

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.

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

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 monomers, 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.

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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.

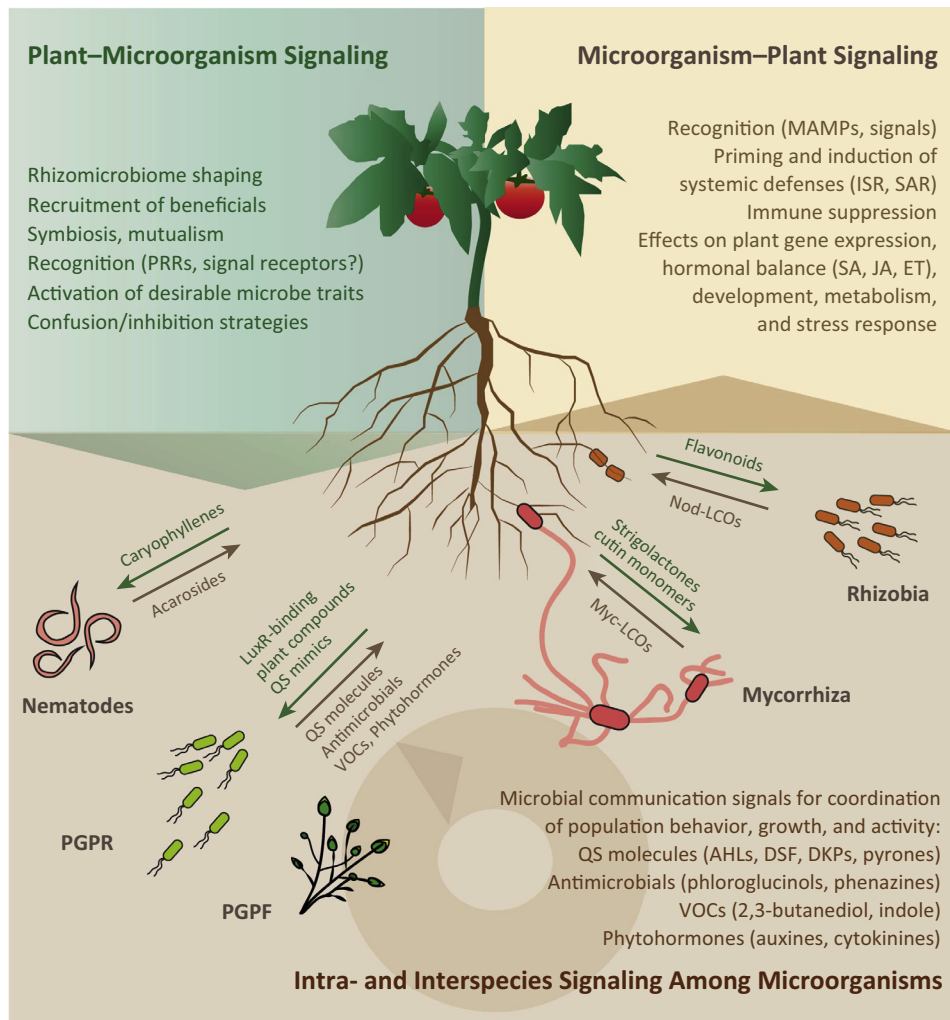
Rhizobial bacteria: legume root-nodule bacteria that induce the formation of special structures (nodules) on the roots of their host plants and fix nitrogen.

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.



