
Plant-Microbial Interaction: A Dialogue Between Two Dynamic Bioentities

Khyatiben V. Pathak and Sivaramaiah Nallapeta

Abstract

Since the time of evolution, the earth's plant floral community remained associated with ubiquitous population of microbes by a wide array of interactive relationships, ranging from symbiotic to parasitic. The ecology of plant-microbial association has influenced the plant's diversity, metabolism, morphology, productivity, physiology, defence system and tolerance against adversities. Similarly, the microbial population has also been affected in terms of morphology, diversity, community composition, etc. In plant-microbial association, microbes obtain shelter, protection and nutrients from the plants either positively or negatively without affecting the plant's health. In symbiotic plant-microbial interaction, plants provide habitat, nutrients and protection against the adverse environment, while in return, the microbes render several benefits such as protection against pathogens, plant growth promotions, resistance towards abiotic stress, improved nutrient uptake and fitness. The microbial endophytes and epiphytes are generally regarded as plant symbionts. The antagonistic association between these two living systems, in which the plant antagonist kills the microbial pathogens by producing toxic phytochemicals or the microbial parasite adversely affects the plant's fitness by withdrawing essential plant nutrients for their own survival and altering the physiology of the host plant. How do the plants cross talk to the microbes to establish the associations? Various response-related signals drive such cross talks. The omics (genomics, proteomics and metabolomics) approach is being used to unveil the role of complex cryptic signalling process in the plant and microbe interaction. In this chapter, the existing understandings about the plant-microbial interactions and the roles of signalling mechanisms in such interactions have been discussed.

K.V. Pathak (✉)
Bioclues Organisation, IKP Knowledge Park,
Secunderabad 500009, AP, India
e-mail: Khyati835@gmail.com

S. Nallapeta
Bioclues Organization, IKP Knowledge Park, Picket
Secunderabad 500009, AP, India

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1 Introduction

During the course of evolution, microbes have developed association with the plant environment by establishing various interactions. Almost all the plants existing on earth harbour a single microbe or a variety of microbes (Lindow and Brandl 2003; Rosenblueth and Martínez-Romero 2006; Saharan and Nehra 2011). The microbes colonize in the plants for shelter, nutrient and protection against the adverse conditions, while in return microbes offer several interactive relationships ranging from symbiosis to parasitism (Rosenblueth and Martínez-Romero 2006; Wu et al. 2009; Reichling 2010). Sometimes, plants also exhibit defence-related responses towards the microbial pathogens by producing microbial-inhibitory phytochemicals or inducing self-defence in response to the chemicals secreted by microbes (Reichling 2010; Radulović et al. 2013). This association influences the plant's diversity, metabolism, morphology, productivity, physiology, defence system and tolerance against adversities (Lindow and Brandl 2003; Rosenblueth and Martínez-Romero 2006; van der Heijden et al. 2008; Wu et al. 2009; Saharan and Nehra 2011). Similarly, the microbial population residing in the plant is also affected in terms of morphology, diversity and community composition (Lindow and Brandl 2003; Montesinos 2003; Bever et al. 2012). In symbiotic association, the microbes and their host plant both get benefits from each other. The symbiotic interaction confers several benefits to the host plant such as plant growth promotion, protection from the phytopathogens, improved nutrient availability and uptake, plant fitness and improved tolerance to the abiotic stress (Lindow and Brandl 2003; Rosenblueth and Martínez-Romero 2006; Saharan and Nehra 2011). In some plant-microbial interactions, microbes colonize plant tissue without causing any benefits or deleterious effects to the host, and the host plant also accepts such flora as a component of the innate plant system. Such plant-microbial interactions are

regarded as a neutral relationship. The microbial pathogens invade the plant tissues, consume nutrients and release toxins that affect plant health. Such interactions can affect plant growth, development, nutrient dynamics, defence system, etc.

