Journal of Advanced Research 19 (2019) 29–37

Contents lists available at ScienceDirect

Journal of Advanced Research

journal homepage: www.elsevier.com/locate/jare

Review

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

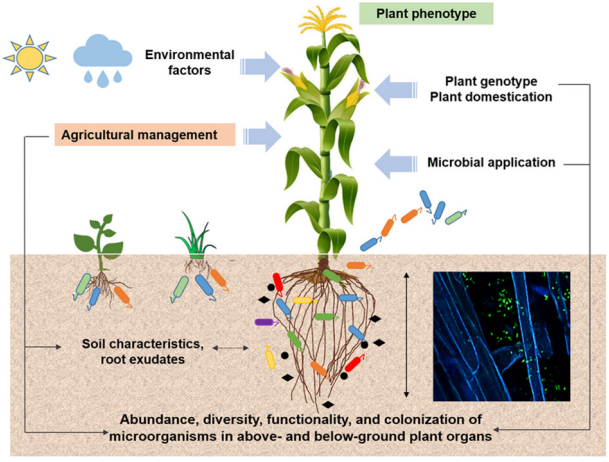
Stéphane Compant, Abdul Samad, Hanna Faist, Angela Sessitsch *

AIT Austrian Institute of Technology GmbH, Center for Health & Bioresources, Bioresources Unit, Konrad-Lorenz-Straße 24, 3430 Tulln, Austria

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



ARTICLE INFO

Article history:
Received 20 December 2018
Revised 13 March 2019
Accepted 13 March 2019
Available online 20 March 2019

Keywords:
Plant microbiome
Composition
Functionalities
Inoculation
Farming practices
Plant microbiome modulation

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.

Peer review under responsibility of Cairo University.

* Corresponding author.
E-mail address: angela.sessitsch@ait.ac.at (A. Sessitsch).

https://doi.org/10.1016/j.jare.2019.03.004
2090-1232/

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 sensus 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 unaffected. 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, Zhalnina 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 Gemmatimonatedes [22–25]. In the roots of rice, *Rhizobiaceae*, *Comamonadaceae*, *Streptomycetaceae*, 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*, *Curtobacterium*, *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 secret an enzyme, 1-aminocyclopro pane-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 keystone 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 biomass 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
Arabidopsis thaliana, growth chamber, non-sterile soil	*Xanthomonas* sp. WCS2014-23, *Stenotrophomonas* sp. WCS2014-113, *Microbacterium* sp. WCS2014-259/ field soil with endemic *Arabidopsis* plants	*Hyaloperonospora arabidopsidis*	Less fungal spores and higher plant fresh weight	[74]
Solanum lycopersicum cv. Moneymaker, growth chamber	*Bacillus megaterium* SOGA_2, *Curtobacterium ceanosedimentum* SOGA_3, *Curtobacterium* sp. SOGA_6, *Massilia aurea* SOGA_7, *Pseudomonas coleopterorum* SOGA_5, 11 and 12, *Pseudomonas psychrotolerans* SOGA_13, *Pseudomonas rhizosphaerae* SOGA_14 and 19, *Frigoribacterium faeni* SOGA_17, *Xanthomonas campestris* SOGA_20/phyllosphere of field-grown tomato plants	*Pseudomonas syringae* pv. tomato	Fewer pathogen DNA copies on leaf disks	[58]
Solanum tuberosum cv. Lady Clair, cv. Victoria, cv. Bintje, leaf disks in petri dishes	Double or triple combinations of *Pseudomonas* spp. R32, R47, R76, R84, S04, S19, S34, S35, S49/rhizosphere and phyllosphere of field-grown potatoes	*Phytophthora infestans*	Reduced fungal sporangiophore development	[56]
Lycopersicon esculentum cv. Jiangshu, greenhouse pots with soil	*Pseudomonas* spp. CHA0, PF5, Q2-87, Q8R1-96, 1M1-96, MVP1-4, F113, Phl1C2/pea, wheat, cotton, tomato, sugar beet, tobacco	*Ralstonia solanacearum*	Reduced disease severity and pathogen abundance	[78]
Blue maize CAP15-1 TLAX/greenhouse pots with vermiculite	*Pseudomonas putida* KT2440, *Sphingomonas* sp. OF178, *Azospirillum brasilense* Sp7, *Acinetobacter* sp. EMM02/unknown	Dessica-tion	Increase of shoot and root dry weight, plant height and plant diameter	[75]
Capsicum annuum, *Vitis vinifera* cv. Barbera, growth chamber, greenhouse	*Acinetobacter* sp. S2 and *Bacillus* sp. S4, *Sphingobacterium* sp. S6, *Enterobacter* sp. S7 and *Delftia* sp. S8/*Vitis vinifera* rhizosphere and endosphere	Drought	Increased fresh root, aerial biomass and photosynthesis	[73]
Nicotiana attenuate, field	*Arthrobacter nitroguajacolicus* E46, *Bacillus mojavensis* K1, *Pseudomonas frederiksbergensis* A176, *Arthrobacter nitroguajacolicus* E46, *Bacillus cereus* CN2, *Bacillus megaterium* B55, *Bacillus mojavensis* K1, *Pseudomonas azotoformans* A70, *Pseudomonas frederiksbergensis* A176, *Bacillus megaterium* B55, *Pseudomonas azotoformans* 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, nutrient 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

