REVIEW ARTICLE

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Rhizosphere microbiome: revisiting the synergy of plant-microbe interactions

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Abstract
Sustainable enhancement in food production from less available arable land must encompass a balanced use of inorganic, organic, and biofertilizer sources of plant nutrients to augment and maintain soil fertility and productivity. The varied responses of microbial inoculants across fields and crops, however, have formed a major bottleneck that hinders its widespread adoption. This necessitates an intricate analysis of the inter-relationships between soil microbial communities and their impact on host plant productivity. The concept of "biased rhizosphere," which evolved from the interactions among different components of the rhizosphere including plant roots and soil microflora, strives to garner a better understanding of the complex rhizospheric intercommunications. Moreover, knowledge on rhizosphere microbiome is essential for developing strategies for shaping the rhizosphere to benefit the plants. With the advent of molecular and "omics" tools, a better understanding of the plant-microbe association could be acquired which could play a crucial role in drafting the future "biofertilizers." The present review, therefore aims to (a) to introduce the concepts of rhizosphere hotspots and microbiomes and (b) to detail out the methodologies for creating biased rhizospheres for plant-mediated selection of beneficial microorganisms and their roles in improving plant performance.

Keywords Biased rhizosphere · Microbial inoculants · Microbiome · Rhizosphere engineering · Root border cells

Introduction

Biofertilizers are preparations containing specialized living organisms that can fix, mobilize, solubilize, or decompose nutrient sources which, when applied through seed or soil, enhance nutrient uptake by plants. Biofertilizer research started with "Nitragin," the first commercially produced and patented culture of *Rhizobium*, by Nobbe and Hiltner in 1895 (Nobbe and Hiltner 1896). The introduction of yellow seeded soybean in India in the 1960s led to a spurt in demand for soybean inoculants in the region. This intensified research in development of microbial formulations for pulses, groundnut, and even forage legumes. The discovery of *Azotobacter*, *Azospirillum*, blue-green algae and a host of other beneficial microorganisms soon followed. Interestingly, "biofertilizer" is a misnomer and the term "microbial inoculants" better suit

these plant growth-promoting organisms, which are capable of exerting beneficial effects on plants. Generally, 60–90% of the total applied fertilizer is lost and in this regard, microbial inoculants have prominence in sustainable integrated nutrient management systems (Bhardwaj et al. 2014). Moreover, the utility of poor-quality native nutrients in soil necessitates microbial interventions. For example, approximately 90% of total soil K is found in crystalline, insoluble mineral forms like feldspars and mica, which plants cannot utilize (Meena et al. 2014). To make them available for plant nutrition, microorganisms which can solubilize and release K should be deployed.

While positive responses have been recorded in a range of field trials, the beneficial effects from the application of microbial inoculants are found to differ greatly under different agro-environmental conditions and this has resulted in inconsistency in responses across crops and regions (Table 1). There are also reports on the efficacy of microbial inoculants on particular varieties of crops, but not others. For example, the *Rhizobium* strain G_2, which increased the yield of four chickpea varieties—T_3, $Gwalior_2$, G-130, and Pusa-53—was ineffective on the varieties R.S.II and N-59 (Sundara Rao 1974). This suggests the host plant-specificity and strain-specificity

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Table 1 Varied responses of crops to microbial inoculation

Microbial inoculant	Crop	Remarks	Reference
Bacillus megaterium	Vegetable crops, grains, and potatoes	Yield increases of 0%–70%	Smith et al. (1961)
Rhizobium	Chickpea	Yield ranging from 30 to 610 kg/ha	Subba Rao (1976)
Arbuscular mycorrhizal fungi	Various crops	Negative interactions to 14-fold yield increase	Black and Tinker (1979), McGonigle (1988), Owusu-Bennoah and Mosse (1979)
Associative nitrogen-fixing bacteria	Rice	Yield increases of 10%–30%	Chongbiao (1990)
Azotobacter	Wheat	Yield ranging from 34 to 247 kg/ha	Hegde and Dwivedi (1994)
Azospirillum brasilense and *Bacillus circulans*	Flax and cereals	Yield increases of 8%–30%	Mikhailouskaya and Bogdevitch (2009)
Azospirillum	Wheat	12.9%–22.5% increase in dry weight	Veresoglou and Menexes (2010)
Pseudomonas, Azospirillum, Azotobacter, Bacillus	Maize, wheat, sunflower, lettuce	Yield increases of 19%–40%	Rubin et al. (2017)

associated with microbial inoculants. Several physical, chemical, and biological factors affect the survival and functioning of microorganisms in the soil. Soil water deficit and high temperature are the major abiotic factors that affect their performance in dryland agriculture. Inadequacy of soil organic matter further aggravates the problem as the non-symbiotic microorganisms depend on organic matter for energy and growth. Microbial inoculation in soil also influences the activity of indigenous microflora, ultimately having a bearing on their own survival (Ramos et al. 2003). This is because the introduced microorganism must adhere to the plant roots, compete for space and nutrients released through root exudation, and must be able to occupy the new niche in sufficient numbers so as to exert its effect on the host plant (Barriuso et al. 2008b). Often, the native inhabitants of soil, which are better adapted to the environmental conditions, outcompete the inoculated population. Development of an effective microbial inoculant thus requires the presence of multiple fitness traits that can facilitate its colonization and survival under harsh environmental conditions (Rana et al. 2011). To facilitate this, bioprospecting for more tolerant strains and novel methodologies for understanding the plant-microbe interactions are necessitated.

