



Review

A review on the plant microbiome: Ecology, functions, and emerging trends in microbial application



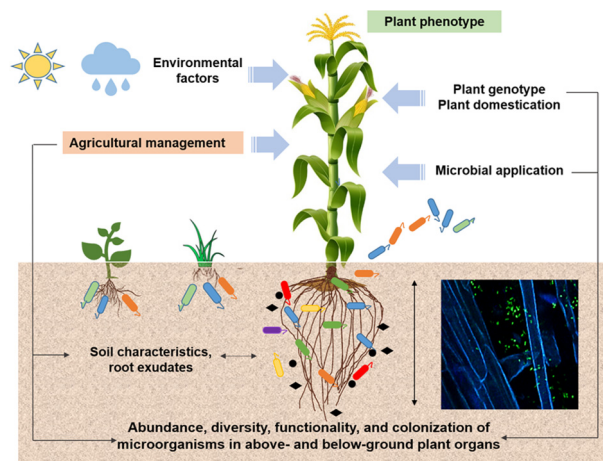
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HIGHLIGHTS

- Microbiota are important for plant growth, health and stress resilience.
- Inoculation with key microbiota members can improve plant traits.
- Tailored selection and delivery of microbial strains or consortia is required.
- Microbiome improvement may be achieved by appropriate agro-management practices.
- Plant breeding for improved interaction with microbiota will be of benefit.

GRAPHICAL ABSTRACT



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ABSTRACT

Plants have evolved with a plethora of microorganisms having important roles for plant growth and health. A considerable amount of information is now available on the structure and dynamics of plant microbiota as well as on the functional capacities of isolated community members. Due to the interesting functional potential of plant microbiota as well as due to current challenges in crop production there is an urgent need to bring microbial innovations into practice. Different approaches for microbiome improvement exist. On the one hand microbial strains or strain combinations can be applied, however, field success is often variable and improvement is urgently required. Smart, knowledge-driven selection of microorganisms is needed as well as the use of suitable delivery approaches and formulations. On the other hand, farming practices or the plant genotype can influence plant microbiota and thus functioning. Therefore, selection of appropriate farming practices and plant breeding leading to improved plant-microbiome interactions are avenues to increase the benefit of plant microbiota. In conclusion, different avenues making use of a new generation of inoculants as well as the application of microbiome-based agro-management practices and improved plant lines could lead to a better use of the plant microbiome. This paper reviews the importance and functionalities of the bacterial plant microbiome and discusses challenges and concepts in regard to the application of plant-associated bacteria.

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Introduction

Studies of the last decade have revealed highly complex microbial assemblages associated with different plants and specific plant organs [1–3]. The microbial component of the plant holobiont, also termed as plant microbiota (comprising all microorganisms) or the plant microbiome (comprising all microbial genomes) in the rhizosphere, phyllosphere and endosphere has important functions supporting plant growth and health [2–5]. Revealing the functionality of plant-microbe interactions and factors involved in community assembly can lead to a better understanding of the plant as a meta-organism and how plants can benefit from their microbial partners [3,6]. Nowadays, crop production is facing many challenges such as climate change, the demographic development, and there is an increasing demand of sustainable production. As microorganisms have shown the potential to be applied as biofertilizers or biopesticides there is increasing interest to integrate them as alternatives to chemical products in agricultural practices [7,8]. Since the 80's, many researchers have addressed the topic of microbial inoculants [9], however, with limited success in the field. Having more information on plant microbiota in regard to biotic and abiotic stresses, plant genotype, and environmental conditions, it might be feasible to find better suitable candidates or approaches for inoculation in a given environment [7]. Plant microbiota consist of different types of organisms including fungi, archaea and bacteria. Due to the wealth of information available on bacteria and interest from the industry, this review focusses on the bacterial component of plant microbiota and discusses functionalities as well as challenges and concepts in regard to the application of plant-associated bacteria.

The keywords for database search were: plant holobiont, microbiome, core microbiome, colonization, endophytes, PGPR, PGPB, plant growth promotion, consortia, beneficial bacteria, formulation, field, agricultural practices, and plant breeding. The main databases were PubMed and Google Scholar.

