



# Recent Advances in Plant-Microbe Interaction

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## Abstract

The association of plants and microbes has begun since their evolution. Microbes and plants have coevolved and interacted with each other to meet their demands. Their relationship might be cordial symbiotic as in case of interaction between plants and beneficial microbes or detrimental as in case of interaction between plants and phytopathogens. Numerous genera of microbes are known to be associated with the plants and their rhizosphere. The interaction among these diverse microbial communities and their ability to excel the competition decides the overall plant health. In the past decades, agricultural microbiologists had given more emphasis to plant growth-promoting rhizosphere microbes and soil-borne phytopathogens and their interactions, which has resulted in the identification and use of promising microbial strains with biocontrol and biofertilizing properties. With recent advancement in molecular diagnostics, it is evidenced that in addition to rhizosphere microbes, the interactions between plant microbiomes, *viz.* epiphytes and endophytes, colonizing the entire plant and the plant genome (holobiont) significantly affect the fitness of the plant. Scientific studies evidence that the plant genotype, biostage, soil biogeochemistry and microbe-microbe interaction decide the nature of associated microbiomes. Recent research shows that artificial inoculation of beneficial microbiomes instead of a single or a

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consortium of microbial strains would improve the success rate of establishment and functioning of the introduced microbial community. This chapter highlights the recent advancements in plant-microbe interaction and ways it could be explored and exploited to enhance plant health, thereby improving crop production qualitatively and quantitatively supporting sustainable agriculture.

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**Keywords**

Plant microbiome · Holobiont · Microbial diversity · Beneficial microbes · Phytopathogens · Molecular tools · Sustainable agriculture

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## 2.1 Introduction

Majority of the terrestrial plants are harboured in soil which is a huge and richest reservoir of diverse microbes (Tringe et al. 2005). It is estimated that a gram of soil contains  $10^7$  microbial species, of which bacterial diversity alone ranges up to  $5 \times 10^4$  with a population of  $10^{10}$  bacterial cells  $\text{gm}^{-1}$  of soil (Gans et al. 2005; Roesch et al. 2007; Raynaud and Nunan 2014). Microbes and plants have coevolved and are interdependent. Microbial association with host plants could be ectophytic or endophytic, and their intimacy may be beneficial to both the host plant and the microbe or may be favourable to the associated microbes alone posing a health risk to the host plant. Vogl (1898) cultured the first symptomless endophyte from *Lolium temulentum* seeds. Hartmann et al. (2007) documented that as early as 1901, Hiltner was able to predict the role of plant root exudates in shaping different microbial communities associated with plants and emphasized that the ‘plant microflora’ composition decides the resistance of plants towards pathogens. Plant root acts as a bridge paving the entry of selected soil bacteria into plants which multiply within the plants either as benign endophytes enhancing plant growth or as phytopathogens hampering plant growth. Beneficial benign endophytes offer a variety of services to the associated host plants such as plant growth promotion, yield enhancement and plant protection against various biotic (phytopathogens, invertebrate herbivores) and abiotic (temperature, drought, salinity, heavy metals) stress by influencing the host plants’ metabolism. The host plants recognize microbe-associated molecular patterns (MAMPs) and initiate immune responses which modulates the association and multiplication of the microbe (Rosenblueth and Martinez-Romero 2006). Majority of the microbes inhabiting the plant rhizosphere belonging to the genera *Pseudomonas*, *Bacillus*, *Rhizobium*, *Azospirillum*, *Acetobacter*, *Streptomyces*, *Trichoderma*, *Glomus*, *Acaulospora*, *Scutellospora*, *Enterphospora*, etc. have evidenced to play a beneficial role in plant health and ecological fitness. Most of them colonize the rhizosphere region, while few others possess intracellular and intercellular endosymbiosis with host plant and act as an interface between the plant and the soil medium channelling the effective transmission of nutrients, minerals and water from soil. The microbes rely on plants for dwelling space and derive their nutrition from root exudates and in turn supply plants with nutrients, vitamins,

growth-promoting hormones and disease-evading biomolecules as well as trigger plant immune system, thereby protecting the plant from various biotic and abiotic stresses. On the other hand, soil also contains various phytopathogenic species belonging to the genera *Rhizoctonia*, *Fusarium*, *Phomopsis*, *Phytophthora*, *Agrobacterium*, etc., which causes dreaded disease in plants. The ratio and competitive ability between the good and bad microbes decides the overall plant health and fitness. Until the last decade, more emphasis was given to explore the potential rhizosphere microbes to utilize them as biofertilizers and biopesticides. There are growing evidence that the composition of plant microbiomes (those living as endophytes and epiphytes in all plant parts), their networking and signalling decide the plant health. Recent advances in molecular diagnostics like metagenomics, metabolomics, proteomics, high-throughput sequencing, etc. have opened new insights and a better understanding of uncultivable microbes and their role in maintaining plant health. This chapter briefs about plant-associated microbiomes, factors affecting their establishment and their role in preserving the health of the plants, techniques used in studying the holobiont and their potential application in agriculture to boost the yield in the most sustainable manner.

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## 2.2 Plant Microbiomes

Plant microbiome includes all microbial partners associated with plants underground and aboveground. Underground microbes include epiphytic and endophytic microbes colonizing the roots (rhizosphere and rhizoplane), while aboveground microbes are those inhabiting the phyllosphere as endophytes and epiphytes and include microbes dwelling in caulosphere (stem), phylloplane (leaves), anthosphere (flowers) and carposphere (fruits). Plants offer space, protection, nutrients and supports the dissemination of associated microbes. The microbes, in turn, provide substances that help in seed germination, plant growth and development and resistance to salinity, drought and water stress and activate plants' defence against herbivore pest and phytopathogens (Stanley and Fagan 2002). Though a microbe belonging to a specific taxon provides a specific functional advantage, other members in the microbiome are essential to support or synergize the effect of the key candidate. Thus, knowledge on holobiont (plants and associated microbes) will help us understand their evolution, biodiversity, interdependence and functionality of the ecosystem which has ample applications in food security and safety. Attempts made by evolutionary biologists to study the evolution of plant microbiomes showed that arbuscular mycorrhizal (AM) symbioses were primogenital which might have helped in the establishment of terrestrial plants (Brundrett 2002; Parniske 2008). Evolutionary theory also suggests that endophytes that are systemic and vertically transmitted in grasses pose greater resistance to host plants against invertebrate herbivores and phytopathogens as compared to horizontally transmitted endophytes inhabiting woody plants (Stanley and Fagan 2002). Studies on genetic linkages between fungal and bacterial symbiosis opens up the possibility of the involvement

of rhizobial root nodule symbiosis from functional aspects of mycorrhiza (Parniske 2008; Oldroyd et al. 2009).