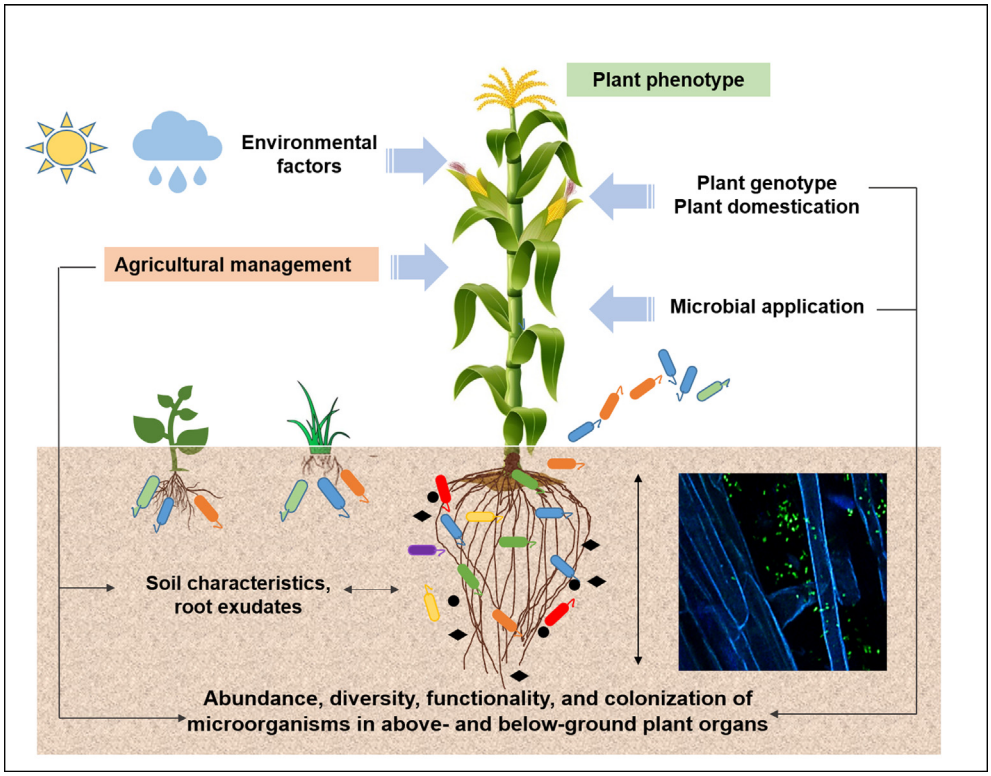


Fig. 1. Complex interactions determining plant phenotype and traits.

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.

Acknowledgements

HF and AS have received funding from the European Union's H2020 research and Innovation Programme under grant agreement No 727247 (SolACE).

