## **Rhizosphere Biology**

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Vadakattu V. S. R. Gupta • Anil K. Sharma Editors

# Rhizosphere Biology: Interactions Between Microbes and Plants



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#### Preface

Rhizosphere plant–microbe interactions are diverse, spatially and temporally dynamic, influenced by plant, soil biophysical environment, and are critical to plant health and crop productivity. It is well established that bacteria and fungi around a plant's root in the rhizosphere, the miniature ecosystem around the root, can influence both the root's form and its physiology. The rhizosphere concept, coined in 1904 by Lorenz Hiltner about the roles of soil microorganisms in plant nutrition and health, has initiated a century-long research and discussion about organismic interactions between plants and microbes. More than 50 years ago, Dr Ralph Foster's (CSIRO, Adelaide) electron micrographs revealed the intricate structure of rhizosphere, rhizoplane, and endosphere environments and the interplay between plant root, microflora, and protozoa. Rhizosphere microbiota provides a valuable potential resource of plant probiotic and growth-promoting functions capable of conjugating crop productivity within sustainable agricultural systems. It is, therefore, important to understand the dynamics of rhizosphere interactions in order to develop practical strategies that would help improving yield and maintain ecosystem health.

During the last decade, there has been a renewed interest in exploring the dynamics of the rhizosphere, using *omics* tools, for its composition and organismal interactions occurring in the complex spatial structuring at the root–soil interface and their key drivers during the crop growth. Recent research has shown structural and functional diversification of root-associated microbial communities of crop varieties, wild and domesticated accessions of barley, maize, canola, peas, and various *Arabidopsis* accessions, etc. Some of these findings also identified bacterial taxa which were positively correlated with crop performance or yield. This led to an intense effort to identify the plant-based traits that modulate the genetic structure and diversity, gene expression, and functional profile from the outer realms of rhizosphere to inside the root. This new understanding has highlighted an attractive avenue that would help to better harness beneficial outcomes from plant–microbiome interactions.

This book is a compilation of the latest knowledge on plant and microbial aspects of rhizosphere biology covering different ecological, molecular, and biochemical characteristics of rhizosphere and endosphere interactions. It contains 15 chapters, each prepared by authors who are internationally recognized for their knowledge and expertise in a particular area of rhizosphere interactions. Additionally, it covers the cross-talk between plants and microbes including quorum-sensing signal molecules, plant interactions with abiotic factors, and potential ways rhizosphere microbial composition and functionality could be manipulated for enhanced and efficient benefits. The different chapters cover key areas such as (1) factors driving rhizosphere biology and interactions, (2) diversity of phenotypic and functional groups, (3) functional significances of rhizosphere interactions, and (4) how best to manipulate rhizosphere interactions. A special feature of the papers is that they highlight the benefits of using the latest omics (metagenomics, transcriptomics, and metabolites involved in the multitrophic interactions.

Endophytic bacteria, those that colonize the internal tissue of the plant showing no external sign of infection or negative effect on their host, have been found in all plants and form a range of relationships including symbiotic, mutualistic, commensalistic, and trophobiotic interactions. This type of plant microbiome is now considered as the second genome of the host plant and concepts such as "holobiont" comprising the plant with its endophytic microbiome as an extended phenotype and a unified system. In the chapter on bacterial endophytes, Tosi et al. (Chap. 1) present a comprehensive summary of the latest knowledge about the diversity and functions of bacterial (including actinobacteria) endophytes, their influence on plant fitness, and the potential to manipulate their functions in agroecosystems. The presence of a taxonomic overlap between endophytic and rhizospheric communities and clear community shifts between these compartments confirms the idea that rhizosphere is a key habitat regulating endophytic communities. Although soil type can have a major influence, strong and significant host genotype effects on the diversity resulting in distinct taxonomic composition of endophytic bacteria have been shown with a variety of plants. However, the observation of differential abundance, core microbiomes, new knowledge on the heritability of the specific taxa and their links to plant genotype through genome-wide association studies is needed in order to develop designer plant-microbiome combinations that maximize beneficial functions. The involvement of root exudates as carbon and nutrient sources in modifying the rhizosphere microbial communities, as proposed by Albert Rovira more than 50 years ago, is now extended to include signal molecules and root architecture influencing the microbiome composition. In Chap. 9, Haichar and Achouak describe how newly introduced and modified genes in plants influence the quality and quantity of root exudates and in turn rhizosphere microbiome. It is increasingly becoming clear that the ability of soil microbes to colonize a particular plant species is fuelled and modulated by the release of signals by either or both partners and are only recognized by the right partner. Taking the knowledge from legume-rhizobia and plant-mycorrhizal symbioses, Antar et al. summarize (Chap. 13) the latest knowledge about the signals involved in other beneficial plant-microbe interactions and microbe-microbe signal interactions. In spite of recent findings about the intricacies of rhizosphere interactions, the exact molecular mechanisms governing the complex root-soil-microbe interactions remain largely unknown. Balasubramanian et al. present (Chap. 14) a review of what is known about the strategies for manipulating the rhizosphere region with a focus on engineering the root H+ efflux and organic anions, secondary metabolite composition of root exudates, alterations in root biomass accumulation, and below-ground carbon allocations for improved plant performance.