2 Plant Niches and Plant-Microbial Communications

The plant-microbial interactions are much more diversified in terms of their physiological and pathological functions. The plant system offers several ecological niches for the colonization of microbes and produces diversified bioactive phytochemicals in response to the microbial interactions (Narasimhan et al. 2003; Reichling 2010; Garcia-Brugger et al. 2006; Radulović et al. 2013). The microbial system also releases several active metabolites for communication with host plants to maintain a wide range of interactive relationships (Shulaev et al. 2008; Ryan et al. 2008; Braeken et al. 2008; Saharan and Nehra 2011). The plant comprises three major niches such as the rhizosphere, phyllosphere and endosphere for the entry of atmospheric and soil microbes. The interactive relationship between plants and microbes is mostly governed by the chemical signals, and they play a major role in the plant's growth, development and fitness (Bais et al. 2004; Shulaev et al. 2008; Braeken et al. 2008; Mandal and Dey 2008).

3 Rhizospheric Root Microbial Communication

The soil microbes generally enter in the plant system via rhizospheric roots. The root surface and exudates are nutrient-plenteous niches and attract the soil microflora (symbionts, pathogens). The thin layer of rhizosphere around plant roots is densely populated with a variety of microbes

such as bacteria, fungi, actinomycetes and algae. Among these microbes, bacterial population is found to be the highest in rhizosphere. This microbial diversity around the rhizosphere may influence the plant's physiology as a result of competitive colonization by rhizospheric flora in the plant roots for nutrients and habitat (Morgan et al. 2005). The symbiotic microbes offer protection to the plants against phytopathogen by competing for food and shelter. The interaction of plant microbes requires recognition of each other. Plants and microbes both produce diversified signalling molecules for recognition and communication (Bais et al. 2004; Badri et al. 2008a; Braeken et al. 2008; Mandal and Dey 2008). Root exudates comprise of various signalling molecules such as carbohydrates, proteins, phenolics, flavonoids and isoflavonoids (Narasimhan et al. 2003; Bais et al. 2004). The secretion of these molecules in the root exudates plausibly controlled by the expression of transporter proteins in the root system and the variation in the composition may depend upon the types of microbial interaction with roots (Sugiyama et al. 2006; Loyola-Vargas et al. 2007; Badri et al. 2008a, b). The root exudate of *Arabidopsis* is composed of sugars, amino acids, organic acids, flavonols, lignins, coumarins, auronones, glucosinolates, anthocyanins, carotenes and indole compounds (De-la-Peña et al. 2008; Mandal and Dey 2008). Liquid chromatography coupled with electrospray mass spectrometry (LC-ESI-MS) enabled the identification of more than 149 metabolites including 125 secondary metabolites in the *Arabidopsis* root exudates (De-la-Peña et al. 2008). The plant sugars and amino acids have a major role in energy metabolism and polymer biosynthesis which is essential for the growth and development of the plant. The sugars, amino acids and organic acids are chemoattractants which guide the motility of microbes (Smeekens and Rook 1997; Welbaum et al. 2004). Some exudates are also composed of antimicrobial compounds which provide protection to the plant system against phytopathogens (reviewed by Bais et al. 2004). This suggests that plants selectively allow certain microbes with the capability to detoxify antagonizing chemical agents to colonize in the plant. The composition and concentration of such chemoattractants and

antimicrobials secreted by the plant system are controlled by genetic and environmental factors (Bais et al. 2004). For instance, the endophytic bacteria exhibited a fivefold increment in chemotactic response induced by rice exudates than the non-plant-growth-promoting bacteria present in the rice rhizosphere (Bacilio-Jiménez et al. 2003). De Weert et al. (2002) have reported that root colonization of *Pseudomonas fluorescens* in tomato root is dependent upon the induction of flagellar chemotaxis by root exudates. The variation in the degree of chemotactic response induced by chemoattractants (sugars, organic acids and amino acids) among the *Azospirillum* strains has been observed by Reinhold and group (1985). This suggests that microbial competence is greatly dependent upon their capability either to take benefit of the specific plant environment or to adjust themselves against the altering conditions. The protection of a delicate unprotected plant from the attack of phytopathogens is mediated by the secretion of phytoalexins, defence proteins and certain phenolic compounds by plant roots in response to the pathogens (Garcia-Brugger et al. 2006; Mandal et al. 2010). This response is known as systemic acquired resistance. Certain phenolic acids and their derivatives, such as cinnamic acids, ferulic acid, hydroxy benzoic acids, syringic acid, salicylic acid, p-coumaric acid, 4-hydroxy aldehyde, tannic acid, vanillic acid, vanillin, vanillyl alcohol and glycosides, produced by the plant have a role in the induction of symbiotic rhizospheric plant-microbial interactions (reviewed by Mandal et al. 2010). Thus, the root exudate is a library of a complex mixture of biologically active molecules exerting several benefits to the plant and also an ideal source of novel biochemicals.