References

[1] Reinhold-Hurek B, Bünger W, Burbano CS, Sabale M, Hurek T. Roots shaping their microbiome: global hotspots for microbial activity. Annu Rev Phytopathol 2015;53:403–24.
[2] Vorholt JA. Microbial life in the phyllosphere. Nat Rev Microb 2012;10:828–40.
[3] Hardoim PR, van Overbeek LS, Berg G, Pirttilä AM, Compant S, Campisano A, et al. The hidden world within plants: ecological and evolutionary considerations for defining functioning of microbial endophytes. MMBR 2015;79:293–320.
[4] Brader G, Compant S, Vescio K, Mitter B, Trognitz F, Ma L-J, et al. Ecology and genomic insights into plant-pathogenic and plant-nonpathogenic endophytes. Annu Rev Phytopathol 2017;55:61–83.
[5] Lemanceau P, Blouin M, Muller D, Moënne-Loccoz Y. Let the core microbiota be functional. Trends Plant Sci 2017;22:583–95.
[6] Hacquard S. Disentangling the factors shaping microbiota composition across the plant holobiont. New Phytol 2016;209:454–7.
[7] Mitter B, Pfaffenbichler N, Sessitsch A. Plant–microbe partnerships in 2020. Microb Biotechnol 2016;9:635–40.
[8] Mendes R, Garbeva P, Raaijmakers JM. The rhizosphere microbiome: significance of plant beneficial, plant pathogenic, and human pathogenic microorganisms. FEMS Microbiol Rev 2013;37:634–63.
[9] Glick BR. Plant growth-promoting bacteria: mechanisms and applications. Scientifica 2012;963401.
[10] Fierer N. Embracing the unknown: disentangling the complexities of the soil microbiome. Nature Rev Microbiol 2017;15:579–90.
[11] Liu Y, Zuo S, Xu L, Zou Y, Song W. Study on diversity of endophytic bacterial communities in seeds of hybrid maize and their parental lines. Arch Microbiol 2012;194:1001–12.
[12] Hardoim PR, Hardoim CC, van Overbeek LS, van Elsas JD. Dynamics of seed-borne rice endophytes on early plant growth stages. PLoS ONE 2012;7:e30438.
[13] Hartmann A, Schmid M, van Tuinen D, Berg G. Plant-driven selection of microbes. Plant Soil 2009;321:235–75.
[14] Hiltner L. Über neuere Erfahrungen und Probleme auf dem Gebiete der Bodenbakteriologie unter besonderer Berücksichtigung der Gründüngung und Brache. Soil Biol Biochem 1904;98:59–78.
[15] Donn S, Kirkegaard JA, Perera G, Richardson AE, Watt M. Evolution of bacterial communities in the wheat crop rhizosphere. Environ Microbiol 2015;17:610–21.
[16] Kawasaki A, Donn S, Ryan PR, Mathesius U, Devilla R, Jones A, et al. Microbiome and exudates of the root and rhizosphere of *Brachypodium distachyon*, a model for wheat. PLoS ONE 2016;11:e0164533.
[17] Hartmann A, Rothballer M, Schmid M. Lorenz Hiltner, a pioneer in rhizosphere microbial ecology and soil bacteriology research. Plant Soil 2008;312:7–14.
[18] Hu L, Robert CAM, Cadot S, Zhang X, Ye M, Li B, et al. Root exudate metabolites drive plant-soil feedbacks on growth and defense by shaping the rhizosphere microbiota. Nature Commun 2018;9:2738.
[19] Zhalnina K, Louie KB, Hao Z, Mansoori N, da Rocha UN, Shi S, et al. Dynamic root exudate chemistry and microbial substrate preferences drive patterns in rhizosphere microbial community assembly. Nature Microbiol 2018;3:470–80.
[20] Fitzpatrick CR, Copeland J, Wang PW, Guttman DS, Kotanen PM, Johnson MTJ. Assembly and ecological function of the root microbiome across angiosperm plant species. Proc Natl Acad Sci USA 2018;115(6):E1157–65.
[21] Compant S, Reiter B, Sessitsch A, Nowak J, Clément C, Ait Barka E. Endophytic colonization of *Vitis vinifera* L. by plant growth-promoting bacterium *Burkholderia* sp. strain PsJN. Appl Environ Microbiol 2005;71:1685–93.
[22] Burns KN, Kluepfel DA, Strauss SL, Bokulich NA, Cantu D, Steenwerth KL. Vineyard soil bacterial diversity and composition revealed by 16S rRNA genes: differentiation by geographic features. Soil Biol Biochem 2015;91:232–47.
[23] Zarraonaindia I, Owens SM, Weisenhorn P, West K, Hampton-Marcell J, Lax S, et al. The soil microbiome influences grapevine-associated microbiota. mBio 2015;6(2):e02527–e2614.
[24] Samad A, Trognitz F, Compant S, Antonielli L, Sessitsch A. Shared and host-specific microbiome diversity and functioning of grapevine and accompanying weed plants. Environ Microbiol 2017;19:1407–24.
[25] Faist H, Keller A, Hentschel U, Deeken R. Grapevine (*Vitis vinifera*) crown galls host distinct microbiota. Appl Environ Microbiol 2016;82:5542–52.
[26] Edwards J, Johnson C, Santos-Medellín C, Lurie E, Podishetty NK, Bhatnagar S, et al. Structure, variation, and assembly of the root-associated microbiomes of rice. Proc Natl Acad Sci USA 2015;112:E911–20.
[27] Correa-Galeote D, Bedmar EJ, Arone GJ. Maize endophytic bacterial diversity as affected by soil cultivation history. Front Microbiol 2018;9:484.
[28] Compant S, Clément C, Sessitsch A. Plant growth-promoting bacteria in the rhizo- and endosphere of plants: their role, colonization, mechanisms involved and prospects for utilization. Soil Biol Biochem 2010;42:669–78.
[29] Compant S, Mitter B, Colli-Mull JG, Gangl H, Sessitsch A. Endophytes of grapevine flowers, berries, and seeds: identification of cultivable bacteria, comparison with other plant parts, and visualization of niches of colonization. Microb Ecol 2011;62:188–97.
[30] Wallace J, Kremling KA, Kovar LL, Buckler ES. Quantitative genetics of the maize leaf microbiome. Phytobiomes J 2018. doi: https://doi.org/10.1094/PBIOMES-02-18-0008-R.
[31] Kecskeméti E, Berkelmann-Löhnertz B, Reineke A, Cantu D. Are epiphytic microbial communities in the carposphere of ripening grape clusters (*Vitis vinifera* L.) different between conventional, organic, and biodynamic grapes? PLoS ONE 2016;11:e0160852.
[32] Campisano A, Antonielli L, Pancher M, Yousaf S, Pindo M, Pertot I, et al. Bacterial endophytic communities in the grapevine depend on pest management. PLoS ONE 2014;9:e112763.
[33] Steven B, Huntley RB, Zeng Q. The influence of flower anatomy and apple cultivar on the apple flower phytobiome. Phytobiomes J 2018;2:171–9.
[34] Aleklett K, Hart M, Shade A. The microbial ecology of flowers: an emerging frontier in phyllosphere research. Botany 2014;92:253–66.
[35] Barret M, Briand M, Bonneau S, Préveaux A, Valière S, Bouchez O, et al. Emergence shapes the structure of the seed microbiota. Appl Environ Microbiol 2015;81:1257–66.
[36] Johnston-Monje D, Raizada MN. Conservation and diversity of seed associated endophytes in *Zea* across boundaries of evolution, ethnography and ecology. PLoS ONE 2011;6:e20396.
[37] Rodríguez-Escobar C, Mitter B, Barret M, Sessitsch A, Compant S. Commentary: seed bacterial inhabitants and their routes of colonization. Plant Soil 2018;422:129–34.
[38] Glassner H, Zchori-Fein E, Yaron S, Sessitsch A, Sauer U, Compant S. Bacterial niches inside seeds of *Cucumis melo* L. Plant Soil 2018;422:101–13.

