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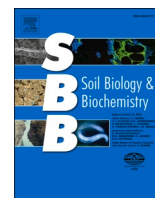
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Legacy effects of rhizodeposits on soil microbiomes: A perspective

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A B S T R A C T

Plant legacy effects observed in plant-soil feedback experiments have largely been attributed to the root or litter material of the previous plant. The legacy effects of rhizodeposits are defined as changes in the soil microbiome that remain after a plant has died or been removed from the soil and caused by the release of substances of various compositions by living plants (rhizodeposits). Rhizodeposit-mediated legacy effects have been largely ignored mainly due to the high spatial and temporal variability of rhizodeposits and difficulties quantifying and tracking them in the rhizosphere. In this perspective article, we discuss what is known about the legacy effects of rhizodeposits and provide ideas for future experiments to improve understanding of this phenomenon. Only a few studies separate rhizodeposit-mediated plant legacy effects from legacy effects of root decomposition. Results from these experiments indicate that rhizodeposit-mediated legacy effects on soil microbial communities may persist for several months to several years, especially if the same crop is cultivated persistently for several years in a ‘conditioning’ phase. Rhizodeposit-mediated legacy effects on fungal communities usually last longer than those on bacterial communities due to fungal life-cycle strategies (spore formation) and slower reproduction rates, compared to bacterial communities. We highlight the need for further experimentation to investigate the influence that the length of a conditioning phase has on the persistence of the legacy effect, differentiate the effect of root exudates from the effects of sloughed root cells, separate the influence of simple sugars from that of high molecular-weight exudates and plant derived compounds with antimicrobial properties, and explore whether plant species diversity influences the nature of the legacy. To address these questions, we propose the use of contemporary tools such as stable isotope probing, plant genetics, and reverse microdialysis. We think that harnessing rhizodeposit-mediated plant legacy effects could be a promising approach to improve sustainable crop production by creating disease-suppressive soils and simulating plant growth-promoting micro-organisms within soil systems.

1. Introduction

Soil legacy effects are defined as the influence of previous soil conditions on the subsequent ability of the soil to perform functions in the future. Legacy effects are the manifestation of ‘soil memory’ (Targulian and Bronnikova, 2019) and are typically the result of the adaptation of soil (micro)biota to changing environments (Vermeersch et al., 2022). Soil legacy effects have been observed in response to soil temperature (Adekanmbi et al., 2022), rainfall intensity (Evans and Wallenstein, 2012), drought (Canarini et al., 2021), and grazing intensity (Wang et al., 2021). Soil legacy effects can also be a result of plant-soil interactions and may be mediated by rhizodeposits. However, relatively little is known about rhizodeposit-mediated legacy effects, or how they could be used to benefit crop production.

Leaf litter composition (Austin et al., 2014) and plant community species richness (Cong et al., 2015) have been described as major drivers of plant-soil interactions. As a result of plant-soil feedback, legacy effects

on the soil can strongly impact the growth of the subsequent plant or alter the composition of the subsequent plant community (van de Voorde et al., 2011; Mariotte et al., 2018; Crawford et al., 2019; Beals et al., 2020). Typical experiments to study plant-soil feedback include a ‘conditioning’ phase followed by a ‘responding’ phase (van de Voorde et al., 2011). The conditioning phase is characterized by soil cropped with a single plant species, or a mixture of plant species. In the responding phase, the same (‘conspecific’) or a different (‘hetero-specific’) plant species is/are grown in the same soil. Plant-soil feedback can be driven by abiotic (e.g. nutrient provision or depletion) or biotic (e.g. suppression or stimulation of pathogens and mutualists) factors (Bennett and Klironomos, 2019). The observed effects on following plants are the net outcome of both positive and negative legacy effects. The role of litter (Veen et al., 2019), plant species (Garbeva et al., 2008), and plant communities as a whole (Heinen et al., 2020; Schmid et al., 2021) on soil legacy effects have been largely described. However, the role of rhizodeposits, and how the composition of root exudates affects

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the plant-soil-feedbacks, remains a mystery.

