From rhizosphere to detritusphere – Soil structure formation driven by plant roots and the interactions with soil biota

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ABSTRACT

Roots and the associated soil directly affected by root activity, termed the rhizosphere, have both been extensively studied and recognized for their crucial role in soil functioning. The formation of the rhizosphere is primarily driven by the effect of roots on shaping the physical structure of the soil, which in turn has direct feedbacks on the interactions between physical, biological and chemical processes. As a result, the rhizosphere is a hot spot for microbial activity, cycling of nutrients and turnover of organic matter. Despite the pivotal role of soil structure in controlling rhizosphere processes, we still lack a quantitative description and understanding of the interrelationships of root-systems and soil in the creation and stabilization of soil structure.

We provide a comprehensive review of current knowledge and novel insights into processes that drive the formation and stabilization of soil structure in the rhizosphere. These processes are regulated by multiple indirect and direct pathways, involving root growth, the production of rhizodeposits and root hairs, as well as the activity of soil microorganisms and fauna. Further, we highlight that rhizosphere processes may persist and evolve after root death to an extent currently largely unknown. Finally, we identify five pertinent challenges that should be addressed to fully apprehend rhizosphere processes and thus harness the potential resilience of plant-soil interactions. These challenges include refining structural assessment and sampling of rhizosheaths, examining the rhizosphere in-situ and bridging the gap between solid phase and pore scale research. In our view, overcoming these obstacles can be accomplished by combining the power of imaging and isotopic approaches, especially at the field scale, encompassing diverse soils and plant species. The ultimate objective of future research should be to upscale rhizosphere processes by conducting more field experiments in concert with modeling efforts, under the umbrella of collaborative interdisciplinary research.

1. Introduction

Soils sustain the growth of higher plants by providing nutrients and water, as well as physical strength to hold plants in place. The obvious locus of belowground plant-soil interactions is the root system, which forms the vital plant part that ties together the abiotic and biotic world in the soil, connecting it to the aboveground plant organs and thus to the atmosphere. The soil volume around plant roots that is directly affected by their activity, i.e. the rhizosphere, forms a distinct soil structure with pores and interfaces that represents a hot spot and habitat harbouring

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numerous ecological processes and plant-microorganism-soil interactions (Darrah, 1993; Hinsinger et al., 2009). Plant growth is sustained via root activity through multiple mechanisms that are triggered within the rhizosphere, such as nutrient, water and oxygen transport, as well as mobilisation of resources by soil biota (Hinsinger et al., 2009).

Solute and gas transport in soils are determined by the complex spatial arrangement of solids (organic and inorganic matter) and pores which are variably filled with water and gas. Thus, soil structure exerts a significant control over most physical, chemical and biological processes in soils. Soil structure and aggregate formation are fostered by water menisci and biological processes that influence the binding of soil mineral and organic particles (Totsche et al., 2018). As a result, the structure of soils is a dynamic property that can be affected by moisture fluctuations (e.g. shrink-swell processes) and biological activity, including root growth (Amelung et al., 2023; Peth et al., 2013; Phalempin et al., 2021; Pires et al., 2007). While soil structure is recognized to play a fundamental role in soil functioning (Rabot et al., 2018), we still lack a thorough quantitative description and understanding of the interrelationships of root-systems and soil in the creation and stabilization of soil structure (Erktan et al., 2018; Ghezzehei, 2012; Lucas et al., 2019a; Marin et al., 2022; Naveed et al., 2017).

One of the main challenges in rhizosphere research is its exact definition and thus the spatial demarcation of the soil volume around a root to be considered as rhizosphere (York et al., 2016). Methods and definitions vary depending on the scientific discipline, observation scale, objectives and process in question (Kuzyakov and Razavi, 2019; Vetterlein et al., 2020). The rhizoplane, which corresponds to the root surface, represents the actual hot spot for the allocation of root derived OM and nutrient uptake (Schmidt et al., 2018). The rhizosheath is operationally defined as the soil material adhering to the root after it has been removed from the soil and shaken, and often considered as the rhizosphere for subsequent analyses and measurements (Aslam et al., 2022; McCully, 1999). However, the rhizosphere is suggested to extend beyond the physical association of roots and adhering soil particles (i.e., the rhizosheath) to a complex domain with functionally overlapping zones (Hinsinger et al., 2021; York et al., 2016). Even the distinction of the root surface is difficult as frequently root hairs are not included in the spatial domain of the root-soil interface because of their small size and transient nature (Raynaud, 2010). However, these cellular extensions of the root epidermis are considered important for nutrient acquisition as they significantly increase the absorptive surface area thus improving soil exploration (Jungk, 2001; Keyes et al., 2013; Koebernick et al., 2017, 2019; Marschner et al., 2011).

Our limited understanding of soil structure formation in the rhizosphere stems from its opaque and complex 3D nature, or even 4D if we consider its temporal dynamics. Progress has also been hindered until recently by a lack of suitable analytical techniques. It is also due to the intertwined physical, chemical and biological processes in the rhizosphere that are not easy to disentangle but need to be addressed by developing interdisciplinary concepts and approaches (Vetterlein et al., 2020).

In the following we will discuss the current knowledge on soil structure formation due to biological, chemical and physical rhizosphere processes, and we will demonstrate avenues for future research, leading to a holistic view and understanding of structure-related rhizosphere functioning. Our view is that plant roots are inherently bound to soil structure dynamics. The interconnections between roots, soil particles and soil biota provide a complex system of interactions that are highly diverse and in which biological processes are more resilient to external stresses than the surrounding soil (Hallett et al., 2022; Preece and Penuelas, 2016). The structural properties of the soil in close vicinity to plant roots are modified by a range of processes occurring during plant growth, which in turn affect the environment plant roots encounter (Hinsinger et al., 2009; Philippot et al., 2013; Vetterlein et al., 2020). Soil structure itself influences root growth and morphology (Alessa and Earnhart, 2000; Gregory, 2006; Lippold et al., 2021, 2022; Phalempin

et al., 2022; Vetterlein et al., 2022), and vice versa roots affect soil structure (Lucas et al., 2019a; Phalempin et al., 2022). The structure of the present review is guided by the view that root effects on soil structure formation and stabilization are the result of entangled direct and indirect pathways. These pathways include the physical effects induced by root growth (section 1.1) and rhizodeposition (section 1.2). The chemical nature of rhizodeposits (section 2.1) is also key in attracting microorganisms (section 2.2) and soil fauna (section 2.3) that further affect the structure of the rhizosphere. Beyond the life of the plant, processes induced in the rhizosphere may persist and evolve after root death (section 3). We end our review with five challenges that should be addressed in future research to fully apprehend rhizosphere processes (section 4).