[39] Mitter B, Pfaffenbichler N, Flavell R, Compant S, Antonielli L, Petric A, et al. A new approach to modify plant microbiomes and traits by introducing beneficial bacteria at flowering into progeny seeds. Front Microbiol 2017;8:11.

[40] Stone BW, Weingarten EA, Jackson CR. The role of the phyllosphere microbiome in plant health and function. Annu Plant Rev online 2018;1:1–24.

[41] Ladygina N, Hedlund K. Plant species influence microbial diversity and carbon allocation in the rhizosphere. Soil Biol Biochem 2010;42:162–8.

[42] Chaparro JM, Badri DV, Vivanco JM. Rhizosphere microbiome assemblage is affected by plant development. ISME J 2014;8:790–803.

[43] Aleklett K, Leff JW, Fierer N, Hart M. Wild plant species growing closely connected in a subalpine meadow host distinct root-associated bacterial communities. Peer J 2015;3:e804.

[44] Bulgarelli D, Garrido-Oter R, Münch PC, Weiman A, Dröge J, Pan Y, et al. Structure and function of the bacterial root microbiota in wild and domesticated barley. Cell Host Microbe 2015;17:392–403.

[45] Toju H, Peay KG, Yamamichi M, Narisawa K, Hiruma K, Naito K, et al. Core microbiomes for sustainable agroecosystems. Nat Plants 2018;4:247–57.

[46] Pfeiffer S, Mitter B, Oswald A, Schloter-Hai B, Schloter M, Declerck S, et al. Rhizosphere microbiomes of potato cultivated in the High Andes show stable and dynamic core microbiomes with different responses to plant development. FEMS Microbiol Ecol 2017;93(2). pii: fiw242.

[47] Hanski I. Dynamics of regional distribution: the core and satellite species hypothesis. Oikos 1982;38:210–21.

[48] Magurran AE, Henderson PA. Explaining the excess of rare species in natural species abundance distributions. Nature 2003;422:714–6.

[49] Jousset A, Bienhold C, Chatzinotas A, Gallien L, Gobet A, Kurm V, et al. Where less may be more: how the rare biosphere pulls ecosystems strings. ISME J 2017;11:853–62.