On average, 17% of carbon fixed by photosynthesis is released by plant roots as rhizodeposits (Nguyen, 2009). The direct influence of rhizodeposits on the diversity and composition of the (rhizosphere) soil microbiome is well described (Paterson et al., 2007; Huang et al., 2014; Tian et al., 2020). However, their effects – through soil legacy – on subsequent plants are largely ignored and seldom studied. It is nevertheless likely that rhizodeposits play an important role in plant-soil feedback via rhizodeposit-mediated soil microbial legacy effects (Bakker et al., 2018). Here, we define rhizodeposit-mediated soil microbial legacy effects as changes in the soil microbiome that can be attributed to rhizodeposition and that remains after a plant has died or has been removed from the soil. Better understanding of rhizodeposit-mediated soil microbial legacy effects may lead to greater insights into plant succession in natural ecosystems. Moreover, it may also lead to the design of novel crop rotations, to the introduction of new plant cultivars, or to the use of artificial biostimulants that mimic the positive plant legacy effects (Bakker et al., 2020; Koyama et al., 2022).

In this perspective we (i) introduce rhizodeposition and the methodological challenges of studying the rhizosphere microbiome; (ii) provide a critical overview of the existing evidence for rhizodeposit-mediated soil microbial legacy effects; (iii) outline the importance of separating the effects of rhizodeposit-mediated plant legacy effects from root decomposition legacy effects; (iv) discuss the factors influencing the persistence of rhizodeposit-mediated plant legacy effects; (v) highlight the role of plant species diversity and identity on rhizodeposit-mediated plant legacy effects; and (vi) suggest possible avenues for future research that involve the use of contemporary techniques such as stable isotope probing, plant gene knockouts, and reverse microdialysis.

2. Rhizodeposition: a complex mix of compounds with high spatial and temporal variability

Rhizodeposits (including sloughed root cells, mucilage, and root exudates) stimulate microbial growth in the rhizosphere, compared to the surrounding soil environment, due to the accessibility of relatively labile substances within their constitution (Paterson et al., 2007; Dennis et al., 2010). Rhizodeposits contain a multitude of compounds (Uren, 2007) and the release of rhizodeposits is highly spatially and temporally variable (Neumann and Romheld, 2007). For example, the release of polymeric substances is greater in older parts of the root, in contrast to sugars and other carbohydrates that are typically found in the root hair

and root elongation zone (Farrar et al., 2003; Prosser et al., 2006). Consequently, responses of the rhizobiome to rhizodeposits differs along different portions of the rhizoplane and soil profile (Wei et al., 2019, 2021), which further leads to micro-spatial fluctuation in plant-soil feedbacks. As a result, the germination and plant growth in the responding phase will depend on the spatial distribution of exudation by previous plants in the soil profile and the location of plant roots in the responding phase (Neumann and Romheld, 2007; Bennett and Klironomos, 2019).

The release of rhizodeposits in the form of low molecular weight compounds (e.g. sugars and amino acids) primes the decomposition of soil organic matter and the mineralization of nutrients, often improving plant nutrition (Meyer et al., 2017; Mwafurirwa et al., 2017). However, other components of rhizodeposits can perform specific functions and can have specific effects on soil microbiomes, soil biogeochemical processes, and plant disease suppression (Table 1). Some of them, such as tannins can persist in soil for several months and thus cause durable effects on soil microbial properties that may contribute to rhizodeposit-mediated plant legacy effects (Adamczyk et al., 2011).

Legacy effects, especially on plant communities, are often attributed to the presence and relative balance between beneficial and pathogenic organisms (Bennet and Klironomos, 2019). The root exudate composition might hence affect the following plants through modulation of this balance. Furthermore, root-exudate mediated allelopathy can affect soil microbial legacies (Bais et al., 2004; Li et al., 2019b). However, the fate of the root exudates in soils is only realised if the root exudates reach and affect the soil microbiome. This happens only in the absence of root uptake, rapid microbial degradation, and/or absorption to surface-reactive particles of pertinent compounds (Uren, 2007).

Due to the heterogenous nature of the rhizosphere, and the short timescales over which degradation of compounds and interactions occur, quantification and identification of root exudates in the soil environment is challenging (Oburger and Jones, 2018; Pantigoso et al., 2021). This limitation makes it difficult to separate the direct effects of a plant root (depleting nutrients and changing the physical structure of a soil) from the indirect effects that are due to rhizodeposits and their legacy on soil microbial communities and functions. Hence, without knowing the composition and quantity of the compounds in root exudates, and the persistence of their effects on soil microbes, we cannot comprehensively understand their contribution to soil microbial legacies.

Techniques for collecting rhizodeposits have traditionally involved

Table 1

Summary of key types of rhizodeposits, the cause of their release, their mode of action, and their potential legacy in soil.

