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Editorial: Rhizosphere Functioning and Structural Development as Complex Interplay Between Plants, Microorganisms and Soil Minerals

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Editorial on the Research Topic

Rhizosphere Functioning and Structural Development as Complex Interplay Between Plants, Microorganisms and Soil Minerals

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The rhizosphere, the soil volume, which is directly affected by root activity (Hinsinger et al., 2009), is an important hot spot for a multitude of biotic and abiotic processes (Lambers et al., 2009). Carbon transfer from plants to microorganisms and to soil takes place in these small volumes around living roots, creating chemical gradients and zones of microbial activity over distinct temporal and spatial scales. Hydraulic and biogeochemical properties of the rhizosphere and the formation of complex three-dimensional structures such as micro- and macroaggreates in turn, result from complex feedbacks between physical, chemical and biological processes. The aim of this Research Topic is to advance our understanding of rhizosphere interactions by collating 16 original contributions across disciplines, including original research, reviews and specific methods on the processes taking place in the rhizosphere, to shed new light on one of the most important interfaces for the diversity of life on earth.

Growing roots are at the core of the rhizosphere and dynamically impact soil structure through the spatial rearrangement of mineral soil particles due to the physical pressure exerted by their growth. Continued growth and branching resulting in constantly changing root architectures that continuously alter the spatial extent of the rhizosphere. To account for these constant spatiotemporal changes, Schlüter et al. developed a new method to model root architecture and estimate rhizosphere volume via a combination of time-lapse μCT imaging, image registration and root distance modeling. Besides exerting pressure, roots also secrete mucilage from their tips, which impacts the physical properties of the rhizosphere microenvironment (Carminati et al., 2011). Haas et al. used gel-like model substances to understand the behavior of mucilage in soils. They found that the capacity of these substances to stabilize soil particles depends on their deformation capacity. In addition, mucilage dynamically modifies mechanical properties of the soil matrix such as the penetration resistance (Haas and Horn) and hydraulic properties of the soil solution (Benard et al., 2019). While the importance of mucilage for rhizosphere hydration and root growth is well-recognized (Carminati et al., 2011), direct measurements of mucilage in intact soils remain challenging. Holz et al. present a promising approach using infrared spectroscopy to measure the distribution of mucilage in the rhizosphere, making use of the C-H signals of mucilage fatty acids. By the application of exudate mixtures via artificial rhizospheres to top- and sub-soils, Baumert et al. demonstrate that higher levels of root exudates lead to an increased macro-aggregation of subsoil material. The authors thus demonstrate soil structure formation driven by root exudation in a soil compartment that was previously thought to be determined mainly by physical rather than biological processes. However, the mechanisms of root exudation of primary metabolites are not yet fully understood. In a comprehensive review, Canarini et al. propose that root exudation rates are regulated via source-sink driven dynamic processes, rather than occurring as a passive leaking of exudates.

Growing roots and hyphae of mycorrhizal fungi release tremendous amounts of organic carbon derived from photosynthesis into soil compartments at depths that otherwise receive only small amounts of dissolved organic matter leached from litter. The exudation of organic compounds into the rhizosphere can prime the decomposition of previously stabilized inherited soil organic matter (Baumert et al.). In addition to the roots themselves, mycorrhiza fungi function as vectors for plant derived organic matter into the root free bulk soil, where the "hyphosphere" fosters nutrient acquisition, soil aggregation and the allocation of initially plant derived organic matter into more stable organo-mineral associations (Gorka et al.; Vidal et al.). Although being structurally different to the rhizosphere, the mycorrhizal hyphosphere thus may extend some of the rhizosphere's functions, including soil structure formation and the sequestration of initially plant derived organic carbon.