4 Phyllosphere and Microbe Interaction

The rhizospheric and atmospheric microbes move to the above-ground parts of the plant and generally colonize in the outer layer of the plants. These microbes are known as epiphytes (Lindow and Brandl 2003). They generally remained associated to the plant surface. In the phyllosphere, leaves are more exploited for studying the diversity and interactive relationship with microbes than buds

and flowers (Beattie and Lindow 1995; Jacques et al. 1995; Hirano and Upper 2000; Andrews and Harris 2000). The phyllosphere is considered to be a very large habitat for microbes ($\sim 6.4 \times 10^8 \text{ km}^2$) (Morris et al. 2002). Based on the surface area, the phyllosphere bacterial population of 10^{26} cell could be estimated for the tropical plants (Morris et al. 2002). The microbial population density of phyllosphere is large enough to establish beneficial, detrimental or neutral interactions with phyllosphere. The phyllosphere allows the colonization of diversified microbial genera including bacteria, yeast, fungi, algae, protozoa and nematodes with the highest population of bacteria ($\sim 10^8$ cells/g of aerial tissue) (Beattie and Lindow 1995; Jacques et al. 1995; Hirano and Upper 2000). The filamentous fungi are ephemeral and mostly colonize in the phyllosphere in the form of spores, while the rapidly sporulating fungi and yeast are actively colonizing the phyllosphere (Andrews and Harris 2000). The microbial population on the plant surface varies in their population size, shape within the plant of the same species over a short time period and change in environmental conditions (Hirano and Upper 1989; Ercolani 1991; Legard et al. 1994). The nutritional and physical conditions of the phyllosphere also affect its microbial ecology (Wilson and Lindow 1994). The peculiar difference in the above- and underground atmosphere suggests the significant difference among the phyllospheric and rhizospheric bacterial population. The failing attempt to colonize two of the most common rhizosphere-specific microbes, i.e. *Rhizobium* and *Azospirillum*, in the plant leaf tissues provides an evidence of environmental-dependent differential specificity in microbial colonization of plant niches (Fokkema and Schippers 1986). Many physico-chemical factors restrict the colonization of microbes in the phyllosphere. To inhabit the phyllospheric tissues, microbes capable of modifying the microhabitat and utilizing the nutrients must be selected by the phyllosphere to colonize in it (Lindow and Brandl 2003). Microbes can improve the wettability by producing biosurfactants which facilitate penetration of microbes in the phyllosphere (Lindow and Brandl 2003). For instance, a biosurfactant tolassin

produced by *Pseudomonas tolaasii* had facilitated the motility of bacteria on the phyllosphere (Hutchison and Johnstone 1993). A biosurfactant syringomycin production by a common pathogenic as well as nonpathogenic epiphyte, *Pseudomonas syringae*, on the phyllosphere can affect the ion transport by triggering the formation of ion channels which release metabolites from the cell and cause cell lysis (Hutchison et al. 1995). The nonpathogenic strain also induces the release of a low concentration of syringic acid metabolites (Hutchison et al. 1995). Some of the bacterial epiphytes produce plant growth regulator indole-3-acetic acid (IAA) and their derivatives. IAA production by an epiphyte, *Pantoea agglomerans*, has been demonstrated for their role in the maintenance of fitness of the plant during drought condition (Brandl and Lindow 1998). At low concentration, IAA releases the plant cell wall saccharides (Fry 1989). This phenomenon can be correlated with the plant's fitness by IAA-mediated nutrient availability upon the release of plant cell wall saccharides (Fry 1989). The phyllospheric microbial community secretes cell wall exopolysaccharides and forms a slimy and sticky layer. This layer provides protection to the phyllosphere and its bacterial community against desiccation and reactive oxygen species (Kiraly et al. 1997). The sticky matrix of microbial epiphytes may increase the nutrient concentration in order to provide nutrients to the microbial epiphytes to survive on a nutrient-deficient phyllospheric environment (Costerton et al. 1995). The pathogenic bacteria are known to alter the environment of the host plant to facilitate interaction to modulate the metabolism of the host plant for its own benefit. The interaction of *P. syringae* with its host plant has been studied with great care to understand the role of various molecular determinants in their interactions (Hutchison and Johnstone 1993; Hutchison et al. 1995; Costerton et al. 1995). The hypersensitive response and pathogenicity regulated by *hrp* genes in *P. syringae* have been investigated in detail. A complete set of type III secretion protein pathways and related proteins encoded by *hrp* gene cluster is critical for the growth and fitness of *P. syringae* in the phyllosphere (Hirano et al. 1997, 1999; He 1998). The studies also