Type of rhizodeposit	Cause of release	Mode of action	Potential legacy	References
Essential oils, tannins, resins, saponins and phytoalexins, and Rosmarinic acid	Pathogen attack	Plant protection against pathogens	Reduce the abundance of potential pathogens, thus reducing plant pathogenicity	(Rahimi et al., 2019; Winkelmann et al., 2019; Niazian and Sabbatini, 2021; Malzarz et al., 2022)
Phytosiderophores	Iron-deficiency	Enhance the mobilization of Fe in soil and their uptake by crops	Increase Fe accessibility	Dotaniya et al. (2013)
Organic acids i.e. oxalic, citric, and malic acids	Phosphate deficiency	Increase phosphate solubilization from insoluble calcium phosphate	High availability of plant available phosphorous	(Perry et al., 2007; Zhu et al., 2021)
	High concentration of Al ³⁺ ion	Detoxification of Al by forming Al-organic acid complexes	Reduce the Al toxicity and acidification	Ma (2000)
Methyl 3-(4-hydroxyphenyl) propionate	Higher concentration of inorganic nitrogen	Biological nitrification inhibition	Reduce denitrification and N ₂ O emission	Nardi et al. (2020)
Flavonoids (signaling compounds)	To initiate symbiotic process	Legume-rhizobia symbiosis	Increase the availability of inorganic nitrogen forms	Cooper (2004)
Extracellular DNA and Proteins	Pathogen attack	Act as extracellular traps for fungal pathogens	Reduce the abundance of potential fungal pathogens thus reduced pathogenicity	Hawes et al. (2011)
Enzymes e.g., Phosphomonoesterases	Nutrient uptake	Catalyze the conversion of organic to inorganic P	Higher availability of nutrients	Uren (2007)
Mucilage	Water deficit	Increase water-holding capacity of the rhizosphere	Increased drought tolerance	(McCully and Boyer, 1997; Kroener et al., 2014)

hydroponics (O'Sullivan et al., 2017) or percolating nutrient solutions through a solid cultivation media (Vranova et al., 2013). These methods ignore the spatial heterogeneity of root exudation (Neumann and Romheld, 2007; Wei et al., 2021), alter root morphology and root exudation rate (Groleau-Renaud et al., 1998), and do not account for the interactions between plant roots and microbes (Wang et al., 2020). New techniques (e.g. microfluidic devices that mimic some attributes of the soil environment (Aufrecht et al., 2022)) offer more promise to more realistically quantify rhizodeposition. Techniques based on the extraction of root exudates from the rhizosphere of real soils is hampered by low extraction yields and fast degradation of extracted root exudates by active microbes within the extract, and thus cannot distinguish root exudates from compounds produced or modified by the rhizosphere microbiome. Williams et al. (2021) proposed a hybrid method based on the removal of roots from soil and the collection of root exudates in hydroponic solution. This method captures the effects of both the soil and its microbiome on root exudation but does not account for the degradation of the compounds released and does not give spatial information. The development of novel methods of root exudate quantification is a key challenge that must be overcome to adequately investigate the role played by rhizodeposit-mediated soil microbial legacies in plant-soil feedback.

3. Evidence for rhizodeposit-mediated plant legacy effects

Plant legacy effects on the abundance of soil-borne pathogens are relatively well understood in crop monoculture systems and mitigated in agricultural practice by alternating crops in rotation to suppress pathogens and deprive them of multiple host plants in sequence. This indicates that crop rotations can enhance the disease suppressive capacity of soil microbiomes or directly prevent proliferation of certain plant pathogens (Peralta et al., 2018). A major question is: "Which part of this legacy is mediated by rhizodeposits?" Evidence shows that many of the effects on pathogens are indeed modulated by root-exudates. For example, Chen et al. (2018) demonstrated that the addition of potato-onion root exudates helps to suppress clubroot in Chinese cabbage (*Brassica rapa* subsp. *pekinensis*) more than the application of potato-onion residues. The inclusion of pineapple in rotation with banana decreased *Fusarium* wilt disease, likely through root exudation which stimulated the growth of fungi that are able to outcompete the pathogen (Yuan et al., 2021). Resistance against *Fusarium* wilt disease in watermelon was also demonstrated by either applying wheat root exudates or companion cropping watermelon with wheat, indicating a role for both the exudates and the associated microbiome (Li et al., 2019a). Zhang et al. (2022) attributed greater resistance to inter-annual variability and reduced presence of potentially pathogenic microbes to a greater amount of fixed carbon translocated to the belowground and more complex and stable microbiome networks observed when introducing bahiagrass (*Paspalum notatum* Flugge) into a peanut-cotton rotation. These examples highlight the potential for rhizodeposit-mediated suppression of pathogens which could be exploited by the application of bioactive compounds that act as prophylactic bioprotectants against specific pathogens as part of an integrated pest management strategy that maintains disease suppressive soils.

