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Editorial overview: Environmental microbiology: #PlantMicrobiome

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Roeland Berendsen is a research scientist working at the Institute of Environment Biology at Utrecht University, the Netherlands. He obtained his PhD also at Utrecht University working on the ecology and control of *Lecanicillium fungicola*, an important pathogen of the white-button mushroom. In 2012, he started working on the plant microbiome. His work focuses on how plant-beneficial microbes affect the plant's immune system and vice versa how the plant's immune system is involved in shaping the plant microbiome. He is especially interested in the mechanisms by which plants, upon attack, cry out for help and recruit beneficial microbes. His ambition is to apply these mechanisms in agriculture for sustainable food production.

Plants associate with a multitude of microorganisms that collectively function as a microbiome. In accordance with the concept of 'The Extended Phenotype', we only appreciate the full functional capacity of a plant until we understand the fundamental significance of its associated microbes [1]. It has long been recognized that microbes can have marked impact by either improving or compromising plant performance [2–4]. Also the realization that these microbes function in a community has been appreciated for decades [5,6] as well as the framework of a microbiome being their 'theatre of activities' [7]. However, the advent of high-throughput sequencing a decade ago has fueled #PlantMicrobiome research and improved our understanding how plant-microbe interactions are affected by a complex of (a)biotic interactions. In recent years, plant microbiomes from numerous species have been described, but also in the plant microbiome field 'this collection phase is coming to an end' [8] and is moving to more hypothesis driven research, uncovering mechanistic principles that drive plant microbiome organization and functioning.

In this special issue of *Current Opinion in Microbiology*, we present the state and the art of #PlantMicrobiome research. The issue provides current opinions on how the plant microbiome impacts the host with special emphasis on #PlantHealth, #PlantNutrition or resistance to #AbioticStress. Further topics concern the relevance of identifying a #CoreMicrobiome, the importance of #MultikingdomInteractions and the #Mycobiome in microbiome functioning and a review discusses reductionist #SynCom approaches for manipulative microbiota experiments. The issue also covers recent views on the communication between plants and associated microbes based on #RootExudates, the effects of #Domestication and the recent progress in microbial ecology of the #Phyllosphere. Finally, this issue provides frameworks for plant microbiome #Application in Agriculture and the control of #ParasiticWeeds. Below we introduce the individual contributions and highlight how these reviews and topics are interlinked.

#PlantMicrobiome and stress

Teixeira, Colaianni, Fitzpatrick and Dangl review microbiome contributions to #PlantHealth. The authors argue that the plant microbiome is an extension of the immune system acting as an additional layer of defense against pathogens. The plant immune system not only protects against invading pathogens but also sculpts composition of the plant microbiome. Vice versa, it is becoming increasingly apparent that like pathogens also commensal beneficial' microbes need to suppress or evade default plant immune responses to successfully colonize their host. In addition, it emerges that the immune system is integrating cues from the environment, suggesting that plants coordinate microbiome assembly, functioning in a context-dependent manner.

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Klaus Schlaeppi is lecturer at the Institute of Plant Sciences at the University of Bern, Switzerland. He studied plant-microbe interactions at the University of Fribourg (Switzerland) and obtained his PhD investigating plant defences against pathogens. As postdoctoral scientist at the Max-Planck-Institute for Plant Breeding Research in Cologne (Germany), he contributed characterization of the root microbiota of *Arabidopsis* and related Brassicaceae species. As junior group leader at Agroscope he broadened his research to microbial agro-ecology. His research addresses fundamental questions of root microbiome biology such as the root microbiome's contribution to plant growth, how plants communicate to their root microbiota and how plants take influence on their activities. The translational ambition of his research program is to make use of plant microbiomes in smart and sustainable agriculture.

Also Getzke, Thiergart and Hacquard discuss recent progress in understanding microbiome contributions to #PlantHealth. The authors identify that #MultikingdomInteractions, in particular among bacteria and fungi keeping each other in check, are key to community stability and ultimately for the functionality of host-associated microbial communities. An imbalance in fungal-bacterial interactions can result in disease as commensal bacteria counterbalance the growth of potentially pathogenic fungi in the community.

The review by Rolfe, Griffiths and Ton extends host immune contributions to #RootExudates that manipulate root microbiome membership for improving #PlantHealth. Recent evidence suggests that plants respond to biotic attack by changing root exudate chemistry and therewith they assemble a more health-promoting microbiome. Such disease-induced 'cry-for-help' provides a mechanistic explanation for the development of disease-suppressing soils, and the authors propose that similar context-dynamic mechanisms may shape microbiomes to cope with #AbioticStress.

Drought challenges plants and the plant microbiomes can help to mitigate this form of #AbioticStress. Xu and Coleman-Derr feature a current update about the plant microbiome's responses to drought. The authors hypothesize that the enrichment of monoderm bacteria, which is typically found in roots of drought-stressed plants, is a result of drought-induced shifts in plant metabolism and possibly mediated by #RootExudates. They discuss that increased abundance of monoderms may promote increased drought tolerance of the host, again indicating that plants 'cry-for-help' and recruit microbes to cope with adverse conditions.