2. Physical aspects – root growth and rhizosheath formation

2.1. Mechanical aspects of root growth

Growing roots have a strong and complex mechanical effect on the structure of the surrounding soil (Lucas, 2022). There are various mechanisms that lead to micro- and macrostructural changes. The most obvious one is that roots exert a mechanical stress due to radial and longitudinal expansion which compacts the soil and thus potentially decreases the porosity around roots. Decreasing soil porosity toward the root surface has long been postulated in a conceptual model by Dexter (1987) and was more recently directly observed by Aravena et al. (2011) in small soil cylinders filled with soil aggregates. However, Helliwell et al. (2019) reported an increase in porosity at the immediate root surface above the root tip in different soils and for different plant species, indicating the complexity of spatial rearrangement of soil particles due to plant activity. This was confirmed by Koebernick et al. (2019) in a Synchrotron-CT experiment, where the pore space was analysed at a micrometer resolution. The authors proposed that differences in shape between the cylindrical root surface and convex soil particles resulted in a higher porosity directly at the root surface and developed a conceptual model of this effect. Phalempin et al. (2021) showed that root growth could result in an increase or decrease of soil porosity in the root vicinity depending on the local conditions determined by initial soil physical characteristics. Roots may also directly create pores by root-shrinkage, which generates large and continuous paths for water and air flow (Carminati et al., 2009). The alignment of clay particles around root channels (Bruand et al., 1996) creates pore walls that remain stable after root decay because of the generated dense cylindrical structure (Dexter, 2004). On the contrary, when roots exert pressure to the pore wall, e.g., while thickening, local shear failure may occur along zones of weakness in the complexly structured aggregated rhizosphere, resulting in cracks which subsequently may affect the connectivity of the pore network (Materechera et al., 1992a, 1992b).

The mechanical deformation of the soil around roots depends also on soil water content and the texturally specific related capillary forces, which are affected by the uptake of water, and the release of complex mixtures of organic compounds that impact surface tension, contact angles, mechanical strength and aggregation (Aravena et al., 2011; Bengough, 2012; Carminati, 2013; Landl et al., 2021; Read et al., 2003; Read and Gregory, 1997; Rosskopf et al., 2022). These mechanical and hydraulic changes in physical rhizosphere properties can generate feedback mechanisms on root development by interacting directly with root growth (Lucas et al., 2019a). This was for instance also demonstrated by Colombi et al. (2017), who showed that root elongation in compacted soils is positively affected by low root tip diameter to length ratio. It has to be noted that the magnitude of soil structural changes in the rhizosphere is likely to not only depend on soil texture (Helliwell et al., 2017), but also on antecedent bulk density and soil friability. Systematic studies on the combined effects of plant species and soil properties on rhizosphere structure alterations are therefore needed and are starting to emerge (Phalempin et al., 2021). In such studies

combining multiple effects, one key remaining challenge is to ensure the comparability between treatments which is highly dependent on sampling conditions. For instance, water content (or water potential) has a large effect on the amount of rhizosphere collected and its structure, and the soil water content can vary according to the plant and soil characteristics (Basirat et al., 2019; Rahim et al., 2023; Steiner et al., 2024). One option to tackle this challenge is to ensure that the sampling is performed at comparable water contents (or water potentials).

2.2. Rhizodeposits and root hairs trigger rhizosheath formation

Rhizosheaths are soil structures bound to the root surface that result from rhizodeposits gluing soil particles together during drying (Mo et al., 2023; Watt et al., 1993). According to Albalasmeh and Ghezzehei (2014), the primary mechanism of rhizosheath formation is the deposition of exudates at inter-particle contacts during drying. Besides root exudates, bacterial products also play an important role in the formation of the rhizosphere structure (Sher et al., 2020; Watt et al., 1993), which will be further discussed in section 2.2. Repeated wetting-drying cycles of rhizodeposits and bacterial derived substances promote the fixation of organic matter (OM) to soil particles as well as the aggregation of soil particles (Ghezzehei and Albalasmeh, 2015; Mo et al., 2023; Watt et al., 1994). It is likely that water repellency (even when subcritical – i.e. contact angles <90°) that reduces rewetting kinetics, might promote aggregate stability (Goebel et al., 2005). Thus, the fact that the rhizosphere of several species (e.g. lupin, maize) turns hydrophobic upon drying (Ahmed et al., 2016; Moradi et al., 2012; Zarebanadkouki et al., 2016) is likely to enhance the aggregate stability in the rhizosphere. The production of mucilage, a gel like OM exuded at the root tip (Oades, 1978), also results in the formation of filaments and interconnected surfaces upon drying (Benard et al., 2019; Schnepf et al., 2022). The high water adsorption of mucilage, for a given soil water potential, decreases the suction and thus the forces pulling soil particles together during soil drying. This might sustain a higher porosity in the rhizosphere counteracting the effect of soil compression around roots (section 1.1).

Apart from mucilage, root hairs are considered another key element in rhizosheath formation and soil aggregation in the rhizosphere (Aslam et al., 2022; York et al., 2022). Root hairs entangle soil particles contributing to rhizosheath stability and have been shown to increase the extension of rhizodeposition radially from the root surface and longitudinally along the root (Holz et al., 2017, 2020b). Koebernick et al. (2017) showed that root hairs counteract the effect of root-induced soil compaction by significantly increasing the pore volume fraction at the root–soil interface. Through water extraction, root hairs also indirectly increase soil tensile strength and create new pores, which results in intensified drying and wetting cycles (Materechera et al., 1992b; Rasse et al., 2000; Segal, 2008) or local compression, modifying the hydraulic properties around the roots (Aravena et al., 2011; Marin et al., 2022).

3. Rhizodeposition – multiple routes towards soil structure formation

3.1. Soil structure formation via direct sorptive effects of rhizodeposits

Rhizodeposits have the potential to alter soil structure directly by acting as gluing agents that attach individual soil particles to each other, thereby forming aggregates (Baumert et al., 2021). Yet, the capacity of rhizodeposits to directly alter soil structure strongly depends on the nature of the rhizodeposit considered. For instance, mucilage was demonstrated to have a strong effect on aggregate stability (Morel et al., 1991). Morel et al. (1991) assumed a direct adhesive effect because it occurred immediately after incorporation of mucilage to soil. However, the effect of this single pulse addition decreased rapidly due to the microbial decomposition of the added mucilage. The effect of mucilage on

aggregate stability may vary with plant species and age, but also with the chemical environment encountered (e.g., pH, concentration of divalent cations in soil solution) (Knott et al., 2022; Werner et al., 2022). The effect of mucilage on soil structure is also partly controlled by its chemical composition. For example, Galloway et al. (2018) showed that soil particle aggregation is promoted by the polysaccharide xyloglucan, which is released to the soil by roots of many angiosperm plants. Akhtar et al. (2018) also identified xyloglucan, together with chitosan, β-1, 3-glucan, gum tragacanth, and xanthan, that are compounds contained in mucilage, as one of the most effective polysaccharides contributing to soil adhesion. Interestingly, it was shown in several studies that hydrophobic rather than hydrophilic substances, such as xyloglucan, foster the stability of soil aggregates, likely by limiting the penetration of water within aggregates (Behrends Kraemer et al., 2019; Chenu and Cosentino, 2011; Piccolo and Mbagwu, 1999). It has to be noted that root-derived compounds, which initially contribute to the formation of soil structure, may not retain their stability over time.

For low molecular weight root exudates with a high solubility in water such as glucose, there is little evidence for a direct effect on soil structure because small uncharged molecules do not bind strongly to soil minerals (Pojasok and Kay, 1990). Furthermore, such soluble root exudates are easily assimilated by microbes (Paterson et al., 2007), thus acting more in an indirect way by promoting microbial activity and specific microbial community structures (section 2.2) (Williams and de Vries, 2020).

