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The Rhizosphere Talk Show: The Rhizobia on Stage

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From bacterial quorum sensing to the signals of bees, communication is the basis of biotic interactions. Frequently, more than two organisms can take part in the speeches, resulting in a complex network of cross-talks. Recent advances in plant-microbe interactions research have shown that communication, both inter-kingdom and intra-kingdom, is shaped by a broad spectrum of factors. In this context, the rhizosphere (i.e., the soil close to the root surface) provides a specific microhabitat where complex interactions occur. The complex environment that makes up the rhizosphere can select for certain microbial populations, which are adapted to this unique niche. Among them, rhizobia have emerged as an important component of the rhizospheric microbiome. The aim of this review is to explore the components of such a rhizospheric Talk Show in the frame of the rhizobium-legume interactions. This symbiosis is a complex process that involves several signals that can be shaped by plant rhizospheric exudates and microbiome composition. The relationship established by rhizobia with other rhizospheric organisms, together with the influence of the environmental factors, results in their beneficial role on host plant health. Here, we resume research accounting strategies, molecules, and organisms that influence the place of rhizobia in the rhizosphere. The focus is on the most recent approaches for the study and subsequent exploitation of the diversity of the organisms. Indeed, the study of plant-microbes communication and evolution is fundamental to develop highly efficient inoculants able to reduce the use of fertilizers in agriculture.

Keywords: rhizosphere, rhizobia, communication, microbial communities, plant-microorganisms interaction

THE TALK SHOW IN THE RHIZOSPHERE

Prokaryotes and eukaryotes have interacted for millions of years, evolving and refining over time their communication systems. As proposed by Hauser in 1996 (Hauser, 1996), biological signals and the exchange of information are part of the definition of communication, while the signals themselves are considered as “every structure able to shape the behavior of the organisms” (Smith and Harper, 2003; Schott-Phillips, 2008). Consequently, the signals can evolve and persist thanks to the interaction between signals producers and receivers. Then, cooperation and fitness improvement are the basis of biological communication (Zahavi, 2008).

In a particular environment, individuals can communicate and interact with multiple partners, and the nature of interaction can determine variable costs and benefits to the partner, as a biological market (Werner et al., 2015). One of the most fascinating environments

where complex biological interactions occur is the rhizosphere. Indeed, a large number of signals can be exchanged involving the plant itself, insects, fungi and microbes. This all take place in a high-density environmental niche. Usually, communication is the result of chemical responses of cells to signatory molecules coming from other cells. These signals affect both the metabolism and transcription of genes activating several regulatory mechanisms.

Frequently, in the rhizosphere more than two organisms (and species, across the tree of life) can take part in the communication, resulting in a complex network of interactions and cross-talks which can influence the fitness of all participating partners. Thus, this environment can be considered a hot spot for numerous inter-kingdom signals exchange, which involves plant-associated microbial communities (rhizobiome). The microbial community's composition is mainly shaped and recruited by hundreds of metabolites released in the soil by plant roots, which normally facilitate the interactions with the biotic and abiotic environment. Often the plant can modulate their diversity based

on the benefits in terms of growth and health (Plant Growth Promoting, PGP) (Hartmann et al., 2009). Nevertheless, a large number of nutrients issued by the plant can be of interest for the pathogenic organisms, which can take advantage of plant products for their survival in the rhizosphere (Rasmann and Turlings, 2016).

It stands to reason that the plants play a fundamental role in the rhizosphere scene (Bending, 2017) (Figure 1). Indeed, because of the chemical signals conveyed by nutrient-rich exudates released by the plant roots, a large variety of microbes can first colonize the rhizosphere and then gradually penetrate the root and the overall plant tissue (endophytes) (Hardoim et al., 2008). Otherwise, they can colonize the host plant establishing a lasting and beneficial symbiotic relationship (Chi et al., 2005). To date, numerous investigations on root exudates composition have been performed (Hartmann et al., 2009; Bulgarelli et al., 2013; Venturi and Keel, 2016).

