



# Special issue: Rhizosphere spatiotemporal organisation: an integrated approach linking above and belowground

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Received: 19 August 2022 / Accepted: 20 September 2022  
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The resilience of soils, i.e. their ability to maintain functions or recover after disturbances, is closely linked to the root-soil interface, the powerhouse of the soil. Recently, it has been hypothesised that resilience arises from self-organised spatiotemporal patterns that are the result of complex and dynamic feedbacks between physical, chemical and biological processes in the rhizosphere (Vetterlein et al. 2020). To test this hypothesis, several challenges need to be overcome: (i) methods are needed to repeatedly, ideally in situ, measure radial rhizosphere gradients non-invasively

in the field with high spatial ( $\mu\text{m}$  to  $\text{mm}$ ) and temporal (hours to days) resolution; (ii) combining measurements of different parameters at the same time and place would be desirable; (iii) integration of physical (structure, mechanics, water), chemical (exudates, metabolites, complexation, sorption) and biological (gene expression and proteome, microbiome composition, activity and function) data will help to decipher the local interactions; (iv) upscaling from local measurements (pore, root segment) or single time points to the scale of the whole plant/soil profile or growing season is needed to link the local interactions to the emerging system-level properties; and finally (v) one must always keep in mind the close interplay between above- and below-ground processes. All this will eventually help to assess how and under which circumstances certain root and rhizosphere characteristics may contribute to a better integration of nature-based solutions into our cropping systems.

Many of the contributions in this special issue are directly related to a major research initiative (PP 2089) funded by the German Research Foundation (DFG), which aims to address the above challenges by bringing together different disciplines working in the same experimental system to create complementary datasets and find a common language (Vetterlein et al. 2021). Here, a particular focus was placed on root hairs as a plant-related driver of rhizosphere processes and on soil texture as a soil-related driver of rhizosphere processes. A number of contributions were added to expand the available methodological

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Responsible Editor: Hans Lambers.

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toolkit, increase the number of root/rhizosphere features covered and integrate rhizosphere processes into assessment schemes.

### Linking rhizosphere processes across scales

Schnepf et al. (2022) present a series of case studies of state-of-the-art simulations in an opinion paper which provides an introduction to the multi-scale, multi-process problems that must be addressed to integrate processes in the rhizosphere, from the single root to the plant level. They show which mathematical tools can be used to move from image based models at the pore scale to the continuum scale, but also provide examples of how models operating at different scales can inform each other. Examples are given of combined modelling of root and root hair growth/architecture and exudation, and of exudation and P uptake or mucilage and water flow. Finally, an approach for explicit integration of microbial processes and their interaction with the distribution of particulate organic matter, nutrients, exudates, water and soil structure is presented.

### Rhizosphere traits and water uptake

Experimental data on the role of soil texture and root hairs for the development of drought stress have been interpreted using modelling approaches at the laboratory scale for the juvenile phase (Köhler et al., 2022) and at field scale during the whole growing period in two consecutive years (Jorda et al., 2022). Jorda et al. (2022) show that the root capacity was large enough to absorb all available soil water and that the onset of drought stress was primarily related to shoot size. Neither study could demonstrate a direct influence of roots hairs on soil–plant conductance for the selected maize genotypes, but proved an effect of soil texture on water use. The potential role of mucilage for water uptake at the pore scale is addressed in case study four by Schnepf et al. (2022), demonstrating that the interaction between mucilage, water and soil particles increases the connectivity of the liquid phase across the rhizosphere. Knott et al. (2022) add to this topic, establishing how physical properties of mucilages change with pH and the presence of divalent cations. Furthermore, Werner et al. (2022) have shown

that not only the chemical environment changes the mucilage properties, but that mucilage composition strongly depends on the growth conditions, the collection system and the age of the plant.

### Root traits, texture, soil structure and mechanical impedance

Lippold et al. (2021, this issue) for the laboratory scale, and Vetterlein et al. (2022) for the field scale, could not confirm earlier reports suggesting that the absence of root hairs is compensated by a greater investment in fine root growth or stronger interaction with mycorrhiza. At both scales, a surprisingly large effect of soil texture on root diameter was found, which was not related to differences in soil mechanical impedance. The latter was investigated by Roskopf et al. (2022) at field scale accounting for different soil matric potentials. They found changes in soil stability within a short period of time, but no consistent difference in mechanical impedance between soil textures. Not only soil texture, but also differences in soil structure (presence of macroaggregates) affect root distribution in soil (Lippold et al., 2022). However, these differences are local adaptations to the heterogeneity in nutrient availability and penetration resistance, which have little effect on shoot growth.

### Plant-microbe-soil interface

The (molecular) mechanisms at the plant–microbe–soil interface have been reviewed by Oburger et al. (2022a), providing an excellent overview of the identified mechanisms triggered/influenced by individual compounds or compound classes in root exudates. This is a prerequisite for merging spatially resolved datasets for gene expression (Ganther et al., 2021), microbiome composition (Yim et al., 2022) and exudation, which have so far been interpreted separately. The gene expression and microbiome data revealed that soil texture is a much more important factor compared to the presence of root hairs. For enzyme activity, reflecting root and/or microbial activity, a new micro-zymography approach was developed by Ghaderi et al. (2022). Yuan et al. (2022) presented a new method for

in-situ measurements of small-scale, spatially and temporally resolved sampling of soil pore water. For the quantification of exudation, Oburger et al. (2022b, this issue) present a rapid and cheap method for determination of C in exudate samples, which can be used for samples obtained from hydroponics or from a soil-hydroponic hybrid approach. The latter method is of particular relevance as it allows information to be obtained at the field level. The quantification of rhizodeposition and, in particular, the change in carbon partitioning between shoot, root and rhizodeposition during ontogeny was the aim of the comprehensive study of Remus et al. (2022). They showed that the ratios of the relative  $^{14}\text{C}$  fluxes in the root-soil-soil gas system changed considerably during plant development and that the relative and absolute C fluxes of rhizodeposition followed different trends.

### Relevance of Rhizosphere traits at system scale

Liu et al. (2021) demonstrated in a laboratory experiment that an identified mechanism (citrate efflux for complexation of  $\text{Al}^{3+}$ ) can be used to promote root growth in a specific environment (subsoil acidity, Al toxicity and drought stress) and thereby enhance biomass production. Vetterlein et al. (2022) demonstrated the role of hairs in nutrient uptake and shoot growth at field scale with greater effects on loam than on sand, which was hypothesized based on mechanistic knowledge gained by other researchers in laboratory experiments over the years. Both examples show that knowledge gained in small scale, reductionist approaches can be extrapolated to the field, but the community needs to do this, and surprises that arise from complex environments, such as the strong impact of soil texture, are picked up and identified for further research. For rhizosphere research to be recognised by other actors outside this research community, approaches for deriving simple indicators for assessing rhizosphere processes, such as those described by Mira et al. (2022), are very important. Such indicators could also be valuable for polluted sites, as described by Minkina et al. (2022).

**Authors contribution** D.V., A.C. and A.S. together wrote this editorial, D.V. prepared the submission.

**Funding** Open Access funding enabled and organized by Projekt DEAL. Large part of the work presented in this special issue was funded by the DFG, German Research Foundation (project number 403801423) within the framework of the priority programme 2089 “Rhizosphere spatiotemporal organisation—a key to rhizosphere functions”.

### Declarations

**Conflict of interest** All authors declare no conflict of interest.

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