revealed that certain secretory metabolites induce *P. syringae* interaction with the host plant and modulate the host plant system in its favour (Hutchison and Johnstone 1993; Hutchison et al. 1995). Thus, this type III secretion pathway may also have a role in the colonization of the host plant phyllosphere by nonpathological strains.

Certain epiphytic bacteria interact with each other for shelter and nutrients. Such bacterial interactions may provide benefits to host plant by providing protection against phyllosphere pathogen and frost injury to the plant surface. The population epiphytic bacteria always remain affected due to the presence of antagonist on the phyllosphere (Lindow 1985). Certain phyllospheres such as flowers of deciduous trees, leaves of susceptible herbaceous plants and tropical tree species are generally susceptible to frost injury (Lindow 1985). The epiphytic bacteria with ice nucleation activity (Ice⁺ bacteria) have a role in frost injury (Lindow 1987). The *P. syringae* is an Ice⁺ bacterium which avoids damaging ice formation (Lindow 1987). The population of these bacteria on epiphytes has a positive effect on the ice nucleation temperature essential for the ice nucleation activity (Lindow 1995). Thus, the increase in population leads to an increase in ice nucleation temperature which makes the plant vulnerable to frost injury (Lindow 1987). The population size of such bacteria on the susceptible young phyllospheric region is generally very low and it increases over time. Thus, the protection of the phyllosphere from frost injury can be achieved by removing the Ice⁺ bacteria from the phyllosphere (Lindow 1987, 1995). The colonization of bacterial antagonists of Ice⁺ bacteria on the phyllosphere can be the potential strategy to control Ice⁺ bacterial population (Lindow 1995). The competitive colonization of Ice⁻ bacteria on the phyllosphere also provides an effective way of biological control (Lindow 1985, 1987, 1995). The use of lyophilized preparation *P. fluorescens* A506 for foliar spray application in order to manage population of Ice⁺ bacteria and protect agricultural crop from frost injury has been commercialized (BlightBan A506; Nufarm Americas, Inc., Sugar Land, TX). The precolonization or competitive colonization of antagonistic bacteria on the disease-prone phyllosphere provides an effective strategy of biocontrol of the phyllosphere

pathogen. The bacterial blight disease of apple and pear caused by *Erwinia amylovora* is the most devastating bacterial disease to the plant phyllosphere (Mercier and Lindow 2001; Pusey 2002). This pathogen establishes itself on the phyllosphere before the onset of infection, and prevents the colonization of this pathogen. The prior colonization of bacterial antagonist strains *P. fluorescens* A506 and *P. agglomerans*, on the phyllosphere, has been proven to be an effective way to suppress the colonization of *Erwinia amylovora* which resulted in the drastic reduction in disease symptoms (Lindow et al. 1996; Pusey 2002). The microbial population of the phyllosphere always undergoes changes upon the change in environment and also takes up a wide variety of plasmids leading to the increase in the rate of mixing of genes in the bacterial population (Lilley and Bailey 1997; Bailey et al. 2002). This indicates that the phyllosphere, specifically the leaf surface, is the ideal place for the horizontal transfer of genetic information and may provide a significant base for raising the diversified microbial ecology.