Trends in Plant Science

Figure 1. Known Molecules and Events Involved in Intra- and Interspecies Signaling among Microorganisms and Interkingdom Signaling Between Microorganism and Plants in the Rhizosphere. The rhizosphere is populated by a diverse community of microorganisms, including rhizobial bacteria, mycorrhizal fungi, plant growth-promoting bacteria and fungi (PGPR and PGPF), and nematodes, which all undergo interactions with the plant that are often beneficial. To coordinate their behavior and to control their growth and activity, these microorganisms produce a diversity of signals, among them quorum-sensing (QS) molecules such as *N*-acyl homoserine lactones (AHLs), diffusible signal factor (DSF), and diketopiperazines (DKPs), antibiotics at subinhibitory concentrations, phytohormone-like molecules, volatile organic compounds (VOCs), and, in the case of nematodes, specific pheromones (acarosides). These communication molecules can also function as interkingdom signals that elicit various effects on plant developmental processes and on local and systemic immune responses (i.e., ISR, induced systemic resistance; and SAR, systemic acquired resistance) and involve interactions with plant hormonal signaling via salicylic acid (SA), jasmonic acid (JA), and ethylene (ET). The plant recruits, shapes, activates and sustains its rhizomicrobiome via the release of root exudates (not shown) and signaling molecules of which only few are known to date. To recognize its associated rhizomicrobiome, the plant uses dedicated pattern recognition receptors (PRRs) and presumably other as yet unknown receptors to detect particular microbe-associated molecular patterns (MAMPs) and likely the signals presented by the microorganisms. Recruitment of plant-beneficial rhizosphere microorganisms results in the intimate symbioses undergone by mycorrhiza and rhizobia, which are initiated by the exchange of specific plant signals (strigolactones and flavonoids, respectively) and microbial signals (Myc and Nod factors, respectively), and other mutualisms such as those involving PGPR, PGPF, and entomopathogenic nematodes. In addition to hosting beneficial microorganisms as guards, the plant also uses confusion and inhibition strategies (e.g., QS mimicry and quenching) to ward off harmful microorganisms.

Box 1. Rhizosphere Signaling

Rhizosphere signaling can be divided into three categories according to direction of the binary communication taking place: microbe-to-microbe, microbe-to-plant, and plant-to-microbe. (i) Microbe–microbe signaling: intra- and interspecies communication via small molecules among microorganisms, which serves to control and coordinate microbial behaviors in uniform and mixed communities. (ii) Signaling from plants to microorganisms: plant-produced compounds are detected and affect gene expression, growth, activity, and plant interaction by microorganisms. (iii) Signaling from microorganisms to plants: compounds produced by microorganisms are detected and affect gene expression, growth, development, and immune and stress responses in plants.

Major effects/outcomes of rhizosphere interkingdom signaling between plants and microorganisms. This signaling occurs via low molecular weight signals produced by bacteria or the plant. (i) Recruiting, shaping, and activity control and maintenance of the rhizosphere microbiome. (ii) Inducing plant immunity and keeping microbial pathogens away. (iii) Sustaining plant growth, health, nutrition, and stress tolerance. (iv) Modulating below–aboveground (and vice versa) interactions.

discovered which produce DSF, including rhizosphere-inhabiting species such as *Burkholderia* spp. and *Stenotrophomonas maltophilia* [12]. Interestingly, bacterial DSF signals have also been recently determined to elicit innate immunity in plants, hence acting as interkingdom signals [13]. Many Gram-positive bacterial residents in the rhizosphere use peptides (also known as pheromones) as QS signaling molecules [14,15]; these signals are likely to play many regulatory roles both at the intra- and interspecies level. Another potential class of bacterial signals are antibiotics which have been proposed to function, at low and non-inhibitory concentrations, as intra- and interspecies signaling molecules [16]. Future work will need to determine whether antibiotics truly function as signals and whether this has a role in shaping the microbiome. Many fungal species inhabiting the rhizosphere (mostly ascomycetes) secrete molecules for communication (in many cases alcohols) which are most often associated with particular developmental processes [17]. Whether fungi and bacteria undergo interspecies signaling is a subject of current investigation [18], and this type of molecular communication will be an important aspect in the process leading to the establishment and stabilization of mixed rhizosphere microbial communities.

An important characteristic is also the ability of microorganisms to release an array of **volatile organic compounds** (VOCs), many of which are still uncharacterized [19,20]. However, the chemical structures of several VOCs have been reported and they are typically small molecules (100–500 Da, usually alkenes, alcohols, benzenoids, aldehydes, ketones, terpenes) originating from a wide range of bacterial and fungal species. Microbial VOCs are believed to play an important role in long-distance interactions in microbial communities and have been implicated in microbe–microbe as well as plant–microbe interactions in the rhizosphere [21]. With respect to microbe–microbe interactions, they can behave as chemical weapons by exhibiting antimicrobial activity; alternatively they have also been reported to interfere with and thus affect other QS systems [19,20]. In addition, VOCs can act as intraspecies as well as interspecies signals by coordinating gene expression and influencing microbial behaviors such as biofilm formation, virulence, and stress tolerance [19]. Finally, VOCs have also been reported to be regulators of plant growth and stress resistance, and a few compounds have been studied which affect root architecture, plant immunity, and expression of plant genes involved in defense and hormonal signaling pathways [21]. VOCs have therefore been implicated in several signaling mechanisms and are likely to have an impact on the rhizomicrobiome; however, research is at an early phase and future work will unravel their likely importance.

