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Current Opinion in Microbiology

Next generation microbiome applications for crop production — limitations and the need of knowledge-based solutions

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Plants are associated with highly diverse microbiota, which are crucial partners for their host carrying out important functions. Essentially, they are involved in nutrient supply, pathogen antagonism and protection of their host against different types of stress. The potential of microbial inoculants has been demonstrated in numerous studies, primarily under greenhouse conditions. However, field application, for example, as biofertilizer or biocontrol agent, is still a challenge as the applied microorganisms often are not provided in sufficiently high cell numbers, are rapidly outcompeted and cannot establish or require specific conditions to mediate the desired effects. We still have limited understanding on the fate of inoculants and on holobiont interactions, that is, interactions between plants, micro-biota and macro-biota and the environment, under field conditions. A better understanding will provide the basis for establishing models predicting the behaviour of strains or consortia and will help identifying microbiome members being able to establish and to mediate desired effects under certain conditions. Such models may also inform about the best management practices modulating microbiota in a desired way. Also, smart delivery approaches of microbial inoculants as well as the selection or breeding of plant genotypes better able to interact with microbiota may represent promising avenues.

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Current Opinion in Microbiology 2019, **49**:59–65

This review comes from a themed issue on **Environmental microbiology**

Edited by **Roeland Berendsen** and **Klaus Schlaeppi**

For a complete overview see the Issue and the Editorial

Available online 12th November 2019

https://doi.org/10.1016/j.mib.2019.10.006

Introduction

Plants host highly diverse and dynamic microbiota, which have important functions for their host. Similar to the contribution of microbiota to human health, plant-associated microorganisms protect their host against pathogens and pests, contribute to nutrition and improve the plant stress tolerance. Although some symbionts, such as N_2-fixing rhizobia or arbuscular mycorrhizal fungi, are well known for more than a century and are components of several microbial bio-fertilizer products, (other) plant microbiota have only recently received greater attention. A high number of publications has demonstrated the huge potential of plant-associated microorganisms for improving plant nutrition, yield and tolerance towards abiotic stress and pathogens [e.g. reviewed by Backer *et al.* [1], Syed Ab Rahman *et al.* [2•], Compant *et al.* [3], Berendsen *et al.* [4]], particularly under greenhouse conditions. Generally, the better understanding on the beneficial functions of plant microbiota and the need to develop more sustainable strategies in plant production have led to a high interest in the development of microbiome-based solutions. We are getting more and more information on the complexity of plant microbiota, their genomes and putative functions as well as mechanistic understanding of individual strains or strain combinations (synthetic communities), mostly in combination with model plants, but lack behind in ecological and mechanistic insights serving field applications. Here we address major limitations on current microbial applications and development issues and propose avenues potentially leading to the development of more efficient and reproducible ways to make use of microbial functions in crop production.

Bottlenecks in making use of microbial solutions for crop production

The general aim of any agricultural application must be that the applied strain or consortium is able to establish after field application and fulfils its required function in the agricultural environment. Applications and products are needed, which are appropriate in a wide diversity of agricultural settings, each having specific environmental conditions and different native microbiota any inoculant strain or consortium has to compete with. A wide range of environmental abiotic factors influence the performance and outcome of the biological interactions. These are light intensity, temperature, pH, soil type and pH, nutrient and rare element content [5•]. These factors together with the biotic component do not only directly influence the applied microorganisms, but also the whole holobiont, that is, the host (crop) plant and its associated macro-biota and micro-biota, which in turn may influence the effectiveness of the applied microorganisms [6]. The effect of inoculation, especially of synthetic communities, on the plant microbiome, its relevance and the opportunity to improve holobiont and plant performance has been discussed by Sanchez-Cañizares *et al.* [7]. Better understanding of these interactions, the establishment of microorganisms in an agricultural environment, their ecology and ability to perform required functions in targeted agricultural environments need to be addressed to enable field application [6,8,9•]. We also require very practical solutions to deliver microbial inoculants in the required doses and to ensure inoculant quality as well as appropriate formulations. Formulation development still represents a challenge, in particular for Gram-negative bacteria [10].