The rhizosphere is the biologically active interface and per gram of root contains nearly  $10^{11}$  microbial cells with 30,000 diverse species which determines plant health (Berendsen et al. 2012; Pathma et al. 2019). The total surface area of phyllosphere has been estimated to be approximately  $10^9$  km<sup>2</sup> globally which acts as a house for various beneficial and pathogenic microbes with a microbial density of  $10^7$  cells/cm<sup>2</sup> of leaf surface (Lindow and Brandl 2003; Farre-Armengol et al. 2016). Early studies focussed on plant-microbe interaction at tissue level, but the advancement of biochemical and molecular diagnostics has enabled us to understand the interaction of microbe at the cellular level of plants which acts as the interface for molecular conversation between plants and microbes. The microbial effectors delivered into the host plant cell shapes the dialogue between them. This acts as the beginning for a plethora of changes at the cellular level which could be compatible leading to beneficial symbiotic interactions (rhizobacteria, mycorrhiza) or incompatible leading to detrimental pathogenic infections by phytopathogenic fungi, bacteria and viruses (Panstruga and Kuhn 2015). In both cases, genetic signatures of the host plant and the associated microbes are the drivers that shape their associations and the outcome. The host plant produces specific cues which are recognized by the microbes enabling their orientation with the host plants. Also microbes produce specific chemical cues which attract or repel another microbe and decide the taxonomical diversity of the microbial community associated with the host plant. In case of pathogenic association, virulence which decides the success of infection is the combination product of plant-pathogen interaction and not the individual trait of plant or the pathogen. Both host plant and pathogen genotype are key factors deciding the success of infection (Ebert and Hamilton 1996).

Plants' immune system initially recognizes all microbial infection as harmful invasions after which they discriminate between pathogenic and beneficial microbes (Pel and Pieterse 2013). Microbes have specific molecular signatures, and microbial infections induce plants' systemic resistance. In case of infection of plants with microbes, the pattern recognition receptors (PRRs) present in the plasma membrane of plants recognize microbe- or pathogen-associated molecular patterns (MAMPs or PAMPs) and activate the MAMP- or PAMP-triggered immunity (MTI/PTI) that inhibits infection in case of phytopathogen, while the MTI does not evade beneficial infections. There occurs continuous molecular signalling between the host plant and associated microbe and phytohormones, viz. jasmonic acid, salicylic acid and ethylene which plays an important role in the defence responses triggered by both beneficial and pathogenic microbes. Successful phytopathogenic microbes secrete effector proteins which alter resistance signalling, and plants, in turn, had evolved a more specific immune response called effector-triggered immunity (ETI) where the microbial effector proteins are recognized and handled by plant resistance (R) proteins. PTI provides immunity before the pathogen gains entry into the plant, while R proteins come to rescue once the infection occurs (Glazebrook 2005; Chisholm et al. 2006; Van Wees et al. 2008; Trda et al. 2015).

### 2.3 Key Players Shaping and De-shaping Plant Microbiomes

Soil and host plants were considered to be the key factors responsible for shaping the plant-associated microbiomes. However, ranking their degree of influence in deciding the associated microbiomes are debatable as the results of scientific experiments were contradictory. Factors influencing plant microbiomes are illustrated (Fig. 2.1). Few investigations emphasized that diversity of plant-associated microbial community was greatly influenced by host plants (Grayston et al. 1998; Costa et al. 2006), while few studies highlighted the role of soil factors in shaping the plant microbiome (Buyer et al. 1999; Girvan et al. 2003; Horner-Devine et al. 2004; Fierer and Jackson 2006). Other abiotic factors include temperature, humidity, precipitation, wind patterns and light (quality and quantity), etc., which vary with season and have a profound effect on plant physiology and biochemistry, which in turn has a cascading impact on the native microflora of the soil and thereby the host plant. Marschner et al. (2001) reported that plant genotype and soil type should be considered as dependent variables to analyse their complex interactions in shaping associated microflora for better understanding and accurate results.