[50] Mallon CA, Poly F, Le Roux X, Marring I, van Elsas JD, Salles JF. Resource pulses can alleviate the biodiversity–invasion relationship in soil microbial communities. Ecology 2015;96:915–26.

[51] Hol WHG, Garbeva P, Hordijk C, Hundscheid MPJ, Gunnewiek PJAK, van Agtmaal M, et al. Non-random species loss in bacterial communities reduces antifungal volatile production. Ecology 2015;96:2042–8.

[52] Hol WHG, de Boer W, Hollander MD, Kuramae EE, Meisner A, van der Putten Wim H. Context dependency and saturating effects of loss of rare soil microbes on plant productivity. Front Plant Sci 2015;6:485.

[53] Rascovan N, Carbonetto B, Perrig D, Díaz M, Canciani W, Abalo M, et al. Integrated analysis of root microbiomes of soybean and wheat from agricultural fields. Sci Rep 2016;6:28084.

[54] Mansfield J, Genin S, Magori S, Citovsky V, Sriariyanum M, Ronald P, et al. Top 10 plant pathogenic bacteria in molecular plant pathology. Mol Plant Pathol 2012;13:614–29.

[55] Rudrappa T, Czymmek KJ, Paré PW, Bais HP. Root-secreted malic acid recruits beneficial soil bacteria. Plant Physiol 2008;148:1547–56.

[56] de Vrieze M, Germanier F, Vuille N, Weisskopf L. Combining different potato-associated *Pseudomonas* strains for improved biocontrol of *Phytophthora infestans*. Front Microbiol 2018;9:2573.

[57] Hopkins SR, Wojdak JM, Belden LK. Defensive symbionts mediate host–parasite interactions at multiple scales. Trends Parasitol 2017;33:53–64.

[58] Berg M, Koskella B. Nutrient- and dose-dependent microbiome-mediated protection against a plant pathogen. Curr Biol 2018;28:2487–92.

[59] Santhanam R, van Luu T, Weinhold A, Goldberg J, Oh Y, Baldwin IT. Native root-associated bacteria rescue a plant from a sudden-wilt disease that emerged during continuous cropping. Proc Natl Acad Sci USA 2015;112:E5013–20.

[60] Durán P, Tortella G, Viscardi S, Barra PJ, Carrión VJ, Mora La, et al. Microbial community composition in take-all suppressive soils. Front Microbiol 2018;9:2198.

[61] Gómez Expósito R, Bruijn Id, Postma J, Raaijmakers JM. Current insights into the role of rhizosphere bacteria in disease suppressive soils. Front Microbiol 2017;8:2529.

[62] Schlatter D, Kinkel L, Thomashow L, Weller D, Paulitz T. Disease suppressive soils: new insights from the soil microbiome. Phytopathology 2017;107:1284–97.

[63] Trivedi P, Delgado-Baquerizo M, Trivedi C, Hamonts K, Anderson IC, Singh BK. Keystone microbial taxa regulate the invasion of a fungal pathogen in agro-ecosystems. Soil Biol Biochem 2017;111:10–4.

[64] Carrión VJ, Cordovez V, Tyc O, Etalo DW, Bruijn ID, Jager CL, de Victor,, et al. Involvement of *Burkholderiaceae* and sulfurous volatiles in disease-suppressive soils. ISME J 2018;12:2307–21.

[65] Backer R, Rokem JS, Ilangumaran G, Lamont J, Praslickova D, Ricci E, et al. Plant growth-promoting rhizobacteria: context, mechanisms of action, and roadmap to commercialization of biostimulants for sustainable agriculture. Front Plant Sci 2018;9:1473.

[66] Hungria M, Campo RJ, Souza EM, Pedrosa FO. Inoculation with selected strains of *Azospirillum brasilense* and *A. lipoferum* improves yields of maize and wheat in Brazil. Plant Soil 2010;331:413–25.

[67] Berger B, Patz S, Ruppel S, Dietel K, Faetke S, Junge H, et al. Successful formulation and application of plant growth-promoting *Kosakonia radicincitans* in maize cultivation. BioMed Res Int 2018:6439481.

[68] Fukami J, Nogueira MA, Araujo RS, Hungria M. Accessing inoculation methods of maize and wheat with *Azospirillum brasilense*. AMB Express 2016;6:3.

[69] Kecskés ML, Choudhury ATMA, Casteriano AV, Deaker R, Roughley RJ, Lewin L, et al. Effects of bacterial inoculant biofertilizers on growth, yield and nutrition of rice in Australia. J Plant Nutr 2015;39:377–88.

[70] Samad A, Antonielli L, Sessitsch A, Compant S, Trognitz F. Comparative genome analysis of the vineyard weed endophyte *Pseudomonas viridiflava* CDRTc14 showing selective herbicidal activity. Sci Rep 2017;7:17336.

