

**Review article**

Rhizosphere signaling nurturing phyto-microbiome niche

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Abstract: In an ecosystem, terrestrial plants do not exist all alone but live in complex associations with diverse microorganisms. The interaction between plant and microbiome is an outcome of a very long co-evolution. The knowledge of the microbial community in the rhizosphere is getting more transparent due to the advancement of technologies and genetic tools. The functional taxonomy, identification of genes and metabolite profiling has gathered much of information on this beneficial association between plants and plant growth promoting microorganisms. The metabolites produced by plant growth promoting rhizobacteria (PGPR) are diverse and the clear understanding of mechanisms by which they act either way is still required. The metabolites produced and secreted by plants in the rhizosphere affect the diversity and specificity of the microbiome. While, the metabolites produced by the microbiome of a plant induce beneficial responses like growth promotion, nutrition acquisition and defense in plants. Each plant shows a specific microbiome flourishing in its rhizosphere and it is the chemicals secreted by both plants and microbiome helps in signaling and assembling mutual relationships. This review will focus on the signaling compounds used by plants and rhizobacteria and ways by which rhizobacteria impart defense benefits to the plants.

Keywords: Rhizobacteria - Metabolite - Plant-Microbe interactions.

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INTRODUCTION

Every multicellular organism particularly eukaryotes exist with a microbiome relationship. Microbes in nature tend to function as communities, creating a complex network of microbial interaction. A terrestrial plant continuously grows in a complex community and is always associated with regulated and well-structured microbial communities. The microbiome associated with the plant community is called phyto-microbiome, that assist plants to confront various environmental challenges and giving access to nutrients. The community of microbes allows the formation of specific microbial ecological niche at the vicinity of plant roots generally termed as 'Rhizosphere'. The rhizosphere is inhabited by various organisms including fungi, bacteria, nematode, arthropod, etc, hence is known to be one of the complex ecosystems on earth (Venturi & Keel 2016). Although there are different kinds of organisms found in the rhizosphere but diversity among them is very low. This is due to the selective pressure exerted by plants on the microbiome residing in this zone. Hence, differential microbial communities are found to be associated with the rhizosphere of different plants (Zhang *et al.* 2017). The interaction between plant roots and microbial community is done in a sophisticated manner through chemicals signals released by plant roots and microbial community within the rhizosphere, thereby leading the formation of an association between plants and beneficial microbes. This association provides plants various beneficial properties like protecting them from the pathogenic microbes. The beneficial microbial species generally bacteria, found in the rhizosphere are termed as plant growth-promoting rhizobacteria (PGPR). The PGPR genera that are commonly found in the rhizosphere include, *Bacillus*, *Pseudomonas*, *Acinetobacter*, *Enterobacter*, *Arthrobacter*, *Burkholderia* and *Paenibacillus* (Zhang *et al.* 2017).

Mutual relationships are established by selective communication and signaling between the microbiome and the plants. Plants possess various extracellular and intracellular signaling molecules forming complex and intricate signaling pathways via transmitting signals and thus giving specific responses as required. The major

signaling pathways triggered in plants in response to environmental stimuli are hormone signaling, calcium signaling, and mitogen activated protein kinase (MAPK) signaling. Hormone signaling is activated by plant hormones like auxin, cytokinin, salicylic acid (SA), ethylene (Zhao *et al.* 2014, Jalmi *et al.* 2018). Initiation of calcium signaling deploys a multitude of calcium-sensing proteins like Calmodulins (CaMs), CaM like proteins (CMLs), Calcineurin B-like proteins (CBLs), and Ca²⁺-dependent protein kinases (CDPKs) that bind to Ca²⁺ and trigger different downstream signaling pathways (Dodd *et al.* 2010, Jalmi *et al.* 2018). Apart from these, the most predominant and complex is the (MAPK) signaling composed of three-tier phosphorylation module MAPKKKs (Mitogen Activated Protein Kinase Kinase Kinase), MAPKKs (Mitogen Activated Protein Kinase Kinase), and MAPKs (Mitogen Activated Protein Kinase) (Hamel *et al.* 2006). MAPKs are substantially known in providing tolerance against biotic and abiotic stress (Rodriguez *et al.* 2010, Jalmi & Sinha 2015, Jalmi & Sinha 2016). Once chemical signals are perceived and transmitted by the plants there is an alteration in the gene expression and release of an array of plant metabolites that are required as signals for flourishing selective microbiome. The use of metabolomics approach has enabled researches to study metabolites secreted by microorganisms and plants. Different types of signaling metabolites are reported for different types of communications. The different kinds of communication allowed in the rhizosphere mainly includes bacteria-bacteria interaction, bacteria-plant interaction. Further, section will focus on different signaling molecules used for communication between rhizobacteria and plants.