The rhizospheric hotspot of plant microbiome

In spite of the vast microbial diversity in soil, microorganisms are congregated in small pockets which constitute only 1% of the total soil volume (Young et al. 2008). These microhabitats wherein microorganisms are aggregated to form colonies or biofilms are characterized by faster rates of different biogeochemical processes than bulk soil (Kuzyakov 2009). Kuzyakov and Blagodatskaya (2015) defined these soil volumes as "microbial hotspots" and identified four such hotspots in soil. These include (a) rhizosphere, the region of soil surrounding living roots which is under the influence of

plant root exudates; (b) detritusphere, the soil region associated with decomposition of plant litter and turnover of soil organic matter; (c) biopores, formed by deep growing roots and burrowing fauna; and (d) the soil aggregate surfaces (Kautz 2015; Kramer et al. 2016; Kuzyakov and Blagodatskaya 2015). These regions provide inputs of labile and recalcitrant organics for bioprocesses and are also relevant with respect to the factors like soil moisture, oxygen availability, and nitrogen nutrition, which limit microbial activity (Kuzyakov and Blagodatskaya 2015).

The localized availability of labile carbon and other readily utilizable nutrients leads to a concentration of events like respiration, gas exchange, nutrient and moisture utilization, and other bioprocesses in the rhizosphere (Richter et al. 2011). The major phenomenon underlying the establishment of such distinct rhizosphere characteristic is rhizodeposition, wherein plant roots secrete a wide range of low- and high-molecular weight compounds including sugars, organic acids, amino acids, polysaccharides, vitamins, and other secondary metabolites into the surrounding soil (Badri and Vivanco 2009). These rhizodeposits account for ~ 11% of net photosynthetically fixed carbon and 10–16% of total plant nitrogen (Jones et al. 2009). These exudates play an important role in shaping the rhizosphere by altering soil chemistry in the immediate vicinity of plant roots and by serving as substrates for the growth of selected soil microorganisms (Yang and Crowley 2000). Components of plant root exudates get varied, both qualitatively and quantitatively, depending on the nutritional status of the plant, growth stage, and even in time and space relative to the position of the root (Hartmann et al. 2009; Malusà et al. 2016). This creates a strong selective pressure in the rhizosphere leading to a plant-driven selection of specific rhizosphere microbial communities. Interestingly, only 2–5% of the rhizosphere microorganisms promote plant growth (Antoun and Kloepper 2001) and plants naturally select for these

beneficial microorganisms which help in their growth and survival, especially under constrained conditions (Lareen et al. 2016). The rhizosphere microorganisms may also enter the roots and migrate to the plant's aerial surfaces (phyllosphere) (Thapa and Prasanna 2018) and internal tissues (endosphere). Hence, plants are often associated with communities of microorganisms, living on or within them, exhibiting mutually beneficial symbioses. This entire genome of microbial community, referred to as the microbiome, plays vital roles in host's nutrient uptake, metabolic capabilities and tolerance to biotic and abiotic stresses (Bulgarelli et al. 2013; Sessitsch and Mitter 2015). Therefore, defining a host plant's core distinct microbiome that supports its growth is the preliminary step in improving the plant's characteristic traits.

Significance of plant microbiome on crop growth

In an ecological perspective, plants are more than individual entities as they co-habit with the plant microbiota that impact plant growth and productivity. The microbial diversity of soil and rhizosphere microbiomes is highly underestimated as only 5% of microorganisms have been cultured by current methodologies (Mendes et al. 2013). The plant-associated microbiomes consist of beneficial organisms like nitrogen-fixing bacteria, mycorrhizal fungi, other plant growth-promoting rhizobacteria (PGPR), and biocontrol agents, as well as organisms that are deleterious to plant growth like pathogenic microorganisms. Next-generation sequencing technologies based on 16S rRNA gene have illustrated the vast diversity of microorganisms, particularly bacteria, present in the core microbiome of plants (Table 2). Hawkes et al. (2007) conducted a meta-analysis of clone libraries obtained from the rhizosphere of 14 different plant species and found that the plants were associated with more than 1200 bacterial taxa and the phylum *Proteobacteria* was the most dominant. These assemblages of plants and microorganisms deal with perturbations in the surroundings by detecting and responding to environmental stimuli, resulting in specific adjustments in their growth and development. As opined by Gopal and Gupta (2016), the overall fitness of the plant depends greatly on the ecological services of plant-associated microorganisms that include biofertilization, protection from diseases and tolerance to abiotic stresses.

Role of plant microbiome in nutrient acquisition

Research on plant microbiome actually started with the earliest observations of legume-*Rhizobium* and mycorrhizal symbiotic relationships. Rhizobia fix atmospheric nitrogen in a form that is utilized by legumes and in turn depend on host

for photosynthates and for some of the genes involved in nitrogen fixation (Hunter 2016). Mycorrhizal fungi enhance the nutrient absorptive capacity of roots by increasing the effective surface area and the release of hydrolytic enzymes. Besides nutrient translocation, mycorrhizae also improve soil structure by creating stable soil aggregates (Rillig 2004). The similarity in signaling crosstalk and the similar cellular responses of the rhizobial and mycorrhizal symbionts led to the establishment that the rhizobium-legume symbiosis recruited mechanisms established to support the more ancient endosymbiotic relationship with arbuscular mycorrhizal fungi (Rogers and Oldroyd 2014; Streng et al. 2011). However, understanding the fundamental differences between the two responses is crucial in realizing the age-old dream of developing *in planta* systems to transform cereals into autonomous N-fixing plants, by engineering into them the legume symbiosis pathway (Geurts et al. 2012).