In summary, it must be noted that many rhizosphere microorganisms have been shown to produce and respond to QS signals, and it is likely that most if not all are able to at least respond to one class of microbial signals. This intense and complex communication among microorganisms is likely to play a fundamental role in recruiting and shaping the microbial community in the rhizosphere. In addition, many of these microbially produced signals can most probably act

as interkingdom signals affecting plant gene expression. These microbial signals could therefore be an important tool to use in the future for tailoring the rhizomicrobiome.

Signaling from Plants to Microorganisms

Plants in the rhizosphere serve as hosts to an overwhelming diversity of commensal, mutualist, or parasitic microorganisms, signifying that secretion of phytochemicals is crucial for these plant–microbe interactions [22]. Surprisingly, so far only a few plant signaling molecules affecting rhizosphere microbiology have been studied and elucidated in detail (Figure 1). Probably the best-deciphered signaling network between plant and rhizosphere microorganisms is in legumes with different endosymbiotically growing nitrogen-fixing **rhizobial bacteria**. Upon signal exchange between the host plant and the bacterial symbiont, a developmental program begins which will give rise to a nodule. Rhizobial bacteria then colonize root nodules, fix atmospheric nitrogen inside, and transport usable forms of nitrogen to plants, thereby facilitating their growth. The role of plant signals in the establishment of root nodules has been the subject of extensive investigations during the past 20 years, and results have been regularly reviewed, even recently [23,24]. Consequently we will not discuss in detail this **interkingdom signaling** network. The first signals to be exchanged between the host plant and its rhizobial symbiont are plant-produced flavonoid compounds (2-phenyl-1,4-benzopyrone derivatives), which induce bacterial *nod* genes [25,26]. These genes are then responsible for producing and secreting lipo-chitooligosaccharides (LCOs), also known as nodulation (Nod) factors, which are the central signal molecules for initiating nodule formation [27]. These LCOs are then perceived by the plant via receptor kinases at the root epidermis, thereby activating a well-characterized signal cascade leading to nodule formation (reviewed in [24,28,29]).

Interestingly, LCO signals are also involved in symbiotic associations of plants and arbuscular mycorrhizal fungi (AMF or AM), one of the most important rhizosphere mutualisms. **Mycorrhizal symbiosis** is very primal: fossil records date it back to at least 400 million years ago with the appearance of the earliest land plants. This symbiosis is therefore well established and enables nutrient exchange between the two partners. The fungus increases the capacity of roots to access nutrients from the soil, especially immobile phosphates, whereas the plant provides carbohydrates to the fungus. Despite the ecological importance, the molecular and genetic mechanisms of the signaling underlying this symbiosis are only partially understood. This chemical dialogue is most probably continuous, to establish long-lasting colonization, but apparently is not very specific because there is no plant host specificity. This indicates that either the plant signals are conserved throughout the plant kingdom or possibly that a broad range of plant compounds are involved. It was already established some time ago that a set of legume mutants of LCO-induced signaling that are unable to undergo rhizobial interkingdom communication are also impaired in mycorrhizal symbiosis [30]. This strongly suggested that, first, mycorrhizal fungi produce similar LCO-type signaling molecules (named Myc-LCOs), as now recently has been demonstrated [31], and second that most likely during evolution rhizobia co-opted the mycorrhizal signaling machinery. Importantly, some molecules secreted from plant roots act as signals for AM fungi [32]; for example, the strigolactone plant hormones are considered to be one of the primary signals for initiating AMF symbiosis [33,34]. Strigolactones have been associated with multiple functions because they can act as an *ex planta* stimulus for mycorrhizal hyphae [35] and also act as plant hormones interfering with auxin transport [36,37]. Intriguingly, root-parasitic plants such as *Striga* spp. and *Orobanchae* spp. hijack strigolactone signals to detect their host and induce seed germination in vicinity of the roots [33,38]. The property of mediating multiple functions could be the scenario for several molecules which act as signals in the rhizosphere and have also a role *in planta*. Recently, cutin monomers have been implicated as a specific class of plant signaling factors which play a crucial role for AMF stimulation. Two loci, *RAM1* and *RAM2* ('required for arbuscular mycorrhization'), have been identified in *Medicago truncatula* mutants seriously affected in AM symbiosis; they encode a

GRAS domain transcription factor and a acyl transferase, respectively, involved in the production of cutin monomers [39,40]. Importantly, these cutin monomer signals also play a role as elicitors in appressoria formation in aerial fungal pathogens [41]. Strigolactones and cutin monomers are thus examples of plant signals which are perceived by beneficial as well as pathogenic organisms.