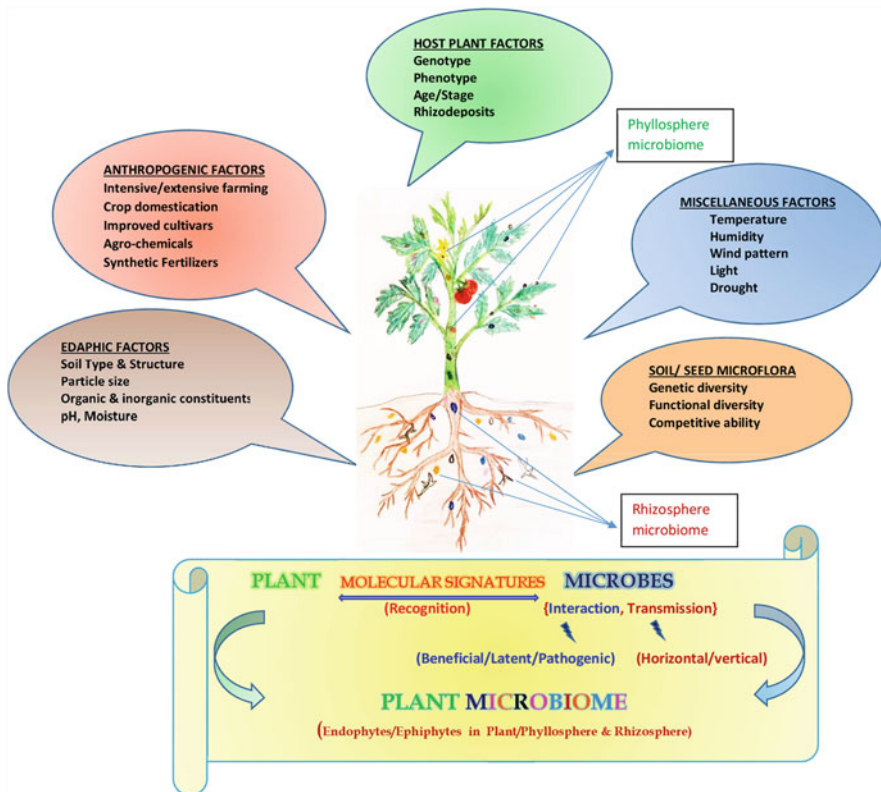


Fig. 2.1 Factors influencing plant-microbe interaction

### 2.3.1 Crop Domestication

Plants and their microbial partners have coevolved, and this statement holds good for all organisms on Earth and their associated symbiotic microbes. Anthropogenic activities and crop domestication have significantly affected the plant genetic makeup due to continuous selection for a preferred trait which was mostly focussed on yield and quality enhancement. This selection not only increased the desired alleles in the subsequent progenies but had also swept away genomic sections close to target regions leading to the loss in diversity of other desired traits related to plant morphology, biochemistry, etc., which may offer protection against insect herbivores, phytopathogens or influence the patterns of nutrition acquisition as well as recruitment of beneficial microbes from the soil, etc. Loss of genetic diversity due to domestication has been reported in crops like paddy (Ram et al. 2007), wheat (Haudry et al. 2007), barley (Bulgarelli et al. 2015), common bean (Bitocchi et al. 2013), sugar beet (Zachow et al. 2014) and lettuce (Cardinale et al. 2015). Germida and Siciliano (2001) reported that ancient plant races possessed diverse rhizobacterial community structure with pseudomonads being predominant followed by *Aureobacter*, while the modern cultivars exhibited less rhizobacterial diversity. Wild ancestral cultivars of legumes showed ability to attract and colonize diverse rhizobacterial species as compared to the domesticated pea (*Pisum sativum*), broad bean (*Vicia faba*), soya bean (*Glycine max*) and chick pea (*Cicer arietinum*) (Mutch and Young 2004; Kim et al. 2014). Similar studies on mycorrhizal association with wild primitive ancestors and modern crop cultivars showed that the primitive cultivars showed higher preference for mycorrhizal colonization and dependence as compared to improved modern cultivars of wheat (Kapulnik and Kushnir 1991; Hetrick et al. 1993; Zhu et al. 2001), breadfruit (Xing et al. 2012) and maize (Sangabriel-Conde et al. 2015). However, there were few exceptions where modern cultivars of annual crops were more responsive to mycorrhizal symbiosis as compared to ancestral ones in a meta-analysis (Lehmann et al. 2012).

Though crop domestication aimed to improve the quality and quantity of production as compared to their wild relatives, domesticated crops were poor supporters of self-sustained production systems and were unable to tap ecosystem services provided by nature and demanded assistance through external inputs in the form of synthetic fertilizers and plant protection chemicals which in turn polluted the ecosystem and hampered numerous beneficial interactions between host plant and microbes due to the loss of soil microbial diversity. The bacterial communities in domesticated agricultural fields were different from the adjacent native tall grass prairie ecosystem (Fierer et al. 2013), and conversion of Amazon rainforest to cultivable land showed a drastic reduction in microbial diversity (Rodrigues et al. 2013). Ramirez et al. (2012) showed that synthetic nitrogen amendments will suppress microbial biomass and soil respiration increasing copiotrophs (Actinobacteria and Firmicutes) and reducing oligotrophs (Acidobacteria and Verrucomicrobia). Weese et al. (2015) reported that continuous use of nitrogen fertilizers had resulted in reduced evolution of mutualistic rhizobia. Anthropogenic interventions and crop domestication affected the soil physiochemical properties and

thereby reduced its microbial density and diversity (Garcia-Palacios et al. 2013). In fact, human interference has significantly disrupted the coevolutionary pattern between host plants and their beneficial and pathogenic microbial counterparts and had posed a serious threat to healthy sustainable crop production.

### 2.3.2 Plant Genotype

Plant genotype is a key modulator of its microbiome composition. Host plant DNA fingerprints have proved its significance in drafting the diversity of root-associated microbes (Ofek et al. 2014; Matthews et al. 2019). Increase in evolutionary distance between plant species shows a proportional increase in the diversity of the assembled microbial community (Bouffaud et al. 2014). Apart from different plant species, genotypic variation within the same plant species also shows a profound difference among the associated microbiomes (Inceoglu et al. 2011; Peiffer et al. 2013). Plant genotype decides its phenotype including leaf morphological features like hairs, stomata, veins, etc., which influences microbial colonization (Lindow and Brandl 2003). Similarly, root architecture as influenced by the host plant genotype also affects microbial colonization. Fitzpatrick et al. (2018) showed that the diversity of endophytes increased with an increase in root hair density, while the diversity of rhizosphere microbes decreased with an increase in root length in case of angiosperms. Variation among microbial communities associated with different cultivars of potato (Weinert et al. 2011), maize (Peiffer et al. 2013), sweet potato (Marques et al. 2014) and barley (Bulgarelli et al. 2015) has been documented. Plant genotype determines the chemistry of root exudates and their blend. Root exudates contain sugars, organic acids, amino acids, flavonoids, nucleotides, enzymes and antimicrobial compounds and supply the rhizosphere with carbon-rich compounds which chemotactically attract or deter the soil microbes. Root exudates' chemical composition and proportion determines the quality and quantity of associated rhizosphere microbes (Micallef et al. 2009). Thus, rhizodeposits which are specific to plant genotype influence microbial community assemblage. It reduces the diversity of associated microbes but enriches the abundance of microbes belonging to specific taxa (Bulgarelli et al. 2012; Lundberg et al. 2012). The citric acid found in root exudates of cucumber was evidenced to attract *B. amyloliquefaciens* SQR9, while fumaric acid from root exudates of banana attracted *B. subtilis* N11 and stimulated biofilm formation (Zhang et al. 2014). Rhizodeposits of paddy primarily contained amino acids, viz. alanine, histidine, glycine, proline and valine, and carbohydrates, viz. glucose, mannose, arabinose, galactose and glucuronic acid, which facilitates the orientation of endophytic bacteria *Bacillus pumilus* and *Corynebacterium flavesces* (Bacilio-Jimenez et al. 2003). Plant roots also secrete compounds such as phenols and terpenoids which play a defensive role and suppress infection by phytopathogens. Cinnamic acid derivatives, namely, phenylpropanoids, were secreted by the roots of barley plant infected by *Fusarium graminearum* (Lanoue et al. 2010). Badri et al. (2013) documented that phytochemicals, especially phenolic compounds, played a major role in recruiting microbes in *Arabidopsis* rhizosphere.