SIGNALING IN PLANT-RHIZOBACTERIAL ASSOCIATION

The complex signaling machinery present in plants helps them to perceive environmental signals and act accordingly giving responses. Plants can generate defense response depending on the environmental stimuli and array of transcriptional activities initiated by the specific signaling pathway. Plants can recognize both PGPR and pathogenic microbes similarly. Both classes of microorganisms are recognized based on the microbe associated molecular pattern (MAMPs) or the chemical compounds and secondary metabolites secreted by the microbial community (Van Wees *et al.* 2008). However, the response given by the plants is different for the pathogen and rhizobacteria. The mechanism behind this is not fully understood but it might be different and specific signaling pathways conveying signals from the pathogen and rhizobacteria. The different types of compounds or metabolites used for the signaling and maintaining the beneficial association between rhizobacteria and plants are discussed below.

SIGNALING METABOLITES IN BACTERIA

Bacteria in the rhizosphere are very well known to release an array of metabolites used as signaling molecules, helping bacteria to set up a symbiotic relationship with plants and providing beneficial properties to plant. Bacteria also produce compounds to communicate among the bacterial species in the rhizosphere thus promoting the growth of specific bacteria and inhibiting others. The different compounds secreted by rhizobacteria are discussed in this section.

The most important compounds used for communication among the bacteria are volatile organic compounds (VOCs). These are aromatic molecules and mainly include low weight lipophilic compounds and are by-products of the different metabolic pathways. VOCs are well documented in promoting plant growth, inducing defense responses and expression of plant ion transporters (Zhang *et al.* 2009, Farag *et al.* 2013). Numbers of VOCs are studied to be produced by rhizobacteria including alkanes, alkenes, alcohols, ketones, terpenoids and sulfur compounds. Rhizobacteria use these compounds as signals to cognate receptors for cell-cell communications (Hassan *et al.* 2016). Rhizobacterial derived VOCs used as signals for communication with plants include 2-heptanol, 2-endecanone, and pentadecane (Ryu *et al.* 2003).

Many of bacteria in the rhizosphere employ quorum sensing (QS) communication underlying intra- and inter-species interaction occurring in rhizo-microbiome. Both gram negative and gram positive bacteria use QS as a mode of interaction with distinct differences in signaling molecules and type of response. Gram negative rhizobacteria communicate through QS by producing an extracellular signal molecule called auto-inducers (AI). The most commonly studied AIs produced by gram negative bacteria are Acyl homoserine lactone (AHLs), consisting of invariant lactone ring and an acyl side chain of varying length, saturation and hydroxyl group (Chernin 2011). AHLs then perceived by the plants, inducing distinct responses in plants, altering gene expression of defense response, hormone synthesis, secondary metabolite synthesis and cytoskeleton remodeling (Miao *et al.* 2012, Schikora *et al.* 2016), thus contributing to the bacterial-plant symbiotic association (Hassan *et al.* 2016). The most studied AHLs are, 3-oxo-C6-HL and 3-oxo-C8-HL and their signaling in plants is mediated through G-protein coupled receptors GCR1 and GPA1. *Arabidopsis* calmodulin AtCaM and transcription factor

MYB44 are known to be involved in root elongation response mediated by 3-oxo-C6-HL (Zhao *et al.* 2016). Apart from AHLs, cyclodipeptides (CDPs) are also among QS molecules produced by PGPR used as an inter-kingdom signaling molecule. Several CDPs from *Pseudomonas* spp. are found to stimulate lateral root growth by acting as an inducer of auxin signaling (Ortíz -Castro *et al.* 2011). The CDPs show feedback regulation controlling their own synthesis by acting directly on LasR AHLs QS system (González *et al.* 2017).

