Metabolic coupling on roots

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Abstract
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Disciplines
Agricultural Science | Agriculture | Plant Biology | Plant Pathology | Soil Science

Comments
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When a seed germinates, it commits to living through good times and bad in a given plot of soil. This sessile state of plants provides strong incentive to establish beneficial partnerships with other organisms. Members of root-associated microbial communities, known as rhizosphere microbiomes, can provide benefits to plants that range from enhancing nutrient availability to bolstering the plant’s defenses against biotic and abiotic stresses. Plants help shape the rhizosphere microbiome, as evidenced by differences among plant species in their microbiome composition, but how they recruit and influence these communities are poorly understood. In this issue of *Nature Microbiology*, Zhalnina et al. provide evidence that metabolic coupling of plant exudation of specific nutrients with microbial nutrient utilization preferences contributes to the assembly of the rhizosphere microbiome. Moreover, developmental patterns in root exudate composition suggest an ability of plants to regulate their metabolic interactions with microbes, thus potentially fostering beneficial communities and enabling breeding or engineering to manipulate root microbiomes.

Soils are rich with microorganisms. As roots develop, these soil communities serve as a seed bank of microbes that can potentially respond and flourish on growing roots. Only a small subset of bulk soil microbes establish populations on roots, and these bulk soil communities remain distinct from those on roots in composition, structure, and transcriptional responses to root exudates. Zhalnina et al. investigated the mechanisms by which microbes in the bulk soil respond to roots and the extent to which their responses are predictable and generalizable. They assembled a collection of microbes representing the seed bank in a native soil supporting the annual grass *Avena*. Using this collection, they elegantly integrated data from microbial community profiling, microbial comparative genomics, plant metabolomics, and exometabolomics, i.e., metabolomics of the extracellular milieu, to probe the metabolic interactions that help drive the assembly of the rhizosphere microbiome.

Microbial community profiling captures the demographics of entire communities based on molecular signatures of community members in the absence of cultivation. In a previous study, several of the authors used amplicon sequence data as molecular signatures to document the successional dynamics of microbial communities on *Avena* roots and in the neighboring bulk soil throughout plant development. These data served as a critical resource for linking cultivated isolates from a seed bank to their likely responses to roots. In particular, Zhalnina and colleagues used sequence similarity to match their cultivated isolates to taxa in the community profiles, and then assigned isolates that matched taxa that were abundant in the bulk soil to distinct response groups based on their successional dynamics on *Avena* roots. Isolates that matched taxa that increased in
relative abundance during *Avena* growth were called positive responders, whereas those that matched taxa that decreased or did not change were called negative responders and undefined responders, respectively. These designations reduced the complexity of the system to a manageable level, and supported the creation of a powerful reference set of isolates for exploring mechanistic linkages between traits of seed bank microbes and microbial responses to roots.

Plants release 16 to 50% of their photosynthetically-fixed carbon into the soil, with this veritable waterfall of nutrients supporting the rhizosphere microbiome. Identifying the key chemical drivers influencing the microbiome has been challenging, however, because of the diverse and dynamic nature of both the microbes and the root exudate metabolites. Recent studies with rhizosphere communities highlighted a link between the expression of metabolic genes for specific substrates and the presence of those substrates in exudates. Zhalnina *et al.* used comparative genomics to examine microbes beyond those only in rhizosphere communities. By focusing on traits associated with the acquisition and turnover of carbon substrates, they found that positive responders had a greater abundance of organic acid and amino acid transporters than negative responders, whereas negative responders had a greater abundance of macromolecular depolymerases. Collectively, these findings illustrate potentially distinct nutrient acquisition strategies, with positive responders adapted to the uptake of easily assimilated organic and amino acid monomers, and negative responders adapted to breaking down complex substrates.

An exciting aspect of this work was the powerful functional demonstration that microbial substrate utilization preferences are coupled with the exudation of specific substrates. Root exudate metabolomics demonstrated compositional shifts during *Avena* development as in other species, consistent with genetic programming of root metabolite release, and a notable increase in the exudation of aromatic compounds during vegetative growth. Using exometabolomics, Zhalnina *et al.* profiled the depletion of metabolites due to the growth of specific microbes in root exudates, thus linking substrate utilization to the succession of substrates produced. Interestingly, isolates designated as positive responders depleted significantly more amino acids and organic acids than negative responders, and the metabolites that most strongly differentiated positive responders from negative responders were aromatic organic acids. Moreover, a model predicting microbial responses to roots successfully predicted the responses to roots of three of four isolates examined, illustrating that these metabolite utilization capabilities may be particularly good predictors of rhizosphere colonization.

The question of how the chemical environment on roots shapes the rhizosphere microbiome is important to agriculture, as it is central to the breeding and optimization of plant-microbe partnerships for crop health and productivity. Many questions remain to be addressed, including how rhizosphere microbes influence root exudation patterns, how antimicrobial compounds in root exudates influence microbial enrichment patterns, and how metabolite sorption to minerals influences bioavailability and the metabolome profiles in soil matrices rather than the liquid matrices used these studies. The report by Zhalnina and colleagues, however, is a strong advance in providing compelling functional evidence.
for metabolic coupling between root production of specific metabolites, particularly aromatic organic acids, and microbial preferences for using these metabolites, thus deepening our insights into the process of rhizosphere microbiome assembly.

Figure. Metabolic synchronization of microbial substrate utilization traits and root exudation traits is a major driver of rhizosphere microbiome assembly. Plants are genetically programmed to release a succession of root exudate metabolites through their development (distinct metabolites are shown as distinct shapes diffusing from plant roots). The microbes in the bulk soil function as a seed bank of microorganisms that vary in their genetic potential to import and utilize distinct metabolites as substrates. The substrate use preferences of these microbes within the complex chemical milieu of the rhizosphere determines which microbes flourish in response to growing roots. Microbial community assembly patterns can therefore be predicted from models coupling substrate use preferences and chemical succession in the rhizosphere. Knowledge of these patterns can help guide strategies to engineer microbial communities that are favorable for plant health.