The most known plant-microbe dialogue on the rhizosphere scene, which determine direct and indirect advantages to the

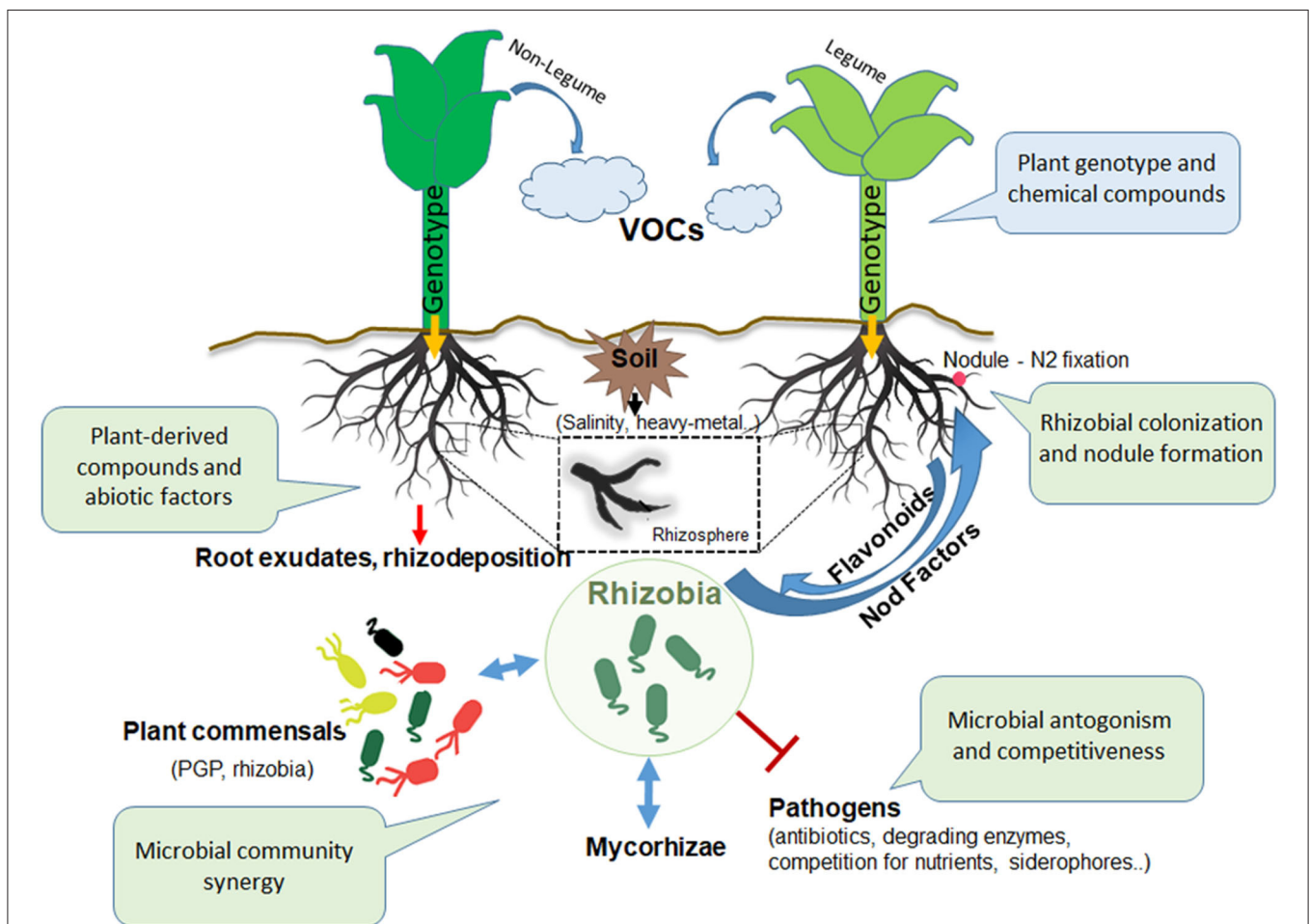


FIGURE 1 | Actors and interactions in the rhizosphere. Inter-kingdom and intra-kingdom communication involving plants and microbes in the rhizosphere: the consistent role of rhizobia. VOCs, volatile organic compounds; PGP, plant growth promoting; AMF, arbuscular mycorrhizal fungi.