For instance, canavanine, the amino acid present in the root exudates, attracted a particular group of microbes and deterred few other taxa, thereby shaping soil microbial community. Lebeis et al. (2015) reported the role of salicylic acid in sculpturing the root-associated microbiomes in *Arabidopsis*.

The composition of sugars and organic acid in root exudates varies in quantity and quality with plant species and developmental stage which in turn modulates antibiotic biosynthesis and offers protection against soilborne phytopathogens (Kravchenko et al. 2003). Acetosyringone and hydroxyacetosyringone (phenylpropanoids) secreted by damaged plants serve as an attractant for *Agrobacterium tumefaciens* (Dixon 1995). Rhizodeposits contain flavonoids which were evidenced to regulate quorum-sensing (QS) signals for *Pseudomonas aeruginosa* PAO1 (Vandeputte et al. 2011) and nodulation genes in rhizobia (Hassan and Mathesius 2012). Chen et al. (2015) evidenced that the vacuolar sugar transporter gene in *Arabidopsis* (*SWEET2*) controlled the glucose efflux from *Arabidopsis* roots, thereby inhibiting infection by *Pythium*. Szoboszlay et al. (2016) reported that the bulk soil treated with a flavonoid 7,4'-dihydroxyflavone commonly found in *Medicago sativa* root exudates showed enhanced species richness of bacteria belonging to the taxa *Acidobacteria*, *Nocardioidaceae*, *Thermomonosporaceae* and *Gaiella*. Candidate gene approach by mutation studies revealed the effect of plant genotype on the microbial community of *Arabidopsis thaliana* phyllosphere microbes. Cuticle formation was affected in *pec1* and *lacs* mutants, and this condition increased the diversity of microbial community composition as well as bacterial abundance. Additionally, ethylene signalling gene (*ein2*) of the host also influenced the composition of the microbial community (Bodenhausen et al. 2014). Vellend and Agrawal (2010) recorded that four main processes, namely, dispersal, drift, speciation and selection, influence the microbial community composition and its diversity.

### 2.3.3 Plant Developmental Stage

Structural and functional diversity of the microbial community associated with the plants is dynamic and changes throughout the plant phenology. Plant age and stage is another driver that shapes the associated microbial community. Microbial association and interaction starts from seed material. Seeds acquire their microbiome from the parent plant and transport them to the new environment by seed dispersal. In turn, the microbiome protects the seeds from pathogenic infections. Seed-borne microbes gain a competitive advantage and close association with the host plants on seed germination as compared to the opportunistic microbes from the surrounding soil. Though plant genotype determines the chemistry of root exudates, their titre is influenced by the age of the plant. Thus, the age of the plant impacts the rhizodeposits which concurrently influences the associated rhizosphere microbial community (Bulgarelli et al. 2013). Quantity and quality of rhizodeposits of the same plant species vary with age. In most cases, especially in annuals, the rhizodeposits decrease with increase in plant age. Rhizodeposits of young plants



were rich in low molecular weight compounds as compared to older plants (Vestergard et al. 2008). Plant age had a significant correlation with molecular and functional diversity of rhizosphere microbes as evidenced in case of many other crops including maize (Baudoin et al. 2002), *Medicago* (Mougel et al. 2006), wheat, pea and sugar beet (Houlden et al. 2008). Epiphytic bacteria are found to exceed in number as compared to the endophytes. Younger plants were found to have a higher population of endophytes as compared to the mature ones as evidenced by the concentration of endophytic bacterium *Herbaspirillum* in paddy, and this might be attributed to the fact that the non-pathogenic endophytes could not withstand the plant defence mechanisms which increases with the age of the plant (James et al. 2002). Denaturing gradient gel electrophoresis (DGGE) analysis of the *Arabidopsis* rhizosphere bacterial communities showed that exudates during seed germination attract more diverse rhizosphere microbes and the titre of exudates slowly declines with plants aging resulting in negligible differences between microbes in rhizosphere and the bulk soils (Micallef et al. 2009). Metatranscriptomics analysis of *Arabidopsis* rhizosphere microbiome showed that different stages of development of plants, viz. seedling, vegetative, bolting and flowering, expressed unique transcripts as the plants select the subset of associated microbes and shape their assemblage to tap their services (Chaparro et al. 2014). Sugiyama et al. (2014) observed that in soyabean the population of *Bacillus*, *Bradyrhizobium* and *Stenotrophomonas* was higher in the flowering stage as compared to other vegetative and pod-setting phase; however, no such differences were traced with the fungal communities.

### 2.3.4 Microbe-Microbe Interaction

Microbial species present in a community also influence the survival and performance of their microbial counterparts belonging to different taxa by the process of niche construction or modification. Competition for space and nutrition, production of secondary metabolites, effector proteins, polysaccharides, induction of plant defences, etc. by the microbial partners decide the species richness of the microbial community occupying the particular niche in the host plant. Primary microbes produce effector proteins and secondary metabolites that modify the host metabolism and establishment of other secondary microbes, thereby shaping the plant microbiomes. Certain microbes produce exopolysaccharides (EPS), phytoalexins, etc., which protect themselves and the other bacterial immigrants. Arbuscular mycorrhizal fungi (AMF) infection in plants was evidenced to alter the other microbial members in the community including bacteria which might be due to the effect of antibiotics or stimulatory compounds they produce (Marschner et al. 2001; Vestergard et al. 2008). Poza-Poza-Carrion et al. (2013) evidenced that the primary colonizers, viz. *Pseudomonas fluorescens*, *P. syringae* and *Erwinia herbicola*, determine the colonization of lettuce leaf by a human pathogenic strain of *Salmonella enterica*. The resident epiphytes assist the colonization by the immigrant by providing resistance to desiccation. Investigations on *Arabidopsis* leaf microbiome

sampled in different seasons documented six microbial hubs including fungi (*Udeniomyces*, *Dioszegia*), oomycete (*Albugo*) and bacteria (*Caulobacter* and two species of order Burkholderiales). An artificial infestation of *Arabidopsis* with *Albugo laibachii* has a negligible effect on the phyllosphere microbiome structure, while *Dioszegia* sp. infestation showed 100-fold reduction in *Caulobacter* sp. evidencing the disproportionate role played by microbial hubs in structuring the microbiomes (Agler et al. 2016). Hyperparasitism of primary colonizers is another mechanism used by microbes in shaping their community structure. *Pythium oligandrum*, an oomycete, effectively parasitizes another oomycete, *Phytophthora infestans*, causing late blight of potato. This opens up an avenue for use of the mycoparasitic *Pythium oligandrum* as an effective biocontrol agent of *Phytophthora* (Horner et al. 2012). Fungal endophytes *Neotyphodium* sp. and *Epichloe* sp. harboured in fescue species produced secondary metabolites loline which not only protected the plant from herbivory but also shaped the establishment of epiphytic microbes such as *Burkholderia ambifaria* that could utilize lolines as a source of carbon and nitrogen (Roberts and Lindow 2014).