[71] Chowdhury SP, Hartmann A, Gao XW, Boriss R. Biocontrol mechanism by root-associated *Bacillus amyloliquefaciens* FZB42 – a review. Front Microbiol 2015;6:780.

[72] Parnell JJ, Berka R, Young HA, Sturino JM, Kang Y, Barnhart DM, et al. From the lab to the farm: an industrial perspective of plant beneficial microorganisms. Front Plant Sci 2016;7:1110.

[73] Rolli E, Marasco R, Vigani G, Ettoumi B, Mapelli F, Deangelis ML, et al. Improved plant resistance to drought is promoted by the root-associated microbiome as a water stress-dependent trait. Environ Microbiol 2015;17:316–31.

[74] Berendsen RL, Vismans G, Yu K, Song Y, de Jonge R, Burgman WP, et al. Disease-induced assemblage of a plant-beneficial bacterial consortium. ISME J 2018;12:1496–507.

[75] Molina-Romero D, Baez A, Quintero-Hernández V, Castañeda-Lucio M, Fuentes-Ramírez LE, Bustillos-Cristales MDR, et al. Compatible bacterial mixture, tolerant to desiccation, improves maize plant growth. PLoS ONE 2017;12(11):e0187913.

[76] Raaijmakers JM, Weller DM. Natural plant protection by 2,4-diacetylphloroglucinol-producing *Pseudomonas* spp. in take-all decline soils. Mol Plant-Microbe Int 1998;11:144–52.

[77] Herrera Paredes S, Gao T, Law TF, Finkel OM, Mucyn T, Teixeira PJPL, et al. Design of synthetic bacterial communities for predictable plant phenotypes. PLoS Biol 2018;16:e2003962.

[78] Hu J, Wei Z, Friman V-P, Gu S-H, Wang X-F, Eisenhauer N, et al. Probiotic diversity enhances rhizosphere microbiome function and plant disease suppression. mBio 2016;7(6):e01790–e1816.

[79] Hu J, Wei Z, Weidner S, Friman V-P, Xu Y-C, Shen Q-R, et al. Probiotic *Pseudomonas* communities enhance plant growth and nutrient assimilation via diversity-mediated ecosystem functioning. Soil Biol Biochem 2017;113:122–9.

[80] Chamam A, Sanguin H, Bellvert F, Meiffren G, Comte G, Wisniewski-Dyé F, et al. Plant secondary metabolite profiling evidences strain-dependent effect in the *Azospirillum-Oryza sativa* association. Phytochemistry 2013;87:65–77.

[81] Santos-Medellín C, Edwards J, Liechty Z, Nguyen B, Sundaresan V. Drought stress results in a compartment-specific restructuring of the rice root-associated microbiomes. mBio 2017;8(4):e00764–e817.

[82] Kerr A, New PB. Biological control of crown gall: field measurements and glasshouse experiments. J Appl. Microbiol 1972;35:279–87.

[83] Syranidou E, Christofilopoulos S, Gkavrou G, Thijs S, Weyens N, Vangronsveld J, et al. Exploitation of endophytic bacteria to enhance the phytoremediation potential of the wetland helophyte *Juncus acutus*. Front Microbiol 2016;7:1016.

[84] Thijs S, van Dillewijn P, Sillen W, Truyens S, Holtappels M, ÓHaen J, et al. Exploring the rhizospheric and endophytic bacterial communities of *Acer pseudoplatanus* growing on a TNT-contaminated soil: towards the development of a rhizocompetent TNT-detoxifying plant growth promoting consortium. Plant Soil 2014;385:15–36.

[85] Khan MU, Sessitsch A, Harris M, Fatima K, Imran A, Arslan M, et al. Cr-resistant rhizo- and endophytic bacteria associated with *Prosopis juliflora* and their potential as phytoremediation enhancing agents in metal-degraded soils. Front Plant Sci 2015;5:755.

[86] da Costa PB, Granada CE, Ambrosini A, Moreira F, de Souza R, dos Passos JFM, et al. A model to explain plant growth promotion traits: a multivariate analysis of 2,211 bacterial isolates. PLoS ONE 2014;9(12):e116020.

[87] Armanhi JSL, de Souza RSC, Damasceno NdB, de Araújo LM, Imperial J, Arruda P. A community-based culture collection for targeting novel plant growth-promoting bacteria from the sugarcane microbiome. Front. Plant Sci 2017;8:2191.

[88] Islam S, Akanda AM, Prova A, Islam MT, Hossain MM. Isolation and identification of plant growth promoting rhizobacteria from cucumber rhizosphere and their effect on plant growth promotion and disease suppression. Front Microbiol 2015;6:1360.