Rhizobia and AM fungi are examples of close symbiotic relationships between plants and microorganisms in the rhizosphere, and the signaling pathways have been thoroughly studied and will continue to provide data on signals and cascade mechanisms between plants and microorganisms in the rhizosphere. Because many different microorganisms live in the rhizosphere, albeit not in such close association with plants, questions arise on the role of plant-secreted signals which affect gene expression of members of the rhizomicrobiome. Many rhizobacteria undergo cell density-dependent signaling mechanisms known as QS [42]; this occurs via the production and response to quorum levels of signals. Many plant-associated bacteria require QS for colonization of the plant-associated environments and regulate a wide range of phenotypes including rhizosphere competence, virulence, conjugation, secretion of hydrolytic enzymes, and the production of secondary metabolites (see above) [43,44]. As mentioned above, the most common QS system in Gram-negative bacteria uses AHLs as signals. The archetypical AHL QS system comprises a LuxI family synthase synthesizing the AHL, which then interacts at quorum concentrations with the cognate LuxR family regulator affecting gene expression [8]. Importantly, AHLs have also evolved to act as interkingdom signals affecting plant gene expression (see below) [10]. Plant-produced compounds have been reported to interfere with QS acting as agonists or antagonists of bacterial AHL QS systems [45]. Only a few of these compounds, which are believed to act on the LuxR family protein, have been identified [46]. However, the significance of this plant interference with AHL QS is still an open question.

It has been recently discovered that many different plant-associated bacteria possess proteins very closely related to QS LuxRs which do not bind and respond to AHLs but instead to plant low molecular weight compound(s) [47]. This is henceforth regarded as a bacterial subfamily of LuxR proteins which evolved away from binding AHLs and can now respond to plant signals, thus representing a widespread novel interkingdom signaling circuit. Members of this subfamily have been recently studied in strains of plant-pathogenic xanthomonads as well as in beneficial rhizosphere rhizobia and pseudomonads, demonstrating that this interkingdom signaling system is involved in regulating traits important for *in planta* colonization (reviewed in [10,47]). In rhizosphere pseudomonads, one of these proteins called PsoR is involved in transcriptional regulation in response to plant compound(s) of various antimicrobial related genes and in biocontrol [48]. In this common plant–bacteria signaling system, the pivotal step is now to identify the plant signal(s) which is governing this communication and is likely to be a widespread low molecular weight plant secondary metabolite(s).

Plants have also evolved the ability to produce and release an array of volatile compounds from their leaves, flowers, fruits, and roots [49]. These volatiles are estimated to constitute approximately 1% of plant secondary metabolites (mainly represented by terpenoids, phenylpropenoids, and fatty acid and amino acid derivatives) and are believed to cross membranes freely and to be released into the atmosphere or soil. Their main functions are to defend plants against herbivores and pathogens or to provide reproductive advantages. In the roots, volatiles can act as antimicrobial substances or as attractants for enemies of root-feeding herbivores [50]. A well-studied example of an attractant is the volatile (E)- β -caryophyllene emitted by the roots of maize in response to feeding by the larvae of the Western corn rootworm (WCR) [50,51]. This volatile is highly attractive to an entomopathogenic nematode which parasitizes and kills WCR within a few days. This illustrates very well the signaling role of volatiles in roots and they are likely to be involved in many other tritrophic interactions.

In summary, to date several plant molecules including flavonoids, strigolactones, cutin monomers, and volatiles, as well as so far unidentified plant low molecular weight compound(s), which bind a widespread subfamily of bacterial LuxR proteins, have been recognized as signals which are sensed by and to which microorganisms respond and regulate gene expression. It is very likely that many more of the chemical signals generated by the plant play fundamental roles in shaping and tailoring the rhizomicrobiome.