partners, was properly addressed as early as 1904 when Hiltner described the symbiotic interaction among legumes and rhizobia (Hartmann et al., 2008). This symbiosis is a highly specific process in which the genetic and chemical communication signals are strictly plant-bacterium specific. In this mutualistic interaction, rhizobia positively influence the host's growth thanks to the nitrogen fixation process and at the same time can benefit from the nutrients provided by the plant.

This symbiosis has been extensively studied over the last few decades, and many studies on the communication and the signaling between the two partners at different steps of the symbiosis (from root infection to nodules development) have been elucidated (Oldroyd et al., 2011; Oldroyd, 2013). However, the knowledge about the earlier steps of rhizosphere colonization, namely the opening line at the root surface, remains poorly characterized. Nonetheless, increasing data have shown the importance of intraspecies and multispecies communications among rhizospheric biotic components for the improvement of rhizobia-legumes interaction. In addition, it has been shown that rhizobia are part of the rhizosphere of a wide variety of non-legume plants where they can play a role as PGP components, recovering a central role in plant core microbiome (Yeoh et al., 2016).

This review provides an outline of the most studied intra- and inter-kingdom communication strategies in the rhizobium-legume cross talk, defining the most relevant mechanisms of rhizospheric communication. We conceived the exchange of signals between plants and microorganisms as an intricate Talk Show *discussion*, in which a large variety of *dialogues* can take place, regulated and coordinated by a defined line-up, but at the same time, free to influence each other.

THE PLACE OF RHIZOBIA: SETTING UP THE SCENE

Rhizosphere complexity makes it difficult to identify and analyze the microbiome components and in particular, the laws governing the dynamics and the maintenance of plant associated microbial communities. Among factors able to influence those microbial communities, nutrients availability and soil composition have a strong influence (Naylor and Coleman-Derr, 2018). At this level, the root soil interface is rich in exudates that can differently alter gas and soil composition, thus selecting for certain microbial populations adapted to this unique niche. Root exudates contain a large variety of secondary metabolites, such as organic acids, amino acids and sugars, which are mainly used to attract microbes (PGP or pathogenic microorganisms) through chemotaxis process, and phenolic compounds such as flavonoids, fundamental for the signaling mechanism that allowst the symbiotic interaction with rhizobia and mycorrhizal fungi to start. Interestingly, several phytohormones and antimicrobial compounds (phenolics and terpenoids) are secreted by roots and used by plant as defense weapons against soil-born pathogens, to select among beneficial microbes (Baetz and Martinoia, 2014). Additionally, roots are able to produce volatile organic compounds (VOCs), which fulfill the role of rhizosphere microbial growth regulator (as antimicrobial compounds) or as

significant carbon source (Peñuelas et al., 2014). Therefore, the rhizodeposition makes microbial composition of the rhizosphere significantly different from that found in bulk soil (de Oliveira et al., 2017).

The plant acts as a *mediator* in the rhizospheric stage, consistently contributing to the balance of soil microbiome composition (Hartmann et al., 2009). On the other hand, the soil microbial community actively participates in the composition of the rhizospheric environment, taking part in degradation and production of organic compounds, for its own benefit (Paterson et al., 2007).

Among bacteria living in the rhizosphere and in association with plants, rhizobia can impact on surrounding microbial population by affecting legumes rhizosphere's composition and structure of the soil microbiome (Nwoke et al., 2008; Fan et al., 2018). The role of rhizobia as the main actor is mediated by a plethora of chemical and molecular signals that regulate bacterial invasion and intracellular colonization, modulate host plant defense response and nutrient exchange (Gibson et al., 2008).