Diversity and functional potential of plant microbiota

Below-ground plant microbiota

Plants actively recruit their microorganisms from surrounding microbial reservoirs such as the soil/rhizosphere, the phyllosphere (i.e. the aerial plant habitat *sensu lato* or the leaf surface in relation to the external environment), the anthosphere (the external environment of flowers), the spermosphere (the exterior of germinated seed) and the carposphere (the external fruit environment) [3]. Root microbiota are mostly horizontally transferred, i.e. they derive from the soil environment, which contains highly diverse microorganisms, dominated by Acidobacteria, Verrucomicrobia, Bacteroidetes, Proteobacteria, Planctomycetes and Actinobacteria [10]. However, bacteria may be also vertically transmitted via seeds. Seeds also represent an important source of microorganisms, which proliferate in the roots of the developing plant [11,12]. Plants with their root system provide unique ecological niches for soil microbiota which colonize the rhizosphere, roots and to a certain extent above ground parts [13]. The narrow layer of soil under the direct influence of plant roots, i.e. the rhizosphere, is considered as a hot spot of microbial activity and represents one of the most complex ecosystems [14]. Recently, Donn et al. [15] showed root-driven changes in bacterial community structure of the wheat rhizosphere and found a 10-fold higher abundance of actinobacteria, pseudomonads, oligotrophs, and copiotrophs in the rhizosphere as compared to bulk soil. Moreover, the authors also reported that rhizosphere and rhizoplane communities were altered over time, whereas the bulk soil population remained unaf-

ected. Similarly, Kawasaki et al. [16] reported that the *Brachypodium distachyon* (a model for wheat) rhizosphere was dominated by Burkholderiales, Sphingobacteriales and Xanthomonadales, while the bulk soil was dominated by the order Bacillales. Root exudates such as organic acids, amino acids, fatty acids, phenolics, plant growth regulators, nucleotides, sugars, putrescine, sterols, and vitamins are known to affect microbial composition around roots, the so-called rhizosphere effect [8,17]. For instance, a group of defensive secondary metabolites like benzoxazinoids (BXs) released by maize roots alter the composition of root-associated microbiota, and microorganisms belonging to Actinobacteria and Proteobacteria were found to be most affected by BXs metabolites [18]. Furthermore, Zhálnina et al. [19] investigated the mechanisms underlying the bacterial community assembly in the rhizosphere of *Avena barbata* and found that the combination of root exudation chemistry and bacterial substrate preferences drive bacterial community assembly patterns in the rhizosphere. Fitzpatrick et al. [20] reported numerous rhizosphere bacterial taxa particularly belonging to *Pseudoxanthomonas* having significant differential abundances across 30 angiosperm plant species. Overall, different plant species and genotypes, depending on the type and composition of root exudates, influence the composition of rhizosphere microbiota.

Plant roots are colonized also internally (root endosphere) by a diverse range of bacterial endophytes. The entry of bacterial endophytes inside root tissues often occurs through passive processes or root cracks or emergence points of lateral roots as well as by active mechanisms [21]. The colonization and transmission of endophytes within plants depend on many factors such as the allocation of plant resources and the endophyte ability to colonize plants. Diverse range of bacterial taxa can gain entry in root tissues, for example, the most abundant phyla often found in grapevine roots were Proteobacteria, Acidobacteria, Actinobacteria, Bacteroidetes, Verrucomicrobia, Planctomycetes, Chloroflexi, Firmicutes and Gemmatimonadetes [22–25]. In the roots of rice, *Rhizobiaceae*, *Comamonadaceae*, *Streptomyetaceae*, and *Bradyrhizobiaceae* were found as most dominant families [26]. As another example, Correa-Galeote et al. [27] found Proteobacteria, Firmicutes, and Bacteroidetes as predominant phyla inside the maize roots and the abundance of these phyla was influenced by soil cultivation history.

Above-ground plant microbiota

Above-ground plant tissues such as the vegetative foliar parts, leaves and floral parts, provide unique environments for endophyte and epiphyte diversities, however, there are major differences in the ecology of endosphere and phyllosphere bacteria. Most endophytes spread systemically via the xylem to distinct compartments of the plant like stem, leaves, and fruits [28], although they can also enter plant tissues through aerial parts of the plant such as flowers and fruits [29]. Depending on plant source allocation, different above-ground plant compartments host distinct endophytic communities. It has been reported that phyllosphere bacteria also derive from the soil environment and are driven by the plant and by environmental parameters, however, the latter having a more profound effect [2,23,30]. Consequently, different microorganisms are found in the endosphere and phyllosphere at the genus and species level. For instance, the structural analysis of phyllosphere or carposphere microbiota of the grapevine revealed *Pseudomonas*, *Sphingomonas*, *Frigoribacterium*, *Curto-bacterium*, *Bacillus*, *Enterobacter*, *Acinetobacter*, *Erwinia*, *Citrobacter*, *Pantoea*, and *Methylobacterium* as predominant genera [23,31], whereas analysis of endophytes of grape berries revealed a dominance of the genera *Ralstonia*, *Burkholderia*, *Pseudomonas*, *Staphylococcus*, *Mesorhizobium*, *Propionibacterium*, *Dyella* and *Bacillus* [32].

