Special Issue: Unravelling the Secrets of the Rhizosphere

Review

Metabolomics in the Rhizosphere: Tapping into Belowground Chemical Communication

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The rhizosphere is densely populated with a variety of organisms. Interactions between roots and rhizosphere community members are mostly achieved via chemical communication. Root exudates contain an array of primary and secondary plant metabolites that can attract, deter, or kill belowground insect herbivores, nematodes, and microbes, and inhibit competing plants. Metabolomics of root exudates can potentially help us to better understand this chemical dialogue. The main limitations are the proper sampling of the exudate, the sensitivity of the metabolomics platforms, and the multivariate data analysis to identify causal relations. Novel technologies may help to generate a spatially explicit metabolome of the root and its exudates at a scale that is relevant for the rhizosphere community.

Communication in the Rhizosphere

By nature, soil communities are extremely diverse. As a consequence, the rhizosphere is populated with myriad organisms, including nematodes, fungi, bacteria, and arthropod herbivores (Figure 1) [1]. Each of these organisms, alone and in combination, may interact with the plant. Given that other forms of communication are not feasible belowground, soil organisms mostly rely on chemical **communication** (see Glossary). Indeed, plants secrete a large array of primary and secondary plant metabolites into the rhizosphere to facilitate interactions with their biotic and abiotic environment. Even the **root exudate** of a small plant species, such as arabidopsis (*Arabidopsis thaliana*), may contain over 100 different metabolites [2]. Recent advances in untargeted **metabolomics** allow us to detect and, to some extent, identify increasingly more of the compounds that are secreted by plants and the organisms interacting with them in the rhizosphere. Reliable quantification and identification will require well-designed experimental set-ups and an answer to the question of which conditions should be applied during exudate collection [3]. Moreover, the experimental designs should be such that they provide a realistic insight into what happens under field conditions.

Here, we review recent advances in metabolomics and the identification of compounds exuded into the rhizosphere, and what is known about their role in the interaction between plants and soil biota. We focus on insect herbivores, nematodes, and beneficial microbes, because the role of exudates in defence against microbial pathogens was recently reviewed elsewhere [4,5]. We specifically focus on the role of plant secondary metabolites because they often have a critical role in species-specific communication between interacting organisms [6]. Finally, we discuss

Trends

Metabolomics is becoming accepted as a tool for the (untargeted) analysis of metabolites in root exudates.

The importance of the rhizosphere microbiome for the functioning of plants is becoming increasingly clear.

Statistical analysis and genetic mapping are used to establish relations between metabolites and (other) traits.

The increased understanding of metabolic engineering in plants will allow the critical assessment of the role of individual compounds in plant–rhizosphere communication.

Novel chemical-analytical platforms, such as laser-assisted electrospray ionisation (LAESI), will allow for spatial metabolomics on the scale of roots and interacting organisms.

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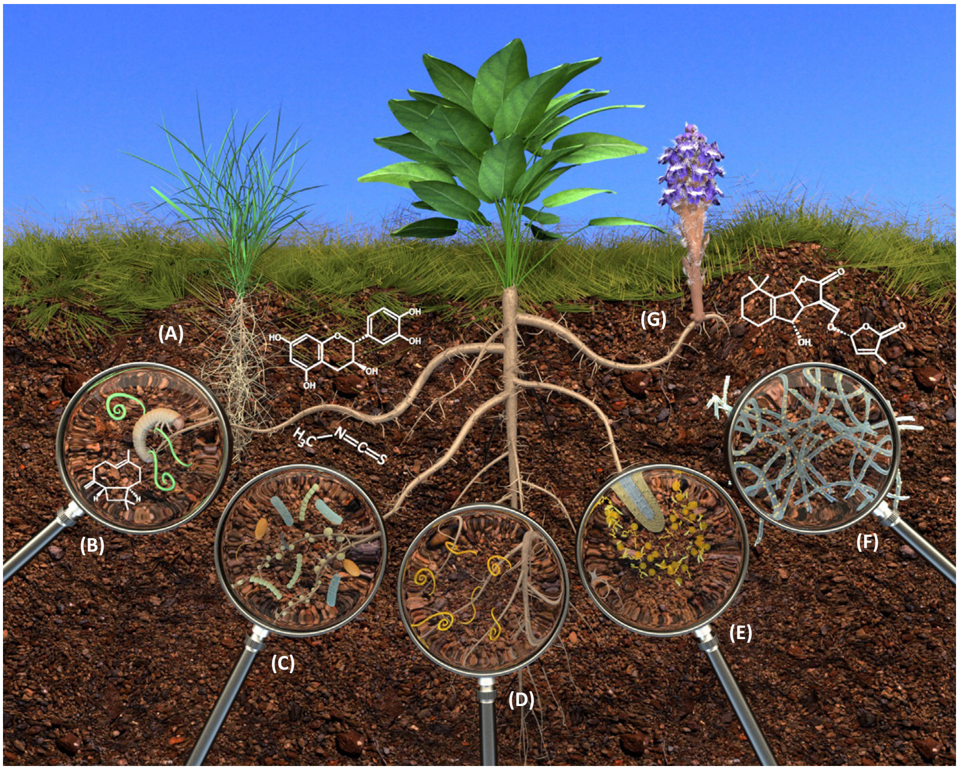

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Trends in Plant Science

Figure 1. Belowground Chemical Communication of Plants with other Organisms. (A) Plants exude phenolic compounds to inhibit the germination or growth of other plants (allelopathy); (B) insect larvae feeding on the roots induce the production of volatiles, such as sulfur-containing compounds or the terpene (*E*)-β-caryophyllene, attracting entomopathogenic nematodes; (C) the root exudate of plants affects colonisation by rhizosphere bacteria and initiates the colonisation and root nodule formation by *Rhizobia*; (D) root exudates induce hatching of cyst nematodes and attract juvenile nematodes towards the root; (E) the root cap at the tip of the roots is the site of most active exudation; (F) strigolactones in the root exudate induce hyphal branching in arbuscular mycorrhizal fungi, a process required for colonisation; and (G) the germination of parasitic plants is induced by strigolactones in the root exudate of their host.

challenges and opportunities with regard to exudate collection and analysis, data analysis, and the interpretation of the ecological role of the secreted metabolites.

Metabolomics of Root Exudates

It has long been acknowledged that root exudates constitute a significant source of organic carbon in the soil; up to 50% of the total plant photosynthetic production may be exuded into the rhizosphere. A primary function of root exudates is to mobilise recalcitrant and limiting nutrients, such as phosphorous (P), and to detoxify heavy metals by the excretion of organic acids. Therefore, the analysis of exudates is often limited to organic acids and other primary compounds, such as sugars [7,8]. However, the recent development of broad-spectrum and highly sensitive (nano- to picomolar range) **metabolomics platforms** now potentially allows a more comprehensive view on exudate composition.

The principal aim of metabolomics is to analyse as many compounds as possible in a single run. However, the analytical platform chosen greatly determines the classes of compound that can be detected. When studying rhizosphere interactions mediated by volatiles, **gas chromatography-mass spectrometry** (GC-MS) is the platform of choice. By contrast, water-soluble