Furthermore, water deficiency, salinity, heavy metals, acidity, as well as low nutrients levels are all abiotic factor that frequently can interfere with the role of rhizobia in the rhizosphere *scene* (Fagorzi et al., 2018; Bellabarba et al., 2019).

In addition, recent data have revealed that under identical soil conditions, the plant genotype, through its phenotypic features, can filter and modulate the microbial community structure and function, as well as the diversity of root associated bacteria (el Zahar Haichar et al., 2008; Berg and Smalla, 2009) carrying out a partner choice in rhizobia mutualism (Simms and Taylor, 2002).

Increasing field studies including large-scale rhizosphere samplings are now emerging with the aim to better understand the rhizospheric microbiome rules, focusing on the structure, the preservation and on the importance of communication occurring among the plants. In every case, the abiotic environmental factors (positive or negative), together with the communication among plants and rhizobial/non-rhizobial species are able to influence the rhizosphere Talk Show, giving order to the existing messy *scenario*.

SYNERGIC EFFECTS OF INTRA-KINGDOM BACTERIAL INTERACTION

The communication of microorganisms in the rhizosphere is mediated by a large diversity of microbial metabolites and physical signals, as happens in a noisy Talk Show, in which every *dialogue* can influence the success of the performance. The soil bacteria attracted by root exudates (**Figure 1**), root cell lysates and mucilages, profusely colonize the rhizosphere, thus starting the rhizosphere *dialogue*. Quorum sensing (QS), the bacterial population-dependent regulatory mechanism, is involved in bacterial cell aggregation and in the first phases of rhizosphere colonization through biofilm formation (Ng and Bassler, 2009). Indeed, rhizobia typically produce and release into the surrounding environment diffusible N-acyl homoserine lactone (AHL) molecules, which are used as signals for the control of plant- microbe interaction. The recognition of AHL molecules by bacterial cells starts and controls several processes

as the biofilm formation, Extracellular Polymeric Substances (EPS) production, bacterial motility and expression of bacterial genes relevant for symbiosis and nitrogen fixation (Loh et al., 2002; Sanchez-Contreras et al., 2007; Yang et al., 2009).

The rhizobial QS is based on the LuxR – LuxI type regulatory system. It is dependent on the threshold level of AHL which allows to induce expression of specific target genes (Veliz-Vallejos et al., 2020).

Actually, at least three LuxRI-type QS regulatory systems have been identified (Zheng et al., 2015b), and their role in interspecies communication also in co-inoculation experiments has been well demonstrated (Miao et al., 2018). Since several decades, extensive investigations of the role of the QS in rhizobial biofilms all along the root surface and inside the plants (i.e., endophytes) have been performed. Thus, strains with an effective roots colonizing ability through biofilm formation (Velmourougane et al., 2017) and flagellar-dependent chemotaxis ability (Zheng et al., 2015a) are always more advantaged than those strains without biofilm formation capabilities. Furthermore, a large variety of strategies are important for rhizobial roots colonization, such as the secretion of antibiotics and/or cell-wall degrading enzymes, which have been reported to be important for the protection against root phytopathogens (Siddiqui et al., 2000; Chandra et al., 2007) (**Figure 1**).

A wide spectrum of other physiological traits plays an important role in the rhizosphere by contributing to the complex phenomenon of nodulation competitiveness (Triplett and Sadowsky, 1992). These traits include swarming motility, type III secretion system, plasmid transfer, cell division, metabolism and transport (Calatrava-Morales et al., 2018). It is of note that their occurrence varies among species.

Microbial communities in the rhizosphere can compete for nutrients and for the plant roots colonization. Several rhizobia are able to interfere with the infecting capability of other strains through the production of bacteriocins, antimicrobial compounds that act on relative close phylogenetic species (Oresnik et al., 1999; Venter et al., 2001). *Sinorhizobium meliloti*, one of the most studied symbiotic species, is able to produce high-affinity siderophores which deprive antagonists of the available iron, thus limiting their plant growth (Arora et al., 2001).

