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Special Issue: Unravelling the Secrets of the Rhizosphere

Review

Signaling in the Rhizosphere

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Signaling studies in the rhizosphere have focused on close interactions between plants and symbiotic microorganisms. However, this focus is likely to expand to other microorganisms because the rhizomicrobiome is important for plant health and is able to influence the structure of the microbial community. We discuss here the shaping of the rhizomicrobiome and define which aspects can be considered signaling. We divide signaling in the rhizosphere into three categories: (i) between microbes, (ii) from plants to microorganisms, and (iii) from microorganisms to plants. Signals act on diverse organisms including the plant. Mycorrhizal and rhizobial interkingdom signaling has revealed its pivotal role in establishing associations, and the recent discovery of signaling with non-symbiotic microorganisms indicates the important role of communication in shaping the rhizomicrobiome.

Trends

The plant and the rhizomicrobiome strongly influence each other via the secretion and detection of signaling compounds.

Signaling between plants and rhizosphere microorganisms has been mainly studied in intimate symbiotic associations, in particular those involving mycorrhizal fungi and rhizobial bacteria; it is now evident that this is a more widespread phenomenon also involving non-symbiotic microorganisms.

The rhizomicrobiome is a very rich and complex microbial community which undergoes intraspecies as well as interspecies signaling.

Thus far, plant molecules including flavonoids, strigolactones, cutin momoners, and as yet unidentified low molecular weight compounds have been recognized as signals which are sensed by microorganisms.

Microorganisms produce signals which affect plant growth and induce plant systemic resistance mainly via a process called priming.

The Rhizosphere and the Rhizomicrobiome

The **rhizosphere** (see Glossary) is a highly complex ecosystem consisting of the narrow zone of nutrient-rich soil that surrounds, and is influenced by, plant roots. It is densely populated by diverse microorganisms including fungi, bacteria, protists, nematodes, and invertebrates. Plant roots secrete an assortment of primary metabolites (e.g., organic acids, carbohydrates, and amino acids) and secondary metabolites (e.g., alkaloids, terpenoids, and phenolics) which are believed to shape, signal, interfere with, or in some way affect the rhizosphere microflora. This release or exudation in the rhizosphere of a large assortment of chemicals comes at a significant cost of carbon and nitrogen for the plant, with the ultimate benefit of attracting and promoting beneficial microorganisms while combating pathogenic or otherwise harmful ones.

The rhizosphere microbiota extends the capacity of plants to adapt to the environment, and the establishment of a particular microbiota member in the rhizosphere can be regarded as niche colonization. As mentioned, the impact of the rhizosphere microbiome (**rhizomicrobiome**) is believed to rely heavily upon the chemical exudates, which also mediate interactions via signaling molecules which are produced and secreted by both plants and microbes. The extent to which root and microbial exudates affect the rhizosphere microbial structure and function is a subject of ongoing research; in particular, how the plant selects the rhizomicrobiome and most importantly the beneficial microbial partners [1–4]. Studies have been mostly focused on bacteria, but the recent extensive census of fungi and protists [5–7] will allow developing a much broader view of the rhizosphere microbiome in the future. Apart from a handful of well-studied examples, which will be discussed below, the signaling and impact of the rhizosphere chemistry on the microbial community remains largely unknown. Scientists often refer to this aspect using several general terms such as underground interactions, signaling or communication highways, rhizosphere chemical language, and complex plant–microbe interactions, but two main questions remain – what constitutes signaling in the rhizosphere and what are the underlying mechanisms?

The shaping and recruitment of the rhizomicrobiome by the rhizosphere chemistry can be regarded as occurring via two general processes. First, via stimulation by the rhizodeposits or

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root exudates (this accounts for approximately 10% of photosynthetically fixed carbon and 15% of total plant nitrogen) of microbial multiplication in the vicinity of roots. This is an active and pivotal way for recruiting, shaping, and tuning microbial rhizosphere communities from the reservoir of microorganisms present in the soil, involving processes that support, restrict, or terminate microbial growth and activity. We believe that this important role of chemicals in determining rhizosphere residents cannot be considered signaling.

