The Soil-Borne Legacy

Peter A.H.M. Bakker,[1,*] Corné M.J. Pieterse,[1] Ronnie de Jonge,[1,2,3] and Roeland L. Berendsen[1]
[1]Plant-Microbe Interactions, Department of Biology, Faculty of Science, Utrecht University, Padualaan 8, 3584 CH Utrecht, the Netherlands
[2]Department of Plant Systems Biology, VIB, Ghent, Belgium
[3]Department of Plant Biotechnology and Bioinformatics, Ghent University, Ghent, Belgium
*Correspondence: p.a.h.m.bakker@uu.nl
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Plants greatly rely on their root microbiome for uptake of nutrients and protection against stresses. Recent studies have uncovered the involvement of plant stress responses in the assembly of plant-beneficial microbiomes. To facilitate durable crop production, deciphering the driving forces that shape the microbiome is crucial.

The rhizosphere microbiome extends the functional repertoire of plants beyond imagination. Exciting developments in high-throughput molecular analyses of the plant microbiome pinpointed enhanced nutrient uptake, improvement of root architecture, and protection of the host against biotic and abiotic stress as key functions of the microbiome. Currently, the life processes that shaped the co-evolution between plant hosts and their beneficial microbiota members gradually come to surface. It appears that plants evolved adaptive strategies by which they utilize root-associated microbiota to optimize both nutrient acquisition and immunity. Knowledge on the mechanisms and plant genetic pathways involved provides great potential for sustainable microbiome-based improvements of our future crops.

Disease-Suppressive Soils and the Cry-for-Help Hypothesis

One of the most intensively studied microbiome functions is protection of the host against infectious diseases. A recent study in common beans has shown that the rhizosphere microbiome provides a first line of defense against the soil-borne fungal pathogen *Fusarium oxysporum* (Mendes et al., 2018). *Fusarium*-resistant genotypes supported a higher abundance of specific plant-beneficial families in their rhizospheres, including Pseudomonadaceae and Bacillaceae. Moreover, metagenome analysis showed that the rhizosphere bacterial communities of *Fusarium*-resistant genotypes were enriched for biosynthetic genes that encode antifungal traits, such as phenazine and rhamnolipids (Mendes et al., 2018). The protective effect of the rhizosphere microbiome became well known from the discovery of disease-suppressive soils, which typically develop in mono-cultured crops in response to a severe disease outbreak (Raaijmakers and Mazzola, 2016). Such soils accumulate plant-protective microbiota that protect future generations of plants against the pathogen that triggered the suppressiveness. Specific microbes that are enriched in disease-suppressive soils and their plant-protecting metabolites have only rarely been identified (Raaijmakers and Mazzola, 2016). For instance, in a soil suppressive to the fungal pathogen *Rhizoctonia solani*, the sugar beet rhizosphere microbiome was enriched for the bacterial families Oxalobacteraceae, Burkholderiaceae, Sphingobacteriaceae, and Sphingomonadaceae, while stress-related bacterial genes representing antifungal activities were specifically upregulated (Chapelle et al., 2016). It was postulated that invasion by *R. solani* could affect the microbiome composition of the infected plant, leading to enhanced antifungal activity in the root microbiome community, thereby restricting pathogen growth. Whether the disease-mediated effects on microbiome composition and activity were a direct effect of pathogen-derived metabolites—for example, production of antimicrobial oxalic acid—or were indirectly mediated via pathogen-inflicted changes in root exudate profiles remained undetermined.

In a recent study, the effect of foliar pathogen infection on root microbiome changes was investigated, excluding possible direct effects of the pathogen on the rhizosphere microbiome. Inoculation of *Arabidopsis* leaves with the downy mildew pathogen *Hyaloperonospora arabidopsidis* resulted in an enrichment of a *Microbacterium* sp., a *Stenotrophomonas* sp., and a *Xanthomonas* sp. in the rhizosphere microbial community (Berendsen et al., 2018). When applied to soil as a synthetic consortium, the recruited bacteria protected *Arabidopsis* against aboveground downy mildew infection via the onset of induced systemic resistance, a well-characterized disease-resistance mechanism in which the plant immune system is systemically primed for enhanced defense against a broad spectrum of plant pathogens (Verbon et al., 2017). Interestingly, preconditioning of the soil with downy mildew-infected plants resulted in reduced susceptibility to the disease in a next generation of plants that were grown on this preconditioned soil (Berendsen et al., 2018). Thus, plants can "cry for help" from their root microbiome when they are under attack by pathogens, leading to selective enrichment of plant-protective microbes and microbial activities in the soil. This soil-borne legacy, or suppressive soil memory (Raaijmakers and Mazzola, 2016), benefits future plant generations growing on the same soil.