[89] Suleman M, Yasmin S, Rasul M, Yahya M, Atta BM, Mirza MS. Phosphate solubilizing bacteria with glucose dehydrogenase gene for phosphorus uptake and beneficial effects on wheat. PLoS ONE 2018;13(9):e0204408.

[90] Passari AK, Mishra VK, Gupta VK, Yadav MK, Saikia R, Singh BP. *In vitro* and *in vivo* plant growth promoting activities and dna fingerprinting of antagonistic endophytic actinomycetes associates with medicinal plants. PLoS ONE 2015;10:e0139468.

[91] Baldan E, Nigris S, Romualdi C, D'Alessandro S, Clocchiatti A, Zottini M, et al. Beneficial bacteria isolated from grapevine inner tissues shape *Arabidopsis thaliana* roots. PLoS ONE 2015;10:e0140252.

[92] Liu K, Newman M, McInroy JA, Hu C-H, Kloepper JW. Selection and assessment of plant growth-promoting rhizobacteria for biological control of multiple plant diseases. Phytopathology 2017;107:928–36.

[93] Tiryaki D, Aydın İ, Atıcı Ö. Psychrotolerant bacteria isolated from the leaf apoplast of cold-adapted wild plants improve the cold resistance of bean (*Phaseolus vulgaris* L.) under low temperature. Cryobiology 2018. doi: https://doi.org/10.1016/j.cryobiol.2018.11.001.

[94] Akinrinlola RJ, Yuen GY, Drijber RA, Adesemoye AO. Evaluation of *Bacillus* strains for plant growth promotion and predictability of efficacy by *in vitro* physiological traits. Int J Microbiol 2018:5686874.

[95] Cardinale M, Ratering S, Suarez C, Zapata Montoya AM, Geissler-Plaum R, Schnell S. Paradox of plant growth promotion potential of rhizobacteria and

their actual promotion effect on growth of barley (*Hordeum vulgare* L.) under salt stress. Microbiol Res 2015;181:22–32.
[96] Callahan BJ, McMurdie PJ, Rosen MJ, Han AW, Johnson AJA, Holmes SP. DADA2: high-resolution sample inference from Illumina amplicon data. Nat Methods 2016;13:581–3.
[97] Berninger T, González López Ó, Bejarano A, Preininger C, Sessitsch A. Maintenance and assessment of cell viability in formulation of non-sporulating bacterial inoculants. Microb Biotechnol 2018;11:277–301.
[98] Köhl J, Postma J, Nicot P, Ruocco M, Blum B. Stepwise screening of microorganisms for commercial use in biological control of plant-pathogenic fungi and bacteria. Biol Control 2011;57:1–12.
[99] Marks BB, Megías M, Ollero FJ, Nogueira MA, Araujo RS, Hungria M. Maize growth promotion by inoculation with *Azospirillum brasilense* and metabolites of *Rhizobium tropici* enriched on lipo-chitooligosaccharides (LCOs). AMB Express 2015;5:71.
[100] Oliveira ALM, Santos OJAP, Marcelino PRF, Milani KML, Zuluaga MYA, Zucareli C, et al. Maize inoculation with *Azospirillum brasilense* Ab-V5 cells enriched with exopolysaccharides and polyhydroxybutyrate results in high productivity under low N fertilizer input. Front Microbiol 2017;8:1873.
[101] Preininger C, Sauer U, Bejarano A, Berninger T. Concepts and applications of foliar spray for microbial inoculants. Appl Microbiol Biotechnol 2018;102:7265–82.
[102] Perez JJ, Francois NJ, Maroniche GA, Borrajo MP, Pereyra MA, Creus CM. A novel, green, low-cost chitosan-starch hydrogel as potential delivery system for plant growth-promoting bacteria. Carbohydr Polym 2018;202:409–17.
[103] Timmusk S, Seisenbaeva G, Behers L. Titania (TiO2) nanoparticles enhance the performance of growth-promoting rhizobacteria. Sci Rep 2018;8(1):617.
[104] Dal Cortivo C, Barion G, Ferrari M, Visioli G, Dramis L, Panozzo A, et al. Effects of field inoculation with vam and bacteria consortia on root growth and nutrients uptake in common wheat. Sustainability 2018;10:3286.
[105] Mendes R, Kruijt M, Bruijn Id, Dekkers E, van der Voort M, Schneider JHM, et al. Deciphering the rhizosphere microbiome for disease-suppressive bacteria. Science 2011;332:1097–100.
[106] Sugiyama A, Bakker MG, Badri DV, Manter DK, Vivanco JM. Relationships between *Arabidopsis* genotype-specific biomass accumulation and associated soil microbial communities. Botany 2013;91:123–6.
[107] Bainard LD, Koch AM, Gordon AM, Klironomos JN. Growth response of crops to soil microbial communities from conventional monocropping and tree-based intercropping systems. Plant Soil 2013;363:345–56.
[108] Panke-Buisse K, Poole AC, Goodrich JK, Ley RE, Kao-Kniffin J. Selection on soil microbiomes reveals reproducible impacts on plant function. ISME J 2015;9:980–9.
[109] Postma-Blaauw MB, de Goede RGM, Bloem J, Faber JH, Brussaard L. Soil biota community structure and abundance under agricultural intensification and extensification. Ecology 2010;91:460–73.
[110] Longa CMO, Nicola L, Antonielli L, Mescalchin E, Zanzotti R, Turco E, et al. Soil microbiota respond to green manure in organic vineyards. J Appl Microbiol 2017;123:1547–60.
[111] Hendgen M, Hoppe B, Döring J, Friedel M, Kauer R, Frisch M, et al. Effects of different management regimes on microbial biodiversity in vineyard soils. Sci Rep 2018;8:9393.
[112] Hartmann M, Frey B, Mayer J, Mäder P, Widmer F. Distinct soil microbial diversity under long-term organic and conventional farming. ISME J 2015;9:1177–94.
[113] Hartman K, van der Heijden MGA, Wittwer RA, Banerjee S, Walser J-C, Schlaeppi K. Cropping practices manipulate abundance patterns of root and soil microbiome members paving the way to smart farming. Microbiome 2018;6:14.
[114] Wei Z, Jousset A. Plant breeding goes microbial. Trends Plant Sci. 2017;22:555–8.
[115] Abhilash PC, Powell JR, Singh HB, Singh BK. Plant-microbe interactions: novel applications for exploitation in multipurpose remediation technologies. Trends Biotechnol 2012;30:416–20.
[116] Gopal M, Gupta A. Microbiome selection could spur next-generation plant breeding strategies. Front Microbiol 2016;7:1971.
[117] Pérez-Jaramillo JE, Mendes R, Raaijmakers JM. Impact of plant domestication on rhizosphere microbiome assembly and functions. Plant Mol Biol 2016;90:635–44.

