

Special Issue: Unravelling
the Secrets of the
Rhizosphere

Spotlight The Soil-Borne Supremacy

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The rhizosphere microbiome plays an important role in plant growth, nutrition and health. Recent research unearthed that plant genotype-dependent navigation of microbial community composition in the rhizosphere is associated with fitness consequences for the host plant, providing great promise for breeding soil-borne supremacy traits into future crops.

Rhizosphere microbiomics

Plants invest a significant proportion of their photosynthetically-fixed carbon sources in the maintenance of rhizosphere microbiota, for example, via exudation of sugars, amino acids, organic acids, mucilage, and dead border cells. In return, beneficial microbes in this so-called rhizosphere microbiome provide important services to the plant as they improve root architecture, enhance nutrient uptake, and provide protection against plant pathogens (Figure 1) [1]. In recent years, advances in next-generation sequencing technology greatly boosted the field of host microbiomics. Detailed analysis of microbial community assembly in the rhizosphere and phyllosphere revived the notion that the microbial composition of the soil is a major determinant of rhizosphere microbiome composition. It also showed in unprecedented detail that root interior, root surface, soil close to the root surface, and unplanted bulk soil have distinct microbiomes [2], and that soil serves

as an important microbial reservoir for microbial community assembly in the phyllosphere [3]. Underlying principles of plant-microbiome interactions have been nicely described in the microbial market theory [4], in which economic market characteristics, such as exchange of commodities between trading partners (plant vs. microbe and microbe vs. microbe), 'price wars' (best return of investment), supply and demand dynamics, and elimination of the competition, drive community assembly of microbiota at the root-soil interface.

Plant genotype-microbiome interactions

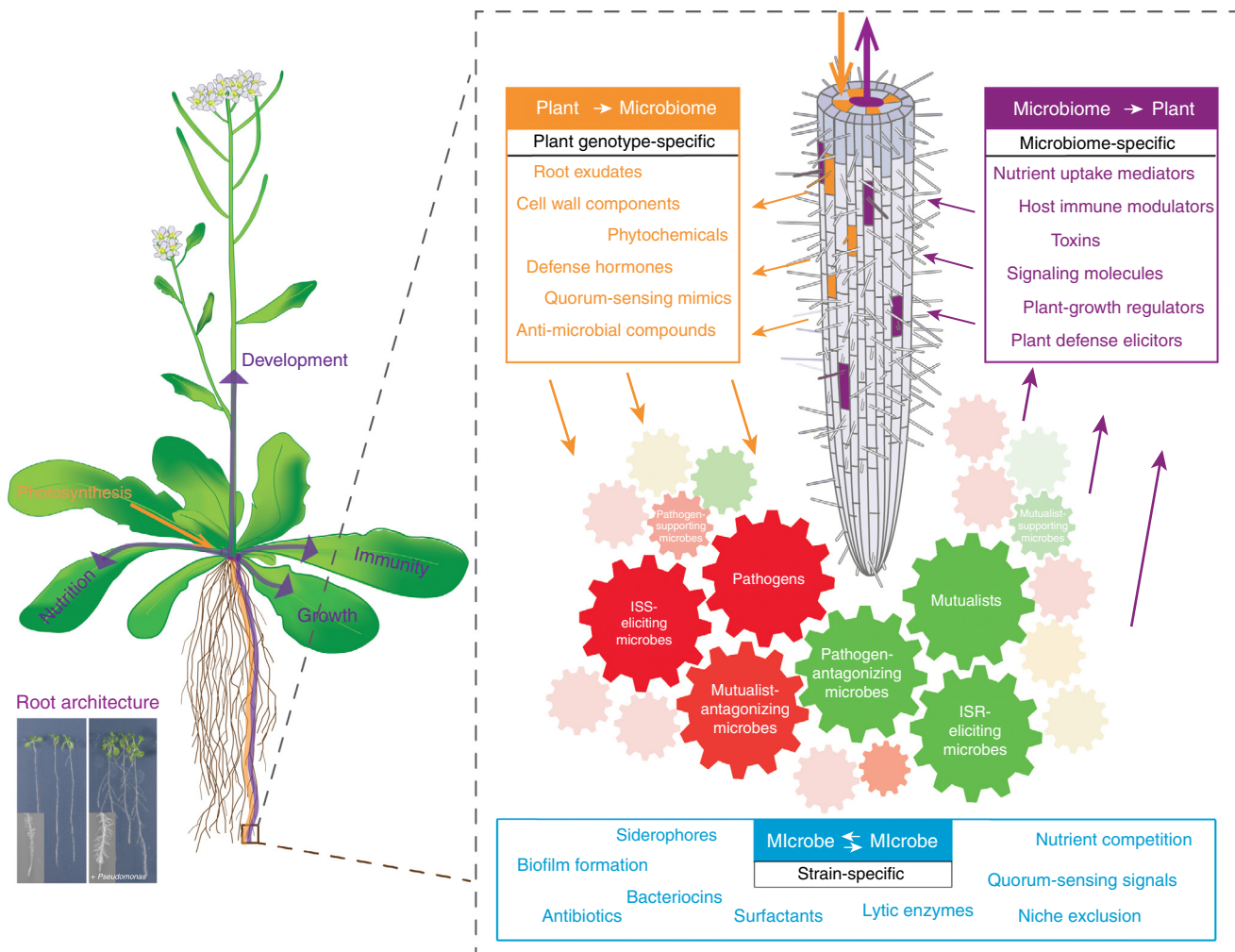
In agricultural systems and other non-natural plant-soil combinations, the effect of host genotype on the composition of rhizosphere microbial communities is much smaller than that of soil type, whereas in natural ecosystems with long-term co-evolution of plant-microorganism interactions, the effect of plant genotype is thought to be bigger [5]. Haney *et al.* recently showed that even small host genotype-mediated effects on microbiome composition can have large effects on host health [6]. They found that a collection of 109 wild *Arabidopsis thaliana* (arabidopsis) accessions differ in the ability to support colonization by beneficial *Pseudomonas* bacteria and that this is associated with consequences for plant fitness. Among the naturally occurring arabidopsis accessions were lines that suppressed growth of *Pseudomonas* bacteria in the rhizosphere, while others supported bacterial growth. This effect of host genotype specifically affected members of the Pseudomonaceae in the root microbiome and was likely caused by the differential production of antimicrobial compounds. Importantly, Haney *et al.* showed that differential support of *Pseudomonas* growth translated into effects on rhizosphere community composition, plant growth promotion, and rhizobacteria-induced systemic resistance (ISR) or susceptibility (ISS) to subsequent pathogen infection [6]. This study nicely highlights that both