### 2.3.5 Soil Factors

Soil type and physio-chemistry, viz. texture, structure, water retention potential, nutrient availability, pH, organic matter content, etc., decide the native microbial community structure and functioning evidencing their role in nutrient cycling in bulk soils. The same is true with rhizosphere soils as the soil physiochemical properties influence the availability of root exudates and in turn its role in microbial recruitment (Ho et al. 2017). Root exudates of seedlings of *Pinus radiata* that are grown in phosphate-deficient soils have been documented to produce double the amount of amino acids and amides than under normal conditions (Bowen 1969). Soil type plays a major role in determining the rhizobial community in soya bean, as compared to the plant genotype which has also been reported to influence rhizosphere microbiology. DGGE and sequence analysis showed that members belonging to Acidobacteria, Actinobacteria, Bacteroidetes, Proteobacteria, Firmicutes, Nitrospirae and Verrucomicrobia (Xu et al. 2009) and fungi belonging to Ascomycetes and Basidiomycetes (Wang et al. 2009) were predominant inhabitants of soyabean rhizosphere. Both the above experiments were carried out by the same research group in which they documented that black soils (Mollisol) supported the diversity of rhizobacteria, while dark brown soil (Alfisol) supported the diversity of fungal communities. Comparison of the bacterial community in differently sized soil particles from field subjected to long-term fertilization by 16S rRNA genes and TRFLP analyses showed that fine particles harboured diverse microflora and included members of *Holophaga* and *Acidobacterium*, while coarse particles supported lesser diversity and were enriched with  $\alpha$ -Proteobacteria. Additionally, this study evidenced that soil particle size initially determined the specificity of the associated microbial taxon as compared to fertilizer amendments (Sessitsch et al. 2001). Studies on soil microbial diversity at a continental scale by ribosomal DNA

fingerprinting showed that microbial diversity was affected by ecosystem type and the major factor being soil pH with neutral soils supporting rich diversity and acidic soils have a poor diversity (Fierer and Jackson 2006). Long-term fertilization significantly impacted the soil pH, soil carbon content and community diversity of bacteria and mycorrhiza in maize rhizosphere (Toljander et al. 2008). Soil deficient in nitrogen enhances the plant grown in it to secrete more of flavonols and flavones which initiates rhizobia-legume symbiosis evidencing the effect of soil chemistry in orchestrating plant rhizosphere microbiomes (Davidson and Robson 1986; Zhang et al. 2009). Similarly, plants grown in iron-deficient soils are evidenced to excrete more phenolic compounds via their roots, which greatly impacts the microbial community colonizing the rhizosphere region (Jin et al. 2014). In addition to the use of synthetic fertilizers and agrochemicals that deprive the soil microbial diversity and efficacy, cropping systems (Xiong et al. 2015a, b), and other agriculture practices including logging (Hartmann et al. 2014), soil tillage (Souza et al. 2016), etc. disturbs the soil integrity, its aggregation patterns, infiltration capacity and organic carbon content indirectly impacting structural and functional diversity of associated microbiomes. Conservation agriculture, which supports zero tillage and practises organic manuring positively influences, strengthens and stabilizes microbial community diversity and biomass (Wang et al. 2017).

### 2.3.6 Miscellaneous Environmental Factors

Several hypotheses including ‘niche theory’ and ‘neutral theory’ attempt to explain the species assemblage in microbial community, and both the theories emphasize the selective role of environmental variables on species assemblage (Mendes et al. 2014). Factors like soil temperature and water availability also influence the plant microbiome. Soil moisture has been evidenced to influence the composition of root exudates. Plants grown in conditions with limited soil moisture showed an increase in amino acid production which in turn affected the microbiology of rhizosphere (Katznelson et al. 1955). The temperature has a profound impact on the plant metabolism, on biochemistry and in turn on the root exudates. Studies revealed that root exudates of strawberry plants grown in low soil temperatures ranging between 5 and 10 °C produced more amino acids that affected the pathogenicity of *Rhizoctonia fragariae* and its infection in strawberry as compared to plants grown in 20–30 °C (Husain and McKeen 1963). Warmer and humid conditions of the tropics favour microbial richness especially those in the phyllosphere as compared to temperate ones (Vorholt 2012). Copeland et al. (2015) reported the effect of seasonal variation in phyllosphere microbiome succession. Toljander et al. (2008) from their scientific investigations hypothesized the impact of temporal variation and crop harvest in the bacterial community composition. Studies based on RNA operon copy numbers indicate that in environments subjected to disturbance as in case of agro-ecosystems, the microbial community contains organisms highly responsive to nutrient inputs but metabolically less active (Nemergut et al. 2016). Drought conditions are known to impact microbes associated with Poaceae plant roots causing a shift in the community structure (Santos-Medellín et al. 2017).

## 2.4 Role of Plant Microbiome in Preserving Plant Health

All living organisms have core microbiomes which act as secondary genomes which are tenfold larger than the host genome, and they decide the overall health and fitness of the host plant in a given ecosystem (Berg 2009; Bulgarelli et al. 2013; Gopal et al. 2013). The advent of molecular tools such as functional genomics and system biology approach depicts that the plant microbiomes are highly structured and forms complex networks which play a key role in plant health as well as the functioning of the ecosystem. Key stone species shapes the microbial hub taxa which in turn impacts the plant performance (van der Heijden and Hartmann 2016). Plant microbiomes, apart from determining the overall plant health and its ecological fitness by promoting plant growth (by enhancing nutrient and mineral availability and secretion of plant growth regulators) and evading abiotic stress (temperature, salinity, drought and heavy metals) and biotic stress (by reducing pests and disease incidence), also play a key role in biogeochemical cycle by the way of nitrogen fixation, denitrification, carbon fixation and release, methanogenesis, mineral fixation, solubilization, etc. Microbes interacting with plants in the ago-ecosystem are responsible for the release of a significant amount of methane and nitrous oxide from the system leading to greenhouse effects. Zolla et al. (2013) documented that core microbiome of soil under study contained members of *Aminobacter*, *Acidiphilum*, *Bacillus*, *Burkholderia* and *Phormidium* which were involved in alleviating abiotic stress in plants grown in them. Beneficial bacteria belonging to genera *Azospirillum*, *Achromobacter*, *Azotobacter*, *Bacillus*, *Burkholderia*, *Enterobacter*, *Microbacterium*, *Methylobacterium*, *Pseudomonas*, *Rhizobium*, *Pantoea*, *Paenibacillus* and *Variovorax* have been reported to promote plant growth (Pathma and Sakthivel 2013) and provide tolerance to abiotic (Grover et al. 2011) and biotic stress (Pathma et al. 2019).