Recently, Wallace et al. [30] studied the maize leaf microbiome across 300 diverse maize lines and found sphingomonads and methylobacteria as predominant taxa. They also showed that the phyllosphere microbial composition was largely driven by environmental factors. In apple flowers, Steven et al. [33] identified *Pseudomonas* and *Enterobacteriaceae* as predominant taxa. Similarly, numerous studies on apple, almond, grapefruit, tobacco and pumpkin flowers found *Pseudomonas* as the most abundant genus [34]. Only recently, seed-associated bacteria have been addressed and found to comprise mostly Proteobacteria, Actinobacteria, Bacteroidetes and Firmicutes [11,35–37]. Seed microbiota are related to soil microbiota but also to those of flowers and fruits [28,38,39]. Generally, above-ground plant microbiota mainly originate from soil, seed and air and adapt for life on or inside the plant tissue where several factors including soil, environmental and farm management shape community composition. Host and compartment-specific assembly indicate a strong functional relationship between the plant and its above-ground microbiota, however, more research is still required to understand this relationship. Endophytes as well as above-ground microbiota are well known for their potential to promote plant growth, improve disease resistance and alleviate stress tolerance [3,40].

Factors affecting plant microbiota

In any plant organ microbial composition is influenced by a range of biotic and abiotic factors. These factors may include soil pH, salinity, soil type, soil structure, soil moisture and soil organic matter and exudates [10], which are most relevant for below-ground plant parts, whereas factors like external environmental conditions including climate, pathogen presence and human practices [3] influence microbiota of above- and below-ground plant parts. The plant species and genotype recruit microorganisms from the soil environment where root morphology, exudates, and type of rhizodeposits play a significant role in the recruitment of plant microbiota [1,13,41,42]. Plant species growing in the similar soil environment recruited significantly different microbial communities in both rhizosphere and root compartments [6,24,43]. Using a 16S rRNA gene sequencing and shotgun metagenome approach, Bulgarelli et al. [44] investigated the root microbiota of different barley accessions and found that the host innate immune system and root metabolites mainly shaped root microbial community structure. Other host-related factors like plant age and developmental stage, health, and fitness are also known to influence plant bacterial community structure through affecting plant signaling (i.e. induced systemic resistance, systemic acquired resistance) and the composition of root exudates [1,43].

Core and satellite microbiomes

Microorganisms that are tightly associated with a certain plant species or genotype, independent of soil and environmental conditions, are defined as the core plant microbiome [45]. Pfeiffer et al. [46] identified a core microbiome of potato (*Solanum tuberosum*) particularly comprising of *Bradyrhizobium*, *Sphingobium*, and *Microvirga*. Similarly, Zarraonaindia et al. [23] found a grapevine core microbiome belonging to *Pseudomonadaceae*, *Micrococcaceae*, and *Hyphomicrobiaceae* independent of soil and climatic conditions. Edwards et al. [26] found bacteria particularly belonging to Deltaproteobacteria, Alphaproteobacteria, and Actinobacteria as a member of rice core microbiome. The core plant microbiome is thought to comprise keystone microbial taxa that are important for plant fitness and established through evolutionary mechanisms of selection and enrichment of microbial taxa containing essential functions genes for the fitness of the plant holobiont [5]. By contrast, some microbial taxa that occur in low abundance in a

reduced number of sites are called satellite taxa [47,48]. Satellite taxa can be defined on the basis of geographical range, local abundance, and habitat specificity [49]. The importance of satellite taxa is increasingly being recognized as drivers of key functions for the ecosystem. A recent study further demonstrated that taxa occurring in low abundance are critical for reducing unwanted microbial invasions into soil communities [50]. Similarly, low abundance bacterial species largely contributed to the production of antifungal volatile compounds that protect the plant against soil-borne pathogens [51]. Hol et al. [52] found that the loss of rare soil microbes can have a negative impact on plant productivity. Numerous studies suggest that satellite taxa (rare taxa) provide critical functions that might be disproportionate to their abundance. There are various ecological reasons that explain satellite to core dynamics that need to be addressed to better understand the functions and buffering capacity of plant microbiome against various environmental stresses.