Positive heterospecific legacy effects are often attributed to the direct suppression of a pathogen under diverse crop rotation. Positive conspecific legacy effects are generally observed when the same plant is grown in sequence. These legacy effects have been attributed to the chemical 'cry for help' of the previous plant by secreting chemo-attractants into the rhizosphere to recruit beneficial symbionts and confer resistance or suppress a pathogen (Pascale et al., 2020). For example, Berendsen et al. (2018) observed that *Arabidopsis thaliana* infected by *Hyaloperonospora arabidopsidis* left a soil-mediated legacy that conferred resistance to the next *A. thaliana* plant growing in the same soil. Yin et al. (2021) showed that successive plantings of wheat engineered a microbiome that was suppressive against soilborne

pathogens during successive plantings. Hu et al. (2018) implicated benzoxazinoids released by maize roots, and their metabolites, in changes to rhizosphere microbial communities and enhanced defences to diseases and herbivores in the following generation. The authors suggested that soils could be conditioned with benzoxazinoids to enhance plant defence, despite a negative conspecific legacy effect on plant growth observed. Harnessing the effect of rhizodeposits to select crop sequences that promote disease-suppressive soils or to design new plant growth promoting soil conditioners could help to enhance or maintain crop yields while reducing the requirement for synthetic plant protection products (Raaijmakers and Mazzola, 2016; Koyama et al., 2022).

Despite the potential for using novel crop sequences that promote disease-suppressive soils, many studies have noted that the impact of the conditioning plant on the soil microbiome is most pronounced during the period of vegetative growth and that the legacy effects of the previous plant in an arable rotation on the soil microbiome are sometimes not detected (Hellequin et al., 2021; Kamau et al., 2021; Struijk et al., 2022). The result of this failure to differentiate the rhizodeposit pathway from the litter pathway is that the mechanism cannot be unequivocally elucidated. Because the specific responsible compounds cannot be identified, the observation cannot be used to breed or modify plants to produce specific rhizodeposits (Ahkami et al., 2017) or to artificially synthesise compounds that mimic beneficial rhizodeposit-mediated legacy effects and apply them as soil amendments (Arif et al., 2020). A mechanistic understanding which separates rhizodeposit-mediated plant legacy effects from root decomposition legacy effects is required to advance the field.

4. Separating rhizodeposit-mediated plant legacy effects from root decomposition legacy effects

Most plant-soil feedback studies do not separate the effects due to rhizodeposition from those due to compounds released during the degradation of plant root residues (De Long et al., 2019). Plant-soil feedback experiments have revealed clear plant legacy effects (Van der Putten et al., 2013; Cortois et al., 2016; Mariotte et al., 2018; Crawford et al., 2019; Beals et al., 2020) and the application of collected or artificial root exudates to soil has implicated the role of rhizodeposition in driving such legacy effects (Hu et al., 2018; Li et al., 2019a; Wen et al., 2021). However, relatively few attempts have been made to account for the legacy effect on the soil microbiome that is specifically due to *in-situ* rhizodeposition and distinguish the quantitative contributions of root exudates, mucilage, and entire root cells grown in a real soil (i.e. the rhizosphere) from the effect of plant root litter from the previous plant (i.e. the detritosphere). Different microbial guilds are responsible for decomposition in the rhizosphere and the detritosphere (Nuccio et al., 2020). This indicates that faster growing microbes utilizing simpler sugars (such as bacteria, moulds, and yeasts) would be more affected by the quantity and quality of rhizodeposits (Hannula et al., 2020), while slower growing organisms such as litter-decomposing fungal saprotrophs would be more affected by litter-mediated legacy effects.

One might expect that pathogens and beneficial plant-associated micro-organisms are likely to be more affected by rhizodeposits than saprotrophs. This is confirmed in two studies that separated rhizodeposit-mediated legacy effects from detritosphere legacy effects by removing thicker roots at the end of the conditioning phase of their experiments (Heinen et al., 2020; Hannula et al., 2021). Although thin roots remained in the soil, it is reasonable to assume that their degradation is similar to that of root border cells released by plant roots, included in rhizodeposition. Heinen et al. (2020) observed that plants in the conditioning phase negatively affected the growth of plants of the same functional type in the responding phase, likely due to legacy effects of the conditioning plants on the composition of (pathogenic) fungal communities in the rhizosphere.