Beneficial bacteria support plant growth directly by nitrogen fixation; phosphorous, potassium, calcium, zinc and silica solubilization and mobilization (Edwards and Burrows 1988); production of plant growth regulators such as indole-3-acetic acid (IAA), cytokinins, gibberellins and aminocyclopropane-1-carboxylate (ACC) deaminase; etc. (Glick 1995; Penrose and Glick 2002). They indirectly promote plant growth by evading biotic and abiotic stress. Beneficial microbes produce antimicrobial compounds, including antibiotics, siderophores, hydrogen cyanide and hydrolytic enzymes such as pectinase, chitinase, DNase, lipase etc., which protect the host plant from the invading phytopathogens and herbivores. Among the plant-associated microbes members of genus *Pseudomonas*, *Bacillus* and *Streptomyces* are known to be prolific producers of antibiotics that protect the host plants from phytopathogenic invasions. The compounds produced include phenazines, phloroglucinols, phenolics, pyrrole-type compounds, polyketides, peptides, bacteriocins, lantibiotics, cyclic lipopeptide, macrolactones, phospholipids, coumarins, aminopolyols, adenine nucleotide analogues, polyacetylene derivatives, aminoglycoside, quinones, etc. (Pathma et al. 2011). Members of *Pseudomonas* and *Bacillus* with inhibitory effect against many phytopathogens including *Xanthomonas* spp., *Agrobacterium tumefaciens*, *Erwinia amylovora*,

*Colletotrichum* spp., *Fusarium* spp., *Rhizoctonia solani*, *Helminthosporium* sp., *Pestalotia theae*, *Macrophomina phaseolina* and *Sarocladium oryzae* have been reported (Ho et al. 2017; Pathma et al. 2019). *P. fluorescens* WCS417r and *P. fluorescens* CHA0 induced systemic resistance in carnation and tomato, respectively, and protected them from infection by *F. oxysporum* (Van Peer et al. 1991; Ardebili et al. 2011). Endophytes *P. fluorescens* 89B-61, *Achromobacter* sp. F2feb.44, *B. licheniformis* AE6 and *Streptomyces* sp. Zapt10 were used to induce systemic resistance in cucumber and protect it from downy mildew caused by *Pseudoperonospora cubensis* (Kloepper and Ryu 2006; Sen et al. 2014). Similarly, plant-associated microbiomes also evidenced protection against herbivore pests. This includes control of lepidopterans, coleopterans and nematodes by *Brevibacillus laterosporus* (Ho et al. 2017); cotton aphids by *Bacillus pumilus* INR-7 (Stout et al. 2002); and wheat aphids by a mixture of *Pseudomonas* sp. strain 6 K and *Bacillus* sp. strain 6 (Naeem et al. 2018). PGPR strains were also lethal to blue-green aphids (Kempster et al. 2002), green peach aphids (Boughton et al. 2006) and termites (Sindhu et al. 2011).

Plant growth-promoting rhizobacterium, *Burkholderia phytofirmans* PsJN, was reported to impart cold tolerance in grapevine plants inoculated with it (Barka et al. 2006). Verma et al. (2015) reported plant growth-promoting properties of a psychrotolerant epiphytic strain *Methylobacterium phyllosphaerae* IARI-HHS2-67, isolated from wheat phyllosphere. *Pseudomonas* sp. DSMZ 13134, *Bacillus simplex* and *B. amyloliquefaciens* subsp. *plantarum* were reported to protect maize against cold stress (Bradacova et al. 2016), and members of *Pseudomonas*, *Arthrobacter*, *Flavobacterium*, *Pedobacter* and *Flavimonas* protected tomato seedlings from chilling injury (Subramanian et al. 2016). *Pseudomonas* sp. strain AKM-P6 offered protection to sorghum against increased temperature (Ali et al. 2009), while *P. putida* AKMP7 provided thermotolerance and growth promotion in wheat under heat stress (Ali et al. 2011). The mechanisms involved included increased production of cellular metabolites, proteins, amino acids such as proline, chlorophyll and sugars and reduced activity of antioxidant enzymes and reduced membrane damage. *Pseudomonas stutzeri*, *P. aeruginosa* and *P. fluorescens* provided halo tolerance in tomato plants (Tank and Saraf 2010), endophytic *P. pseudoalcaligenes* offered salinity tolerance in paddy (Jha et al. 2011), rhizobacteria *Dietzia natronolimnaea* protected wheat from salt stress (Bharti et al. 2016) and *Achromobacter piechaudii* ARV8 and *P. fluorescens* Pf1 protected tomato (Mayak et al. 2004) and green gram (Saravanakumar et al. 2011), respectively, from water stress. *Kluyvera ascorbata* protected canola from nickel toxicity (Burd et al. 1998), while *Photobacterium halotolerans* strain MELD1 offered protection to *Vigna unguiculata* ssp. *sesquipedalis* against mercury toxicity (Mathew et al. 2015). An endophyte *Achromobacter xylosoxidans* F3B detoxified aromatic pollutants from *Chrysopogon zizanioides* and *A. thaliana* (Ho et al. 2013).

Thus, plant microbiomes are potential reservoirs that could be tuned and recruited systematically so as to offer maximum beneficial services for agriculture and thereby to mankind. The continuous evolution of plants and associated microbes both good and bad needs constant research to update knowledge and find prominent solutions

to the selection pressure caused by phytopathogens. Microbial diversity can be employed as efficient biomarkers to identify healthy microbiomes and utilize them systematically in breeding and biological control programmes which will help us conserve the biodiversity preserving ecosystem health and ensure self-sustainable agricultural production systems (Berg et al. 2017).