Other than these, rhizobacteria as well as some pathogenic microorganisms are known to secrete some plant hormones like auxins (IAA), cytokinins, abscisic acid (ABA), gibberellins (GA), salicylic acid (SA), and jasmonic acid (JA), which triggers changes in plant transcriptome and unable association with plants. It is due to the activity of these phytohormones secreted by rhizobacteria they are known for plant growth promoting ability (Gamalero & Glick 2011, Fahad *et al.* 2015). The strains of rhizobacterium, *Bacillus amyloliquefaciens*, *Pseudomonas fluorescens*, *Bradyrhizobium japonicum*, *Paenibacillus polymyxa* are studied to produce a significant amount of the hormones IAA, GA, zeatin, ethylene, and ABA (Kamilova *et al.* 2006, Boiero *et al.* 2007, Idris *et al.* 2007).

SIGNALING METABOLITES IN PLANTS

Plants produce a number of signaling metabolites used for communication and association of symbiotic relation with microbiome. These metabolites are secreted by the plant roots in the form of root exudates. The secreted metabolites in root exudates greatly depend on plant species and environmental factors and the type of root exudates has a direct effect on the rhizosphere community. Specific plant species produce specific compounds to select specific species. Some organic acids present in root exudates are known to attract and allow the growth of various rhizobacteria including *Bacillus* and *Pseudomonas* species (Kravchenko *et al.* 2003, Zhang *et al.* 2014). Flavonoids found in root exudates of legume plants initiate production of lipochitooligosaccharides (LCOs) by inducing nod genes in bacteria, thus helping in nodulation process in plant roots (Kondorosi *et al.* 1989, Hassan & Mathesius 2012). The LCOs has a key feature that makes them different from chitin (associated with fungi exoskeleton) is the presence of N-acyl moiety with fatty acid chain with varying saturation, length and substitution groups. The difference in the side chains presents specificity to different rhizobial strains and plant targets (Oldroyd 2013). The relation between rhizobia and legume plants is set up once these LCOs are directly perceived by plant LysM receptors. These receptors are lysine motif containing receptor like kinase found in plants that perceive MAMPs including chitin (Liang *et al.* 2014). This binding of LCOs by LysM receptors initiates signaling events including an increase in calcium level leading to calcium signaling, accumulation of cytokinin leading to hormonal signaling, subsequently helping in the rhizobial infection process (Oldroyd *et al.* 2011, Rose *et al.* 2012). The process of nodulation operated by the signaling events results in the formation of nodules, wherein symbiotic bacteria thrive and fix atmospheric nitrogen (Limpens *et al.* 2015).

Apart from these, different types of low carbon molecules are also found in the root exudates that serve as precursors for biosynthesis of phytohormones in bacteria. Examples of low carbon compounds are tryptophan used as a precursor in the biosynthesis of auxin indole-3-acetic acid. Also, aminocyclopropane-1-carboxylic acid (ACC), is secreted by plants which is used as a precursor for ethylene biosynthesis and also used as carbon and nitrogen source by rhizobacteria (Haichar *et al.* 2012).

STRESS TOLERANCE BY RHIZOBACTERIA

Plant growth promoting rhizobacteria (PGPR) found in the rhizosphere are known for their plant promoting activities and imparting tolerance to plant against many environmental stresses including abiotic and biotic. Stress responses are positively regulated by bacteria resulting in differential expression of genes involved in hormone biosynthesis (ACS, ACO, MYC2, PR1), genes encoding antioxidant enzymes (SOD, CAT, APX, GST), genes for transcription factors like NAC1, DREB1A and genes for dehydrins like DHN and LEA. Here are listed studies showing the role of PGPR in conferring abiotic stress tolerance. A study showed that PGPR *Pseudomonas putida* conferred drought tolerance to chickpea by providing ROS scavenging ability, accumulation of osmolytes like proline, total soluble sugar (TSS) and modulating membrane integrity (Tiwari *et al.* 2016). Another species *Pseudomonas fluorescens* is known to help rice plants coping with submergence. This tolerance is imparted by ACC deaminase secreted by *P. fluorescens* (Etesami *et al.* 2014). *Bacillus thuringiensis* also known to confer stress tolerance by modifying root length, total ABA content, nitrogen content increasing nodule biomass (Prudent *et al.* 2015). ACC deaminase produced by *Variovorax paradoxus* is also known to confer salt tolerance in pea plants. The plants inoculated with this PGPR had increased photosynthetic activity, electron transport and balance ion homeostasis. *Bacillus amyloliquefaciens* in maize