5. Factors influencing the persistence of rhizodeposit-mediated plant legacy effects

A further question to address is: “How long do rhizodeposit-mediated plant legacy effects last in the soil?”. This is important to determine if they will have a meaningful effect on the plant grown during the responding phase. Few studies so far have addressed the persistence of legacy effects. Heinen et al. (2020) observed that the legacy effects on the composition of bacterial rhizosphere communities were less persistent (about 3 months after plant removal) than those on fungal rhizosphere communities (about 5 months after plant removal), which was supported by Hannula et al. (2021). It was speculated that this difference in legacy observed between fungal and bacterial communities was due to the higher stability of fungal communities as a result of their life cycle strategy (spore formation) and slower reproduction rates, compared to bacterial communities (Hannula et al., 2021). Therefore, it seems that legacy effects on fungal communities may last longer than those on bacterial communities.

Examples of persistent legacy effects have been reported in the recent literature. For example, Schmid et al. (2021) studied the legacy effects of plant species richness on fungal and bacterial richness and evenness in an experiment in which topsoils were excavated, sieved to remove root residues, and re-established in field plots. Comparing unsterilized (plant legacy) treatments with gamma sterilized treatments (no plant legacy) after four years of growth, the authors found that rhizodeposit-mediated plant legacy markedly increased bacterial richness and evenness, but decreased fungal evenness. The finding that the legacy of the previous plant community, cultivated for 4 years, on the soil microbial community persisted indicates that the legacy of rhizodeposition by a previous plant community on the soil microbiome may be quite a persistent phenomenon. Persistent legacy effects have also been reported for biological nitrification inhibitors released as root exudates by savanna grass (*Hyparrhenia diplandra*) after more than 80 years growth (Koffi, 2019). A legacy of considerable biological nitrification inhibition lasted several decades after savanna grass was removed (Lata et al., 2022). The

persistence of the biological nitrification inhibitor should be simulated so as to confirm the duration of its effects by applying annual additions to soil under controlled conditions.

6. The role of plant species diversity and identity on rhizodeposit-mediated plant legacy effects

Roots of different plants grown in polyculture may occupy different niches in soil and thus increase the soil volume affected by rhizodeposition (Fig. 1). Mommer et al. (2010) showed that one dicot species increased topsoil root biomass when grown with another dicot. Heuermann et al. (2019) presented data which showed that, while root biomass was greater in polycultures of four catch crops than in monocultures, deep rooting mustard and phacelia dominated the root biomass and suppressed the roots of oat and clover. Greater plant diversity also influences the diversity of root exudates, which, in turn, increases microbial biomass. de Oliveira et al. (2020) showed that wheat-lupin intercropping conferred greater short-term resilience of carbon and nitrogen cycling to heat stress, compared to a monoculture treatment. Future studies could investigate the persistence of rhizodeposit-mediated legacy effects of plants with different root architectures in polycultures to distinguish whether these legacy effects are species specific or general and whether their effects are additive, synergistic, or antagonistic.

Rhizodeposit-mediated plant legacy effects may influence the endophytic community of the responding plant to a greater extent than its ‘free-living’ rhizosphere community. Hannula et al. (2021) observed that the endophytic community of plants growing in soil previously inhabited by a conspecific species was different from that of the plant growing in the soil previously occupied by heterospecific species, in line with the idea of negative conspecific feedback (Bennett and Klironomos, 2019). Negative feedback and a greater number of pathogens were observed inside the roots when grown in conspecific soils (forbs) or in soils with a legacy of the same functional plant group (grasses; Hannula et al., 2021). This is related to the early ontology of plants when they