Hormonal Modulation of the Rhizosphere Microbiome

The observation that activation of the plant immune system in response to foliar pathogen attack results in changes in the root microbiome indicates that plant immune signaling and root microbiome assembly are functionally linked. Upon infection by microbial pathogens, plants activate systemic defense responses in

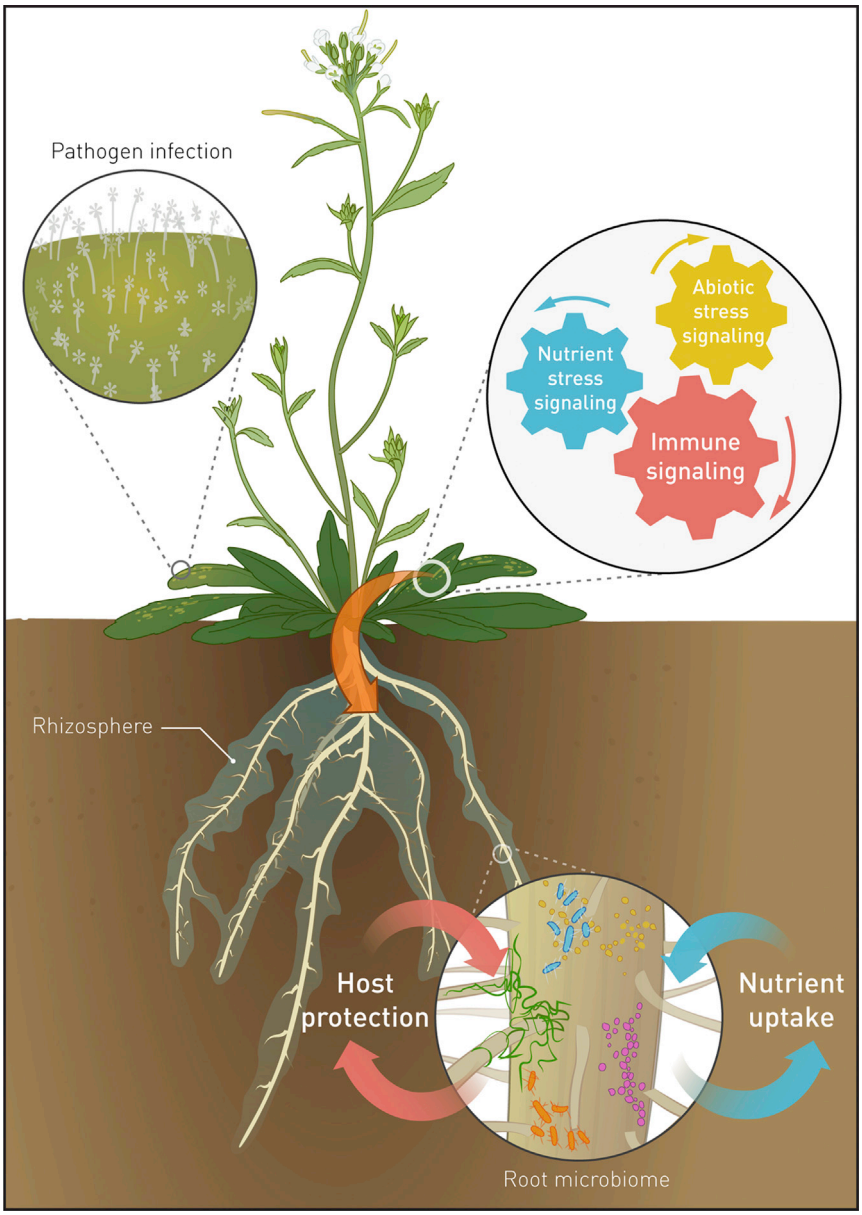

Figure 1. Soil-Borne Legacies: Management of the Root Microbiome
Upon perception of (a)biotic stress, plants respond by adjusting their root exudate profiles. Root exudates can directly relieve stress—for instance, by improving nutrient availability—but also affect the root microbiome. By secreting a mixture of both stimulative and selective metabolites, plants adjust the microbiome in the rhizosphere, the zone of soil surrounding the roots that is influenced by the roots. The distinct biotic, abiotic, and nutrient stress responses are coordinated to stimulate those microbiome functions that the plant most desperately requires. The promoted microbiome members can assist the plant in uptake of nutrients and water or protect against invading species, but they may also serve as a signal of adverse conditions experienced by the plant. In this way, the microbiome can form a soil-borne legacy that benefits a next generation of plants. Illustration: Jan Karen Campbell.

which the hormones salicylic acid (SA) and jasmonic acid (JA) play key roles. SA is essential for protection against biotrophic pathogens that feed on living host cells, such as the downy mildew pathogen *H. arabidopsidis*. In a study with SA-defective *Arabidopsis* mutants, it was established that defects in SA signaling led to an altered root microbiome, possibly due to differences in SA-dependent root exudate profiles (Lebeis et al., 2015). JA is essential for immune response against insect herbivores and necrotrophic pathogens. Both root microbiome composition and root exudate profiles of JA signaling mutants were clearly distinct from those of wild-type plants, demonstrating the involvement of JA signaling in the assembly of the rhizosphere microbiome (Carvalhais et al., 2015). Hence, hormone-dependent secondary metabolites excreted by plant roots have important functions in the communication between the plant immune system and the root microbiome.