How to capitalize on microbiome discoveries in the future

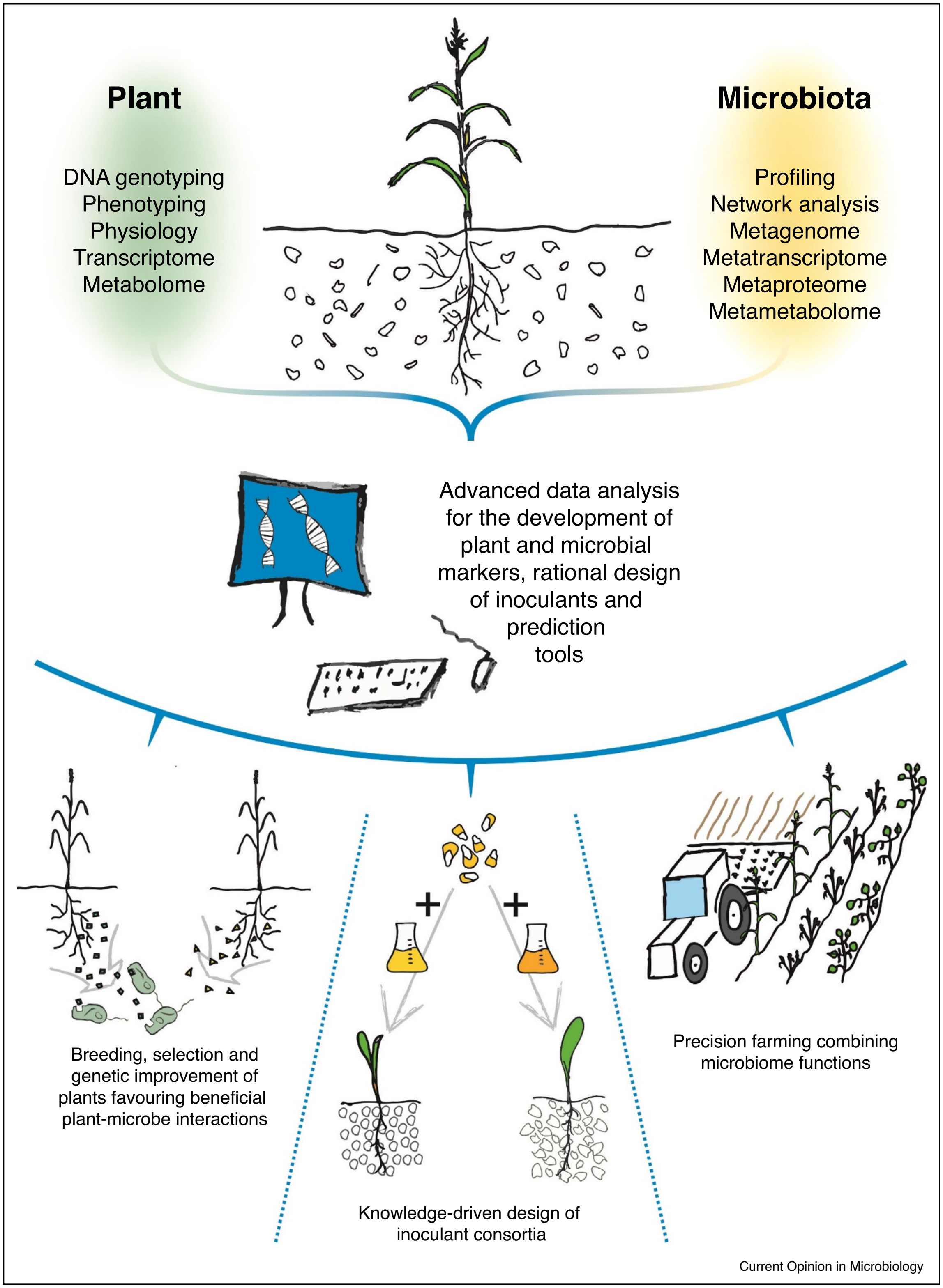
New concepts of inoculation

The huge potential of microorganisms to improve plant health and growth has been demonstrated in numerous studies. However, solutions are required to improve colonization and efficacy under (variable) field conditions to increase reproducibility of beneficial effects. For this, the increasingly available understanding on the interplay between any inoculant strain or consortium and the receiving environment, that is, the target plant and soil, their associated micro-biota and macro-biota, abiotic soil conditions and more generally environmental conditions, will guide us to targeted and more efficient microbial applications. Concepts for combining system biology approaches and 'omic' tools for a better understanding of plant–microbiota interactions for focused improvement of beneficial interactions are ambitious aims [reviewed in Refs. 5•,11••,12], but provide a promising avenue. Important cogs influencing the system and the outcomes of the beneficial interactions are the inoculation method, the applied microorganisms, the plant genotype and plant breeding for improved interaction and agricultural management practices. Also, the inoculant behaviour, together with the applied formulations, in the receiving environment in terms of colonization, expression of desired traits and effects on the target plant are important points to be considered. The increasing capacity to analyse and understand plant–microbiota interactions will for instance enable the design of microbial consortia characterized by different, complementary mechanisms or colonizing different niches [13–15]. Also, the colonization behaviour of these consortia and their activities may be monitored under multiple field conditions greatly supporting the development of more efficient field applications.

With the increasing information on the ecology and temporal dynamics of microbiota in different environments we will be better able to develop specific ecological concepts guiding the modulation of microbiomes [16]. In this context, models will enable us to better predict the outcome of microbial inoculation and to specifically select microbial strains or consortia with functional characteristics required in a specific environment as also proposed by Schlaeppi and Bulgarelli [17] (Figure 1). Some studies have suggested interesting concepts based on sophisticated microbiome network analysis to identify candidate consortia for biocontrol applications [18,19••]. Furthermore, Herrera Paredes *et al.