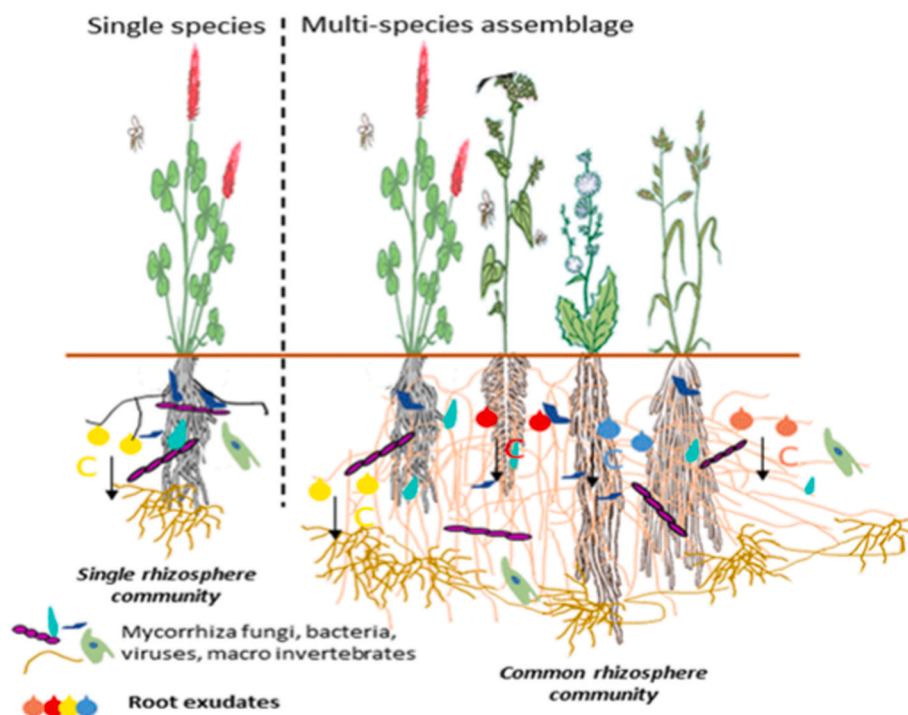


Fig. 1. Hypothetical differences in rhizosphere microbial community between single and multi-species assemblages. Figure is partially adopted and modified from Ehrmann and Ritz (2014).

recruit their endophytes from soils hence potentially amplifying the (recent) effects of rhizodeposits of previous plants (priority effects).

7. Future research

A key knowledge gap that strongly limits our understanding of plant legacy effects emanates from the difficulty in separating the legacy effects caused by plant litter degradation from those caused by rhizodeposition. Even in experiments where plants and visible roots were removed, the presence of fine roots and root litter of the conditioning plant cannot be excluded in the responding phase, both of which may affect the composition of endophytic and ‘free living’ soil microbial communities and consequently plant growth and community composition (Heinen et al., 2020). This prevents an effective unravelling of the mechanisms and prevents the design of appropriate measures to steer plant-soil feedbacks. Here we propose a number of experimental approaches that could be adopted to address this and other knowledge gaps (Fig. 2).

A simple experiment to investigate the legacy effects of rhizodeposition on the soil microbiome could involve growing the conditioning plant with successive plant removal before monitoring the effects over time on the activity, biomass, and composition of soil microbiome with sacrificial replicates (Fig. 2a). This would help to consolidate our knowledge concerning the persistence of legacy effects and enable us to determine whether this is long enough to facilitate meaningful benefits in agricultural soils. The removal of aboveground plant tissues and

visible roots is fairly trivial (Fig. 2b), but the presence of fine non-visible roots and root hairs remains problematic and potentially confounding. Thus, the effect of sloughed root cells, one of the components of rhizodeposition, would be overestimated. This type of design lends itself to experiments to assess the legacy effects of individual plants or mixtures of different plant species, the use of the same plant species under different stress conditions promoting different rhizodeposits, and the comparison of different soil types.

Tracking the flow of photosynthetically-fixed carbon into soil, and its assimilation by the soil microbial community, has provided insights into the effects of plants on the activity, biomass, and composition of the soil microbiome (Hannula et al., 2020; Shu et al., 2022). These insights are obtained by continuously or pulse labelling the plant in a ^{14}C or ^{13}C atmosphere (Van Veen et al., 2007; Hannula et al., 2012, 2017). Thanks to these labelling techniques we know that the quality and quantity of rhizodeposits depend on the plant species, plant age, status of plant physiology, and environmental conditions, and that these factors should be considered when studying the effect of rhizodeposition on activity and composition of microbial communities inhabiting the rhizosphere soil (Wardle et al., 2004; Haichar et al., 2008; Gunina et al., 2017). Thus, ^{13}C labelling of plants *in-situ* may offer an important opportunity to explore the legacy effects of the rhizodeposits after the plants are removed from the soil. The fate of ^{13}C rhizodeposits released into the soil and their use as a carbon source by the microbial community can be quantified by measuring ^{13}C -PLFA (phospholipid fatty acid analysis), DNA-SIP, RNA-SIP (stable isotope probing) profiles (Fig. 2c). ^{13}C -PLFA