Functions of plant microbiota

The members of plant microbiome comprise beneficial, neutral or pathogenic microorganisms. Plant growth-promoting bacteria (PGPB) can promote plant growth by either direct or indirect mechanisms. Some PGPB produce phytohormones like auxin, cytokinin, and gibberellin which affect plant growth through modulating endogenous hormone levels in association with a plant. Moreover, some PGPB can secrete an enzyme, 1-aminocyclopropane-1-carboxylate (ACC) deaminase, which reduces the level of stress hormone ethylene in the plant. Strains of *Pseudomonas* spp., *Arthrobacter* spp. and *Bacillus* spp. and others have been reported to enhance plant growth through the production of ACC deaminase. Rascovan et al. [53] found a diverse range of bacteria including *Pseudomonas* spp., *Paraburkholderia* spp. and *Pantoea* spp. in wheat and soybean roots that showed important plant growth promotion properties like phosphate solubilization, nitrogen fixation, indole acetic acid and ACC deaminase production, mechanisms involved in improved nutrient uptake, growth and stress tolerance.

Some bacteria can cause disease symptoms through the production of phytotoxic compounds proteins and phytohormones. For example, *Pseudomonas syringae* is a well-known plant pathogen having a very broad host range including tomato, tobacco, olive and green bean. Another well-known pathogenic bacterium is *Erwinia amylovora* that causes fire blight disease of fruit trees and ornamentals plants. *Xanthomonas* species, *Ralstonia solanacearum*, and *Xylella fastidiosa* are also associated with many important diseases of crops like potato and banana [54]. The severity of plant disease depends on the combination of multiple factors like pathogen population size, host susceptibility, favorable environment and biotic factors (like plant microbiota) that collectively determine the outcome of plant-pathogen interaction [4]. Both below-ground and above-ground plant-associated bacteria have been shown to enhance host resistance against pathogen infection either through commensal-pathogen interactions or through modulating plant defense [55,56].

There are numerous examples of biocontrol activities against pathogen invasion and disease [57,58] through the production of antibiotics, lytic enzymes, pathogen-inhibiting volatile compounds and siderophores. Some bacteria protect the plant from pathogens through modulating plant hormones level and inducing plant systemic resistance. The continuous use of agricultural soils can build pathogen pressure and can also develop disease-suppressive soils containing microorganisms mediating disease suppression [59,60]. In particular, genera like *Pseudomonas*, *Streptomyces*, *Bacillus*, *Paenibacillus*, *Enterobacter*, *Pantoea*, *Burkholderia* and *Paraburkholderia* have been reported for their role in pathogen sup-

pression [61,62]. Recently, Trivedi et al. [63] identified three key-stone bacterial taxa belonging to Acidobacteria, Actinobacteria, and Firmicutes that controlled the invasion of *Fusarium* wilt at a continental scale. Carrión et al. [64] reported disease-suppressive ability of *Paraburkholderia graminis* PHS1 against fungal root pathogen and linked soil suppressiveness with the synthesis of sulfurous volatile compounds such as dimethyl sulfoxide reductase and cysteine desulfurase. Durán et al. [60] reported the role of endosphere bacterial community on take-all disease (*Gaeumannomyces graminis*) suppression and they identified endophytes belonging to *Serratia* and *Enterobacter* as most promising candidates against *Gaeumannomyces graminis*.

Employment and modulation of the plant microbiome

Microbial inoculation

The development of a single strain application typically starts with a screening of a strain collection for various plant growth-promoting characteristics in the laboratory. Screening assays mainly rely on specific microbial functions like phosphate solubilization, nitrogen fixation or the production of antibiotics, siderophores, plant hormones and ACC deaminase. In a bottom-up approach, the most promising strains are then tested in the greenhouse followed by further testing in the field. Using this approach many bacterial strains show great success in the lab and greenhouse conditions but fail in the field [65] to increase suboptimal plant microbiome. For instance, Hungria et al. [66] found that *Azospirillum brasilense* strain Ab-V5 increased grain yields of maize and wheat up to 30 and 16%, respectively, in field trials. Other researchers tested *Kosakonia radicincitans* formulations effect on maize in three different field plots and bacterial application was highly effective in improving maize silage as well as grain yield [67]. Contrarily, other studies found no significant effects with bacterial inoculation under field conditions. For example, *Azospirillum brasilense* (strain Ab-V5 and Ab-V6) inoculation increased growth of maize and wheat under controlled conditions but showed no significant effect on plant growth in the field [68]. Similarly, *Rhizobium leguminosarum* *bv.* *trifolii* inoculation significantly increased bio-

mass of rice plants in the greenhouse but did not show a significant increase in plant biomass and yield in the field [69]. There are numerous reasons being potentially responsible for the limited success of microbial inoculants in the field and the low reproducibility. It has to be considered that microorganisms in the receiving environment are highly diverse and well adapted and that an introduced microorganism is not able to compete sufficiently with the resident microflora. However, competitive ability of an inoculant strain is usually not a selection criterion. Also, the dosage of introduced cells as well as the physiological activity will influence the competitive ability of an inoculant strain [70]. To warrant the delivery of a certain dosage of cells as well as shelf-life, suitable formulations are key to successful application. An additional important aspect is whether the strain is suited to colonize the respective plant species, genotype or tissue and whether it is also able to exhibit the desired function in the receiving environment. For instance, for certain biocontrol functions (e.g. antagonistic activities) it will be important that the biocontrol strain colonizes the same niches as the pathogen at the same time and also exhibits antagonistic activities. These activities might be tightly regulated and will also depend on microbiome or plant holobiont interactions. In contrast, if biocontrol activity is based on triggering plant defense, as it was shown for the biocontrol strain *Bacillus amyloliquefaciens* FZB42 [71], early colonization is required.