* [20••] have recently demonstrated that rationally designed synthetic bacterial communities allow the modulation of host plant phenotypes under phosphate starvation in a model system. Selecting microbial inoculants or combinations based on their integration/position in microbial networks rather than primarily on functional characteristics will identify microbial inoculants showing more reliable establishment in the field due to more stable interactions with soil resident microbiota. For instance, core microbiota have been recently discussed to comprise keystone microbial taxa, which are highly important for plant performance [21,22]. Core microbiota are well established through evolutionary co-selection and enrichment and are therefore thought to comprise microbial taxa of major importance for their host [23,24]. Specific isolation of core taxa and/or microorganisms (presumably mediating core functions) and testing these microbial strains or consortia for desired effects and performance in the target environment represents a promising approach. Another approach showing that inoculum design based on ecological frameworks can be a promising avenue to improve activity has been proposed by Hu *et al.* [25]. Inoculants containing diverse *Pseudomonas* strains performed better in terms of survival and biocontrol or biofertilizer activity than the individual single *Pseudomonas* strains [25,26••]. These are all highly promising concepts, which have to be brought to the next level, that is, they require further testing and validation in the field, and most importantly precise monitoring fate and activity of the applied consortia. It also remains to be demonstrated how these approaches can be used for various plant traits and how such specifically selected consortia can be brought to the market. Currently, there are important challenges in many countries related to the registration of microbial consortia, particularly for biocontrol applications, as well as related to the production. Any microbial product has to be produced at reasonable costs and has to show sufficient shelf-life and stability requiring suitable formulations meeting the demand of different types of microorganisms.

Wubs *et al.* [27] tested a concept of soil transplantation to introduce new microbiota into soil. They showed that soil transplantation as an inoculation approach was highly

Figure 1



In depth understanding of holobiont interactions and functions will lead to knowledge-based approaches for microbiome applications, for example, i) plant breeding and selection favouring beneficial plant–microbe interactions, ii) complementation of microbial functions by smart selection of microbial inoculants and iii) selection of agricultural management practices to enrich microbiota with desired functions.

efficient in promoting ecosystem restoration and influencing plant community development. These effects were most pronounced when the topsoil layer was exchanged with the soil inoculant, but still significant effects were obtained when the soil inoculant was introduced into intact topsoil. Although this approach might not be practically feasible for large scale agricultural application, it might represent a powerful solution for niche applications such as restoring degraded land or for shifting microbial functions in another direction. This approach might also guide to innovative new products integrating a soil matrix with desirable microbiota.