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## 2.5 Molecular Tools for Analysing Microbial Community Diversity and Their Interaction with Host Plant

Though microbial culturing techniques and biochemical analysis had appreciably contributed for studies on microbial taxonomy and functional diversity as well as their interaction with host plants until the last century, the advent of molecular techniques has added new insights. Some molecular diagnostic tools used for studying plant-microbe interaction are depicted (Table 2.1). Culture-dependent methods enabled us to study only a small portion (< 1%) of microbes especially confining it to aerobic bacteria or particular taxa, viz. *Pseudomonas*, *Bacillus*, etc., (Staley and Konopka 1985). The limitations were addressed by microscopic analysis of environmental samples that could enable visualization of the live or fixed microbe by using high-resolution techniques, viz. confocal microscopy, electron microscopy and fluorescence microscopy including fluorescence in situ hybridization (*FISH*) and photoswitchable fluorophores for single-molecule localization microscopy (SMLM) (Coltharp and Xiao 2012). Though these techniques provide high-resolution images, identification and classification of the microbes in a community becomes challenging even for an experienced taxonomist and at times misleading where biochemical profiling and molecular fingerprinting had come to the rescue (Hugerth and Andersson 2017). An array of techniques including the use of small subunit (SSU) of the ribosomal RNA (rRNA) gene, ribosomal internal transcribed spacer (ITS) (Woese and Fox 1977; Pace et al. 1985), denaturing gradient gel electrophoresis (DGGE) (Muyzer et al. 1993), analysis of phospholipid-derived fatty acids (*PLFA*) (Tunlid et al. 1985; Buyer et al. 1999; Willers et al. 2015), in vivo expression technology (IVET) (Osbourne et al. 1987; Rainey et al. 1997), terminal restriction fragment length polymorphism (T-RFLP) analysis (Liu et al. 1997; Lukow et al. 2000), automated ribosomal intergenic spacer analysis (ARISA) (Fisher and Triplett 1999), fluorescence induction promoter traps (Rediers et al. 2005), microarray based on 16SrRNA (Ehrenreich 2006; Sanguin et al. 2006), 454 pyrosequencing, analysis of total nucleic acids from the environment, metagenomics (Handelsman 2004; Erkel et al. 2006; Leveau 2007), ultradeep sequencing (Velicer et al. 2006), transcriptome analysis (Mark et al. 2005; Yuan et al. 2008), flow cytometry for in situ antifungal gene expression (De Werra et al. 2008), use of isotope probes (Haichar et al. 2008), real-time PCR (RT-PCR), chromatography techniques, Fourier transform infrared spectroscopy (FTIR), nuclear magnetic resonance (NMR) (Wu et al. 2009), differential fluorescence induction (DFI), signature tagged mutagenesis (STM), single-molecule real-time (SMRT) sequencing (Walder et al. 2017), etc. provides clear, detailed insights on plant microbiomes. Multiphasic approaches,

**Table 2.1** Molecular diagnosis of plant-microbe interaction

S. no	Host plant specimen	Associated microbial domain studied	Diagnostic tool	Reveals	References
1	Soybean	Bacteria	Shotgun metagenomics	Identification of beneficial functional traits	Mendes et al. (2014)
2	<i>Jacobaea vulgaris</i>	Bacteria	16S rRNA sequencing and shotgun metagenomics	Assembly of bacterial rhizosphere communities	Yan et al. (2017)
3	<i>Lilium davidii</i> var. <i>unicolor</i>	Bacterial and fungal communities	Illumina MiSeq sequencing of 16S rRNA and ITS gene amplicons	Identification of biological control agents against soilborne pathogens	Shang et al. (2016)
4	<i>Panax notoginseng</i>	Fungi	Illumina MiSeq of fungal ITS gene markers	Rhizospheric soil and root endogenous fungal diversity for plant health and soil fertility	Tan et al. (2017)
5	Boreal pine forest ( <i>Calluna vulgaris</i> , <i>Vaccinium myrtillus</i> and <i>Vaccinium vitis-idaea</i> )	Bacteria	qPCR and next-generation sequencing (NGS) of 16S rRNA	Root- and hyphae-associated bacteria may have a functionally more active role in soil microbiome	Timonen et al. (2017)
6	<i>Saccharum</i> sp.	Bacteria	16S rRNA gene multiplex amplicon sequencing	Identification of community-based culture collection (CBC) having novel plant growth-promoting traits	Armanhi et al. (2018)
7	<i>Vitis vinifera</i>	Bacterial and fungi genera	16S rRNA gene sequencing and of the internal transcribed spacer (ITS)	Identification of dominated bacterial genera in microbial community of <i>Vitis vinifera</i> phyllosphere present in French Mediterranean region	Singh et al. (2018)
8	<i>Populus deltoides</i> and <i>P. trichocarpa</i>	Bacteria	16S rDNA PCR followed by Sanger sequencing	Genomes of plant-associated bacteria are surprisingly consistent across phylogenetically diverse bacterial taxa and that some functions are even shared with PA eukaryotes	Levy et al. (2018)

(continued)



Table 2.1 (continued)

S. no	Host plant specimen	Associated microbial domain studied	Diagnostic tool	Reveals	References
9	<i>Capsicum annuum</i>	Bacteria	16S rRNA PCR-DGGE analysis	95% of in vitro microbiome promotes plant growth and stress resistance	Marasco et al. (2012)
10	<i>Vitis vinifera</i> cv. barbera	Bacteria	16S rRNA PCR-DGGE analysis	Root-associated bacterial microbiome improves plant adaptation to drought through a water stress-induced promotion ability	Rolli et al. (2015)
11	<i>Arabidopsis thaliana</i> Col-0	Bacteria	Transcriptome analysis	A subset of commensals trigger expression of defence-related genes and thereby may contribute to plant health upon pathogen encounter	Vogel et al. (2016)
12	<i>Arabidopsis thaliana</i>	Bacteria	16S rRNA gene sequencing	Salicylic acid controls colonization of specific bacterial families in roots	Lebeis et al. (2015)
13	<i>Arabidopsis thaliana</i>	Fungus ( <i>Piriformospora indica</i> )	Gene expression analysis by qRT-PCR	Suppression of innate immune system in roots confers the colonization of fungus ( <i>Piriformospora indica</i> ) in <i>Arabidopsis</i> roots	Jacobs et al. (2011)
14	<i>Arabidopsis thaliana</i>	Bacteria	16S rRNA and whole-genome sequencing	Identification of taxonomic overlap between the leaf and root microbiota	Bai et al. (2015)
15	<i>Crotalaria pumila</i>	Bacteria ( <i>Methylobacterium</i> sp. Cp3)	16S rRNA gene sequencing	Seed endophyte bacteria ( <i>Methylobacterium</i> sp. Cp3) colonize in the root cortex cells and xylem vessels of the stem under metal stress	Sanchez-Lopez et al. (2018)