plant and microbe genotype contribute to whether a rhizosphere microbiome provides a beneficial or harmful influence on the plant.

Plant genotypic traits shaping microbiomes

Because plants recognize microorganisms as 'nonself', root microbiota are by default warded off by the plant's immune system. Hence, manipulation of the host immune system by beneficial microbes is a first step in the establishment of mutually beneficial relationships. Recently, Lebeis *et al.* showed that the plant defense-related hormone salicylic acid (SA) plays a role in the assembly of the microbiome in the interior of arabidopsis roots [7]. By analyzing the endophytic root microbiomes of SA biosynthesis and signaling mutants, they found signs that SA or SA-mediated plant processes modulate colonization of the roots by specific bacterial families, thereby differentially gating access of specific bacterial taxa to the microbial community in the root interior. These findings pinpoint plant genotypic traits related to plant immunity as players in processes that structure the microbial community in the rhizosphere.

Another mechanism involved in microbial community formation and functioning is quorum sensing. This process controls genes that enable bacteria to carry out important community functions, such as biofilm formation and production of antimicrobial compounds to fight enemies and competitors. Homoserine lactones are important quorum-sensing signals for Gram-negative bacteria, such as *Pseudomonas* species. Recently, Corral-Lugo *et al.* [8] identified rosmarinic acid as a root exudate-derived homoserine lactone mimic that induces a premature quorum sensing response in *Pseudomonas*, thereby manipulating its success in the establishment of a host-microbe interaction. Root exudates consist of a variety of compounds including carbohydrates, amino acids, and organic acids. Their composition is dependent on plant



Trends in Plant Science

Figure 1. Interactions Between Plant Genotype and Root Microbiome Composition Affect the Degree by Which Plants Benefit from Root-Associated Microbes. Plants invest a proportion of their photosynthetically fixed carbon sources in maintaining and shaping the microbial community in and around their roots (i.e., the root microbiome). In turn, plants profit from microbiome-encoded functions, resulting in improved growth, development, nutrition, and/or immunity. The plant genotype affects root metabolism, immune system functioning, and root exudate composition (orange box and arrows), which in turn influences the activity and structure of the root microbiome. The relative success of soil-borne pathogens and mutualists in their respective association with plant roots is affected by the degree of activity of microbes that antagonize or support them. Such microbe-microbe interactions (blue box) are mediated via strain-specific production and perception of molecules with dedicated antimicrobial or probiotic activities that selectively inhibit or support microbial growth. Collectively, microbiota in and around the root provide important services to the plant, such as improved root architecture, enhanced nutrient uptake, promotion of plant growth, activation of induced systemic resistance (ISR), and suppression of soil-borne pathogens and microbes that stimulate induced systemic susceptibility (ISS) (purple box and arrows). *Inset root architecture:* enhanced lateral root formation and increased root hair length in arabidopsis seedlings exposed to beneficial *Pseudomonas* bacteria.