The number of studies that investigated direct effects of rhizodeposits on soil structure is rather limited. Often, the experimental design does not allow for a clear identification of, and thus differentiation between direct and indirect effects. This is the case when effects of rhizodeposition are investigated in non-sterilized soils, such as in the study of Traoré et al. (2000) who tested a variety of different rhizodeposits and found an increased proportion of stable aggregates after 30 days of soil incubation with root mucilage, soluble root exudates, polygalacturonic acid and glucose. The authors reported a longer lasting positive effect on soil aggregation by the addition of mucilage in contrast to more labile soluble compounds, and suggested that whereas labile compounds are rapidly consumed by microbiota in the rhizosphere, mucilage is only gradually decomposed. In general, there is a direct interaction of the type of released OM and microbial activity that fosters the structural stability of soils within the rhizosphere. However, due to the rapid transformation between plant and microbial derived OM and the difficulties to measure chemical gradients from plant to microbial OM in-situ, it is still not clear to which extend plant derived OM or microbially transformed OM affects soil structure formation and stability in the rhizosphere.

New methods, providing explicit spatial gradients for specific organic compounds may help to shed light on this issue (Lohse et al., 2021), due to the ability to differentiate between plant and microbial derived OM. Also correlative microscopy is one way forward to link the physical soil structure of soil micro-environments (e.g. via stacked FIB-SEM images at nm-scale (see Fig. 1) or x-ray μCT at μm-scale (see Fig. 2) with the gradients of plant derived organic compounds and their fate via microbial transformation in intact rhizosphere systems (Lippold et al., 2023; Vidal et al., 2018). Based on the 3D imaging of the physical structure of intact rhizosphere systems, it is possible to target regions of interest for subsequent imaging of microbiota and chemical, as well as isotopic gradients (Lippold et al., 2023; Védère et al., 2022). In both Figs. 1 And 2, a combination of physical, chemical and biological information is demonstrated based on different spectroscopic and microscopic techniques, which allow to study the fate of root derived OM (rhizodeposition) *in-situ* together with its effects on soil microbiota and soil structure.

### 3.2. The microbial route towards soil structure formation

Rhizodeposits may have a direct effect on the formation and/or
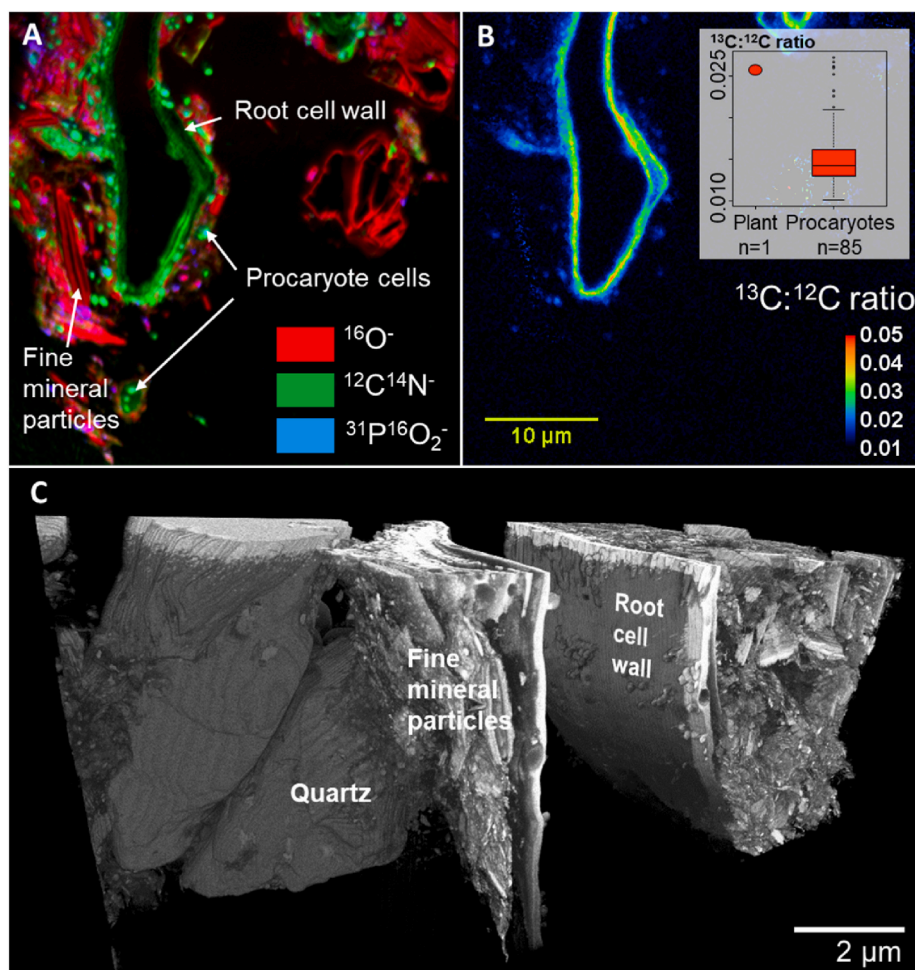
Fig. 1. Demonstrating how the fate of photosynthetically fixed carbon from the plant root into the rhizosphere can be tracked via isotopic imaging, a prerequisite to study the microscale interaction of plants, microorganisms and soil particles at the relevant scale in intact rhizosphere structures. Shown are NanoSIMS and FIB-SEM measurements of a wheat rhizosphere derived from a field experiment with *in-situ* $^{13}CO_2$ enrichment. (A) Composite image of soil minerals ($^{16}O^-$), organic matter ($^{12}C^{14}N^-$) and phosphorus ($^{31}P^{16}O_2^-$) highlighting numerous microbial cells at the rhizoplane (small green dots); (B) $^{13}C^-:^{12}C^-$ ratios of a root cell (section at root tip) and the surrounding unicellular microorganisms; (C) structural assembly of an intact rhizosphere volume measured using FIB-SEM (Vidal et al., 2018). A clear isotopic enrichment is demonstrated via the distribution of ^{13}C that corresponds to the unicellular microbial cells in the direct vicinity of the root cell and the mineral matrix supporting the new formation of MAOM via microbial transformation of rhizodeposits.