Nutritional Stress-Driving Force in Microbiome Assembly

Not only immune responses affect the root microbiome. Drought can substantially alter the composition of the root microbiome and have the largest effect on the endophytic community inside the root, suggesting that the effects of drought on the root microbiome are also plant mediated (Fitzpatrick et al., 2018). Intriguingly, drought and other abiotic stress responses are known to cross-communicate with plant immunity. Recently, Castrillo et al. (2017) provided evidence that the plant's response to nutritional cues, particularly phosphate starvation, interacts with plant immune responses to coordinate the structure of the root microbiome community for their own benefit. It was demonstrated that the master transcriptional regulator of the phosphate starvation response, PHR1, negatively regulates immunity by binding to the promoters of SA- and JA-response genes, and so prioritizing nutritional stress over plant defense. Interestingly, a synthetic, root-derived bacterial community enhanced the activity of PHR1, suggesting an intricate interplay between nutrient uptake, plant immunity, and microbiome assembly.

The phosphate starvation response involves massive changes in gene expression (Castrillo et al., 2017) resulting in the excretion of protons and primary metabolites, such as organic acids, that affect phosphate availability directly (Pant et al., 2015; Sasse et al., 2018). Moreover, biosynthesis of secondary metabolites, like glucosinolates, is altered, leading to changes in the composition of the root microbiome, which in turn indirectly modulate phosphate availability (Pant et al., 2015; Hiruma et al., 2016).

Interestingly, such adaptive root exudation changes show resemblance with those triggered by iron starvation, another nutritional stress response connected with plant immunity and the root microbiome (Verbon et al., 2017). The transcription factor MYB72 was identified as an important regulator coordinating both iron uptake and rhizobacteria-mediated systemic immunity. Hence, the picture is emerging that plant genetic pathways regulating nutrition and defense coordinately shape plant-microbiome interactions in the rhizosphere as part of an adaptive plant strategy that may help to optimize plant survival in nature.