Contrarily, in some cases, soil microbial communities can improve the infection capabilities of particular rhizobia and their communication with the host plant (Mehboob et al., 2013). The recent work by Miao et al. (2018) highlighted that strains of *Rhizobium fabae* are able to improve *Rhizobium etli* nodulation capabilities through a particular intra-species QS mechanism.

In this context, rhizosphere *actors* can participate in setting up the Talk Show by improving their performance. Synergic effects of specific co-inocula formulations should include a fair combination of PGP bacteria and rhizobia (Remans et al., 2008). Indeed, a range of PGP microbes can be used with rhizobia for the improvement of legumes growth and rhizobial mutualistic efficiency. The free - living diazotrophs *Azospirillum*, *Azotobacter*, *Bacillus*, *Pseudomonas*, *Serratia*, and *Enterobacter* are some of the genera that were successfully used with rhizobia as co-inoculants, potentiating growth and yield of several leguminous crops through different strategies, such as the production of phytohormones or biocontrol agents

against rhizosphere phytopathogens (Tchebotar et al., 1998; Tilak et al., 2006; Remans et al., 2008). Presence of *Azospirillum* species can increase the size of the rhizobial infection site, providing space for infection and facilitating the nodulation ability of rhizobia (Tchebotar et al., 1998). Although there are many combinations of bacteria co-inoculation that have been explored for the improvement of rhizobia-legumes symbiosis, there is still the need for advanced comprehensive research in their communication systems. Indeed, a selection of the most appropriate and performing panels of PGP strains, might be used in the near future as inoculants replacing fertilizers by a more environmentally friendly agricultural practice.

THE MOST ACCLAIMED RHIZOSPHERIC INTER-KINGDOM COMMUNICATIONS

A large part of the rhizobia-host communication strategies in the rhizosphere influences the highly regulated and ongoing rhizobial interactions in the root tissue. In compatible legume cultivars, after the establishment in the rhizosphere, rhizobia detect plant-derived flavonoids inducing *nod* genes, which are involved in Nod factors (lipochitooligosaccharides) production (Poole et al., 2018).

Then, rhizobia gradually adhere to roots surfaces, penetrate the plant root tissues and address their lifestyle inside the newly formed root organ, the nodule. Here, rhizobia differentiate into bacteroids, the N₂ fixing form of rhizobia, thus reducing atmospheric nitrogen to ammonia benefiting, in return, of protection and availability of nutrients from the plant (Kereszt et al., 2011). In this scenario, the accessibility to the symbiotic niche is naturally regulated and limited by the host plant to respond to nitrogen needs and by competition among rhizobial strains present in the neighboring soil (Triplett and Sadowsky, 1992).

The bi-directional inter-kingdom interaction between rhizobia and the compatible legume host involves a large panel of molecular signals as well as the exchange of metabolic resources, largely explored by scientist for decades (Oldroyd, 2013; Udvardi and Poole, 2013; Poole et al., 2018). The inter-kingdom molecular communication of these social interactions includes the volatile organic compounds (VOCs) and flavonoids issued by the plant and the bacterial Nod factors responsible for the nodulation signaling pathway. Bacteria cheaters among rhizospheric populations can profit of the plant permission state to escape plant sanctions and infect the plant tissue (Kiers et al., 2003; Sachs et al., 2010; Checcucci et al., 2016; diCenzo et al., 2018).

Representing more than 70% of all lands plants, legumes are able to interact with arbuscular mycorrhizal fungi (AMF) through the recognition of the mycorrhizal oligosaccharides' factors (Myc factors). Plant-fungi association allows the fungal elongation into the root cortex, where AMF can benefit the host mediating the nutrient uptake. It is largely demonstrated that in legumes, the Talk Show *dialogue* between fungi and rhizobia can take place at the root level (Barea and Pozo, 2005; Meghvasi et al., 2008; Kaschuk et al., 2010).