Several other nitrogen-fixing endophytic and free-living rhizobacteria of the genera *Bradyrhizobium*, *Azotobacter*, *Pseudomonas*, *Azospirillum*, *Bacillus*, *Burkholderia*, and *Achromobacter* have been found to have positive impacts on crops by enhancing both above and belowground biomass (Guimarães et al. 2012; Gyaneshwar et al. 2011; Igiehon and Babalola 2018). Several phosphate-solubilizing bacteria (*Pseudomonas*, *Bacillus*, *Alcaligenes*, *Aerobactor*) and fungi (*Aspergillus*, *Penicillium*, *Fusarium*, *Chaetomium*, *Cephalosporium*) are also important members of the plant microbiome (Chen et al. 2006; Sharma et al. 2013; Uribe et al. 2010). They increase the solubility of inorganic phosphorus (P) by releasing protons, OH^-, or CO_2, and organic acid anions such as citrate, malate, and oxalate and can also mineralize organic P by release of various phosphatase enzymes (Marschner et al. 2010). Rhizosphere microorganisms also facilitate the uptake of trace elements such as iron (Fe) and zinc (Zn). Microorganisms release organic acid anions or siderophores that chelate ferric ion (Fe^{3+}) and transfer it to the cell surface where it gets reduced to the soluble ferrous ion (Fe^{2+}) (Mendes et al. 2013). These siderophores include enterobactin, pyoverdine, and ferrioxamines produced by bacteria and ferrichromes produced by fungi (Marschner et al. 2010). Fluorescent pseudomonads have been found to promote iron nutrition via siderophores for Graminaceous as well as dicotyledonous plant species (Shirley et al. 2011). Rhizosphere microorganisms (*Curtobacterium*, *Plantibacter*, *Pseudomonas*, *Stenotrophomonas*, *Streptomyces)* are also known to mobilize zinc (Zn) by acidification of medium via gluconic acid production (Costerousse et al. 2018; Whiting et al. 2001).

The rhizosphere microbiome also plays an important part in organic matter decomposition which enhances soil fertility and ultimately improves plant productivity. Lignocellulolytic fungi like *Trichoderma harzianum*, *Pleurotus ostreatus*, *Polyporus ostriformis*, and *Phanerochaete chrysosporium*

Table 2 Vast diversity of microorganisms identified in the rhizosphere microbiome of plants

Host plant	Dominant members of the rhizosphere microbiome	Reference
Oak	(Characterized by 16S rRNA gene sequencing) identified 5619 bacterial OTUs (operational taxonomic unit) with 38% *Proteobacteria*, 24% *Acidobacteria*, 11% *Actinobacteria*, and 20% unclassified bacteria	Uroz et al. (2010)
Sugarbeet	(Characterized by 16S rRNA gene microarray) Detected 33,346 bacterial and archaeal OTUs, of which 39% were *Proteobacteria* (*Gamma-* and *Betaproteobacteria*), 20% were *Firmicutes*, 9% were *Actinobacteria*	Mendes et al. (2011)
Rice	(Characterized by 16S rRNA gene sequencing) *Bacteroidetes, Firmicutes, Chloroflexi*, and *Betaproteobacteria* (*Rhodocyclaceae, Comamonadaceae*), *Alphaproteobacteria, Deltaproteobacteria*	Edwards et al. (2015)
Sugarcane	(Characterized by 16S rRNA gene sequencing) *Betaproteobacteria* (*Undibacterium, Burkholderia*), *Alphaproteobacteria* (*Bradyrhizobium, Rhizobium*), *Bacteroidetes* (*Niastella, Chitinophaga*), *Gammaproteobacteria* (*Dyella, Frateuria*), *Actinobacteria* (*Streptomyces, Cryocola*), *Chloroflexi* and *Firmicutes* (*Bacillus*)	Yeoh et al. (2016)
Sugarcane	(Characterized by sequencing of 16S and ITS ribosomal RNA genes) Identified 23,811 bacterial OTUs and 11,727 fungal OTUs. Major families were *Chitinophagaceae, Rhodospirillaceae, Hyphomicrobiaceae, Burkholderiaceae, Rhizobiaceae, Sphingobacteriaceae, Sphingomonadaceae, Sistotremataceae, Meruliaceae, Ceratocystidaceae, Chaetosphaeriaceae, Glomeraceae*	de Souza et al. (2016)
Oilseed rape	(Characterized by RNA stable isotope probing and high-throughput sequencing) *Verrucomicrobia, Proteobacteria, Planctomycetes, Acidobacteria, Gemmatimonadetes, Actinobacteria, Flavobacterium, Rhodoplanes, Sphingomonas, Streptomyces, Chloroflexi, Rhizobium*	Gkarmiri et al. (2017)
Arabidopsis thaliana	(Characterized by sequencing of the ITS2 region) *Ascomycetes* (542 OTUs) and *Basidiomycetes* (145 OTUs) were the abundant phyla, and *Archaeorhizomycetes, Leotiomycetes, Dothideomycetes, Eurotiomycetes* and *Sordariomycetes* were the abundant classes	Urbina et al. (2018)
Canola	(Characterized by sequencing of 16S and ITS ribosomal RNA genes) Identified 6376 bacterial OTUs, 679 fungal OTUs and 49 archaeal OTUs, including *Amycolatopsis* sp., *Serratia proteamaculans, Pedobacter* sp., *Arthrobacter* sp., *Stenotrophomonas* sp., *Fusarium merismoides, Fusicolla* sp.	Lay et al. (2018)
Blueberry	(Characterized by 16S rRNA and 18S rRNA gene sequencing) Abundant bacterial classes were *Proteobacteria* (*Alphaproteobacteria* and *Gammaproteobacteria*), *Acidobacteria, Actinobacteria, Bacteroidetes, Saprospirae, Chloroflexi, Ktedonobacteria*, and *Verrucomicrobia Spartobacteria*. Fungal taxa identified were *Ascomycota, Basidiomycota, Mucoromycota, Glomeromycota*, and *Chytridiomycota*	Yurgel et al. (2018)

and bacteria like *Pseudomonas* sp., *Cellulomonas* sp., *Cytophaga* sp., *Sporocytophaga* sp., *Chryseobacterium gleum*, and *Streptomyces* sp. are known to degrade plant biomass, thereby releasing nutrients not only for their own nutrition, but also for plant nutrition (Ahmed et al. 2018; Mendes et al. 2013; Singh and Nain 2014; Woo et al. 2014). The plant microbiome, therefore, facilitates the growth of plants even in nutrient-poor soils.

