stable SOC content by aggregates formation and chemical bonding. Addition of biochar further increases the stability of root exudates in soil. Exudates also attract micro-organisms. This leads to the emission of CO_2 as a result of their respiration. Created with BioRender (https://biorender.com/).