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EDITORIAL

Rhizosphere 5 - shining light on the world beneath our feet

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Soil-Plant interactions are important for climate change mitigation

The Marschner Review of Silva and Lambers (2021) proposes a quantitative framework for the integrated analysis of plant functional groups under climate change that includes scaling rules by which local soil-plant-atmosphere interactions can be spatially and temporally aggregated to infer emergent ecosystem properties. This model is analysed in the commentary of Penuelas and Sardans (2021), who concluded that it would help to apply soil-plant-atmosphere interaction research in climate-change mitigation and adaptation actions. In other words, this approach can shed light on the feedback between small-scale rhizosphere processes and large-scale climate processes. Although vital for plants, belowground functional traits are studied less because they are hard to measure. One approach to circumvent this problem is to find aboveground proxies that allow conclusions on belowground processes.

Assessing below-ground traits from above-ground observations

Lambers et al. (2021) established that leaf manganese (Mn) concentrations are a signature of phosphorus (P)-mobilising carboxylates in the rhizosphere in low-P soils across 727 species in Australia and New Zealand. In their commentary on this paper, White and Neugebauer (2021) conclude that, although some orders containing species accumulating Mn in their shoots are typically non-mycorrhizal and release carboxylates into the rhizosphere, such as the Proteales, many orders containing species with this trait are characterised by conventional mycorrhizal associations. It remains to be further investigated if mycorrhizas really play a role in P acquisition in these Mn-accumulating mycorrhizal species, or whether carboxylates are more important.

Francioli et al. (2021) investigated the saprophytic fungi associated with roots of eight plant species - either a grass or a forb – along a biodiversity gradient in a grassland experiment. Plant functional group was the main factor driving fungal saprophytic community

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structure of species when growing in monoculture, likely driven by inherent differences in root lignin concentration and C:N ratio between grasses and forbs. This clear differentiation at the level of plant functional groups also worked out when analysing saprotrophic communities in mixed root samples. The saprophytic fungal communities in plant species mixtures represented to a large extent the differences observed in monocultures, suggesting that the root-associated saprophytic community can be predicted using information on plant functional groups in grasslands.

Special root-rhizosphere traits for plant nutrient acquisition can be found around the world

Nutrient-poor soils occur in western Japan, where a native Cyperaceae species is shown to form specialised "dauciform" roots. Masuda et al. (2021) confirmed P mobilization in the rhizosheath soil of the dauciform roots of *Carex lenta* which significantly contributed to P acquisition in its nutrient-poor habitat. Rhizosheath formation can also be important in agricultural crops. In a pot experiment using calcareous soil at three levels of soil Zn and P, He et al. (2021) investigated zinc (Zn) and P interactions of alfalfa, a deep-rooted leguminous perennial plant (*Medicago sativa*) that is widely cultivated for forage and hay. Rhizosheath properties of alfalfa showed strong P-Zn interactions in the calcareous soil-plant system that significantly affect Zn bioavailability, plant growth, accumulation of Zn and P, and partitioning of Zn. Therefore, rational P fertilisation should be considered for efficient Zn biofortification on Zn-deficient soils and phytoremediation of Zn-contaminated soils. Honvault et al. (2021) found that plant P-acquisition strategies are driven by multiple belowground morphological and physiological traits as well as interactions among these traits. Interactions and trade-offs among belowground functional traits, however, remain underexplored, especially for fast-growing crops such as cover crops, limiting our understanding of P cycling in agroecosystems. Examining 13 cover crop species highlighted trade-offs between thicker and thinner roots with thicker roots exhibiting greater carboxylate-release or phosphatase activity in the rhizosheath. Multivariate analysis underlined four main P-acquisition strategies relying primarily on morphological traits, physiological traits, or a combination thereof, and mediated by soil type. The diverse strategies underpin functionally-complementary multispecies crop designs via preferential access to different soil P pools, enhancing P availability and cycling efficiency.

Below-ground traits that explain:

Geographic distribution of plants

Phosphorus availability can partly explain the distribution of two native Australian plant species. Albornoz et al. (2021) established that this can be explained by the plant specie's ability to down-regulate their P-uptake capacity. In their study, they demonstrated that Anigozanthos flavidus, a species with a wider geographic distribution, is much more effective a down-regulating its P-uptake capacity at high P availability than Macropidia fuliginosa, a species with a narrower distribution.