breakdown of soil structure (section 2.1), but also an indirect one by their transformation via microorganisms (Amézketa, 1999; Ndour et al., 2020; Oburger et al., 2022). Organic matter, when decomposed and assimilated by microorganisms, is either mineralized to CO_2, transformed to microbial biomass, or transformed and released as microbial exudates/extracellular polymeric substances (EPS) (sometimes also called microbial mucilage) into the surroundings of the microorganism (Paterson et al., 2007). Pathways of microbial transformation are highly relevant for the formation of soil aggregates through the assimilation of rhizodeposit-carbon (C) (Ma et al., 2022). Given the high microbial density and activity at the rhizoplane (Schmidt et al., 2018) and in the rhizosphere (Bonkowski et al., 2021; Marschner et al., 2012) it could be assumed that only small amounts of root exudates directly bind to mineral surfaces forming mineral-associated organic matter (MAOM), as they are easily assimilated. Based on tracer studies using ^{14}C enrichment of growing plants, it is estimated that after 3–8 months 2–4% of the C from rhizodeposition remains as SOM, for instance adsorbed on fine sized soil minerals (e.g., clay minerals), while 0.8–3.2% is incorporated into rhizosphere microbial biomass (Kuzyakov and Domanski, 2000; van Ginkel et al., 2000). The labile nature and high availability of many rhizodeposits leads to the build-up of specific microbial communities in the rhizosphere with a contrasted abundance and diversity compared to the non-rhizosphere bulk soil (Marilley et al., 1998; Nunan et al., 2017; Pett-Ridge et al., 2021; Semenov et al., 1999; Zhou et al., 2022). The detailed description of the microbial communities around roots, as well as their abundance and diversity, is beyond the scope of the present review and has been previously reviewed (Bonkowski et al., 2021; Bulgarelli et al., 2013; Dennis et al., 2010).The EPS produced by bacteria or fungi have the capacity to aggregate soil (Alami et al., 2000; Amellal et al., 1998; Chenu and Cosentino, 2011; Costa et al., 2018; Sandhya and Ali, 2015) and increase aggregate stability (Amelung et al., 2023; de Caire et al., 1997; Sher et al., 2020). The amount and quality of the rhizodeposition directly affects the composition of the rhizomicrobiome (Dangel et al., 2013; Tian et al., 2020), with specific exudates even fostering the microbial biofilm production. While the term EPS encompasses a variety of compounds, including DNA and protein, in the context of soil structure formation, it is specifically indicative of extracellular polysaccharides (EPS-polysaccharide) (Redmile-Gordon et al., 2014). These EPS play a pivotal role in microbial adhesion to soil particles which leverage the slimy texture and ionic charge of EPS to facilitate their attachment to clay minerals and ions, while also gluing soil particles together (Bettermann et al., 2021; Chenu, 1995). Beyond EPS, rhizodeposition was specifically associated with an increase in fungal biomass in several studies (Baumert et al., 2018, 2021; Griffiths
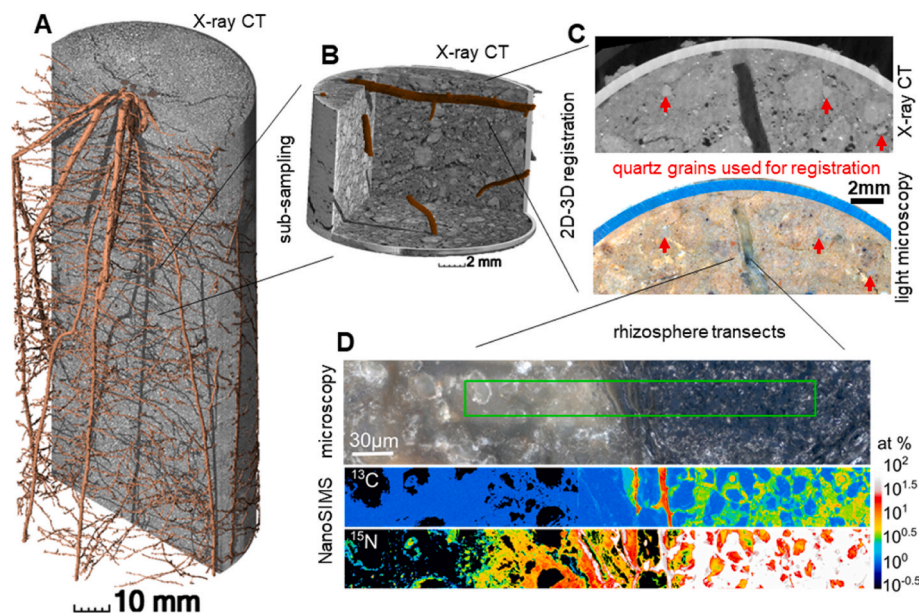
Fig. 2. Correlative imaging workflow demonstrated for a pot experiment with maize grown for three weeks in repacked soil with ^{15}N nitrate labelling of the soil solution prior to planting and $^{13}CO_2$ pulse labelling one day prior to harvest: (A) An X-ray CT scan of the entire soil column (45 μm voxel resolution) is used for targeted sub-sampling. (B) These subsamples are small enough to detect structural changes in the rhizosphere with high spatial resolution (10 μm) and to be used for resin impregnation (Lippold et al., 2023). (C) The exposed surfaces of polished blocks are mapped with light microscopy to identify roots. 2D-3D image registration (Schlüter et al., 2019) is used to project structural information into the microscopy plane. The registration is assisted with landmarks like small quartz grains that are easily identifiable with both imaging techniques. (D) The fate of labelled ^{13}C and ^{15}N and its extent into the rhizosphere is then mapped with NanoSIMS at selected transects. The example demonstrates how intact rhizosphere structures can be correlated with the fate of root derived organic matter from the millimetre up to the micrometer scale. (The NanoSIMS images were acquired and processed by Carmen Hoeschen (TU München) during a test run within the framework of the DFG funded priority program 2089.)

et al., 1998). Previously, considerable attention was directed towards the effect of glomalin on soil aggregate formation. However, it is important to note that glomalin is likely not a singular compound; rather it comprises an operationally defined mixture of compounds more accurately characterized as "glomalin related soil proteins" (GRSP) (Holátko et al., 2021). Further, the origin of GRSP remains not fully elucidated, raising questions about whether GRSP is a direct product of arbuscular mycorrhizal fungi (AMF), is released during the decay of AMF (Purin and Rillig, 2008) as traditionally assumed, or is derived from fungi associated bacteria (Holátko et al., 2021). Regardless of its origin, the concentration of GRSP was observed to correlate positively with the percentage of water-stable aggregates (Rillig et al., 2001; Wright and Upadhyaya, 1996). Rillig et al. (2002) showed that the production of glomalin-like substances by hyphae had a significantly stronger effect on aggregate stability than the hyphae themselves.

Microbial biomass ultimately ends up as microbial necromass that builds up during decomposition of plant-derived soil OM (Angst et al., 2021; Kaestner et al., 2021). After cell death and lysis, micro-aggregates stabilized by microbial materials, especially polysaccharides, remain stable (Totsche et al., 2018), whereas this OM is stored especially as MAOM (Li et al., 2023; Sokol and Bradford, 2019; Vidal et al., 2018, 2021). Teixeira et al. (2024) recently demonstrated that root derived OM predominantly ends up as MAOM with reactive Fe and Al phases playing an important role in the retention of initially root derived OC. The aggregate formation processes accompanied with this retention of OC are amplified by fine roots that cause intense local drying in their surroundings and promote aggregation processes (Rasse et al., 2005; Sher et al., 2020; Tisdall, 1996). A sustained physical stability of aggregates needs a continuous input of organic C, as the amount of organic binding agents is a function of OM input and microbial decomposition (Six et al., 2000). This implies that the persistence of organic C might be fostered in the rhizosphere via a reduced decomposition within stable micro-aggregates (Pett-Ridge et al., 2021; Rossi et al., 2020).