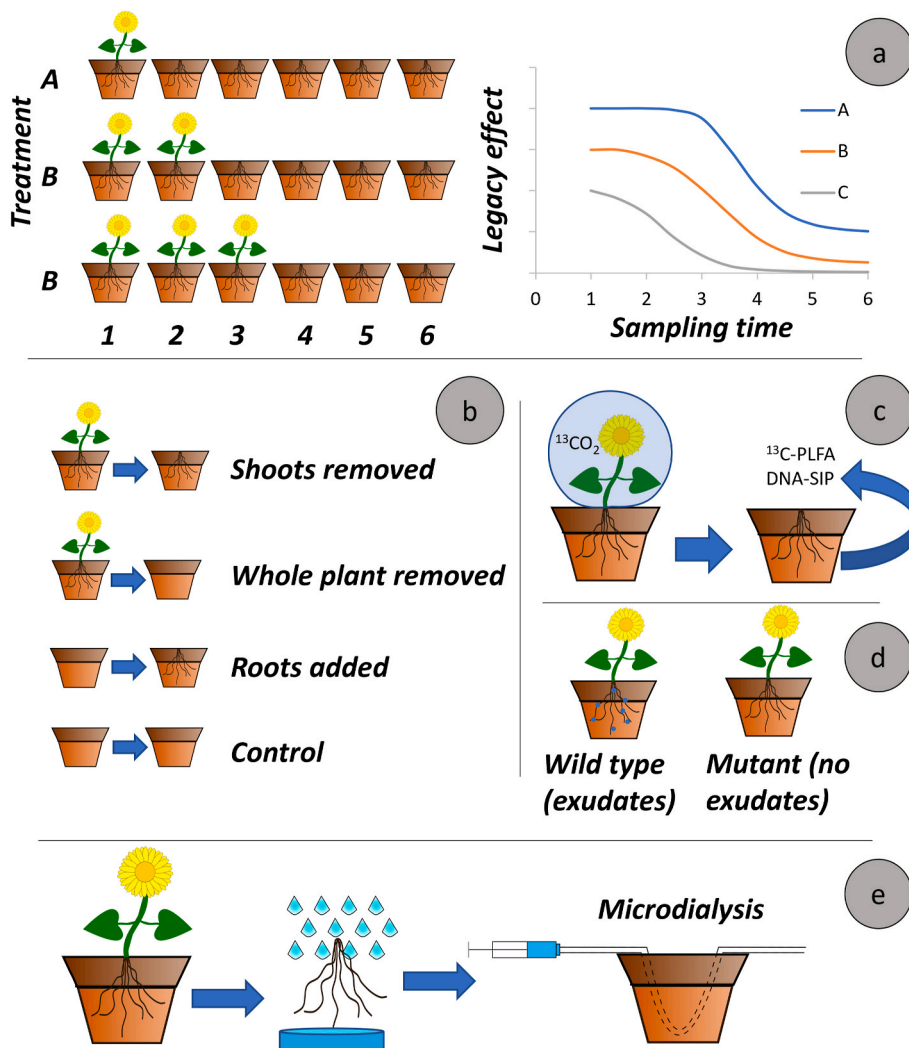


Fig. 2. Potential experimental approaches to study plant legacy effects due to rhizodeposition, including (a) investigating the influence of conditioning and responding phase on plant legacy effects; (b) separating the effect of root biomass decomposition from rhizodeposition; (c) using ^{13}C labelling of plant tissues to deliver and track labelled rhizodeposits in the soil microbial community ^{13}C -PLFA (phospholipid fatty acid analysis) or DNA-SIP (stable isotope probing) profiles; (d) using mutant plants lacking the capability to secrete exudates; (e) collecting rhizodeposits and pumping them into the soil using reverse microdialysis to mimic plant root exudation.

allows the identification of broad microbial groups that are stimulated by rhizodeposition whereas DNA-SIP allows the identification of specific microbial taxa that are stimulated by rhizodeposition. RNA-SIP allows us to identify the function of the taxa stimulated by rhizodeposition. Thus far stable isotope probing has not been used in plant-soil-feedback experiments targeting rhizodeposit mediated legacy effects. However, they would be a potentially effective way to show how the (labelled) rhizodeposits of plants or plant communities in the feedback phase would affect plant growth and establishment in responding phase. Another interesting avenue would be to collect labelled root exudates from plants and add them to soils where following plant is planted to estimate the role of these root exudates in shaping the microbiome composition (using PLFA-SIP, DNA-SIP or RNA-SIP).