The microbiome's protective properties are likely not restricted to microbial attackers. In their review, Masteling, Lombard, de Boer, Raaijmakers and Dini-Andreote conceptually synthesize how plant microbial communities can contribute to control root #ParasiticWeeds. The authors establish a framework of putative direct and indirect mechanisms by which soil and plant microbiomes could be exploited. In particular, they point to the largely unexplored potential of root-associated microbes to interfere with the chemical communication between the host plant and the parasitic plant.

#PlantMicrobiome and nutrition

Bacterial and fungal members of the microbiome contribute to #PlantNutrition. Current progress, mostly of the bacterial part, is summarized by Tao, Kelly and Radutoiu. The authors summarize that nodule-forming rhizobia are not the only microbes assisting plants in the acquisition of nitrogen and that other microbes, associating with healthy plants in nature, comprise an underexplored resource of microbes contributing to plant nitrogen nutrition. These include both epi- and endophytic diazotrophic microbes, but also nitrogen cyclers and mycorrhiza that can supply plants with nitrogen when needed.

Fabiańska, Sosa-Lopez and Bucher largely take the #Mycobiome perspective of #PlantNutrition and review the role of plant nutritional balance in shaping root-microbiome interactions. Low phosphate status progresses the plant's association with arbuscular mycorrhizal fungi (AMF) that support the host with this nutrient stress. The authors highlight that such responses are not restricted to AMF and that other microbial taxa could also very well respond and help deal with nutrients stresses.

The topic of the #Mycobiome is further deepened by Bonfante, Venice and Lanfranco by addressing #MultikingdomInteractions. Fungi host their own microbiome, which also contributes to plant performance. The authors delineate these fungi-associated microbes as often critical for functioning of the fungal host and as such, they indirectly affect the plant. These complex tripartite interactions between plants, fungi and their (endo)bacteria are ancient and can be traced back to the evolutionary transition from water to land.

Assembly of the #PlantMicrobiome

It is clear that microbes perform important functions for the plant, but it is difficult to identify the key microbes from complex microbial communities. Shade and Stopnisek propose a universal approach for the identification of a #CoreMicrobiome, comprising microbes that are consistently detected in higher abundance in a condition of interest, using abundance-occupancy distributions borrowed from macroecology. Their method can prioritize the importance of microbiome members and can help identify drivers of microbiome assembly while taking spatial and temporal heterogeneity of microbiomes into account.

While most of the reviews in this issue focus on root and rhizosphere microbiomes, Leveau discusses community assembly, structure, and (inter)activity of #Phyllosphere microbiomes. Community composition on and in aboveground plant tissues depends on the prevailing conditions, on processes such as immigration and emigration and on the microbe's capacity to survive, produce offspring and disperse. The review dissects the contributions of environment, host plant and microbiome in these interactions and denotes potential benefits of investigating those factors at various scales of resolution.

Escudero and Bulgarelli discuss the evolutionary drivers of plant-microbiome interactions and distinguish between wild plant species that have evolved naturally over long periods of time and those that have undergone specific genetic selection in a relative short time span through #Domestication. The authors frame the current view that host evolution fine-tuned microbiome composition in wild plants, whereas breeding for yield under agrochemical inputs has likely reduced the genetic repertoire of crop microbiomes. The review proposes novel breeding strategies by which the evolutionary trajectory of crops species could be re-wired and functioning of crop microbiomes could be improved for a more sustainable agriculture.

Manipulation of the #PlantMicrobiome

To identify fundamental mechanisms and test hypotheses, researchers need to manipulate microbiome composition. The use of synthetic communities is such an approach that becomes increasingly adopted in the research field. Liu, Qin and Bai reviewed advantages and challenges of such reductionist #SynCom approaches for microbiome research. Although synthetic communities mostly constitute a limited diversity of microbes compared to the more complex communities found outside the laboratory, they allow precise and reproducible experimentation and actual testing of causal relationships between plant phenotypes and microbiome composition.

With regard to manipulating microbiomes at large scale and in an agricultural context, Mitter, Brader, Pfaffenbichler and Sessitsch analyzed what is currently limiting the #Application of microbial inoculants in the field. The authors recapitulate the widely demonstrated potential of microbial inoculants to improve #PlantHealth and #PlantNutrition and they argue that the incomplete knowledge on the fate of inoculants and the simultaneous interactions between the native soil organisms and their environment is currently limiting the success of plant beneficial microbes in agriculture.

We expect that the current vibrant dynamics in the field of #PlantMicrobiome research will continue to contribute uncovering fundamental mechanistic principles of plant microbiome organization and functioning and will further support and stimulate to the exploitation of beneficial microbiome traits in agriculture. It is time that the plant microbiome will redeem its longstanding promises to improve sustainability of crop production by reducing inputs of fossil fuel, water, fertilizers and pesticides that negatively affect the environment. We hope this set of '*Current Opinions*' will inspire scientists around the globe to contribute to this mission. We thank all authors for their contributions and wish an insightful reading.

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