5 Endosphere and Microbial Communication

Some of the rhizospheric or epiphytic microbes colonize the internal tissues (endosphere) without causing any adverse effect to the host plants (Bacon and White 2000). These microbes are endophytes. The endophytes are selected naturally to colonize the endosphere. Some endophytes are seedborne, while others come through horizontal transfer. The endophytes are generally regarded as plant symbionts which can offer a variety of benefits to the plants (Miller et al. 1998; reviewed by Strobel et al. 2004; Compant et al. 2005; Rosenblueth and Martínez-Romero 2006; Ryan et al. 2008). The endosphere offers the habitat for bacteria, fungi and algae. The fungal diversity of endophytes in herbs, shrubs and trees has been studied in great detail for its wide variety of biological applications (reviewed by Strobel et al. 2004; Compant et al. 2005; Rosenblueth and Martínez-Romero 2006; Ryan et al. 2008). The

mycorrhizal fungi are ubiquitously present in most of the plants (Redecker et al. 2000). The fungi spread through the extraradical mycelia in the soil and increase the availability of nutrients to the plant in nutrient-deprived land zones. The mycorrhizal fungal community also solubilizes inorganic phosphorus, nitrogen and other essential nutrients and translocates to the plants from the soil (Finlay 2008). These fungi also impart other benefits such as increased water uptake and improved soil fertility and resistance towards pathogens, drought and herbivores. Moreover, it also helps the plant in carbon cycling to facilitate the carbon supply to the soil aggregates and other microbial communities (Finlay 2008). Like mycorrhizal fungi, other endophytic fungi also have shown to promote plant growth and protect the host plant from herbivores and pathogens by producing chemically novel bioactive metabolites (Finlay 2008; Smith and Read 2008; Kawaguchi and Minamisawa 2010). Some fungal endophytes have the ability to synthesize biologically important plant metabolites. The taxol-producing endophytic fungi such as *Taxus brevifolia* and *Taxus chinensis* are important examples that demonstrate the ability of microbes to synthesize biologically important phytochemicals (Wani et al. 1971; Guo et al. 2006). Taxol is an important phytochemical isolated from the yew tree (Wani et al. 1971). It is most effectively used in the treatment of tumours. Various endophytic proteobacteria, firmicutes, bacteroidetes and actinomycetes have been isolated from the agriculturally important crops (reviewed by Rosenblueth and Martínez-Romero 2006; Wu et al. 2009; Ryan et al. 2008). The species diversity of the microbial flora and their ability to produce beneficial metabolites are dependent on the types of plant niche, host developmental stage, surrounding environment, climate, etc. (Guo et al. 2006; Rosenblueth and Martínez-Romero 2006; Ryan et al. 2008). The endophytic populations in the tomato plants promoted plant growth, while the rhizospheric microbial community failed to do so (Pillay and Nowak 1997). The plant-growth-promoting bacteria of the genus

Azospirillum exhibit their beneficial effects in the rhizosphere, and the colonization in the internal cortical tissue is uncommon (Somers et al. 2004). The endophytic microbes are known to produce phytohormones, antimicrobial agents and siderophore; induce systemic resistance; and improve nutrient availability and uptake (Sturz et al. 1997; Pillay and Nowak 1997; Reiter et al. 2003; Somers et al. 2004; and reviewed by Rosenblueth and Martínez-Romero 2006; Ryan et al. 2008). The nitrogen-fixing bacterial endophytes contribute very less in total endophytic populations. The endophytic bacteria isolated from the sweet potato growing in N-limited soil were found to fix atmospheric nitrogen (Reiter et al. 2003). The presence of nitrogenase (*nifH*) genes further confirmed their ability of nitrogen fixation. The legume nodules also harbour endophytic bacteria. The *Rhizobium rhizogenes* and *R. leguminosarum* pv. *trifolii* have been isolated from the nodule of the red clover (Sturz et al. 1997).

6 Microbial Quorum Sensing and Plant-Microbial Interaction

Bacteria produce chemical signals to communicate with each other. This process is known as quorum sensing (QS). The bacterial cells recognize the signals sent by other bacteria which help the bacterial community to proceed for the particular function (Fuqua et al. 2001). The quorum-sensing signals are very much important in plant-bacterial interactions. In recent years, large numbers of signalling compounds have been identified (reviewed by Braeken et al. 2008). The gram-positive bacteria generally secrete peptide-based signals, while gram-negative bacteria release *N*-acyl homoserine lactone (AHL)-based quorum-sensing signals (Fuqua et al. 2001; Waters and Bassler 2005). The synthesis of AHL autoinducer signals depends upon the LuxI-like autoinducer synthase. The autoinducer signals diffuse freely through the bacterial membrane and bind with cognate LuxR-like proteins to form a LuxR-HSL