Role of plant microbiome in protection from pathogens and host immunity

The rhizosphere antagonistic microorganisms ward off pathogens by producing antibiotics or hydrolytic enzymes and also by competing for nutrients and space (Caravaca et al. 2015; Raaijmakers and Mazzola 2012). Antimicrobial metabolites produced by microorganisms include ammonia, butyrolactones, oligomycin A, phenazine-1-carboxylic acid (PCA), pyoluterin, pyrrolnitrin, and other moieties (Wackett 2013; Whipps 2001). *Pseudomonas fluorescens* suppresses soilborne pathogens like *Meloidogyne incognita* and *Fusarium oxysporum* by production of the antibiotic 2,4-diacetylphloroglucinol (DAPG) (Meyer et al. 2016). Bacteria are also known to parasitize and degrade spores of fungal plant pathogens through the production of extracellular cell wall-degrading enzymes such as chitinase and β-1,3 glucanase (Whipps 2001). Most microbial biocontrol strains produce more than one antibiotic compound with varying degrees of antimicrobial activity. *Agrobacterium radiobacter* produces agrocin 84, which is antibiotic to closely related strains, and polyketide antibiotics which are broad-spectrum in nature (Raaijmakers et al. 2010). Bacterial iron chelators also effectively play a role in the biocontrol of pathogens by sequestering the available iron and making it unavailable to pathogenic microorganisms, thereby restricting their growth. Siderophores produced by *Bacillus subtilis* significantly managed the *Fusarium* wilt of pepper caused by *Fusarium oxysporum* (Yu et al. 2011). Siderophores produced by *Aspergillus niger*, *Penicillium citrinum*, and *Trichoderma harzianum* were found to be effective biocontrol agents and enhanced the growth of chickpeas (*Cicer arietinum*) (Yadav et al. 2011).

Rhizobacteria, particularly *Pseudomonas* and *Bacillus*, could also act as elicitors for inducing systemic resistance against pathogens in some plants. The siderophores produced by *Pseudomonas aeruginosa*, pyoverdine, pyochelin, and its precursor salicylic acid (SA), can induce resistance to diseases caused by *Botrytis cinerea* on bean and tomato, *Colletotrichum lindemuthianum* on bean, and tobacco mosaic virus on tobacco (Bigirimana and Höfte 2002; Höfte and Bakker 2007). Similarly, the catechol-type siderophore produced by *Serratia marcescens* 90-166 induces resistance to fungal, viral, and bacterial pathogens such as *Colletotrichum orbiculare*, *Fusarium oxysporum*, cucumber mosaic virus, *Pseudomonas syringae*, and *Erwinia tracheiphila* in cucumber (Press et al. 2001). The rhizobacterial association trigger either the salicylic acid dependent signal transduction pathway or the jasmonic acid and ethylene signaling pathway for protection against pathogens (Ton et al. 2002). Plants with such induced resistance show strengthening of epidermal and cortical cell walls by deposition of callose, lignin, and phenolics, increased levels of enzymes such as chitinase, peroxidase, polyphenol oxidase, and phenylalanine ammonia lyase, enhanced phytoalexin production, and enhanced expression of stress-related genes (Heil and Bostock 2002; Whipps 2001; Yi et al. 2013). Therefore, multiple microbial interactions in the rhizosphere provide enhanced biocontrol against pathogens, besides modulating the plant immune system.

Role of plant microbiome in tolerance to abiotic stresses

Rhizosphere microorganisms, with their intrinsic metabolic and genetic capabilities, contribute to alleviate abiotic stresses in plants (Gopalakrishnan et al. 2015). Several microflora of the genera *Pseudomonas*, *Bacillus*, *Achromobacter*, *Burkholderia*, *Enterobacter*, *Azotobacter*, *Methylobacterium*, and *Trichoderma* have been widely studied in plant growth promotion by mitigation of multiple kinds of abiotic stresses (Atieno et al. 2012; Meena et al. 2017; Sorty et al. 2016). Wheat inoculated with *Burkholderia phytofirmans* PsJN reported an increased photosynthesis, high chlorophyll content, and grain yield than the control under water deficit in field conditions (Naveed et al. 2014). Treatment of Indian mustard (*Brassica juncea*) with the fungus, *Trichoderma harzianum*, improved the uptake of essential nutrients and enhanced accumulation of antioxidants and osmolytes and decreased Na^+ uptake under saline conditions (Ahmad et al. 2015). Better root colonizing capability of *Pseudomonas* sp. along with its ability to produce exopolysaccharides led to enhanced tolerance towards salinity (Sen and Chandrasekhar 2014). Volatile organic carbons emitted from *Bacillus subtilis* GB03 were found to downregulate the *HKT1* (high-affinity K^+ transporter 1) expression in roots of *Arabidopsis* and upregulate it in shoots, resulting in lower Na^+ accumulation throughout the plant thereby inducing tolerance to salt stress (Zhang et al. 2008). Srivastava et al. (2008) isolated a thermotolerant *Pseudomonas putida* strain NBR10987 from drought-stressed rhizosphere of chickpea and the strain was able to combat stress by producing exopolysaccharides with unique water holding characteristics. Rhizosphere microorganisms also increase tolerance to low nonfreezing temperatures resulting in higher and faster accumulation of stress-related proteins and metabolites (Theocharis et al. 2012). Novel stress tolerant bacteria such as *Brachybacterium saurashtrense*, *Zhihengliuella* sp., and *Brevibacterium casei* have also been reported from plant rhizospheres (Jha et al. 2012). Moreover, the bacteria such as *Pseudomonas*, *Microbacterium*, *Verrucomicrobia*, and *Actinobacteria* and fungi such as *Lewia* sp. and mycorrhizal fungi are potential candidates for rhizoremediation as they alter the mobility and bioavailability of metals, thereby increasing their uptake by plants (Cruz-Hernández et al. 2012; Kawasaki et al. 2012; Yang et al. 2016).