Signaling from Microorganisms to Plants

Rhizosphere-associated microorganisms do not only perceive and interpret signals produced by themselves, other microorganisms, or the plant (see above); they are also capable of influencing their plant host via the release of diverse signaling molecules. Studies have so far been centered on beneficial microbe–plant interactions, which include induction of plant defenses against diseases, pests, and abiotic stressors, and promotion of plant growth and development (Figure 1). Plant-beneficial rhizosphere microorganisms investigated in some detail are mycorrhiza, rhizobial bacteria, **plant growth-promoting rhizobacteria** (PGPR) of the genera *Pseudomonas*, *Bacillus*, and *Azospirillum*, and **plant growth-promoting fungi** (PGPF) such as *Trichoderma* and nonpathogenic fusaria [52–55].

Mycorrhiza, rhizobia, PGPR, and PGPF initially all are recognized as non-self by the plant, which uses dedicated pattern recognition receptors (PRRs) to detect conserved microbe-specific molecules, termed **microbe-associated molecular patterns** (MAMPs) such as lipopolysaccharides, peptidoglycans, flagellin, and chitin [55–57]. The MAMPs trigger a local basal immune defense in the roots, which then can translate into systemic defense responses that are controlled by regulatory networks involving signaling via the plant hormones salicylic acid, jasmonic acid, ethylene, and others [53,57–59]. The plant defense response, commonly induced by root-colonizing PGPR and PGPF, is known as induced systemic resistance (ISR) and acts systemically against various foliar pathogens and even leaf-feeding insects [53]. ISR depends on the jasmonic acid and ethylene signaling pathways, and is distinct from the systemic acquired resistance (SAR) which is most commonly induced by pathogens and involves salicylic acid signaling [59,60]. The innate immune response triggered by rhizosphere beneficial microorganisms is relatively mild and is based on a process called **priming** which prepares the plant, upon sensitization by the microbes, to react more efficiently to abiotic and biotic stress such as attack by leaf pathogens and pests [61,62]. Priming, ISR, and SAR have been the subject of several excellent recent reviews [53,55,59,61], and the reader is referred to these for in-depth information. Beneficial rhizosphere microorganisms counter immune recognitions; the signaling involved in these immune interactions is little understood and has generated considerable interest in these microorganisms in recent years, and research in the field is rapidly evolving [53,55].

Rhizosphere microorganisms elicit plant responses not only via MAMPs and effector proteins but they also do so via diverse signaling molecules. The Nod and Myc factors released by rhizobia and mycorrhiza (see above), respectively, are prime examples of microbial interkingdom signaling molecules: they suppress salicylic acid-dependent defense responses and initiate a common symbiosis signaling pathway [24,55]. Recent studies have provided further insight into the molecular dialogues taking place between mycorrhizal fungi and the plant. In fact, mycorrhiza produce small secreted proteins (SSPs) that act as mutualistic effectors promoting mycorrhization by altering hormonal signaling pathways in their plant host [7,63]. This is illustrated by the ectomycorrhizal fungus *Laccaria bicolor*, which releases the 7 kDa protein MiSSP7 from its hyphae upon root contact. The mini-protein then enters the host cells, localizes to the nucleus, and interacts with plant hormone coreceptors to counteract jasmonic acid signaling and promote symbiosis [64,65]. An SSP mycorrhization effector interfering with hormonal signaling was also identified in the arbuscular mycorrhizal fungus *Rhizophagus intraradices* [66]. Recent research has revealed that PGPR also release various potential signal molecules, which exhibit

interkingdom signaling properties by influencing plant gene expression, defense responses, and developmental processes, but their exact mode of action and plant targets remain to be unraveled. Remarkably, many of these molecules actually function as signal compounds in intra- and interspecies signaling by these rhizobacteria (see above).