It appears clear that microorganisms (bacteria and fungi) affect soil

structure and C persistence through the production of gluing agents (e. g., EPS, glomalin-like substances) and microbial necromass. Yet, how are these rhizodeposition derived products distributed and transported away from roots? The spatial extent at which rhizodeposition alters the surrounding bulk soil and regulates C storage and aggregation in the rhizosphere is decisive for how much of the soil volume is affected by plant roots on the short and long term. Qiao et al. (2014) followed the fate of ^{13}C labelled rhizodeposits of maize into the surrounding soil in a field pulse labelling experiment. Twelve days after the last labelling (11 times multiple labelling) they found the ^{13}C label incorporated to a distance of 14 mm in all aggregate sizes, predominantly in the >2 mm and 1–2 mm macro-aggregates. This indicates that rhizodeposits and/or their metabolites might promote soil aggregation and were occluded within aggregates during soil aggregation. In another ^{13}C labelling experiment, Fahey et al. (2013) followed a large pulse of photo-assimilated ^{13}C into belowground pools in a natural forest. They found that nearly 4 % of the photosynthetic ^{13}C pulse was retained in the mineral soil mostly in micro-aggregates and macro-aggregates after 3 years. It can be assumed that in both cases fungi might play an important role in the translocation of the root derived ^{13}C (See et al., 2022). This is evidenced by recent studies showing that the increased uptake of plant root derived organic C by fungi is associated with the formation of aggregates in the vicinity of roots (Baumert et al., 2021; Gorka et al., 2019).

A growing number of studies looks into the extension of the rhizosphere by fungal hyphae into the so called hyphosphere (Hawkins et al., 2023; See et al., 2022). As the soil structure determines the fungal habitat and thus its functioning and vice versa, we need new concepts and analytical approaches that allow to study intact rhizosphere together with the associated fungi in an intact soil structural environment (Harvey et al., 2020). This may only be achieved if we succeed in tracking fungal hyphae and their translocation of OM in-situ in intact rhizosphere and non-rhizosphere soil compartments, linking physical soil habitat and pore structures with the biogeochemical fate of plant

derived matter at a spatial resolution yet unresolved by CT techniques. Using transparent model systems (e.g. microfluidic systems) is a good entry point to gain a better understanding of the interactions of microbiota and soil habitat structure (Hammer et al., 2024), allowing for the use of light microscopy to track microbiota in defined micro-environments. These systems allow to link physical micro-environments with microbial activity, and thus offer the possibility to study how microbiota and their activity is affected by interaction of physical and biogeochemical processes (Hammer et al., 2024). Such approaches might be combined with the study of roots growing in transparent materials (Aufrecht et al., 2022; Dupuy et al., 2018) and thus allow to study root-microbe interactions at greater detail. However, these methods can only be the starting point as we have to develop novel techniques to study plant-microbe interactions in opaque intact soils in the future. First approaches to combine multiple imaging techniques (e. g. fluorescence microscopy, NanoSIMS) based on physical information about the intact soil micro-environments by CT imaging may lead the way forward (Lippold et al., 2023; Schlüter et al., 2019).

3.3. The soil fauna route towards soil structure formation

The role of soil fauna in altering the soil structure is well known, and is driven by physical (e.g., displacement of soil particles), chemical (e.g., production of mucus) and biological (e.g., enhancing microbial activity) processes (Oades, 1993; Six et al., 2004). The effect of biota on soil structure formation, namely soil aggregation and pore creation, is not solely attributable to a specific taxonomic group but arises from the interplay of a diverse community (Guhra et al., 2022).

The activity of soil fauna results in the production of galleries/burrows (e.g., earthworm and enchytraeids burrows, termite galleries), dejections (e.g., faecal pellets, earthworm casts) and other biostructures (e.g., termite mounds) that have a different structure and composition compared to the surrounding soil or to the organic residues initially ingested (Angst et al., 2019; Guhra et al., 2022; Joly et al., 2018; Jouquet et al., 2011; Kheirallah, 1990; Lee, 1985; Porre et al., 2016; Vidal et al., 2019). According to Guhra et al. (2022) the effect of soil biota on the formation of soil aggregates, e.g., via their excreted OM, can be of either bridging, gluing or separating nature depending on the specific interactions of the biota derived OM, and the respective soil mineral surfaces. The formation of biopores and nutrient-rich biostructures facilitates root penetration, expansion, and ultimately plant growth (Kautz et al., 2014). Thus, by modifying soil structure, soil fauna can alter root growth that, in turn, will further alter soil structure.

The mutual impact of roots and soil fauna on soil structure could also be indirectly controlled by the build-up of specific microbial communities, producing gluing agents and favoring plant growth (section 1.2 and 2.2). For example, earthworms have been shown to indirectly increase plant growth by increasing mycorrhizal colonization of maize roots (Li et al., 2012) and hyphal length density in the soil (Li et al., 2013). Jacquiod et al. (2020) highlighted that plants presented the highest biomass when the interaction between plants and earthworms had resulted in the built up of a specific microbial community in the rhizosphere. Soil microfauna, such as protist or nematodes, are also increasingly recognized for their pivotal contribution in shaping the rhizosphere microbiome, and thus influencing plant growth and health (Bais et al., 2006; Gao et al., 2019). These studies clearly demonstrate that the tight interactions between roots, soil fauna and microorganisms in the rhizosphere can further affect plant growth.

Taken together, soil fauna mostly interacts with roots and affects their growth through its effects on soil structure, microbial communities and biogeochemical cycles. Plants can also initiate a communication strategy with soil fauna via the production of root derived compounds, which could result in altering the rhizosphere soil structure. Roots can repel undesired organisms or attract beneficial soil fauna that depend on the supply of root derived C, making the rhizosphere a refuge for numerous soil organisms. Among multiple examples, Rodger et al.

(2003) showed that border cells produced at the root tip can attract parasitic nematodes, and thus avoid the attacks of these parasites in vulnerable root zones (i.e., between root tip and root hairs). Rasmann et al. (2005) demonstrated that maize roots can produce volatile molecules that attract entomopathogenic nematodes that kill insect larvae colonizing the plant. For a comprehensive review on chemical signals between roots and soil biota, the reader can refer to Bonkowski et al. (2009). While responding to root signals, the soil fauna also interact with the mineral and organic soil particles, thus potentially affecting soil structure formation and stability in the rhizosphere.

4. Root legacy – contribution to soil structure and persistent soil carbon

Plant roots and their remnants, i.e. root litter, are a major trajectory for input of OM into the soil and therefore lead to the formation of soil structure. Thus, where and how roots develop, inject their rhizodeposits and die in the soil controls soil formation and can be modified by soil management. The preferential retention and greater contribution of root derived C to soil organic C compared to above ground C has been reported in several studies (e.g., Balesdent and Balabane (1996); Kong and Six (2012); Rasse et al. (2005); Sokol and Bradford (2019)). A main legacy of roots for soil structure is the formation of rather stable biopores that still exist even after the actual root decayed (Lucas et al., 2019b; Xiong et al., 2022).

Thus, in addition to the interactions between living roots and soil microorganisms (section 3.2) and soil fauna (section 3.3) (and viceversa) as drivers of soil structure formation, dying and dead roots affect soil structure-forming processes and leave a legacy in the form of the detritusphere of dead roots. Indeed, the decomposition of roots within the rhizosphere environment involves saprotrophic communities entering in competition for C and nutrients with other organisms of the rhizosphere (Sokol and Bradford, 2019; Veen et al., 2019) such as protists and collembola feeding on fungi (Radosa et al., 2019; Scheu and Schulz, 1996).