Role of plant microbiome in phytohormone production

Plant growth-promoting rhizobacteria and fungi are known to improve plant growth by the production of phytohormones. These plant hormones are mostly synthesized as secondary metabolites as they are not essential for the growth and reproduction of microorganisms (Shi et al. 2017). Gibberellins were firstly discovered when it was noticed that a chemical synthesized in *Gibberella fujikuroi* can contribute to the disease of rice plants (Kurosawa 2003). Gibberellins can stimulate plant growth and regulate various developmental processes like seed germination, stem elongation, sex expression, and fruit formation (Bömke and Tudzynski 2009). Production of gibberellin-like substances have been reported in numerous bacterial genera including *Azospirillum* sp., *Rhizobium* sp., *Acetobacter diazotrophicus*, *Herbaspirillum seropedicae*, *Bacillus* sp., and *Fusarium moniliforme* (Bottini et al. 2004; Meleigy and Khalaf 2009). Auxin and cytokinin production are thought to be involved in root growth stimulation by beneficial bacteria and in associative symbiosis. Auxin biosynthesis by *Pseudomonas*, *Agrobacterium*, *Rhizobium*, *Bradyrhizobium*, *Azospirillum*, *Botrytis*, *Aspergillus*, and *Rhizopus* are well studied (Costacurta and Vanderleyden 1995; Hui et al. 2007). Apart from synthesis, plant-associated microorganisms also alter the hormonal signaling in plants, in response to environmental stimuli. As stated in a previous section, the systemic resistance response induced in plants by beneficial rhizobacteria is in many cases regulated by the phytohormones jasmonic acid and ethylene (Zamioudis and Pieterse 2012). Therefore, microorganism-mediated phytohormone production is a potent mechanism to alter plant physiology, leading to diverse outcomes from pathogenesis to promotion of plant growth (Spaepen 2014).

Role of microbiome in impairing plant health and productivity

Besides plant growth-promoting microorganisms, the root microbiome also consists of rhizosphere microorganisms which are detrimental to plants, competing for nutrients and space. Plant pathogenic fungi, bacteria, and nematodes cause various plant diseases resulting in substantial economic damage to crops. *Agrobacterium tumefaciens*, *Ralstonia solanacearum*, *Dickeya* sp., *Pectobacterium carotovorum*, *Pythium* sp., *Phytopthora* sp., *Fusarium oxysporum*, *Rhizoctonia* sp., *Gaeumannomyces graminis*, *Colletotrichum* sp., and *Magnaporthe oryzae* are a few of the major plant pathogenic microorganisms prevalent in soils (Dean et al. 2012; Doehlemann et al. 2017; Mansfield et al. 2012). The phenolic compounds present in plant root exudates, in low concentrations, facilitate conidial germination, while in higher concentrations; inhibit mycelia growth (Mendes et al. 2013).

Bacteria and fungi are two major groups of the plant microbiome, and their interactions via antibiosis, modulation of the physiochemical environment, cooperative metabolism, protein secretion, or even gene transfer can lead to either antagonism or cooperation (Chen et al. 2018; Frey-Klett et al. 2007). This implies that an alteration of the rhizosphere characteristics can influence plant growth and in this context, shaping the rhizosphere microbiome provides a sound alternative for the conventional microbial inoculation.

Engineering a biased rhizosphere to promote plant-microbe interactions

Taking into account the role of plant root exudates in attracting rhizosphere microorganisms, altering the root exudate composition, both qualitatively and quantitatively, is a major approach to reshape the rhizosphere microbiome. The creation of a "biased rhizosphere" is a novel procedure which involves the expression of specific genes in transgenic plants that would enable roots to produce the specific nutritional compound, which can be used or recognized by specific beneficial microorganisms (Reddy et al. 2002; Savka et al. 2013). The goal of rhizosphere engineering is to direct the plant-microbe interaction towards enhanced beneficial outcomes including nutrient cycling, mineralization and organic matter decomposition, tolerance to drought, salinity and other abiotic stresses, and resistance to diseases (Marasco et al. 2012; Quiza et al. 2015). The methods of application of microbial inoculants in soil, employment of tillage, plant breeding approaches, and the use of fungicides and antibiotics for plant protection are, to a certain extent, conventional rhizosphere modification strategies. The application of plant growth-promoting rhizobacteria (PGPR), nitrogen fixers, phosphate solubilizers, and arbuscular mycorrhizal fungi (AMF) improve plant performance by enhancing nutrient availability, phytohormone production, and pathogen control. But, maintenance of high population densities of these microorganisms after inoculation is a major constraint owing to their decline over time and distance from the inoculum source (O'Callaghan et al. 2001; Quiza et al. 2015). Similarly, tillage, plant protection measures, and cultivar selection may induce soil vulnerability, even though they may influence microbial populations by inhibiting or enhancing the growth of soil microorganisms (Bakker et al. 2012; Brussaard et al. 2007). Consequently, the avenue of rhizosphere microbiome engineering has emerged which aims to alter the rhizosphere to express a bias towards beneficial microorganisms enabling plants to evolve into better hosts. It harnesses the variations in plant root exudation patterns in order to enhance the favorable rhizosphere microbiome (Philippot et al. 2013; Quiza et al. 2015). Genetic alteration of root exudation patterns could influence microbial communities by enhancing or inhibiting the growth of

selected microorganisms. The important strategies for rhizosphere modification being researched widely include the manipulation of root border cells, engineering of inhibitors and enhancers, and induction of microbial gene expression in host plant cells.