The application of microbial consortia

The application of microbial consortia is an emerging approach to overcome lab to field hurdles [56,72]. The rationale of this approach may be the combination of microorganisms with different traits, either complementing each other to combine different mechanisms needed for different effects such as plant growth enhancement and biocontrol of pathogens. Microbial consortia may also comprise strains showing the same mode of action but tolerate different environmental conditions or plant genotypes. Various studies on grapevine [73], potato [56], tomato [58], *Arabidopsis* [74] and maize [75] have shown that microbial combinations have the potential to increase plant growth-promoting (PGP) effects as compared to single inoculants (Table 1). Moreover,

Table 1
Examples of the application of bacterial consortia.

| Plant and growth conditions | Consortia/origin of bacteria | Stress | Consortia effect | References |
|---|---|--|--|------------|
| <i>Arabidopsis thaliana</i> , growth chamber, non-sterile soil | <i>Xanthomonas</i> sp. WCS2014-23, <i>Stenotrophomonas</i> sp. WCS2014-113, <i>Microbacterium</i> sp. WCS2014-259/ field soil with endemic <i>Arabidopsis</i> plants | <i>Hyaloperonospora arabidopsidis</i> | Less fungal spores and higher plant fresh weight | [74] |
| <i>Solanum lycopersicum</i> cv. Moneymaker, growth chamber | <i>Bacillus megaterium</i> SOGA_2, <i>Curtobacterium ceanosedimentum</i> SOGA_3, <i>Curtobacterium</i> sp. SOGA_6, <i>Massilia aurea</i> SOGA_7, <i>Pseudomonas coleopterorum</i> SOGA_5, 11 and 12, <i>Pseudomonas psychrotolerans</i> SOGA_13, <i>Pseudomonas rhizosphaerae</i> SOGA_14 and 19, <i>Frigoribacterium faeni</i> SOGA_17, <i>Xanthomonas campestris</i> SOGA_20/phylosphere of field-grown tomato plants | <i>Pseudomonas syringae</i> pv. tomato | Fewer pathogen DNA copies on leaf disks | [58] |
| <i>Solanum tuberosum</i> cv. Lady Clair, cv. Victoria, cv. Bintje, leaf disks in petri dishes | Double or triple combinations of <i>Pseudomonas</i> spp. R32, R47, R76, R84, S04, S19, S34, S35, S49/rhizosphere and phyllosphere of field-grown potatoes | <i>Phytophthora infestans</i> | Reduced fungal sporangiophore development | [56] |
| <i>Lycopersicon esculentum</i> cv. Jiangshu, greenhouse pots with soil | <i>Pseudomonas</i> spp. CHA0, PF5, Q2-87, Q8R1-96, 1M1-96, MVP1-4, F113, Ph11C2/pea, wheat, cotton, tomato, sugar beet, tobacco | <i>Ralstonia solanacearum</i> | Reduced disease severity and pathogen abundance | [78] |
| Blue maize CAP15-1 TLAX/greenhouse pots with vermiculite | <i>Pseudomonas putida</i> KT2440, <i>Sphingomonas</i> sp. OF178, <i>Azospirillum brasilense</i> Sp7, <i>Acinetobacter</i> sp. EMM02/unknown | Dessica-tion | Increase of shoot and root dry weight, plant height and plant diameter | [75] |
| <i>Capsicum annuum</i> , <i>Vitis vinifera</i> cv. Barbera, growth chamber, greenhouse | <i>Acinetobacter</i> sp. S2 and <i>Bacillus</i> sp. S4, <i>Sphingobacterium</i> sp. S6, <i>Enterobacter</i> sp. S7 and <i>Delftia</i> sp. S8/ <i>Vitis vinifera</i> rhizosphere and endosphere | Drought | Increased fresh root, aerial biomass and photosynthesis | [73] |
| <i>Nicotiana attenuate</i> , field | <i>Arthrobacter nitroguajacolicus</i> E46, <i>Bacillus mojavensis</i> K1, <i>Pseudomonas frederiksbergensis</i> A176, <i>Arthrobacter nitroguajacolicus</i> E46, <i>Bacillus cereus</i> CN2, <i>Bacillus megaterium</i> B55, <i>Bacillus mojavensis</i> K1, <i>Pseudomonas azotoformans</i> A70, <i>Pseudomonas frederiksbergensis</i> A176, <i>Bacillus megaterium</i> B55, <i>Pseudomonas azotoformans</i> A70/tobacco plants | Natural wilt disease | Less dead plants | [59] |