conferred enhanced stress tolerance with increased photosynthesis, enhanced TSS content, improved peroxidase/catalase activity and ROS scavenging (Chen *et al.* 2016). Some PGPR species like *Serratia nematodiphila*, *Burkholderia phytofirmans*, *Pseudomonas vancouverensis*, *P. frederiksbergensis* are known to confer cold stress tolerance in many plants (Fernandez *et al.* 2012, Kang *et al.* 2015, Subramanian *et al.* 2015).

Apart from their role in conferring abiotic stress tolerance, PGPR are also used as biocontrol agents enhancing defense response in plants against pathogens. The root exudates have found to contain chemicals secreted by microbes that stimulate the PGPR association and inhibit pathogenic bacteria. *Bacillus amyloliquefaciens* is used as a biocontrol agent against a plant pathogenic fungus *Rhizoctonia solani* (Ji *et al.* 2013). The stress tolerance is imparted in the form of balanced reactive oxygen species through the formation of ROS scavengers, modulation of phytohormones, and production of secondary metabolites. *Bacillus* species are known to elevate the jasmonic acid hormone by modulating transcription of genes involved in the synthesis of jasmonate (Zebelo *et al.* 2016). *Enterobacter asburiae* induced resistance against tomato yellow leaf curl virus by upregulating the expression of defense-related genes and antioxidant enzyme (Li *et al.* 2016). *Peanibacillus lentimorbus* is known to work against Cucumber Mosaic Virus and *Sclerotium rolfsii* by producing ACC deaminase, via modulating pathogenesis-related gene expression and antioxidant enzyme activity (Dixit *et al.* 2016, Kumar *et al.* 2016). *Serratia liquefaciens* and *Pseudomonas putida* are known to produce AHLs that elicited induced systemic resistance against *Alternaria alternata* (Teplitski *et al.* 2000).

Besides inducing defense response in associated plants, rhizobacteria are also known in producing antibiotics thus inhibiting the growth of pathogenic microorganisms. *Bacillus* and *Pseudomonas* genera are best studied PGPR producing antibiotics, hence used as biopesticides in plant disease management (Saha *et al.* 2012). Antibiotics namely, 2,4 diacetylphloroglucinol (2,4 DAPG) and Phenazine-1-carboxylic acid (PCA) are produced by *P. fluorescens* that shows effective growth inhibition against the soil-borne pathogen *Sclerotium rolfsii* causing stem rot in groundnut *Gaeumannomyces graminis* var. *tritici* causing wheat disease (Asadhi *et al.* 2013, Lohitha *et al.* 2016). Zwittermicin is another novel antibiotic from *Bacillus subtilis*, effective against a spectrum of soil-borne pathogens (Saraf *et al.* 2014). Apart from the secretion of antibiotics, PGPR are studied to secrete hydrolytic enzymes effective in degrading cell wall components of fungi and oomycetes and hence, protecting plants against pathogenic attack (Bull *et al.* 2002, Saraf *et al.* 2005, 2014).

CONCLUSION

Plants are associated with a wide array of the microbiome in the rhizosphere, exerting a positive effect on plant growth, nutrition and defense. These beneficial effects produced by rhizobacteria in the rhizosphere are due to the production of an array of molecules and metabolites for communication, affecting plants in complex and overlapping mechanisms. While plants may bestow the shaping of the associated microbiome, the metabolites produced by rhizobacteria are diverse and the clear understanding of mechanisms by which they act either way is required. The different omics approach in detecting the chemical and genetic system will help in understanding the root associated microbiome and the corresponding signaling mechanisms. As revealed by many studies, rhizobacterial metabolites directly stimulate genetic and molecular pathways in plants, the current review focuses on the different metabolites and chemicals produced by rhizobacteria and plants in setting up a close association, leading to increase inplant growth and induction of plant defense towards pathogens.

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