AHL-type QS molecules are so far the best-documented class of PGPR signal compounds which exhibit effects on plants [10,67]. Early studies report on extensive changes of protein profiles in roots of *Medicago trunculata* [68] and on gene expression profiles in roots and shoots of *Arabidopsis thaliana* [69] following root treatment with structurally different AHLs. Considerable work identified affected functions, including root development, plant defense, stress response, hormonal balance, and metabolic regulation [69–73]. AHL production by rhizobacteria may also incite the plant host to deploy strategies to interfere with these bacterial signals, for example by producing AHL mimics, by preventing their uptake and transport or by destroying them [10,67,74]. As mentioned above, other bacterial QS molecules with interkingdom signaling properties are less well studied; these include the *Xanthomonas* diffusible signal factor (DSF) and cyclodipeptides, in other words diketopiperazines (DKPs), released by *Pseudomonas aeruginosa*, which affect salicylic acid-, abscisic acid-, or auxin-responsive gene expression *in planta* [13,75,76]. Similar molecules are also produced by PGPR pseudomonads and other soil bacteria, and these warrant further investigation [10,12].

Antimicrobials produced by rhizosphere pseudomonads are another class of microbial molecules shown to elicit systemic plant responses. 2,4-Diacetylphloroglucinol (DAPG) present at sub-inhibitory concentrations on roots or in rhizosphere soil, induced salicylic acid- and ethylene signaling-dependent ISR against fungal and bacterial leaf pathogens in *Arabidopsis* [77,78]. DAPG was also shown to affect root development, and it was suggested that this occurs via an auxin-dependent signaling pathway [79]. Pyocyanin, a phenazine antibiotic produced by *P. aeruginosa*, induces ISR and modulates root development in a similar manner [80]. Remarkably, phloroglucinols and phenazines function also as intra- and interspecies signals of pseudomonads [81–84].

As mentioned above, VOCs constitute another class of microbial signaling molecules, and these are receiving considerable attention also for their effects on plants as growth promoters or inhibitors [85], and as priming agents or elicitors of systemic plant defense and stress tolerance [86,87]. 2,3-Butanediol (2,3-BD) released by *Bacillus* PGPR strains was the first microbial VOC with demonstrated effects on plants: it was shown to promote the growth of *Arabidopsis* [88] and to induce ISR towards phytopathogenic *Erwinia* via ethylene signaling pathways in the model plant [89]. 2,3-BD produced by a *Pseudomonas chlororaphis* PGPR induces ISR against the same pathogen in tobacco (*Nicotiana tabacum*) [90]. 2,3-BD produced by a root-endophytic *Enterobacter* strain enhances the resistance of maize plants against a fungal leaf pathogen and, moreover, affects tritrophic interactions with a herbivorous insect and its parasitoid [91]. Indole, another bacterial signaling VOC produced by various PGPRs [92], affects root development in *Arabidopsis* via the auxin signaling pathway [93]. Interestingly, indole released by plants also functions as a potent volatile signal that primes the producer and neighboring plants against attacks from herbivorous insects [94]. Similarly to AHLs and antibiotics, VOCs can also have multiple biological roles in intra- and interspecies interactions of the producer bacteria themselves [19]. Production of bioactive VOCs is widespread and highly diverse among PGPR and PGPF [92,95,96]. VOC-mediated microbe–plant interkingdom interactions can thus be expected to be by far more complex than uncovered so far.

A further class of microbial molecules with interkingdom signaling properties are phytohormone-like compounds, including auxins, gibberellins, and cytokinins, that are not only produced by

PGPR and PGPF but also by bacterial and fungal pathogens; they affect growth, organ development, immune responses, and hormonal signaling in plants (reviewed e.g., in [97–100].

Rhizosphere microbial signaling with plants so far has been investigated predominantly for soil bacteria and fungi, but the very diverse communities of nematodes and protists present in soil [5] may also communicate with plants. This has been substantiated by recent work in which ascaroside pheromones produced by plant-parasitic nematodes were found to stimulate defense gene expression and resistance to microbial infections in *Arabidopsis* and other host plants [101].

Taken together, the findings so far indicate that inter-kingdom communication from microorganisms to plants via signaling molecules is common, diverse, and widespread in the rhizosphere. Remarkably, a majority of the signaling molecules identified so far also have a role in intra- or interspecies signaling of the producing microorganisms. Depending on the viewpoint, such molecules can be seen as signals used by the microorganisms to manipulate the plant or as signals that the plant evolved to respond to so as to detect communicating microorganisms in its root environment. These signaling molecules affect plant growth and developmental processes as priming agents and as elicitors of plant defenses, and they affect plant hormonal signaling. Their effects take place locally in the root and systemically throughout the plant body, implying the involvement of root–shoot signaling events. Moreover, recent studies suggest that signals might even travel from one root system to another via common mycelial networks such as those formed by mycorrhiza, thus allowing interplant signaling [102,103]. However, how the root perceives the microbial molecules and transmits this input into the signaling pathways of the plant to produce a specific response is largely unclear. A major challenge will be to unravel whether these molecules are indeed specific signals, which are recognized by dedicated plant receptors, or whether they function instead as priming agents that induce a general (mild) stress response, which can be interpreted by the plant host and distinguished from responses induced by MAMPS and effectors. Given that the rhizosphere microbiome is extremely diverse and produces a huge diversity of compounds, a generic perception of these molecules as priming agents appears more plausible.