combinations of bacteria that show no or little PGP effects as single inoculants can show PGP effects in a consortium, ranging from the combination of three bacterial species that live in one biofilm [74] to the application of whole microbiomes [58,76]. However, some consortia have shown to reduce the PGP effect as compared to single inoculants [56,73,77] indicating that a smart and knowledge-driven selection of consortia and strains is required.

One interesting and promising approach has been applied by Hu et al. [78]. The authors present an ecological framework and showed that the survival of introduced *Pseudomonas* consortia increased with increasing diversity. Furthermore, high *Pseudomonas* diversity decreased the incidence of the pathogen *Ralstonia solanacearum* due to intensified resource competition and interference with the pathogen. This concept makes use of ecologically based community rules and the author also showed that a higher diversity of *Pseudomonas* consortia resulted in higher accumulation of plant biomass and more efficient assimilation of nutrients into the plant tissue [79]. *Pseudomonas* strain identity was less important than the diversity effect, which was associated with a higher production of plant hormones, siderophores and solubilization of phosphorus *in vitro*.

In some cases it might be relevant to consider the source of a consortium or consortium member to match the environmental conditions (soil type, climate and plants) of a PGP candidate to the field condition where the inoculant strain will be applied. For example, *Azospirillum* spp. preferred to colonize the rice cultivar they were originally isolated from [80] and *Actinobacteria* are more persistent in drought soils [81]. The strategy of matching conditions of origin field and applied field cannot only increase the success of establishment but also the probability of finding bacteria that exhibit a desired PGP effect. The isolation of bacteria associated to plants exposed to pathogens led to the discovery of the biocontrol agent K84 against the crown gall disease [82] and to a consortium of six endophytes preventing tobacco wilt disease [59]. Likewise, the screening of symptomless plants that are exposed to abiotic stresses led to the identification of bacteria that support plant resistance to metal and organic pollutions and are useful in bioremediation [83–85]. In accordance, nutrient-solubilizing bacteria are more common under nutrient-poor conditions [86]. All in all, the origin of an inoculant strain may provide important information on its ecological behaviour relevant for field application.

The bottom-up selection process to identify candidates for a plant growth-promoting consortium starts with a collection of bacteria and investigates interactions in culture-dependent screenings [87]. Candidates in axenic culture are characterized and selected by bacterial stress resistance (desiccation, temperature or toxic compounds) and plant growth-promoting activities [87–91]. Classical laboratory tests are partly replaced by screening of the underlining PGP genes [5]. Although successfully used in many studies as a selection criterion [5,83,92], the efficiency of PGPB does not necessarily correlate with the abundance of genetic and molecular plant growth-promoting traits in bacteria [93–95]. The utility of the detection of PGP-traits in axenic cultures and in their genomes depends on the mechanistic understanding of a particular trait. Lab screenings may provide only limited information. As an example, one *Pseudomonas* strain that can establish antagonistic activity against *Phytophthora infestans* was outgrown by another *Pseudomonas* strain in co-culture and lost upon co-inoculation its biocontrol ability [56]. However, in nature, bacteria can avoid competition by colonizing different microniches and compartments limiting the usefulness of studying *in vitro* bacteria-bacteria interactions without plants.

With the size of the starting collection of potential PGPB, the possible combinations for PGP-consortia increase exponentially. Furthermore, various abiotic factors (temperature, moisture, nutri-

ent content of soil etc.) lead to variable trade-offs that result in variable PGP-effects in plants [58,72]. To handle this inextricable amount of combinations, networks that use limited input data (e.g. presence/absence of a combination of bacteria, nutrient supply in the growth medium) have been used to predict the plant phenotype (phosphate content of *Arabidopsis thaliana*) [77]. Using this concept improving the selection of PGP-consortia is possible without understanding the mode of action and interactions of the bacterial members. In addition, a synthetic biology approach to design microbial consortia combining desired mechanisms, pathways and interactions is a promising approach.

Top-down approaches allow to study microbiome characteristics at a molecular level and to select for PGP-consortium candidates based on this information. This became feasible with the direct identification of core and satellite microbiota in environmental samples based on single amplicon variants in high throughput sequencing of nucleic acids [96], as described above. The advantages of top-down approaches are a pre-selection of candidates under realistic field conditions exposed to a realistic stress scenario while bottom-up screening approaches mimic field conditions in a simplified environment.