4.1. From labile rhizodeposits to persistent soil carbon

The type and quantity of rhizodeposits (e.g. exudates, sloughed off cells) produced are variable in space (i.e., along the root) and time (i.e., along the plant growth cycle), which induces a heterogeneous impact on root-soil C allocation and thus possible effects on soil structure on a larger scale. Exudates are released at the meristem and above the root tip (Jones et al., 2009), while mucilage is produced mostly at the root tip (Nguyen, 2009) and to a lesser extent by root hairs (Dennis et al., 2010). Thus, it can be expected that the effects of rhizodeposition on soil structure clearly differ along the root. It has to be noted that most studies exploring rhizodeposition processes focused on young roots without considering the entire plant growth cycle (Dennis et al., 2010). However, the amount of C released by the living root can vary according to the growth stage, with an increase in rhizodeposition during growth and flowering, and a decrease after maturity until senescence (Aulakh et al., 2001; Pausch et al., 2013). It is thus estimated that the allocation of carbon to roots and soil could be reduced by 43 and 20%, respectively during plant senescence (Nguyen, 2009). Recently, Remus et al. (2022) demonstrated that the relative and absolute C fluxes of rhizodeposition followed different trends during plant development. As plant size is increasing and hence root length density, total amounts of rhizodeposition continue to increase while rates (per unit root dry weight, length or surface) decrease. This points to the fact that the influence of rhizodeposition on specific soil structure formation may clearly differ between different growth stages.

Rhizodeposits are suggested to represent a major source for persistent C inputs to soil (section 2.2) (Gregory, 2022; Sokol and Bradford, 2019), particularly stored as mineral associated carbon (Villarino et al., 2021), but the mechanistic understanding of this process is largely

unknown. The formation of persistent soil organic C derived from rhizodeposition is largely facilitated by microbial transformation of the plant derived OM and thus the increase in microbial residues (Sokol and Bradford, 2019). To fully capture the legacy of root derived OM we need more specific work that tracks the fate of rhizosphere C beyond the actual plant life. For this, specific root and rhizosphere traits should also be considered as they may control actual root C allocation from plant to soil (Hallett et al., 2022; Rossi et al., 2020). To unravel the interaction of different plant species and root traits on the persistence of root derived C and their effects on soil structure we need to apply more specific isotopic tracing approaches (e.g. multiple tracers, using cultivars lacking specific genes for instance for root hair development or mycorrhizal colonization) that allow to track plant root derived OM in intact rhizosphere samples from plant to microorganisms and soil particles. This work has to advance from highly controlled lab scale approaches to plot and field scale experiments.

4.2. Dead roots and soil structure

A soil structural remnant of the former presence of living roots are biopores of persistent root channels. These biopores formed during root growth generate a porous soil structure that is often also stable after the actual decay of the root (Lucas et al., 2019b; Petzoldt et al., 2020; Xiong et al., 2022). Thus, roots create especially coarse soil pores that promote water infiltration as well as aeration (Uteau et al., 2022). It was shown that these root derived biopores also foster the growth of new roots inside them and thus enhance the ability of the roots to reach nutrients further down in subsoils (Han et al., 2017; Petzoldt et al., 2020; Zhou et al., 2020). Due to the altered physical structure of the soil, the size of biopores was also demonstrated to determine the root diameter of the subsequent crops (Han et al., 2016).

Besides the persistence of biopores beyond the root life span, decaying roots also foster the buildup of soil structure and the formation of persistent soil organic C. Interestingly, dead roots end up in different soil OM pools compared to soil OM from rhizodeposits, and especially exudates. A higher release of exudates might diminish the C stored as particulate organic matter (POM) due to the increase of decomposition via priming of inherited POM (Villarino et al., 2021). However, the rhizodeposition from living roots clearly fosters the formation of MAOM (Neurath et al., 2021; Pett-Ridge et al., 2021). In contrast, dead roots are mainly stored as occluded POM within soil aggregates (Sanaullah et al., 2011), rather than in MAOM. The increase of POM during root decay can promote the formation and stability of aggregates (Blankinship et al., 2016), especially in subsoils (Baumert et al., 2018) or C-depleted soils (Wu et al., 2022). We posit that the dynamic interplay between living and decaying root processes establish a unique yet largely unknown interaction between soluble and solid root derived C input, thereby influencing the fate of the soil OM stored either as POM or MAOM in the vicinity of roots.

The presence of dead roots also provides a source of OM for microorganisms to thrive, thereby affecting soil structure by processes already discussed in section 3.2. Xu et al. (2022) showed that root residue addition increased microbe-derived C more than shoot residue addition in a long-term experiment over 500 days. The input of root derived OM thus leads to a more aggregated soil in the rhizosphere, and also to the altered soil OM composition in the soil volume directly affected by the root OM input and its associated microbiome (Angst et al., 2016; Baumert et al., 2021). The high organic C input linked to an increased formation of more persistent soil structures may explain higher organic C concentration in rhizosphere than in bulk soil (Baumert et al., 2021; Sokol and Bradford, 2019), and thus may overall foster soil OC storage on the long run (Tefs and Gleixner, 2012). In this respect, it is worth noting that the effect of rhizosphere microorganisms on soil structure can persist beyond the ceased substrate availability from the living or dead roots, and even beyond the death of microorganisms. This is evidenced by Dormaar and Foster (1991) who studied the formation of

nascent aggregates in an artificial attapulgite rhizosphere. They found that organo-mineral clusters were formed *de novo* by accumulation of attapulgite particles on root gel, on root cell fragments, and on microbial extracellular polysaccharides. Micro-aggregates were formed by the fusion of attapulgite-coated bacteria, colonies and cell remnants, and persisted after the death of the microbes.

5. Five challenges for future rhizosphere research

We encourage scientific efforts to gain a holistic view on rhizosphere dynamics, including physical, chemical and biological aspects in order to effectively harness the potential of the resilience of the plant-soil interface within the framework of global change. The resilience of the rhizosphere and thus the plant-soil system can be addressed as restoring a specific functionality after disturbance (Holling, 1973; Ludwig et al., 2018). According to Ludwig et al. (2018), the resilience of a soil system, and thus also the plant-soil system, is not due to one distinct factor but rather to a holistic meta-function of a sum of processes driven by biota. An important driver of resilience in the rhizosphere are the legacies of the diverse plant-soil interactions that persist after biological activity ceased or after root death. While legacy as an ecological concept has traditionally been associated with the effect of plants on soil properties, guiding ecological succession (Cuddington, 2011), it also includes the ability of a soil to perform functions in the future (Nannipieri et al., 2023), a notion referred to as 'soil memory' by Targulian and Bronnikova (2019). According to Hastings et al. (2007) the legacy of an ecosystem engineer, here the root and the associated microbiome, is defined as the persistence of the engineered aspects and the related effects on the system that still persist after the death or absence of the biota. Thus, to be able to understand the complex interactions between biota and soil in the rhizosphere that lead to resilience and thus e.g. longer lasting stability of the plant-soil system for crop production or high biodiversity, we need a better understanding of the long lasting effects of rhizosphere activity and thus its legacy. This implies investigating the following research lines.