The carbon inputs by plant roots not only provide the primary source of organic C into the soil modifying rhizosphere microbiome, but the chemical composition of exudates also strongly influences the metabolic potential of rhizosphere-enriched microbes along with mediating nutrient fluxes in the rhizosphere. In Chap. 2, Pett-Ridge et al. provide evidence showing the downstream effects of rhizosphere dynamics on the colonization of nearby soil minerals, degradation of prior season's root litter, and the balance of stabilized versus lost soil carbon. Furthermore, this study provides an excellent example illustrating the benefits of using the latest genomic and isotopic techniques to unravel the mechanisms of C flow between growing plant roots, soil microbial communities, and the surrounding mineral matrix. The beneficial effects of these rhizosphere interactions on nutrient fluxes and availabilities could also improve plant nutrition through increased nutrient use efficiency and, as discussed by Paterson and Mwafulirwa (Chap. 3), provide a realistic means of improving plant health and productivity while potentially also mitigating environmental impacts. Also, recent findings about the diazotrophic communities in the rhizosphere and endosphere in terms of their diversity and functional capacity have rejuvenated the old idea of harnessing the biological N fixation in nonleguminous crops through manipulation of this specific functional group; the chapter by Roley (Chap. 4) presents the latest knowledge on this topic.

The rhizobia-legume and mycorrhizae-plant interactions are two well-established examples of plant-microbe symbiosis with extensive research and knowledge about the mechanistic aspects of the beneficial interactions. Recent research has shown that the interactions of "Arbuscular Mycorrhizal Fungi" (AMF), the obligate biotrophs, in the rhizosphere are not just restricted to host plant but involve bacteria in the rhizosphere and hyphosphere; Wang and Feng discussed (Chap. 11) new insights into interactions between AM fungi and other organisms in the rhizosphere.

Plant health status affected by the presence of pathogens and root disease incidence could be a driver for change in the root microbiome as discussed in the chapter by Barnett (Chap. 8) and it was proposed that microsite-based variation between healthy and diseased niches in the root system could ultimately lead to the development of disease suppressive microbiomes; however, the exact mechanisms for such community changes remain elusive at present. Alternatively, plant–microbe interactions in the rhizosphere can have a significant impact on plant health acting as the first line of defense in the rhizosphere. Therefore, identification of plant genetic traits involved in the recruitment of beneficial microorganisms, i.e. promoting probiotic microbial community, would help improve plant defenses against biotic stresses; the chapter by Chiaramonte et al. (Chap. 7) discusses strategies and potential to explore this option through plant breeding programs.

Plant root-biota associations in the rhizosphere involve complex networks and interactions between micro- and macroorganisms across multiple microsites and in intricate spatial structuring that can vary temporally during crop growth from seedling to maturity. Recent evidence from genomic and transcriptomic studies clearly indicates that there is a strong association between rhizosphere development and taxonomic makeup including the succession in bacterial community in field environments. This has been demonstrated for several crops including cereals, canola, cotton, and other crops (Richardson et al., Chap. 5). The major predators of microorganisms such as protists, faunal nematodes, and microarthropods can modulate the composition of rhizosphere microbiome through preferential feeding, with functional consequences in plant performance by affecting nutrient cycling, pathogen density, etc. (Geisen and Quest, Chap. 12). As rhizosphere food webs are not universally identical, the functional importance of microbial–faunal interactions is modulated by the soil habitat structure and management.

The concept of succession in rhizosphere microbiome dynamics also leads to the idea of "legacy" in that the rhizosphere of crop leaves a footprint in the soil systems affecting the following crops. Since rhizosphere interactions involve modifications in soil physicochemical and biological components, the legacy effects should incorporate physical, chemical, and biological effects that potentially endure beyond the root that created it. In the chapter by Oliver et al. (Chap. 6), they suggest that constraints of destructive sampling can be overcome from the recent advances in micro X-ray computed tomography, but it still requires other complementary techniques to determine the extent of the rhizosphere legacy.

It was considered that the most effective form of manipulation of rhizosphere and endosphere microbiomes is through the use of beneficial microorganisms, "bioinoculants" either singly or as consortia for biocontrol to reduce or eliminate plant disease effects or effects of abiotic stresses such as from drought/water-stress or salinity effects. Through the use of latest *omics* tools (metagenomic, transcriptomics, and metabolomics), it is now possible to describe in-depth the networks of members of rhizosphere microbiomes including the effects of introducing inoculants as well as identifying mechanisms to manipulate and engineer microbiomes (Franco, Chap. 15). For example, recent evidence suggests that rhizobacteria with the capacity to produce ACC deaminase can initiate a cascade of changes in plant physiological and biochemical responses resulting in increased tolerance to abiotic stresses in a broad range of plant species (Sharma et al., Chap. 10).

As a result of fast-changing global climate scenario with predictions for reduced rainfall and increased effects of other abiotic stresses across many agricultural regions worldwide, exploitation of such beneficial plant-microbe interactions to alleviate abiotic stress effects in crops should be one of the key approaches to promote resilience and improve global food production. A majority of the recent research on the makeup and dynamics of rhizosphere microbiome until now has concentrated on taxonomic/phylogenetic makeup of the microbiome mainly about who is present and variations with plant type, management, and soil environment. In view of the extensive diversity and the dynamic spatial and temporal structure of the microbiome, interpretation and extrapolation of variations in phylogenetic makeup in terms of their functional potential and resilience have been found to be not straightforward. Hence future research on plant-trait based microbiome interactions requires investigations targeting specific functional groups associated with key plant traits to help with the development of management interventions that can improve productivity in agricultural systems. Through a combination of genomic, transcriptomic, and isotopic tools, it should be possible to directly follow the dynamics of specific microbial functional group and link it with associated functional fluxes. Such research would facilitate the identification of key drivers from plant, microbial, and process perspectives, thereby assisting in the development of new designer plant holobionts that utilize native soil microbiome through nextgeneration crop breeding, "syncoms" or synthetic communities and management practices for sustainable and resilient food production systems.

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