autoinducer complex to trigger transcription of target genes (Fuqua et al. 2001). The AHL-based QS systems in plant symbionts as well as pathogens influence colonization, swarming motility, biofilm formation, plasmid transfer, stress tolerance and synthesis of antimicrobials, extracellular enzymes, exopolysaccharides, biosurfactants, etc. (reviewed by Braeken et al. 2008; Waters and Bassler 2005). For instance, 3-oxo-C₈-HSL produced by *Agrobacterium tumefaciens* has a role in Ti plasmid transfer (Piper et al. 1993). The *P. aureofaciens* strain produces C₆-HSL which induces rhizosphere colonization and protease and phenazine production (Wood et al. 1997; Chancey et al. 1999; Zhang and Pierson 2001). The 3-oxo-C₁₂-HSL produced by *P. putida* IsoF is essential for the development of biofilm structure (Arevalo-Ferro et al. 2005). Some QS signals such as C₈-HSL and 3-oxo-C₆-HSL produced by *P. corrugate* CFBP5454 trigger hypersensitivity response in tobacco and tomato pith necrosis, respectively (Licciardello et al. 2007). The QS signals are important in nitrogen fixation, nodulation initiation, growth and biocontrol (reviewed by Braeken et al. 2008; Waters and Bassler 2005).

7 Potential Applications of Symbiotic Interaction

A variety of beneficial microbes have been identified and characterized for their beneficiary effects from the rhizosphere, phyllosphere and endosphere of the several plant species. The symbiotic interaction with microbes leads to confer positive effects on the plant's health and productivity. The microbes are known to produce a wide variety of bioactive compounds that have potency to promote plant growth, improve nutrient availability, protect against pathogens, protect from the environmental pollutants by detoxifying them, etc. Such properties of symbiotic microbes have great importance for their commercial applications in agriculture, environmental cleaning and pharmaceutical industry.

8 Plant Growth Promotion

The bacteria- as well as fungi-colonized rhizosphere, phyllosphere and endosphere are found to promote plant growth and development. The plant produces five major groups of hormones such as auxins, gibberellins, ethylene, cytokinins and abscisic acid which have a role in the regulation of plant growth. IAA is a phytohormone which is known as native auxin. IAA has a role in various plant developmental processes such as organogenesis, cell expansion, division, differentiation and gene regulation (Ryu and Patten 2008). The bacteria associated to the rhizosphere, phyllosphere and endosphere region of plants synthesize IAA and its variants (indole-3-pyruvic acid, indole-3-butyric acid and indole lactic acid) (Ryu and Patten 2008). The production of IAA variants is an important feature of the plant-microbial interaction which leads to several effects ranging from phytostimulation to diseased condition (Khalid et al. 2004; Narula et al. 2006). IAA produced by bacteria can promote plant growth at low concentration and also act as a signalling molecule to trigger physiological responses including colonization and defence response (Spaepen et al. 2007). The high concentration of IAA inhibits growth (Spaepen et al. 2007). The response to IAA production varies from plant to plant. At low concentration, it also releases saccharides from the plant cell wall and increases availability of nutrients to the plant (Fry 1989). IAA- and indole acetamide-producing bacteria induce growth and yield in wheat crop (Khalid et al. 2004). IAA production by rhizospheric bacteria positively affects the root and shoot weight in wheat plants (Narula et al. 2006). The bacteria from *Rhizobium*, *Microbacterium*, *Sphingomonas* and *Mycobacterium* genera isolated from the roots of the epiphytic orchid *Dendrobium moschatum* have been identified as the most active IAA producers (reviewed by Saharan and Nehra 2011). *Rhizobium* strains associated to root nodules of *Sesbania sesban* (L.) Merr and *Vigna mungo* (L.) Hepper have also been

