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RHIZOSPHERE INTERACTIONS

THE ROOT MICROBIOME INFLUENCES SCALES FROM MOLECULES TO ECOSYSTEMS: THE UNSEEN MAJORITY[1]

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Plants are teeming with microbial organisms including those that colonize internal tissues as well as those that adhere to external surfaces. In the rhizosphere, the plant-associated microbiome is intricately involved in plant health and serves as a reservoir of additional genes that plants can access when needed. Microbiome regulation of plant trait expression affects plant performance, which in turn influences various ecosystem functions, such as primary productivity and soil health. Understanding these plant- and microbe-driven interactions requires a study of the nature and effects of the plant microbiome. Conceptualizing the microbiome requires a synthesis of microbial ecology, physiology, and bioinformatics, integrated with insight into host biology and ecology. Microbiome structure and function analyses are recognized as essential components to understand the genetic and functional capacity of the host (previously assigned solely to the host) and include vital aspects of metabolism and physiology. Here, as a special section, we present a set of papers that address the complex interactions between plants and root microbiomes in the rhizosphere. This unseen majority spans scales; with its microorganisms numerically dominant in terrestrial ecosystems, the root microbiome is also involved in plant genetics through integral roles in plant trait expression that can effect community composition and ecosystem functions, such as soil health.

Key words: rhizosphere interactions; root microbiome.

Over the past decade, significant advances in understanding host health and immunity have been made, thanks to the concept of the microbiome and the relevance it has to health, disease state, and immune function of the host organism. There is enormous power in the unseen majority—the microbes, and research focused on disentangling microbiome complexity has increased our understanding of this “power of the small”. As an example, we now understand that several human disease states are produced by interactions among the microbiome, the environment, and host genetics and immunity (Greenblum et al., 2012; Koeth et al., 2013). By extension of this concept, the plant microbiome comprises the set of genes present in a specified habitat associated with a particular plant. The habitat is scaled over a range—from the whole organism (individual plants), to specific organs, e.g., roots, leaves, shoots, flowers, seeds, including zones of interaction between roots and the surrounding soil, the rhizosphere.

Attention to belowground interactions among soils, microbes, and plants is not new. This concept of the plant microbiome perceives these soil–plant–microbe interactions at a molecular level. This special section opens by drawing attention to the complex interactions in the rhizosphere that are regulated by plant and microbial exudates, as reviewed by Moe (2013). The rhizosphere microbiome plays a significant role in plant health, effectively serving as a “second genome” to the plant (Berendsen et al., 2012) and documented in the second paper in this special section by Curlango-Rivera et al. (2013). The root microbiome also plays a key role in community dynamics and soil health; examples of these influences are documented in this special section by Kaplan et al. (2013) and Rout et al. (2013). Finally, Gaiero et al. (2013) summarize the influences on endophyte microbiome community structure, the microbes inhabiting the adherent and intracellular habitats of plant hosts. Further, these authors assess the influences affecting microbiome community structure in the context of promoting plant growth and the potential for molecular techniques to enhance our understanding of these complex microbiome communities. Together, the papers presented in this special section highlight root microbiome influences across multiple scales—at the plant cellular level, bacterial and plant functional levels, plant and microbial community levels, and at ecosystem functional levels.

The influence of the rhizosphere microbiome relies heavily upon chemical exudates that create communication highways of signaling molecules produced and secreted by microbes and plants. Through this exudate currency, the plant microbiome serves as an extension of the plant genome. Plant and microbial exudate uptake and release and potential impacts on plant and microbial functions are the focus of the first paper in this special section, “Amino acids in the rhizosphere: From plants to microbes” by Moe (2013). Amino acids, one of the most abundant plant exudates, represent a cellular efflux that communicates between plants and microbes.

Rhizosphere interactions that directly influence the root microbiome structure in addition to plant function are documented by Curlango-Rivera et al. (2013) in their research on cotton cultivars with variation in border cell production. In their paper,

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"Intraspecies variation in cotton border cell production: Rhizosphere microbiome implications," the authors document plant defense responses stimulated by copper chloride by measurement of extracellular trapping of bacteria in the border cells of cotton cultivars. One cultivar demonstrated a nearly 3-fold increase in border cell production in the presence of copper chloride compared to other cultivars. However, the ability to form an extracellular trap was similar among cultivars, and bacterial trapping was reduced in one cultivar. Overall, their findings show that extracellular DNA is a component of the surrounding mucilage, which attracts, traps, and immobilizes pathogens in a host-microbe specific manner.