Mycorrhiza fungi not only facilitate carbon flow into the soil but their primary function for plants seems to be aid in the uptake of mineral nutrients. Arbuscular mycorrhiza fungi (AMF) especially provide the host plant with phosphate. Using a tomato—*Rhizophagus irregularis* (AMF) model system grown in pure sand or sand mixed with goethite Andrino et al. show that plants have to invest more carbon for per unit of fungal-delivered phosphate, when the phosphate is strongly adsorbed to a substrate such as goethite. This implies that mycorrhiza-mediated carbon flow into the rhizosphere may be co-determined by soil physico-chemical properties. Molecular processes underlying arbuscular mycorrhizal nutrient exchange are mainly studied under laboratory conditions, although application of the symbiosis will happen in the field. In his review, Kobae summarizes the current knowledge on arbuscular mycorrhizal phosphate uptake and advocates for more research toward understanding arbuscular mycorrhizal phosphate uptake under complex field conditions. The complexity of plant-fungal-soil interactions is exemplified by Paymaneh et al., who show that the growth of strongly AMF-dependent plant *Antropogon gerardii* is inhibited by the addition of biochar to soil, while growth can be partially recovered after the addition of AMF, the extend of which is dependent on the acidity or alkalinity of the soil. Using split root systems, Henkes et al. show that AMF alter the N-uptake and -allocation patterns facilitated by protists in wheat; and that mycorrhiza and protists together determine the rhizosphere microbial community in a systemic manner.

Volatile organic compounds (VOC) emitted by soil microbes are known to modulate root growth (Sharifi and Ryu, 2018). Schenkel et al. exhibit another example for the complexity of biotic interactions in the soil by demonstrating that several *Fusarium* isolates, reduced VOC emissions from soils thereby allowing increased elongation of Arabidopsis primary roots.

A better understanding of roots and rhizosphere functioning under drought is critical to adaptations to rapid climate change and frequent occurrences of climate extremes. Soil management and plant breeding needs to aim for increasing efficiency in plant water acquisition and for keeping water in the soil. Breeding efforts for producing drought resistant cultivars can lead to distinct alterations in the rhizosphere bacterial communities as demonstrated by Li et al. for drought and insect resistant rice cultivars. As reviewed by Yu and Hochholdinger different plant genotypes also develop different root systems and produce different chemical cocktails in their root exudate, which can determine the physical and chemical properties of the rhizosphere and the species composition of its inhabiting microbiota. They state that the resolution of conventional sampling strategies used to describe root endosphere and rhizosphere microbiota communities is too coarse to capture such differences, and emphasize laser capture microdissection in combination with next-generation sequencing as a promising route to elucidate plant microbe interactions in the future. Interestingly, in grafted cultivated plants such a wine, the endosphere and rhizosphere community differs in function of the rootstock (D'Amico et al.).

Since the rhizosphere is hidden in the soil matrix it was previously difficult to extensively explore its complex interactions. To study intact soil environments like the rhizosphere, different imaging techniques play a crucial role, as for instance approaches to trace enzyme activities like the *in-vivo* imaging of phosphatase activity along intact root systems (Dinkelaker and Marschner, 1992). With the advent of high resolution spectromicroscopic imaging techniques it is now possible to directly study plant-microorganism-soil interactions using a wide array of visualization techniques from infrared spectroscopy to nanoscale secondary ion mass spectrometry (Gorka et al.; Holz et al.; Vidal et al.). As demonstrated by Gorka et al. it is vital to get down to micro and nanoscale measurements to gain a more complete understanding of water and nutrient supply and microbial activity at the relevant process scale. The complex nature of active rhizosphere thus asks for a combined approach of chemical, biological and physical concepts and methods (Gorka et al.; Vidal et al.). Gaining a deeper understanding of the rhizosphere as a driving force in ecosystem functionality, can be fostered by interdisciplinary collaborations involving soil physics, microbiology, plant physiology, and biogeochemistry disciplines (Baumert et al.; Haas et al.; Vidal et al.).

This Research Topic highlights the rapid rate of advancements in rhizosphere research. Continuous improvements in imaging methods together with the combination of interdisciplinary approaches aiming at linking physical, chemical, and biological processes is fostering new understanding of the belowground interactions between soil, microorganisms and plants, as well as of the significance of these processes for plant performance and adaptation to biotic and abiotic stresses.

AUTHOR CONTRIBUTIONS

All authors listed have made a substantial, direct and intellectual contribution to the work, and approved it for publication.

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