In recent years great advancements have been made to understand the biology of plant colonization and niche adaption by microorganisms [reviewed in Ref. 28]. Improved understanding of the routes of colonization of plant reproductive organs has led to the development of innovative application approaches such as the targeted integration of microorganisms into the plant seed microbiome [29]. The seed provides protection and a competitive advantage over soil microorganisms to the inoculant strains. Microbial inoculants packaged in seeds, either carrying beneficial strains without inoculation or carrying desired microbiota inside seeds, have great advantage over 'externally' applied microorganisms. This concept has been also validated in the field showing far better colonization of inoculant strains as compared to conventional application (data not shown) and is a promising approach moving application technologies forward. Similarly, strong and robust colonizers can be used as shuttle for sensitive strains mimicking tripartite symbiosis between plant, endophytic fungi and endofungal bacteria with plant growth-promoting abilities, such as *Rhizobium radiobacter* and its host *Piriformospora indica* [30].

Other smart concepts may make use of signalling molecules released by plants attracting microorganisms and inducing plant invasion [31,32]. Also, microbial metabolites play a crucial role in plant colonization and may find application as amendment to microbial inoculants. For example, exopolysaccharides are required for successful plant colonization by the nitrogen-fixing endophyte *Gluconacetobacter diazotrophicus* [33] and surfactins mediate plant species-specific root colonization in Bacilli [34]. Combining microbial cells with such molecules, either derived from plants or from microbes, for example, in a formulation could improve the success of microbial applications under field conditions. The beneficial effect of applying signal compounds needs to be demonstrated under field conditions considering the influence of relevant parameters and interactions.

Breeding for improved plant–microbe interactions

An important aspect for an improved and effective application of microorganisms in agriculture is breeding for elevated plant response to allow improved interactions and better colonialization of the plant environment. The primary focus of plant breeding has been so far largely focusing on the improvement of harvest yield and development of resistance against pathogens, but these processes have also resulted in reduction of genetic diversity in modern crops [35•,36]. Plants and microbiota mutually interact and the influence of the genotype on microbiome composition has been detected in different crop plants such as barley and durum wheat [37]. In addition, the plant response to associated microorganisms is genotype-dependent and has developed in evolutionary processes [38]. Therefore, it is likely that classical breeding has affected beneficial plant–microbe interactions, for example, the capacity to benefit from beneficial microorganisms may have been lost due to breeding under optimal conditions regarding nutrient availability and absence of pathogens. However, the practical challenges in successful breeding for improved plant–microbe interactions lie in the likely multi-locus dependency of the traits necessary for the establishment of efficient plant–microbe interactions, as well as in additional factors such as effects of the environment and management practices including the form of microbial application and the applied microbial species or strain [11••,35•]. Nevertheless, there is potential to breed or better select genotypes for a more efficient interaction with beneficial microorganisms [2•,11••,37], for example, by altering exudate composition [and references therein] (Figure 1). In resistance breeding, traits from ancient varieties or wild relatives have been successfully introduced to overcome pathogen susceptibility, for example, resistance genes against *Phytophthora infestans* have been introduced into commercial potato varieties [39]. These breeding programmes require several rounds of back-crosses and are time-consuming but show the successful (re-)introduction of traits from wild plants. This is also for beneficial plant–microbe interactions a realistic aim but requires long-term breeding efforts. Mendes *et al.* [40] have also shown that breeding for resistance in common bean has selected microbial taxa with traits complementing plant protection, which further contribute to improved plant resilience to biotic stress. Identifying such traits and taxa will help also plant breeders to select for plant traits that enrich desired microbial groups [40]. Apart from classical breeding approaches, modern biotechnological approaches such as gene editing represent powerful tools to, for example, modulate root exudation and attract beneficial microbiota.