Tailoring root border cells for creation of biased rhizoshere

In the process of exudation, roots are found to release a group of metabolically active cells known as border cells into the surrounding soil (O'Connell et al. 1996). These are actually the sloughed-off root cap cells, which are attached to the root surface by a water-soluble polysaccharide matrix (Hawes et al. 2000). In the presence of water, the middle lamellae of these cells become solubilized by the action of pectinolytic enzymes in the cell wall and get dispersed from root tips (Wen et al. 1999). These border cells serve in mucilage secretion, sensing of gravity, and other environmental signals, synthesis, and export of extracellular chemicals, enzymes, antibiotics, and sugars, which can rapidly attract and stimulate growth in some microorganisms or repel and inhibit the growth of others, thereby mediating rhizosphere processes (Hawes et al. 1998, 2000; Jian-Wei et al. 2002). More importantly, border cells remain viable even after their detachment from the root cap and are characterized by distinct mRNA and protein profiles with respect to that of the root cap cells (Brigham et al. 1995; Zhu et al. 2004). The ability of border cells to engineer the chemical and physical properties of the external environment has been demonstrated by their ability to attract fungal spores, to repel pathogenic bacteria, to synthesize defensive structures against pathogen invasion, and to influence gene expression in symbiotic bacteria (Gunawardena and Hawes 2002; Hawes et al. 2000; Somasundaram et al. 2008). These cells, therefore, are attractive targets to be engineered for developing a biased rhizosphere to facilitate association with beneficial microorganisms.

Chemotactic attraction facilitating the association of plant roots and border cells with soil microflora has been reported. Hawes et al. (2000) studied the interaction of root knot nematode with root border cells of pea and found that the nematodes get attracted and immobilized by the border cells. Experiments also revealed that border cells synthesize and export into the surrounding mucilage, histone-linked extracellular DNA (exDNA), which attracts, traps, and immobilizes pathogens in a host-microbe-specific manner (Hawes et al. 2012). Recently, molecular techniques are being used to identify and manipulate the expression of plant genes that control the production and specialized properties of border cells in transgenic plants. Lilley et al. (2011) reported the targeting of inhibitory peptides specifically to root border cells of potato using a root-cap-specific MDK4–20 promoter of *Arabidopsis thaliana*. The AtMDK4-20 promoter was found

to remain active for a long time in the detached border cells and the transgenic potato plants expressed 94.9% resistance to the potato cyst nematode *Globodera pallid* (Lilley et al. 2011). Similarly, the expression of Cry proteins in roots and border cells of transgenic cotton, which are involved in controlling lepidopteran pests, was investigated by Knox et al. (2007). ELISA was used to quantify the in vitro expression of Cry1Ac and Cry2Ab proteins in root border cells of transgenic cultivars of cotton and it was found to be constitutive and at detectable levels (Knox et al. 2007).

Root border cells are also found to impart resistance to aluminum (Al) toxicity (Yu et al. 2009). The responses of root apices of pea (*Pisum sativum*) to Al exposure in mist culture revealed that border cells enhanced the Al resistance of root apices by immobilizing Al in their cell-wall pectin (Yu et al. 2009). Inhibition of root elongation, induction of callose synthesis, and accumulation of Al were more pronounced in root apices stripped from border cells. Such border cell trapping has also been found to be associated with cadmium, arsenic, copper, lead, mercury, and nickel (Hawes et al. 2016; Huang et al. 2009; Kopittke et al. 2011; Zelko and Lux 2003). Root border cells are also reported to actively take up glucose, and also release it, thereby playing a significant role in the net glucose exchange in rhizosphere (Stubbs et al. 2004). These aspects could be effectively utilized to drive the rhizospheric characteristics towards better plant-microbe associations and plant growth. The ability of root border cells to produce mucilage can be employed for better penetration of root tips through hard soils and mineral surfaces for better uptake of water and nutrients. The negatively charged groups on side chains of mucilagenous polysaccharides of root border cells can also facilitate attraction of cations like Ca^{2+}, providing exchange sites from which roots might absorb nutrients (Brundrett et al. 2016). In this way, the thousands of border cells released by plant roots can be tailored to engineer the rhizosphere to suit plant health and nutrition.

Engineering inhibitors and enhancers in plants to induce rhizosphere bias

Plants can be genetically modified to alter soil organic anion efflux and transportation from roots by engineering plants with a greater capacity to synthesize organic anions and to transport them out of the cell (Quiza et al. 2015). Plants engineered with higher ability to excrete citrate from the roots grew better on P-limited soil than the wild type, indicating their ability to grow in acid soils (Koyama et al. 1999). Root-secreted organic acids, such as malate and citrate, optimize the carbon economy of soil microorganisms as they are easily consumed by the microflora (Wu et al. 2018). Also, the organic acid-chemotaxis regulates the recruitment of beneficial rhizobacteria to the root surface (Rudrappa et al. 2008). In tobacco and alfalfa plants genetically engineered to