Stéphane Compant is working as a scientist on plant-microbe interactions at the AIT Austrian Institute of Technology. He received his PhD from the University of Reims Champagne-Ardenne and his habilitation in ecology from the University of Bordeaux in France. Stéphane Compant was Associate Professor of Microbiology at the National Polytechnic Institute of Toulouse in France before he joined AIT. He is one of the leading experts on microbial ecology of endophytic bacteria interacting with plants, on microscopy of plant-microbe interactions in general, and biocontrol of plant diseases.

Abdul Samad is currently working as a junior scientist at the AIT Austrian Institute of Technology. He received his PhD in microbiology from University of Natural Resources and Applied Life Sciences, Vienna, Austria. His PhD was mainly focused on the structural and functional characterization of plant-associated bacterial communities and biocontrol of weeds. Currently, he is working on biofertilizer development focusing on phosphorus and iron solubilizing bacteria. He has great expertise in the area of plant-microbe interactions, soil science, microbial community analysis and NGS sequence analysis.

Hanna Faist, a junior scientist at the AIT Austrian Institute of Technology, is part of the European Horizon 2020 project SolACE (Solutions for improving Agroecosystem and Crop Efficiency for water and nutrient use). Recently, Hanna Faist unravelled the role of the bacterial community in crops exposed to combined stresses and distinct management practices. Previously, at the University of Würzburg, she investigated the grown gall disease of plants, introduced by pathogenic agrobacteria. This included the characterization of a gene and its influence on the lipidome of crown galls and the bacterial community of diseased and healthy grapevines. Combining computational and molecular biological skills, her research focuses on bacteria-plant interactions.

Angela Sessitsch heads the Bioresources Unit of the AIT Austrian Institute of Technology. She studied biochemistry at the University of Technology in Graz, holds a PhD in Microbiology from the Wageningen University, the Netherlands, and is habilitated at the Vienna University of Natural Resources and Life Sciences. She has pioneered plant-associated microbiomes, particularly in the endosphere, and she is interested in understanding the interactions between plants, microbiomes and the environment as well as to develop applications. Her group explores the diversity and functioning of plant microbiota by applying a range of molecular approaches, interaction modes between plants and model bacteria, colonization behaviour of endophytes as well as various application technologies for biocontrol and crop enhancement applications.