Success of re-vegetation of mining land

Restoration of mined land in semi-arid Western Australia was the focus of Cross et al. (2021a). They found that the growth of six keystone native plant species was compromised at different life cycle stages in restoration substrates compared with natural topsoil. In particular, root development was constrained, primarily because of a lack of available nitrogen (N) and high alkalinity. Their results suggest that the edaphic properties of restoration substrates must be considered early in restoration planning, allowing practitioners to select the most appropriate pioneers and ensure favourable revegetation outcomes. In a further study, Cross et al. (2021b) confirmed this result for most of 40 native plant species and eight crops. Their results suggest that up to 75 % of native floristic biodiversity might be selected against in the ecological restoration of magnetite tailings landforms. The best-performing species were those with calcicole plant strategies and N_2-fixing or cluster-root-producing species, indicating that consideration of plant functional traits such as nutrient-acquisition strategy may be important when selecting species as potential pioneers in ecological restoration and rehabilitation.

Plant nutrient (P, Fe) acquisition

Cawthray et al. (2021) undertook solution culture experiments to measure root-mediated iron (Fe) reduction (FeR) in cluster roots at four stages of cluster-root development, in non-cluster roots and whole root systems for two species of *Banksia* (*B. attenuata* and *B. laricina*) grown at 2 to 300 µM Fe (as Fe-EDTA). Unlike typical Strategy I species, both *Banksia* species showed no significant variation in FeR, for either cluster or non-cluster roots over this wide range of Fe supply. They also observed only minor differences for whole-root system FeR, and even though *B. attenuata* showed signs of leaf Fe deficiency in the 2 µM Fe treatment, its FeR was the lowest of both species across all treatments. Additionally, taking plants through a pulse from low to high Fe supply, then back to low Fe supply, did not elucidate any significant response in FeR. They concluded that although Fe acquisition is tightly controlled in the investigated *Banksia* species, such control is not based on regulation of FeR, which challenges the model that is commonly accepted for Strategy I species.

Mechanisms of endophytic fungi to facilitate salt tolerance in host crops

Gupta et al. (2021) reviewed the functioning of salt-tolerant microorganisms, i.e. endophytic, symbiotic fungi, to plant genetics or soil management to alleviate salt stress in crops. Such functions are attained through the induction of systemic resistance, increase of beneficial metabolites, and activation of antioxidant systems to scavenge reactive oxygen species, as well as modulation of plant phytohormones. Colonisation by the endophytic fungus improves nutrient uptake and maintains ionic homeostasis by modulating ion accumulation, thus restricting sodium ($Na+$) transport to leaves and ensuring a high cytosolic potassium ($K+$):$Na+$ ratio. Participating endophytic fungi enhance transcripts of genes encoding the High-Affinity Potassium Transporter 1 (HKT1) and inward rectifying $K+$ channels KAT1 and KAT2, which regulate $K+$ and $Na+$ homeostasis. In addition, endophyte-induced strigolactones play regulatory roles in salt tolerance by interacting with phytohormones. This progress on endophytic symbioses under salinity sheds light on our understanding of the mechanisms of endophytic fungi to enhance salt tolerance in host crops.

Modelling combined with experiments can be used to quantify specific P acquisition processes

McKay Fletcher et al. (2021) present a new approach that combines microdialysis and modelling to quantify citrate-enhanced P uptake by roots. Microdialysis probes with citrate in the perfusate absorb similar quantities of P to an exuding root. The combination with the model allows to decouple microdialysis and rhizosphere mechanisms. Knowing the microdialysis setup, the model thus allows to determine rhizosphere mechanisms from the measurements. Using their model setup, they found that a plant needs to exude citrate at a rate of 0.73 µmol cm − 1 of root h − 1 for a significant increase in P uptake; a rate much higher than is commonly produced by a single root. Such quantifications can help to understand the effects of root exudation for different types of roots and root systems including cluster roots and dauciform roots.

Root microbiome research as a new imperative in the field of plant-microbe interactions

In their Marschner review, Pieterse et al. (2021) reported that root microbiome research has emerged as a new imperative in the field of plant-microbe interactions. The realisation that thousands of microbial species are an integral part of the biology of plants and expand their genomic potential comes with great new opportunities for microbiome-assisted agriculture. Discoveries that root microbiota support plant growth, nutrition and health fostered bio-based crop system approaches to reduce use of agrochemicals. Since its discovery in 1988, the plant-beneficial rhizobacterium *Pseudomonas simiae* WCS417 served as a model strain in numerous investigations on how free-living mutualists colonise the rhizosphere, modulate plant immunity, promote plant growth, and influence microbe-microbe interactions in the soil. Pieterse et al. (2021) highlight the key discoveries that have been made with this strain and lay out conceptual frameworks of our current understanding on molecular mechanisms involved in beneficial plant-microbe interactions, both in binary interactions and in context of the root microbiome.

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