overproduce citric or malic acid, an increased colonization by mycorrhizal fungi and rhizobacteria has been reported (López-Bucio et al. 2000; Tesfaye et al. 2003). In other studies, rhizosphere pH has been altered by over-expressing the genes controlling proton efflux from plant cells (Ryan et al. 2009). Tobacco plants transformed with a modified plasma membrane proton pump ATPase (H⁺-ATPase) exhibited increased H⁺-efflux from roots and a more acidic rhizosphere (Gévaudant et al. 2007). The edaphic variables, especially pH, shape the structure and function of microbial communities in the rhizosphere (Fierer and Jackson 2006). However, Yuan et al. (2008), by transcriptome profiling and functional analysis, have revealed that an acidic soil pH induces the virulence of *Agrobacterium tumefaciens*. Plants may also be engineered to promote the growth of desired microorganisms by releasing nutritional compounds which only the specific microorganism can catabolize (O'Connell et al. 1996). The phenomenon of *Agrobacterium tumefaciens* mediated transfer of a region of its plasmid DNA that encodes opine biosynthesis to plant cells forms the basis of this strategy. Guyon et al. (1993) have demonstrated that opines produced by roots of transgenic plants increase the population of opine-catabolizing *Agrobacterium*. Similar results have also been obtained by Mansouri et al. (2002) who reported that transgenic *Lotus* plants producing opines specifically favor the growth of opine-degrading rhizobacteria, irrespective of soil type and plant species.

Plants may also be engineered for the production of recombinant proteins in order to overcome the difficulties involved in introducing complex antibiotic synthesis machinery in plants for inhibiting the growth of antagonists. Transfer of genes encoding inhibitory proteins and peptides to plants enables their diffusion into the rhizosphere resulting in the growth of only selected soil microorganisms. This approach is being studied for possible applications in the control of soil-borne pathogens. Pathogens infect plant tissues by producing a wide array of plant cell wall degrading enzymes. To prevent this, polygalacturonase-inhibiting proteins (PGIPs) that inhibit the pectin-depolymerizing activity of polygalacturonases (PGs) secreted by microbial pathogens are made use of (Kalunke et al. 2015). Transgenic tomato plants, expressing a pear (*Pyrus communis* L.) PGIP (PcPGIP), capable of inhibiting the PGs secreted by *Bacillus cinerea* showed 15% and 25% reduction of disease lesions caused by the fungus on ripening fruit and leaves, respectively (Powell et al. 2000). In another study, Jach et al. (1995) detected high-level expression of genes transferred to tobacco for the production of chitinase, β-1,3-glucanase, and ribosome-inactivating protein, under the control of the CaMV 35S-promoter. Fungal infection assays revealed that the expression of individual genes resulted in increased protection against the soil-borne fungal pathogen *Rhizoctonia solani* (Jach et al. 1995). Similarly, simultaneous expression of a tobacco class I chitinase and a

class I β-1,3-glucanase gene in tomato resulted in increased resistance to *Fusarium oxysporum* f. sp. *lycopersici* with 36% to 58% reduction in disease severity (Jongedijk et al. 1995). Strittmatter et al. (1995) reported the inhibition of fungal pathogens by engineering controlled cell death in plants. The expression of bacterial ribonuclease barnase, driven simultaneously by a chimeric pathogen-inducible promoter (prp1-1) from potato and the CaMV 35S promoter, in order to avoid detrimental effects of the RNAse, was studied and the induction of barnase activity at the infection site was found to lead to a significant reduction of *Phytophthora infestans* sporulation on leaves (Strittmatter et al. 1995).

Engineering microbial signaling molecules in plants to bias the rhizosphere

Plants recognize and actively respond to different rhizosphere microorganisms by producing signals that modulate microbial colonization (Haichar et al. 2014). Hence, plant rhizosphere may be modified by engineering plants to release microbial signal molecules like isoflavonoids or lipooligosaccharides which induce microbial gene expression in the rhizosphere. This method can be effectively utilized in ensuring nodule occupancy by the appropriate rhizobial species in leguminous crop plants by utilizing nodule-specific compounds as growth enhancers (Savka et al. 2002). The regulatory mechanism of quorum sensing, which involves the synthesis and accumulation of low-molecular weight signal molecules as a function of the population density of microbes producing these molecules in a given environment, finds applications in this area (Savka et al. 2002). Several microbial functions like biofilm formation, pathogenicity, and iron uptake are regulated via quorum sensing (Abisado et al. 2018; Rutherford and Bassler 2012). The ability to generate bacterial quorum-sensing signaling molecules in the plant opens new avenues for manipulating the plant-microbe interactions. Some of the microbial signals like the N-acyl-L-homoserine lactones (AHLs) and volatile organic compounds, which belong to a class of bacterial quorum sensing signals from Gram-negative bacteria such as *Pseudomonas*, play a role in plant morphogenetic processes (Ortíz-Castro et al. 2009). Transgenic tobacco and tomato plants expressing the *LasI* gene from *Pseudomonas aeruginosa*, responsible for the synthesis of AHLs have been synthesized (Barriuso et al. 2008a). These AHLs produce get diffused across the plasma membranes into the rhizosphere, where they have the potential to affect bacterial processes regulated by such molecules (Ortíz-Castro et al. 2009). Providing transgenic plants with the ability to block or degrade AHL signals, otherwise termed as quorum quenching, may provide an alternative approach for engineering plant resistance to microbial pathogens. Transgenic tobacco and potato plants expressing the *aiiA* gene responsible for AHL degradation have shown resistance to *Erwinia carotovora* pv.
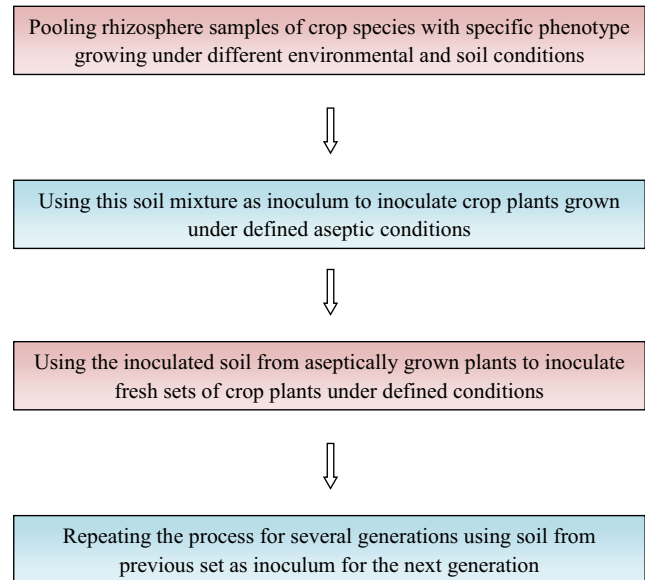
carotovora infections even at very high bacterial inocula (Dong et al. 2000).