Concluding Remarks

Most research activities on signaling in the rhizosphere have concentrated on symbiotic or pathogenic microbe–plant interactions and are now beginning to be studied in other rhizosphere-colonizing microorganisms. It is now becoming evident that plants actively shape the community of microorganisms inhabiting their outer surface and subsequent colonization of their interior [104], but many issues remain unresolved (see Outstanding Questions). We have shown here that signaling taking place in the rhizosphere can be divided into three main categories, with important networks between microorganisms and plants (Box 1). The list of examples in this review is not exhaustive, and in addition many more but currently unknown signals are likely to exist which play a pivotal role in determining and/or shaping the rhizomicrobiome.

The signaling shared by plants and rhizosphere-dwelling organisms occurring at the plant root–soil interface will likely be the subject of many studies in the near future. Our understanding will become clearer through first detecting and quantifying the plant and microbial exudates as well as their effects on gene transcription and translation. This will be greatly enhanced by recent advances in analytical chemistry, particularly gas chromatography–mass spectroscopy (GC-MS), liquid chromatography–mass spectroscopy (LC-MS) and capillary electrophoresis–mass spectroscopy (CE-MS); all these techniques now allow an untargeted qualitative and quantitative approach known as metabolomics. The large-scale chemical analysis of the root exudates (the exudome) can then be combined with transcriptomics to begin to uncover the plant genes involved in the synthesis of the rhizosphere signaling compounds. In addition, other ‘omic’

Outstanding Questions

Are specific interactions between plants and members of the rhizomicrobiome common or limited to few organisms?

To what extent will the new ‘omics’ technologies contribute to the discovery of signaling molecules and to the understanding of the molecular mechanisms involved in signaling in the rhizosphere?

How can we apply the knowledge of rhizosphere signaling to devising novel ways for promoting plant growth and health?

techniques can be involved as well. Metagenomics is a powerful tool that now allows the composition of communities of bacteria, fungi, protists, and other (micro)organisms to be determined from total DNA extracts of the rhizosphere. This can then be combined with other novel techniques such as metatranscriptomics and metaproteomics which can provide insights into the specific expression and translation of genetic loci in the rhizosphere. Moreover, cutting-edge techniques such as different imaging mass spectrometry approaches will further allow direct visualization and quantification of specific chemical (ex)changes in microbe–microbe and plant–microbe interactions [105,106]. The integration of all these approaches will generate an amount of new information which was unimaginable a few years ago, and the challenge ahead will be proper experimental design, interpretation, and appropriate validation of the ‘omics’ data.

Experimental evidence accumulated thus far has established the importance of the root microbiome in plant health, and it is now becoming increasingly evident that the plant is able to control the composition of its microbiome [1,104], to select for specific microbial functions [107], and to exert genotype-level influences on the beneficial activity of specific microbial associates [108]. A recent study identified plant immune signaling via salicylic acid as one of the drivers influencing rhizomicrobiome composition [109]. It is therefore likely that evolutionary selective pressure has resulted in many specific interactions between plants and microorganisms, and future work will bring important insights into this field (Box 1). Rhizosphere signaling research will therefore open new avenues to increase crop productivity and reduce the use of agrochemicals. An example could be via the alteration of plant metabolic pathways of rhizosphere signals as a way to manipulate the rhizosphere inhabitants for the benefit of plant health. Select rhizosphere signaling molecules could also be used directly as chemical cues to foster plant growth and health or to promote the beneficial rhizomicrobiome [110]. These and other ways of microbial related solutions can be devised for a more sustainable agriculture to enrich the rhizomicrobiome for the beneficial members, thereby increasing plant resistance to biotic and abiotic stresses.

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