The other process affecting the rhizomicrobiome occurs via the detection and response to low molecular weight compounds of either plants or microbes, resulting in a cellular response(s) which is not only restricted to the catabolism, transformation, or other aspects (e.g., resistance) of the compound being sensed. This entails a regulatory response/cascade which ultimately leads to the transcription of loci in response to a particular compound. This is what we believe suits the definition of signaling and, to further simplify our understanding of this rapidly growing research field, we divide it into three categories representing the major types of signaling mechanisms known to occur in the rhizosphere (Figure 1 and Box 1): (i) microbial intraspecies and interspecies signaling, which occur mainly via **quorum-sensing** (QS) signal molecules allowing microbial communities to form and synchronize their behavior; (ii) signaling from plants to microorganisms via small plant-secreted molecules, which has been implicated in several specialized symbiotic relationships and most probably occurs frequently in other interactions; and (iii) signaling from microorganisms to plants documented so far by microbially produced compounds affecting plant gene expression, root architecture, and plant defense responses. Some molecules are involved in more than one type of signaling as discussed below. The aim of this short review is to define and highlight these aspects of rhizosphere signaling and to delineate some future directions.

Microbe–Microbe Signaling in the Rhizosphere

Many microorganisms synthesize signaling compounds to synchronize their gene expression in response to cell density in a process known as QS [8]; this has been and is currently the subject of extensive investigations in microbiological research. Importantly, many groundbreaking studies on QS have been generated using models of plant–microbe associations regulating diverse processes such as the production of virulence factors, synthesis of secondary metabolites, formation of biofilms, conjugation, and motility [8]. The signals produced by microbes belong to a wide range of chemical classes, and multiple QS systems using different types of signals often occur within a single organism. It is not the scope here to review exhaustively the QS signals being produced by the rhizomicrobiome but instead to inform the reader of the major trends and directions within the topic of rhizosphere signaling. This type of signaling among microbes is likely to play a fundamental role in shaping and stabilizing the rhizosphere microbial community as well as affecting plant development (Figure 1).

Cell–cell signaling among rhizosphere microorganisms is likely to occur commonly because many strains isolated from the rhizosphere have been reported to produce QS signals. For example, it has become apparent that a variety of proteobacterial rhizosphere isolates produce and/or respond to ***N*-acyl homoserine lactone** (AHL) QS signals, including strains belonging to species or genera of *Pseudomonas chlororaphis*, *Pseudomonas putida, Pseudomonas syringae, Burkholderia, Serratia, Erwinia*, and *Ralstonia*, as well as rhizobial species [9]. AHLs have also evolved to act as interkingdom signals influencing plant gene expression, the induction of systemic plant resistance, and affecting plant growth and development [10]. Recently new types of signals (e.g., pyrones and dialkylresorcinols) produced by Gram-negative bacteria have been discovered which are recognized by LuxR proteins which are very closely related to the AHL-responsive LuxR family [11]; it is currently unknown whether these signals are produced by rhizobacteria. Another class of QS signals in Gram-negative bacteria is the DSF family (diffusible signal factor, which are *cis*-2-unsaturated fatty acids); more bacterial species are currently being

Glossary

Interkingdom signaling: used here to describe signaling between plants and microorganisms via low molecular weight compounds.

Microbe-associated molecular patterns (MAMPS): conserved microbe-specific molecules such as cell wall components which are recognized by the innate immune system of the plant.

Mycorrhizal symbiosis: symbiotic associations between arbuscular mycorrhizal and ectomycorrhizal soil fungi and plant roots.

***N*-acyl homoserine lactone (AHL):** a QS signaling molecule produced by proteobacteria.

Plant growth-promoting rhizobacteria (PGPR) and fungi (PGPF): bacteria and fungi that efficiently colonize the rhizosphere and promote plant growth through stimulating immune defenses, influencing the hormonal balance, warding off pathogens, and mobilizing nutrients.

Priming: used here to describe the physiological alert state of a plant following a stimulus preparing it to produce a faster and more robust defense response when exposed to pathogens, pests, or abiotic stress.

Quorum sensing (QS): a regulatory system that allows bacteria to regulate gene expression in response to cell density.

Rhizobial bacteria: legume root-nodule bacteria that induce the formation of special structures (nodules) on the roots of their host plants and fix nitrogen.

Rhizomicrobiome: or rhizosphere microbiome; represents the total microbial community members present in the rhizosphere.

Rhizosphere: narrow zone of soil that is directly influenced by root secretions and associated soil microorganisms.

Root exudates: a variety of molecules released by roots into the rhizosphere, including acids, sugars, and polysaccharides.

Volatile organic compounds (VOCs): organic chemicals that have a high vapor pressure which allows them to evaporate and enter the surrounding air.