Formulation requirements and delivery approaches

Formulations are needed to ensure long-term viability of cells during storage and the provision of sufficient viable cell numbers to field-grown plants. Unfortunately, suitable formulations are lacking for many microorganisms, particularly for Gram-negative bacteria [97] and viability in formulations is often limited by the tolerance of bacteria to low humidity [98]. Several compounds use on formulations might improve PGP-effects. Experiments adding lipo-chitooligosaccharides (LOCs) isolated from rhizobia to formulations [99] or adapting the growth medium of an inoculant to increase exopolysaccharides (EPS) and polyhydroxybutyrate (PHB) content in the formulation [100] increased for instance the PGP-effects. The mechanisms of bacterial additives are not yet understood, while surfactants adjust droplet size and rheological properties, reduce drift and improve adhesion to hydrophobic cuticular surfaces [101]. Macrobeads that encapsulate PGPB provide a humid environment as well as nanoparticles, which improve adhesion of PGPB to roots [102,103]. In general seed, leaf and soil inoculation techniques of the same PGPB successfully increased yield of wheat in field studies [67]. Seed inoculants might interfere with pesticides employed for seed treatment but establish the plant first and can build up microbial defences (activation of plant immune response, biofilm production), while in mature plants, an existing microbiome must be suppressed for establishment [44,104].

In addition to the classical delivery approaches new methods have been developed. A seed microbiome modulation concept was developed by Mitter et al. [39]. The authors used a spray inoculation of flowers to achieve next generation seeds endophytically colonized by the inoculant strain and a modulation of the seed microbiome. The inoculant strain efficiently colonized the germinated plant, also under field conditions, showing that alternative approaches may lead to improved performance of microbial inoculants.

Modulation of plant microbiomes by agricultural management and plant selection

Impact of agricultural management on plant microbiota

Specific plant microbiota are associated with certain plant traits such as disease suppression [105], biomass production [106] and growth response [107] or the flowering phenotype [108]. Conse-

quently, modulation of plant microbiota or effects of agricultural management will impact plant traits and performance (Fig. 1). This is an alternative to single or microbial consortia inoculation.

Crop diversification, organic approaches, intercropping and other cultural practices have been used for sustainable agricultural production. Albeit few data exist on practices influencing the plant microbiome, fertilization, low or no tillage, protection of biodiversity, and other practices, in general it has been reported that low-input farming systems promote higher abundance and diversity of most organisms [109]. Understanding how cultural practices influence the plant microbiome may lead to strategies to modulate the plant microbiome in a desired direction (Fig. 1). Campisano et al. [32] showed for instance that organic or integrated pest management lead to the build-up of different soil and plant microbiota associated with grapevine. Similarly, Longa et al. [110] showed that different agro-management practices in viticulture (organic, biodynamic or biodynamic with green manure) induce different microbiota, particularly the green manure treatment resulted in major differences as compared to the organic and biodynamic management practices. Vineyards, where integrated, organic and biodynamic management practices had been in place for 10 years, were also assessed. Soil under integrated management had a significantly reduced bacterial species richness compared to organic management but community composition was similar to organically and biodynamically managed soils [111]. In addition, Hartmann et al. [112] demonstrated further the impact of more than two decades of different agricultural management in a long-term field experiment on the soil microbiome. Compared to conventionally managed soils, organic farming appears as increasing the soil microbial richness of winter wheat and grass clover, but also decreased evenness, reduced dispersion and shifted the soil microbiota structure [112]. Authors showed that organic fertilizers influence microbes involved in degradation of complex organic compounds, while pesticides also impact soil microbiota but to a lower degree [112]. Recently, Hartman et al. [113] furthermore

showed pronounced cropping effects on community composition on soil and roots of winter wheat. The authors demonstrated that soil bacterial communities were primarily structured by tillage and root bacteria by management types, whereas fungal communities responded mainly to the management type with additional effects due to tillage. Different practices influence the microbial composition with differences according to soil, roots, bacteria and fungi. Around 10% of variation in microbial communities could be explained by the tested cropping practices [113]. Our understanding of the interaction between practice conditions and the dynamics of the microbial ecosystem has advanced. However, the effects of agro-management and other factors such as environment are highly complex and more understanding is required to make clear-cut recommendations.