Microbiome-based prediction systems and modulation via crop management

Similar to human microbiome research, microbial ecologists are seeking for correlations between the composition of plant-associated microbiota and plant phenotypic traits with the aim to be able to predict plant traits from microbiome data and ultimately to modulate the microbiome for optimal plant performance. Developing tools for the prediction of the functional relationship between microbes and plant phenotype requires research that goes beyond the description of microbial communities and links community data with host functioning. The application of machine learning algorithms is a promising approach for the identification of microbial taxa within communities [41], which impact the phenotype of the host. This can guide screening and selection of microbial inoculants with desired functions [18]. In addition, such algorithms can guide in the future precision farming integrating microbiome functions. For instance, appropriate planting material (e.g. seed or tubers comprising microbiota being responsible for desired traits) or soils (e.g. hosting beneficial microbiota for a specific crop or crop genotype) may be selected implementing a rational design of the plant microbiome supporting plant growth and health.

Alternatively, management of the soil microbiome in a knowledge-driven manner rather than applying microorganisms is another promising approach. This approach is not totally new. For centuries, the so-called three-field crop rotation has been common practice in agriculture. This system contributes to balanced degradation and composition of nutrients in the soil and reduces the infestation of crops with plant diseases and some animal pests [42]. Given that different plant species favour different microbiota in the soil due to differences in root exudation [43], crop rotation might also promote microbial diversity in soil. Similarly, intercropping in which different crops are planted together and roots of different plant species interact directly with each other [44], positively affects soil fertility and microbial diversity and activity [45–47]. Various organic inputs have been shown to contribute to disease suppression [48]. In smart farming approaches, soil management practices such as tillage intensity could be used to manipulate the soil microbiota for enriching plant-beneficial microbial activities to ensure crop yield and at the same time nutrient use efficiency [49••]. Although the beneficial effects of these practices are generally known, a more knowledge-based approach will direct farmers to the most beneficial farming practice for a given farming target (Figure 1). Understanding the phenomenon of disease-suppressive soils will guide us to practices leading to the formation of disease-suppressive soil [13]. However, deep understanding on the role of microorganisms is needed and prediction tools have to be elaborated predicting the functional consequences of various farming practices. Ideally, this approach will be combined with a knowledge-driven amendment of microbiome-modulating signal compounds (e.g. plant extracts), controlled resource-saving fertilisation (e.g. plant-derived waste of manure) or microbial inoculants. Overall, extending the precision farming concept by microbiome functions has great potential. Farmers should get access to tools predicting the suitability of a given soil for a specific farming target, for example, for planting of a specific crop and most suitable farming practice to maximize the benefit from soil and plant microbiota supporting plant nutrition, stress resilience and health. Furthermore, information on the suitability of microbial inoculants and/or compounds or practices promoting the activity of specific microbiota could be made available to farmers.

Concluding remarks

The functions mediated by plant and soil microbiota are essential for plant growth, health and tolerance of adverse environmental conditions. Microorganisms applied in the form of inoculants have partly shown great effects, particularly under greenhouse conditions, but frequently fail when applied in the field. Currently, microbial inoculants are mostly selected based on a bottom-up screening for their plant growth promotion or biocontrol potential and usually inoculant strains show the desired effects under greenhouse conditions before field application. Field application is only to a limited extent knowledge-based in terms of dosage requirements, specific interactions of the inoculant strain with the environment or ecological behaviour of the strain. Also, field conditions, as compared to those found in the greenhouse, differ in many ways further limiting the translation of greenhouse to field conditions. These limitations require more knowledge-based approaches as well as concepts considering the complexity of soil and plant microbiota. Extending precision farming by integrating microbiome function will be a promising approach for the future. Predictive models identifying required/missing functions in a certain environment or suitable farming practices will support this approach. Furthermore, predictive models and ecological frameworks considering the target field environment will allow smart selection of candidate consortia. Innovations regarding the delivery of inoculants, particularly considering seeds and endophytic colonization, may lead to new approaches to apply microbial inoculants. Such models may be also used to inform about suitable agronomic practices to achieve or support a certain plant phenotype by modulating soil microbiota. Finally, selecting the most appropriate plant genotype or breeding for beneficial plant–microbe interactions represent additional promising avenues to make better use of microbiota.

Conflict of interest statement

Nothing declared.

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- •• of outstanding interest

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The authors tested the effect of tillage practices on soil microbiota in both, conventional and organic farming systems, and suggest based on their results that crop management practices such as tillage may allow manipulation of influential microbial members.