Future prospects of plant-microbiome associations

The rhizosphere microbiome facilitates communication between the plant and the surrounding soil environment and they together contribute to creating a productive metagenome which leads to improved crop productivity (Zorner et al. 2018). Studies connecting comparative genomics and metabolomics have shown that specific rhizosphere bacteria are naturally selected depending on the root exudates contents (Zhalnina et al. 2018). For instance, comparison of wild and domesticated common bean (*Phaseolus vulgaris*) grown in agricultural soil revealed that as the genotype transitioned from wild to domesticated, the relative abundance of *Bacteroidetes* (*Chitinophagaceae* and *Cytophagaceae*) decreased while *Actinobacteria* and *Proteobacteria* (*Nocardioidaceae* and *Rhizobiaceae*) increased (Pérez-Jaramillo et al. 2017). The synergistic and complementary mechanisms among microorganisms and of plant-microbe interactions can be unveiled with the use of model plants grown under gnotobiotic conditions as such studies throw light into the phenomenon of microbiome-mediated host plant immunity (Sessitsch and Mitter 2015). Researchers have investigated immune responses elicited by plant microbiomes using the FlowPot system (Kremer et al. 2016). Microbe-free seeds of *Arabidopsis* were grown in sterile, bottom-irrigated pots alongside *Arabidopsis* colonized with diverse microbial communities from various soils. Transcriptome profiling revealed that colonized plants had significantly more defense-associated transcripts involved in innate immunity, when exposed to speck disease of tomatoes, caused by *Pseudomonas syringae* pv *tomato*. The study also revealed a microbiome-influenced host and pathogen gene expression and suggested a "plant-pathogen-microbiome disease triangle" concept for advanced studies of microbial pathogenesis and plant disease resistance. The phenomenon of transfer of microbiome, from disease-suppressive soils to pathogen prevalent soils, for management of crop diseases has also been reported (Gopal et al. 2013; Turner et al. 2013).

Due to the direct influence of microbial interactions on plants and the ability of host plants to mediate microbiome assembly, selection on a host-microbial association is an emerging approach to enhance plant fitness and productivity (Mueller and Sachs 2015). Protocols may be designed targeting the selection of a characteristic host phenotype affected by the microbiome function which then gradually facilitates the transfer of specific trait-associated microbiomes into new plant hosts (Fig. 1). Such studies describing the ability of plant-associated microbiomes to influence different

Pooling rhizosphere samples of crop species with specific phenotype growing under different environmental and soil conditions

⇓

Using this soil mixture as inoculum to inoculate crop plants grown under defined aseptic conditions

⇓

Using the inoculated soil from aseptically grown plants to inoculate fresh sets of crop plants under defined conditions

⇓

Repeating the process for several generations using soil from previous set as inoculum for the next generation

Fig. 1 Process of identification of trait-specific microbiome associated with crop plants. The synergy of plant-microbiome associations forms the basis of this selection which can be utilized to enhance plant fitness and productivity

plant traits including growth, flowering, and abiotic stress tolerance have been reported (Bainard et al. 2013; Sugiyama et al. 2013). Panke-Buisse et al. (2015) used a multi-generation experimental system using *Arabidopsis thaliana* Col to select for soil microbiomes inducing earlier or later flowering times of their hosts. They found that the flowering phenotype was reproducible across plant hosts which showed shifts in flowering time corresponding with the inoculation of early or late flowering microbiomes. Moreover, this resulted in a mutual selection of plant host and the surrounding microbiome (Hunter 2016). As the host plants get co-evolved with their microbiome, this strategy of microbiome selection could be adopted in future crop breeding strategies for low-input sustainable agriculture. Also, the hologenome of host-microbiome association functions as an intermediate between the genotype-environment interaction in shaping the host plant phenotype (Hassani et al. 2018). Considering the functional significance of plant-microbe interactions, an in-depth study into the microbiome function, particularly, the microbiome constituents that are active during the different developmental stages of plant growth and their functions is needed (Mendes et al. 2013).

Genetic improvement of plants focused on an efficient interaction with beneficial microorganisms and selection of agricultural practices with less adverse effects on microbiome therefore need to be evolved (Gopal and Gupta 2016; Sessitsch and Mitter 2015). Application of such works in the field, as opined by Hunter (2016) would permit crops to exploit the beneficial microorganisms in soil, as several commercial crop varieties have lost this capability due to injudicious use of chemical amendments.

Compliance with ethical standards

Conflicts of interest The authors declare that they have no conflict of interest.

Ethical approval No studies with humans/animals have been performed by any of the authors for the purpose of this review article.

Informed consent Informed consent was obtained from all the authors and the authors agreed to the manuscript being submitted to the journal.

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