> Rhizosheaths to quantitatively analyze biogeochemical processes in root affected soil structures – the need for refining the methods for their sampling and structural assessment

Though rhizosheath formation has been studied intensively in the past, we are lacking a comparable approach for their quantification. This is especially important as rhizosheath samples are often vital to quantitatively study the fate of root derived OM, microbial activity and community structures as well as root-soil physical interactions. Further, serving as a footprint of root activity, rhizosheaths hold significant implications for the resilience and legacy of the plant-soil system. On the one hand, the formation of rhizosheaths is reported with varying reference sizes, such as root surface area or root biomass, which hinders the comparability of results. On the other hand, soil water content (or water potential) is the major parameter resulting in varying amounts of rhizosheath collected (section 1 and 2.1). As water content strongly differs in studies reporting rhizosheath formation, and even sometimes between treatments in the same experiment, the comparability of the studies is not given. Rhizosheath soil samples being regularly used to quantify the formation of aggregates in the rhizosphere, results on aggregation are thus also directly affected by the way rhizosheaths are sampled. We therefore strongly encourage future studies to conduct measurements at comparable water contents (or water potentials) and suggest to report results of rhizosheaths production per root surface area to allow for comparison between studies.

> Evaluating the effect of in-situ rhizodeposition and root activity as a whole

The intricate interactions in the rhizosphere between roots,

microorganisms and soil minerals are to a large extend determined by the release of OM by the root. However, much of our understanding is still based on indirect measures and assumptions due to the difficulties to directly study the intact root-microorganism-soil interface in-situ. It is not understood to which extend the root itself or rather the associated microbiome determines the fate of plant derived oranic C in the soil, and how this affects the structure in the vicinity of the root. And in reverse, how does the soil structure and thus the architecture of habitats determine the interactions of the rhizosphere microbiome. Our comprehension of the fate of plant root-derived OM, its microbial transformations, and the regulation of mineralization versus sequestration within persistent soil structures in the rhizosphere remains limited, particularly within the framework of an intact soil structure. Thus, in the realm of rhizosphere research, there is a growing need for refined methodologies to untangle the intricate web of interactions between plant roots, soil microorganisms, and soil structure. The scientific community should develop experiments that allow to differentiate and quantitatively measure the influence of the different single rhizosphere components (root inputs, microorganisms and soil particles) on the whole intact rhizosphere system.

For instance, future investigations should strive to discriminate between the direct influence of rhizodeposits and the indirect effect of microbial-derived secretions, and microbial necromass on rhizosphere formation in general and aggregate formation in the rhizosphere in particular. Stable Isotope Probing (SIP) represents a promising avenue, allowing us to link root-derived carbon to the formation of persistent carbon within the rhizosphere through the microbial assimilation of root-derived carbon and the subsequent formation of microbial necromass. In this context, particular attention should be given to the exploration of the expansion of the rhizosphere into the hyphosphere, investigating the profound influence of fungal hyphae on soil structure and functioning as well as the fate of plant derived OM.

To address the spatial and structural complexity of the intact rhizosphere, innovative concepts and new analytical approaches are required (section 2.1). One notable technique to achieve this is correlative microscopy, which bridges the physical soil structure of microenvironments with the gradients of plant-derived organic compounds and their microbial transformation within intact rhizosphere systems. Utilizing 3D imaging, such as stacked FIB-SEM images at the nanometer scale or x-ray µCT at the micrometer scale, enables researchers to pinpoint regions of interest for subsequent imaging of microbiota and chemical, as well as isotopic gradients. This comprehensive approach allows for an *in-situ* examination of the fate of root-derived OM alongside its impacts on soil microbiota and soil structure. Such approaches are the prerequisite to disentangle the importance of specific physical and chemical properties in rhizosphere micro-environments for the soil structure formation and the fate of plant derived OM as regulated by plants and microbiota.

Furthermore, to fully comprehend the legacy of root-derived OM, there is a demand for more specialized research that traces the destiny of rhizosphere carbon beyond the plant's active life cycle, providing critical insights into long-term soil health and nutrient cycling. So far most work does not differentiate between the effects of rhizodeposition of the living plant and the effects from decaying dead roots (Nannipieri et al., 2023). In this sense, it is vital to better define at which timepoint an active root and its rhizosphere changes into a decaying root and thus a detritusphere system, and which are the important factors that need to be measured during that transformation. While the most direct approach would involve extracting roots from the soil and analysing the effects of living and dead roots individually, an integrated understanding of the effects of rhizosphere and detritusphere on soil structure may be hampered if these components are studied in isolation (Vetterlein et al., 2020). Therefore, we need experiments that span over the whole life time of a plant including its decay.

Bridging the gap between solid phase and pore scale research for advancing rhizosphere research

There are two major approaches to quantify and characterize the soil structure and habitat formed due to root activity, namely non-invasive imaging (e.g. CT) and destructive sampling, e.g., rhizosheath sampling, soil aggregate fractionation. Whereas the imaging approach offers detailed information of soil structure at the pore scale and thus allows to comprehensively quantify and model physical soil structure, it lacks the ability to gain quantitative information on, for instance, organic C allocation and fate between plants, microorganisms and soil particles. The latter is for instance a clear prerequisite to gain robust information (e.g. C and N contents, amount of microbial necromass, microbial activity, POM vs. MAOM) on the importance of roots and root traits as means for soil carbon storage and persistence. We thus can create new angles by connecting quantitative methods that can specify overall solid state structural units/volumes with state-of-the-art imaging techniques that can put these solid entities into relation to pores and thus solute, water and gas fluxes as well as plant resource acquisition. Thus, it is important to develop analytical means and concepts to study both aspects together in complex intact 3D plant-soil structures, rather than the continuation of applying these approaches separately. This will also offer new avenues in connecting soil water status with plant physiology and in connecting the pore view with analysis of solid soil compartments and thus elemental budgets at larger scales (e.g. soil carbon stocks).

Assessing the combined effects of plant species and soil properties on rhizosphere structure formation

In the face of a rapidly changing climate, necessitating resilience in the plant soil system, there is a pressing need for robust insights into plant soil interactions within the root zone, on a global scale. This information is crucial for further understanding water and nutrient acquisition strategies, which, in turn, influence plant productivity and health. This extends to the unknown contribution of soluble vs. solid rhizodeposition and dead roots to the formation of persistent soil carbon in particulate or mineral-associated OM pools. To foster soil carbon sequestration derived from roots by managing root traits, we need to discern the specific rhizosphere structural entities (e.g. macroaggregates rich in POM, microaggregates rich in MAOM) where initially plant derived C ultimately accumulates.

The focus extends beyond extensively studied temperate regions and major crops. It is thus imperative to conduct systematic studies that assess the combined effects of plant species and soil properties on rhizosphere structure formation. These investigations should encompass a wide range of pedoclimatic conditions and soil properties, including texture, in conjunction with various plant species and cultivars. By delving into this complex interplay, we can gain a deeper understanding of how different plant centered factors influence alterations of the rhizosphere structure at a global scale, and thus to more effectively make use of plant-soil interactions to mitigate climate change.

Upscaling of rhizosphere processes

Field-scale studies provide a more realistic analysis of the complex interactions between plants and the environment they interact with in natural and managed ecosystems. This allows researchers to better understand how rhizosphere processes function over time with plant development and in the more relevant agronomical and ecological systems context. Upscaling rhizosphere processes is therefore a needed step to make informed decisions about land use and conservation.