Future studies should further distinguish legacy effects due to the sloughing of root cap cells from the effects of root exudates on the rhizosphere microbiome. The use of plant genetics, and particularly gene knockouts, could help address this challenge. Badri et al. (2009) described an *A. thaliana* mutant with down regulated ATP-binding cassette genes involved in sugar transport and upregulated genes involved in transport of secondary plant metabolites. These modifications resulted in increased exudation of phenolics and decreased exudation of sugars. However, when scientists investigated the effects of salicylic acid-impaired *A. thaliana* on soil microbiomes, they noted little effect of removing one component from root-exudates on composition and biomass of soil microbes (Clocchiatti et al., 2021). At the same time adding synthetic components of root-exudates to the soils had larger effects. However, the use of plant genetics, and particularly gene knockouts, is valuable to gain insights into the role of specific types of compounds released by roots on the rhizosphere microbiome and may allow plants secreting particular exudates to be grown alongside mutants without this capability to create conditioned soils with and without particular rhizodeposits (Fig. 2d).

Microdialysis, which is an emerging tool to mimic the exudation of compounds by plant roots, is another technique that could help to explore plant legacy effects. While this tool has frequently been used to simulate the root-scale uptake of compounds from the soil, mimicking plant root uptake by diffusion (Buckley et al., 2020), it has recently been adapted to secrete compounds into soils (reverse microdialysis) to mimic plant root exudation (Buckley et al., 2022). An opportunity exists to use microdialysis to condition soils with artificial exudates (e.g. simple sugars) prior to growing a plant in the same soil in the responding phase of an experiment (Fig. 2e). This could be further advanced by conditioning soils with real rhizodeposits collected from plants grown in a different soil, possibly in an isotopically labelled environment (i.e. $^{13}\text{C}_2\text{O}_2$) to track the fate of the rhizodeposit carbon in the soil microbiome, soil extracellular environment, and the tissues of the responding plant.

8. Conclusions

Our understanding of the rhizosphere remains, even after several decades of research, incomplete. Knowledge gaps are largely due to the difficulties measuring rhizodeposition composition, and so it is understandable that the legacy effects of rhizodeposition are similarly unknown. One might assume that rhizodeposit-mediated legacy effects are small and limited to the rhizosphere soil for short periods because the soil microbiome is resilient and rhizodeposits are temporally and spatially variable. However, conditioning phases lasting several years have revealed rhizodeposit-mediated plant legacy effects on the soil microbiome that persist for several months and years (Hannula et al., 2021; Schmid et al., 2021). It should also be noted that not all organisms are similarly affected by the rhizodeposition. Fast growing organisms and organisms tightly connected with plants (such as pathogens and beneficial microbes) are more likely to be affected by rhizodeposit mediated legacies and hence also have greater potential to affect the growth of the following plant (Hannula et al., 2020; Heinen et al., 2020).

Future research should improve our knowledge of the underlying mechanisms of the plant legacy on soil microbiome. However, to generalize data to field conditions, it is important to consider that the complex root-soil-rhizosphere microbiome system cannot be entirely understood by studying the behaviour of each component separately (Vetterlein et al., 2020). The microbial community depends on soil properties such as texture, pH, and composition and quantity of nutrients (Samad et al., 2019) and it is unclear whether legacy effects are generally predictable (i.e. consistent across different soil types, pH ranges, and nutrient status), or if they are highly context specific. When testing for the effects of plant species on soils, this should be tested with different soil types, with plants under differing physiological status, and with multiple different plant species belonging to different functional groups to generalize plant legacy effects on soil microbial properties. It should also not be forgotten that microbiota other than bacteria and fungi (e.g. protists, nematodes and archaea) might also have relevant effects on plants and are also known to be strongly influenced by plants. Hence legacy effects are likely to occur also for these groups of microorganisms but appear to be notably poorly understood. Differences may also exist within each microbial group due to differences in function. For example, plant pathogenic nematodes can leave more durable effects than other nematodes if the host plant is present in the conditioning phase.

The potential benefits of understanding rhizodeposit-mediated legacy effects could lead to enormous benefits in agroecosystems by creating disease-suppressive soils or promoting plant growth-promoting rhizobacteria. This outcome may be achieved by designing novel cropping sequences, breeding traits into crops to promote rhizodeposition that benefits the following crop, or by synthesizing biomimetic chemo-attractants that recruit beneficial microorganisms and shape rhizosphere microbiomes for specific crops.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

No data was used for the research described in the article.

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