metagenomics, metaproteomics, metatranscriptomics including next-generation sequencing (NGS) technologies and bioinformatics, had provided a novel, deeper and comprehensive insights on plant-microbe interaction (Turner et al. 2013a, b; Mendes et al. 2014; Hacquard et al. 2015). Ramirez-Flandes et al. (2019) showed that genes controlling the redox potential of the microbes could possibly be used to characterize the microbial assemblies in the corresponding microbiomes which are interlinked to the energetics of the ecosystem, thereby enabling differentiation among microbes in highly dynamic complex associations.

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## 2.6 Engineering Plant Microbiomes for Sustainable Production Systems

Extensive research that would unlock the complexity of plant-associated microbiomes and their ecology will provide us with clues to understand the process of microbial assembly as well as their links and importance in plant performance. The advent of molecular tools had evidenced the advantage of transferring the core soil microbiome over the previous practice of inoculating the crops with single strain or consortium of beneficial microbes since plant growth promotion or biotic and abiotic stress evasion was evidenced to be the combined function of the rhizosphere microbiome instead of a single taxon. Thus, the practice of inoculating the core microbiome as such by transferring the disease suppressive soils as rhizosphere substitutes can improve the success rate of the use of microbes for improved crop production and protection (Berendsen et al. 2012). Construction of synthetic microbiomes with beneficial microbes and inoculating the plant with it artificially is one of the techniques in microbiome engineering. Mueller and Sachs (2015) emphasized the use of host phenotype as a probe for the selection of members of the synthetic microbiome. This technique is termed as host-mediated microbiome engineering. One simple cost-effective means of engineering root microbiomes is mixing up of disease suppressive soils with disease conducive soils which had proved its potential in controlling black root rot in tobacco (Kyselkova et al. 2009), *Rhizoctonia* infection in sugar beet (Mendes et al. 2011) and common scab in potato (Rosenzweig et al. 2012). Analyses of soil metagenome evidenced that core microbiome of the soil contained 17 bacterial communities belonging to Actinobacteria, Firmicutes and Proteobacteria with biocontrol properties that were responsible for the disease suppressive nature of the soil. Among all the studies, bacteria belonging to Pseudomonadaceae was identified as key players responsible for disease suppression (Gopal et al. 2013). Cutting-edge molecular biology techniques, viz. next-generation sequencing, transcriptome profiling of multispecies (Schenk et al. 2012), bioinformatics tools (Lee et al. 2012) and advanced spectroscopy that helps in identification of microbial bioactive molecules (Watrous et al. 2012; Badri et al. 2013), provided deeper insights on the microbiome and the success rate of their use in sustainable agriculture. Apart from data on operational taxonomic units (OUTs), comprehensive data collection on OTU  $\alpha$  and  $\beta$  diversity, spatial and temporal persistence, metabolic networking and their studies in crop model will

assist in proficient assembling of robust microbiomes especially those associated with the rhizosphere as well as successful establishment and functioning of the introduced microbiomes in the new ecosystem (Shade and Handelsman 2012; Lozupone et al. 2012; Scheuring and Yu 2013). Identification and use of members of core microbiomes of plants and genetically engineering them with genes encoding essential proteins or compounds that help in crop protection improves the efficacy of the technique as the engineered microbe infects the host plant efficiently and transfers the required trait. For instance, *Pantoea agglomerans* (33.1), an endophyte of sugarcane with growth-promoting activity, was engineered with cry1Ac7 gene, and it provided excellent control of lepidopteran borer of sugarcane *Diatraea saccharalis*. Similar genetic modification with *Bacillus thuringiensis*  $\delta$ -endotoxin has been attempted in endophytes *Clavibacter xyli* and *Herbaspirillum seropedicae*. Since the endophyte colonizes the sugarcane tissue internally and hence the larval stage of the borer pest occupies the same niche, it could not escape the cry toxins. Thus, this mode of delivery enhances the success rate of the biopesticides than being applied as a foliar spray (Downing et al. 2000; Quecine et al. 2014).

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## 2.7 Future Perspectives and Conclusion

Projects funded by the National Institutes of Health and European Union intensified research on human microbiomes, which opened up new avenues in the field of human medicine. Similar co-ordinated and focussed research on plant microbiome will help us identify and appreciate beneficial microbiomes and integrate them in crop pest and nutrient management programmes and reap benefits of the services they provide. Understanding the plant microbiome and their interaction, which has a huge impact on the holobiont and the associated ecosystem, is an important research prospect and is highly challenging. Sampling techniques and data processing protocols need to be standardized as per research priorities in order to fill the knowledge gaps. In-depth understanding of the microbiome community and their functional diversity by advance molecular approaches like metagenomics and metabolomics can reveal the uncultivable hidden microbial partners and their role in plant health and other ecosystem services and help us utilize this versatile bioresource for sustained eco-friendly agricultural production systems which is the need of the hour to feed the increasing population with depleting resources without posing pollution pressure on the production system. Though plant-microbe interaction studies have been done since the beginning of the twentieth century, it is still a brooding area of research that could benefit the human community by their indispensable role not only in agriculture sector but also in medicine and environmental protection. Genetically modified crops can greatly impact the native microbiomes of the plant leading to unpredicted changes in the diversity of associated microbes which may be fruitful or detrimental. Hence, it is equally important to consider the plant-associated microbiomes while designing better performing hybrids or GM crops. Hence, the use of biotechnological tools in crop breeding and biocontrol programmes should be designed in a way to recruit beneficial communities as well as

to minimize the loss of microbial biodiversity so as to provide a self-sustained production system that enhances plant health, ecological fitness and performance.

**Acknowledgement** The authors wish to thank Dr. R. Nagarajprakash, group leader, Chemical Sciences Research Group, Lovely Professional University, Punjab, India, for his constructive criticism and support in preparing this book chapter.

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