genotype, can change depending on the environmental condition, and are thus an important driving force in the assembly of microbial communities in the rhizosphere [5]. Whether plant-derived quorum sensing signals play a role in the differential support of *Pseudomonas* growth in the study of Haney *et al.* remains to be elucidated.

Microbiomes mutilated through domestication?

In natural ecosystems, plant diversity and productivity is influenced by soil-feedback mechanisms that differentially affect fitness and survival of individual plant species and rhizosphere microbiota [5]. Hence, plant genotype and microbiome composition determine the degree by which plants profit

from their root microbiome. In the past centuries, plant breeding in combination with yield-increasing agricultural practices and the use of chemical fertilizers and pesticides, has resulted in the selection of domesticated plant genotypes that may have become eroded for plant traits that aid in maximizing profitable functions from the root microbiome [9]. Bulgarelli *et al.* [10] found small

but significant differences between the composition of the rhizosphere microbiomes of domesticated barley and its wild ancestors, which suggests that the genetic make-up of modern crops affects the composition of the rhizosphere microbiome. Also the rhizosphere microbiomes of field-grown maize inbred lines showed significant signs of heritable variation in microbial diversity [11]. This indicates that plant genetic traits contribute to microbiome composition and may ultimately be used in plant breeding strategies to optimize plant-beneficial microbe interactions in crops. Plant genomes encompass a large, hidden potential for maximizing profits from rhizosphere microbiota as was recently shown by Wintermans *et al.* [12]. A collection of over 300 wild arabidopsis accessions displayed extensive natural genetic variation in the capacity to initiate root architectural adaptations and to increase shoot fresh weight in response to exposure to plant growth-promoting *Pseudomonas* bacteria (Figure 1). A genome-wide association analysis identified candidate genes related to important plant growth processes, showing that plant genotype can affect the level by which plants profit from microbial functions in the rhizosphere.

Future prospects

The notion that wild plants harbor a reservoir of genetic traits that aid in maximizing profitable functions from rhizosphere microbiota provides great promise for utilization in plant breeding strategies that are aimed at optimizing plant-microbiome interactions in crops. In the past years, advances in plant microbiomics provided important insights into processes underlying phytobiome structure and assembly. The crucial next step is to mine systematically plant-beneficial functions that are encoded in the rhizosphere microbiome, elucidate how these functions operate at the molecular level and translate to plant benefits, and identify which plant genes act in acquiring the profits of these microbiome functions. Detailed knowledge on how these soil-borne supremacy traits are encoded in plant genomes and plant-associated

microbiomes will contribute to the design of future crops that, in combination with dedicated microbial agriculture, can sustainably enhance crop production with less input of harmful chemicals.

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Special Issue: Unravelling the Secrets of the Rhizosphere

Spotlight Small is Plentiful

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Rhizobia are legume symbionts that arise through horizontal transfer of symbiotic genes among soil bacteria. A recent study shows that these transfers occur frequently at a micro-scale, leading to unexpected rhizobial diversity and emergence of symbiovars within species. This confirms the disconnection between function and taxonomy in bacterial communities.

The soil is a formidable reserve of microbial diversity. A single gram of soil contains up to 50,000 different bacterial species that play a central role in biogeochemical processes as well as the nutrition, health and productivity of plants. Increased affordability and power of DNA sequencing technologies has led to an explosion of large-scale sequencing studies exploring environmental and host-associated microbiomes. This field is dominated by cataloguing species and genes present in all habitats as well as by predicting their functional potentials. This has revealed the high local diversity of microbes in the root rhizosphere and endosphere [1,2]. A future challenge is now to identify ecological and evolutionary factors generating this diversity. In a recent study Kumar *et al.* explored the links between microbe identity and ecology using a highly stringent functional prism [3]. The authors analyzed the genomic diversity of bacteria that have taken up residence inside a specific habitat, the root nodule, of two legume species growing in a tiny area of vegetation.

A taxonomically diverse range of free-living soil bacteria, called rhizobia, have