Future Perspective, Claiming the Legacy

Plants seem to have co-evolved with microbial partners to adopt an adaptive life strategy in which they select plant-beneficial functions of the root microbiome (Figure 1). It will be an important future research goal to resolve how the genetic pathways that regulate plant immunity and nutrient acquisition coordinate the selection of microbial traits. The chemical communication between roots and the microbiome at the root-soil interface must be essential in microbiome assembly. Indeed, recent findings have highlighted root exudates produced in response to pathogen infection and nutrient starvation as key players in selection, proliferation, and interactions of microbes in the rhizosphere (Berendsen et al., 2018; Castrillo et al., 2017; Pant et al., 2015; Sasse et al., 2018). However, as of yet, our knowledge of how specific plant root exudates shape the microbiome to the plant's advantage is limited. Regulation at the level of root metabolite biosynthesis and transport is likely, but only a few biosynthesis pathways and corresponding transporters have so far been characterized (Sasse et al., 2018). In-depth insight in plant cues and traits that sculpt the soil-borne microbial legacy may emerge from carefully designed experiments in which metagenomics, metatranscriptomics, and root metabolomics approaches are combined to inform us about how plants recruit their microbiome to maximize both nutrition and defense under often harsh environmental conditions. The soil-borne legacy can then be sensibly exploited in agriculture by introducing specific microbial consortia in combination with microbiome-optimized plant genotypes that sustain their populations and activities and improve crop production with reduced input of chemical pesticides and fertilizers.

REFERENCES

Berendsen, R.L., Vismans, G., Yu, K., Song, Y., de Jonge, R., Burgman, W.P., Burmølle, M., Herschend, J., Bakker, P.A.H.M., and Pieterse, C.M.J. (2018). Disease-induced assemblage of a plant-beneficial bacterial consortium. ISME J. https://doi.org/10.1038/s41396-018-0093-1.

Carvalhais, L.C., Dennis, P.G., Badri, D.V., Kidd, B.N., Vivanco, J.M., and Schenk, P.M. (2015). Linking jasmonic acid signaling, root exudates, and rhizosphere microbiomes. Mol. Plant Microbe Interact. *28*, 1049–1058.

Castrillo, G., Teixeira, P.J., Paredes, S.H., Law, T.F., de Lorenzo, L., Feltcher, M.E., Finkel, O.M., Breakfield, N.W., Mieczkowski, P., Jones, C.D., et al. (2017). Root microbiota drive direct integration of phosphate stress and immunity. Nature *543*, 513–518.

Chapelle, E., Mendes, R., Bakker, P.A.H.M., and Raaijmakers, J.M. (2016). Fungal invasion of the rhizosphere microbiome. ISME J. *10*, 265–268.

Fitzpatrick, C.R., Copeland, J., Wang, P.W., Guttman, D.S., Kotanen, P.M., and Johnson, M.T.J. (2018). Assembly and ecological function of the root microbiome across angiosperm plant species. Proc. Natl. Acad. Sci. U. S. A. Published online January 22, 2018. https://doi.org/10.1073/pnas.1717617115.

Hiruma, K., Gerlach, N., Sacristán, S., Nakano, R.T., Hacquard, S., Kracher, B., Neumann, U., Ramírez, D., Bucher, M., O'Connell, R.J., and Schulze-Lefert, P. (2016). Root endophyte *Colletotrichum tofieldiae* confers plant fitness benefits that are phosphate status dependent. Cell *165*, 464–474.

Lebeis, S.L., Paredes, S.H., Lundberg, D.S., Breakfield, N., Gehring, J., McDonald, M., Malfatti, S., Glavina del Rio, T., Jones, C.D., Tringe, S.G., and Dangl, J.L. (2015). PLANT MICROBIOME. Salicylic acid modulates colonization of the root microbiome by specific bacterial taxa. Science *349*, 860–864.

Mendes, L.W., Raaijmakers, J.M., de Hollander, M., Mendes, R., and Tsai, S.M. (2018). Influence of resistance breeding in common bean on rhizosphere microbiome composition and function. ISME J. *12*, 212–224.

Pant, B.-D., Pant, P., Erban, A., Huhman, D., Kopka, J., and Scheible, W.-R. (2015). Identification of primary and secondary metabolites with phosphorus status-dependent abundance in Arabidopsis, and of the transcription factor PHR1 as a major regulator of metabolic changes during phosphorus limitation. Plant Cell Environ. *38*, 172–187.

Raaijmakers, J.M., and Mazzola, M. (2016). ECOLOGY. Soil immune responses. Science *352*, 1392–1393.

Sasse, J., Martinoia, E., and Northen, T. (2018). Feed your friends: do plant exudates shape the root microbiome? Trends Plant Sci. *23*, 25–41.

Verbon, E.H., Trapet, P.L., Stringlis, I.A., Kruijs, S., Bakker, P.A.H.M., and Pieterse, C.M.J. (2017). Iron and Immunity. Annu. Rev. Phytopathol. *55*, 355–375.