At the community level, the paper in this special section by Kaplan et al. (2013) demonstrates microbiome community structure through the use of molecular techniques. They document that plant community structure is influenced by the microbiome and quantify functional attributes of bacterial isolates from the microbiome. In "A survey of the microbial community in the rhizosphere of two dominant shrubs of the Negev Desert highlands, *Zygophyllum dumosum* (Zygophyllaceae) and *Atriplex halimus* (Amaranthaceae) using cultivation-dependent and -independent methods," the authors show that the microorganisms living in the rhizosphere and in bulk soils of the harsh environment of the Negev Desert of Israel have potential for use as plant-growth-promoting bacteria (PGPB). Many epiphytes and endophytes in the microbiome, associated with these desert perennials, perform a variety of plant-growth-promoting functions including nitrogen fixation, iron chelation through bacterial siderophore production, phosphate solubilization, and secretion of cellulase. Kaplan et al. (2013) suggest that "mining" for plant-growth-promoting bacteria from harsh environments, such as arid deserts, could provide inocula to stimulate crop growth in environments undergoing or anticipated to undergo harsher conditions as a function of climate change. The multiple plant-growth-promoting traits associated with these epiphytic and endophytic microbes support the "dual trait" phenomenon in which plant-growth-promoting bacteria were more effective when they were capable of expressing dual growth promotion traits (Baig et al., 2012). While dual-trait plant-growth-promoting bacteria help the dominant native plants of the Negev Desert persist, they also help invasive plants establish and persist, as documented by Rout et al. (2013). In their paper, "Bacterial endophytes enhance competition by invasive plants," the effects of the rhizosphere microbiome occur at the levels of plant traits and plant communities through perturbations to soil biogeochemical pools and cycles. The invasive grass *Sorghum halepense* produces less biomass, with a >5-fold decline in rhizome growth, when microbiome endophytes are inhibited. This finding suggests a major role for endophytes in the growth and resource allocation of an invasive species and implies that the complex feedbacks between the plant and the microbiome involve hormone signaling and nutrient exchange between partners. In addition, Rout et al. (2013) demonstrate that endophyte isolate physiology correlates with invader effects on biogeochemical cycles of nitrogen, phosphate, and iron. Thus, bacterial endophytes of the microbiome could influence successful plant invasions of this species.

The final paper in this special section is a review by Gaiero et al. (2013), "Inside the root microbiome: Bacterial root endophytes and plant growth promotion." This concept paper reviews the drivers of bacterial endophyte microbiome community structure relating to plant growth promotion, the mechanisms of plant growth promotion, and the use of molecular techniques to study these communities. The authors document the vast number of plant species that have bacterial root endophytes as part of their root microbiome, with some bacterial endophytes shown to positively influence plant growth through a wide variety of plant-growth-promoting functions. Factors influencing endophyte community structure (species diversity, richness, and abundance) within the plant and the dynamic processes that influence the microbiome of the rhizosphere include the abiotic factors of soil conditions and biogeography, and the biotic factors of plant species, microbe–microbe interactions and plant–microbe interactions, spanning scales (micro to macro).

Viewed from either perspective, plant-centric or microbiome-centric, the plant microbiome exerts influence on plant trait expression. By the nature of plant communities, these effects are manifest across scales—from molecules to ecosystems. Many lines of evidence illustrate the range of plant–microbiome associations contributing to plant plasticity under a given set of environmental conditions (reviewed by Friesen et al., 2011). The plant microbiome can be perceived as an integrated component of the plant genome. This aspect of the microbiome expands the ecological concept of "feedbacks" (Bever, 1994), a pivotal concept that integrated the soil–plant–microbe interface. The root microbiome and plants can exert a vast array of influences on these feedbacks, which also vary over time as a function of the flux between attenuation and intensification of microbiome members that span the parasite–mutualism spectrum in their interactions with plants (reviewed by Callaway and Rout, 2011). Plants that can motivate or manipulate their microbiome in ways that increase the likelihood for plant persistence will be favored by selection, particularly under stochastic disturbances (de Bello et al., 2010). The papers in this special section retune our focus to the role that the microbiome plays in regulating plant trait expression, accounting for plant performance, and expand our interpretation of microbiome influences toward understanding the dynamics within the ecosystem functions of biogeochemical cycling and plant productivity. Our understanding of these complex communication pathways within the plant microbiome will become clearer through first detecting, then quantifying the multiple functions of microbial and plant exudates and their effects on gene transcription and translation. The holistic approach to understanding organismal structure and function requires an understanding of the organism in its entirety. Quantifying the impacts of the plant microbiome will advance our conceptual framework in plant biology, with real-world applications that have the potential to increase crop production through enhanced plant trait expression and/or increased utilization of marginal habitats.

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