To scale rhizosphere processes up to the field scale, several approaches can be employed:

Field Experiments: Conducting field experiments that manipulate relevant variables enables the observation of rhizosphere processes within natural environmental contexts. To advance rhizosphere

research, we thus recommend increased emphasis on field-based studies. Various techniques can facilitate this, including stable isotope labeling (^{13}C, ^{15}N), root exudate sampling and post-root excavation rhizosheath analysis. Additionally, innovative imaging methods like the use of optodes as well as exudate collection are now being successfully applied in field conditions (Ahkami et al., 2024; Faget et al., 2013; Holz et al., 2020a). These approaches offer valuable insights into rhizosphere dynamics within real-world settings.

Modeling: Using mathematical models and simulations can help to extrapolate findings from smaller-scale studies to predict how rhizosphere processes function at the soil profile and field scales and how they impact plant functioning. Although current root models are now capable of effectively describing root architecture and including rhizosphere physical and biogeochemical dynamics in an effective way, it remains a gap between microscopic understanding at the rhizosphere scale and how to represent it in macroscopic models (Roose and Schnepf, 2008; Schnepf et al., 2022).

Additionally, the collaboration between experimentalists and modelers has to be considerably intensified in order to allow the better incorporation of data from laboratory experiments and environmental factors into models, setting experimentally informed parameterization and work towards making predictions.

Collaborative Research: It may be obvious, but collaborating within multidisciplinary teams of scientists, including e.g. agronomists, ecologists, and soil scientists, to combine expertise and resources for field-scale research efforts is crucial to successfully upscale rhizosphere processes. Examining individual components of the rhizosphere in isolation does not advance our understanding of its complex interactions. Thus, better understanding rhizosphere processes and upscaling from micro-to root system or plot scales asks for researches that seek consensus in aiming for the added value of multidisciplinary research groups. This requires planning projects and experiments in which researchers from multiple disciplines, including modelers, agree on using common sets of methods, same plant species, cultivars or mutants and work at the same sites or with the same soils, rather than just pursuing their own accustomed procedures (Vetterlein et al., 2020). This is the prerequisite to bring conceptual and experimental approaches into agricultural practice and thus address pressing questions of the mitigation of climate change and resource scarcity.

6. Conclusions

Roots actively alter the physical structure of the surrounding soil via a complex interplay of physical, biological and chemical interactions (Fig. 3), and thus affect water and nutrient availability, as well as carbon storage. While rhizosphere research has thrived in recent decades, the ambition to quantitatively and mechanistically grasp the intricacies of this complex plant-soil interface has not been entirely met. The limitations stem primarily from rather reductionist methodological and conceptual challenges. To unravel the complexities embedded in the spatial and temporal dynamics of the plant-microorganism-soil interface and its resilience to stress, it is imperative to overcome classical disciplinary views. We need a holistic system approach facilitated by collaborative research initiatives. As pointed out by Vetterlein et al. (2020), the establishment of joint research platforms, within larger project consortia or through multiple groups participating in defined experiments, is essential to bring together scientists from diverse disciplines. This will inevitably involve reaching a consensus on necessary methodological compromises. A key focus should be on integrating quantitative bulk analysis (e.g. isotopic tracing, soil OM fractionation) with state-of-the-art imaging techniques (e.g. μCT, NanoSIMS). This is crucial to unravel the multitude of interactions between roots, microorganisms and soil particles, together with process rates in intact rhizosphere micro-environments. In parallel, we encourage a strategic shift towards upscaling mechanistic understanding from the micro-environment to the plot and field scales. This implies the further development of
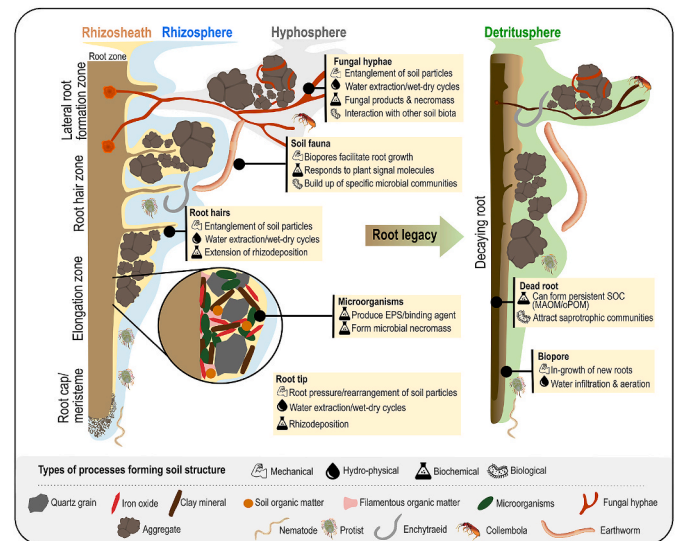
Fig. 3. A holistic and conceptual perspective on the creation and stabilization of soil structure in the root-affected soil. This phenomenon arises from intertwined mechanical, hydro-physical, biochemical and biological processes that occur in close vicinity to plant roots. The influence of living roots on the soil structure extends beyond the physical association of roots and adhering soil particles (i.e., the rhizosheath), encompassing a complex domain with functionally overlapping zones, such as the rhizosphere and the hyphosphere. Roots and the affected rhizosphere form unique soil structural hot spots through various routes, ranging from the physical pressure exerted by growing roots on the surrounding soil to the release of a wide array of soluble and solid rhizodeposits that fuels interactions within the intricate rhizosphere food web. It is important to note that roots can affect soil structure beyond their lifetime. Decaying roots contribute to the formation of relatively persistent soil organic carbon (SOC) forms, including mineral-associated organic matter (MAOM) and occluded particulate organic matter (oPOM). Further, root residues and biopores attract (new) organisms (e.g., microorganism, soil fauna, new roots), further enhancing the long term legacy of dead roots. Note that the scale depicted does not accurately reflect reality and has been adjusted for visualisation purposes. This figure was drawn using Inkscape 1.2.2 (Inkscape Project, 2023).

methods allowing the quantification of plant-microorganism-soil interactions at larger scales, providing higher throughput and temporal resolution. The knowledge derived from these approaches is vital for making well-informed management decisions, especially in the context of managing soil carbon stocks and improving system resilience via root-soil interactions.

CRediT authorship contribution statement

Carsten W. Mueller: Writing – original draft, Visualization, Conceptualization. **Vera Baumert:** Writing – original draft, Visualization. **Andrea Carminati:** Writing – review & editing, Writing – original draft, Conceptualization. **Amandine Germon:** Writing – original draft. **Maire Holz:** Writing – review & editing, Writing – original draft, Conceptualization. **Ingrid Kögel-Knabner:** Writing – review & editing, Writing – original draft, Conceptualization. **Stephan Peth:** Writing – original draft, Conceptualization. **Steffen Schlüter:** Writing – original draft, Visualization, Conceptualization. **Daniel Uteau:** Writing – original draft. **Doris Vetterlein:** Writing – original draft, Conceptualization. **Pedro Teixeira:** Writing – original draft. **Alix Vidal:** Writing – review & editing, Writing – original draft, Visualization, Conceptualization.

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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