Selection of plants for efficient interaction with plant microbiota

Crop breeding programmes have yet to incorporate the selection of adequate plant microbiomes [62] (Fig. 1). Different plant genotypes behave differently in regard to interacting with microbiota and attract different microbiome members conferring resistance to abiotic and biotic stresses or help for plant growth and nutrition [114]. It is therefore possible to design or select plants with the ability to attract beneficial microbiota [115]. Nevertheless, limited understanding exists which plant mechanisms and underlying genes lead to the association with specific microbiota or how certain microbial activities are influenced. Plant breeding programmes have gone through selection of specific and improved plants, however, in many cases with a loss of plant genes compared to wild-type plants or wild relatives [116]. Wild plants have evolved specific microbiota but this selection was disrupted with the domestication of important crops [116]. Domestication has led not only to the loss of genetic plant diversity but also to a reduction of microbial diversity associated with plants and a loss of the capacity to interact with specific plant growth-promoting

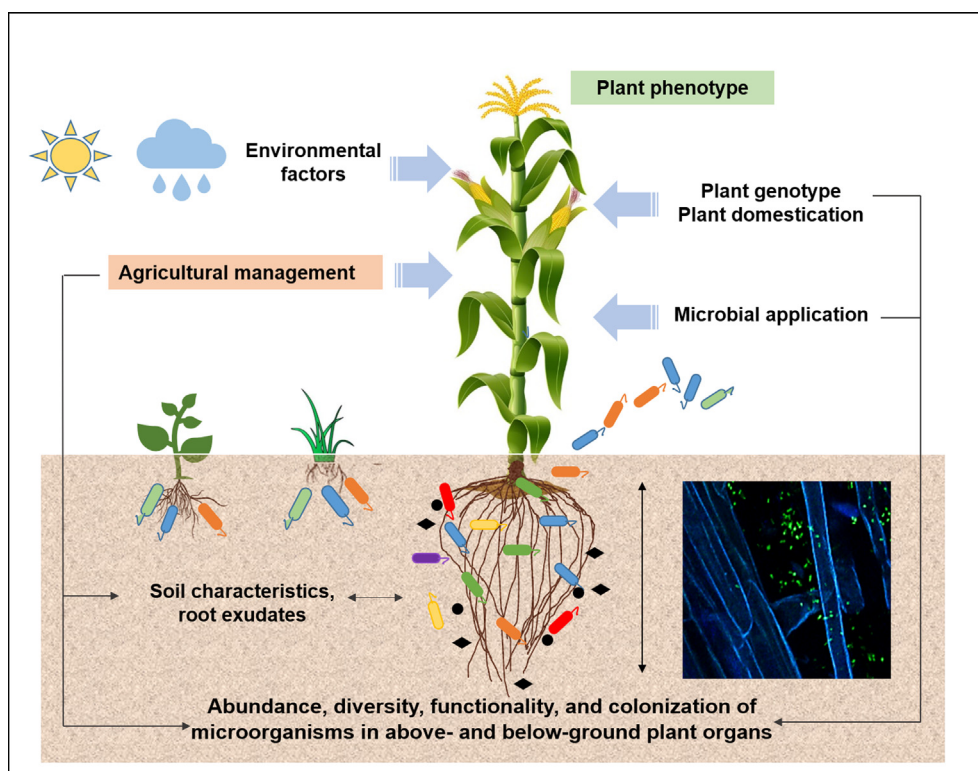


Fig. 1. Complex interactions determining plant phenotype and traits.

microorganisms [117]. Plant breeding should consider the associated microbiome within the holobiont, to confer additional plant traits or to modify them. However, this approach is impeded by still insufficient understanding of microbiome functioning, mechanisms of plant-microbiome interactions and a lack of simple high throughput screening methods. Nevertheless, selection and breeding of plants for their association with beneficial microbiota is highly promising in regard to delivering a new generation of microbe-improved plants.

Conclusions and future prospects

Plant microbiota and their interactions are highly diverse and multiple factors shape community assembly and functioning. While recognized since the 19th century, the investigation of and interest in plant-associated microbiota only started to bloom since the 80's. Due to the high potential of microorganisms to improve plant growth, stress resilience and health, numerous microbial inoculants have been developed, but many of them show poor performance in the field. Several approaches may lead to improved field success such as designing smart microbial consortia, the selection of agricultural management practices favoring microbiota with beneficial functions or a new generation of plant breeding approaches. Last but not least the development of suitable formulations and delivery approaches is highly important for any field application. Our understanding of plant microbiota, its functionality and its exploitation has substantially increased in the last years. However, a better understanding is needed on how inoculants modulate the resident microbiome, how complex microbiota and the holobiont affect the activity of the applied strain or how microbial inoculants colonize the plant environment in the field.

Conflict of interest

The authors have declared no conflict of interest.

Compliance with Ethics Requirements

This article does not contain any studies with human or animal subjects.

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