To our knowledge, Crush was the first researcher who observed that the presence of mycorrhizas stimulated nodulation and consequently plant growth (Crush, 1974). Then, many others reported additional effects produced by the tripartite interaction of Arbuscular Mycorrhizal Fungi – Rhizobia – Plant (ARP): it enhances symbiotic nitrogen fixation and effectiveness in drought soils (Hao et al., 2019; Laouane et al., 2019), increases number and dry weight of nodules (Antunes and Goss, 2005) and root soluble sugar contents (Hao et al., 2019; Tang et al., 2019). For more literature on the arguments, we refer to Anandakumar et al. (2019), Sakamoto et al. (2019), Sui et al. (2019) and Zhang et al. (2020).

Besides positive effects, fungi can act as antagonistic plant pathogens, which rhizobia can counteract as biocontrol agents for multiple plant species (Deshwal et al., 2013). Furthermore, it was demonstrated that the multiple inoculations of fungi, PGP bacteria can improve symbiotic behavior and plant nutrients availability, as was shown in semi-arid and alkaline soils (Requena et al., 1997; Abd-Alla et al., 2014).

It seems that communication which rhizobia can establish with the other components of the stage, can be a potential reserve for the improvement of rhizosphere interactions, and primarily those that contribute to host plant growth (Artursson et al., 2006). Recently, transcriptomic analysis in the presence of fungal exudates has shown their positive role in the transcription of rhizobial genes associated with the chemosensory (Zhang et al., 2020). In the future, further research should be addressed to the development of new technologies and applications to enable the optimization and the subsequent exploitation of ARP tripartite interactions. In particular, the monitoring of expression profiles of genes associated with communication mechanisms, the development of microcosm systems which simulate the natural condition, the analysis of the metabolic potential of microbial (and fungal) consortia in association with host plants, might be good starting points to better understand the multi-organism's rhizosphere communication. The most recent metagenomic approaches for the study of rhizobial microbial communities, as well as the determination of the role of each actor in the rhizosphere scene, will be essential for the understanding and the subsequent exploitation of organism diversity for sustainable agriculture (Faure et al., 2009; Arora et al., 2020).

CONCLUDING REMARKS

The current understanding of the rhizosphere is highlighting the complexity of the communication strategies taking place in this

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model environmental *scenario*. Increasing evidence is pointing out how in this scenario rhizobia occupy an important place that extends to non-legume plants. This niche is a consequence of the influence of several factors (biotic and abiotic), at different levels (intra- and inter-kingdom) and different degrees (competition and cooperation).

Every interaction and exchange of signals taking place in one of the most known complex environments cannot be conceived as uni or bidirectional reactions, but it can be imagined as a complex network of *dialogues*, a model of noisy *discussion* while remaining inexplicably tidy and regulated by the partners themselves. Therefore, the recent studies, focused on microbial community networks models (Melke et al., 2010; Barto et al., 2012; Succurro and Ebenhöh, 2018; Mai et al., 2019), have to be adapted to the complexity of the rhizosphere. The dissection of such rhizospheric communication is essential for the improvement of the benefic aspects of such communication (Mueller and Sachs, 2015; Checcucci et al., 2017; Mueller et al., 2019) with a view to agricultural applications.

The rhizosphere *scene* can be considered as a highly suitable model for the application of a system biology study approach, including the large number of plants and microorganisms sequenced genomes, the studies on partners metabolic functionalities (Korenblum et al., 2020) and on the transcriptomic changes related to different partners interaction (Pathan et al., 2020). It is expected that future studies will continue to explore the selective forces that shape rhizosphere microbiome further elucidate the potential of the communication among the different rhizospheric partners.

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All authors listed have made a substantial, direct and intellectual contribution to the work, and approved it for publication.

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Conflict of Interest: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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