identified as IAA producers (reviewed by Wu et al. 2009; Saharan and Nehra 2011). The rhizobia also have been used as biostimulants and biofertilizer for wheat production due to their ability to produce IAA, uptake minerals (nitrogen, phosphorus and potassium) from the soil and transport to the plant and increase the length of root and shoot (reviewed by Wu et al. 2009; Saharan and Nehra 2011). IAA production has been reported from the phyllospheric as well as rhizospheric microbes which provide total synergistic effect on the plants (Lindow and Brandl 2003; Saharan and Nehra 2011). The isolates *Bacillus*, *Pseudomonas* and *Azotobacter* from the chickpea were also found to produce IAA. In all *Rhizobium* species identified so far, 85.7 % rhizobia have been reported for their ability to produce IAA (Joseph et al. 2007). *Pseudomonas fluorescens* B16, a plant-growth-promoting rhizobacterium, synthesizes plant growth promotion factor and pyrroloquinoline quinone (Choi et al. 2008).

9 Nutrient Availability and Uptake

Plants need micronutrients for growth and development. The micronutrients can work as cofactors in various enzymatic processes. Iron, phosphorus and nitrogen are essential growth elements for all living systems. Though iron is considered as one of the most abundant metals in the earth, the bioavailability of iron is limited in certain environments such as the soil and plants due to the low solubility of Fe^{3+} ion. The limitation of bioavailable iron in the soil as well as the phyllosphere leads to increased competition for iron availability. In these iron-limited conditions, certain plant-associated microbes synthesize low molecular weight iron chelators known as siderophores (Whipps 2001). Microbes secrete siderophores to scavenge iron from the mineral phases and to make the soluble Fe^{3+} complexes which can be transported to the cells. Within the microbes, bacteria generally produce highly diverse types of siderophores. The gram-negative bacteria belonging to genera *Pseudomonas*,

Enterobacter, *Burkholderia*, *Rhizobia*, *Yersinia*, *Azotobacter* and *Escherichia* are known to produce siderophores (reviewed by Saharan and Nehra 2011). Based on the types of ligand used for ferric ion chelation, siderophores are classified into three major groups: catecholates, hydroxamates and carboxylates. The rhizobia produce hydroxamate and catecholate types of siderophores. The hydroxamate siderophores such as ferrioxamine B and pseudobactin are produced by rhizospheric bacteria (Sridevi and Malliah 2008). The gram-positive bacteria *Bacillus subtilis* and *B. anthracis* produce bacillibactin. The enterobactin, azotobactin, pyoverdine, yersiniabactin and ornibactin are the siderophores produced by *E. coli*, *Azotobacter vinelandii*, *P. aeruginosa*, *Yersinia pestis* and *Burkholderia cepacia*, respectively (reviewed by Saharan and Nehra 2011). Certain fungal strains such as *Ustilago sphaerogena* and *Fusarium roseum* also produce siderophores identified as ferrichrome and fusarinine C, respectively. The actinomyces including *Streptomyces pilosus* and *S. coelicolor* produce desferrioxamine types of siderophores (reviewed by Saharan and Nehra 2011). Various experiments have been carried out in recent years to study the effect of siderophore-producing microbes on plant growth. The endophytic *E. coli* strains isolated from the sugarcane and rye grass have the ability to produce maximum siderophores with improvement in the growth of the plants (Gangwar and Kaur 2009). The seed inoculation of *P. fluorescens* and *P. putida* strains resulted in increase in the plant growth and yield of various crops (Kloepper et al. 1980). The siderophore production ability of the plant-associated microbes is an important trait for plant growth promotion by improving iron availability to the plant. These siderophore-producing microbes may be used as potential plant-growth-promoting agents in agriculture.

Phosphate is another micronutrient essential for growth and development. Same as iron, phosphorus is also present in huge quantity but unavailable to plants due to its insolubility. Some microbes have the capability to solubilize phosphorous and make it available to plants.

The phosphate-solubilizing microbes have a role in the plant growth promotion by improving the nutrient uptake of plants. The bacteria that correspond to genera *Bacillus*, *Rhizobium* and *Pseudomonas* have been reported for their phosphate-solubilizing property. Fungi belonging to *Aspergillus* and *Penicillium* genera are also known as phosphate solubilization microbes (Saharan and Nehra 2011). The microbes solubilize phosphate by exuding organic acids and release phosphate in the solution. The combined use of *Bacillus* strains (M3 and OSU-142) resulted in increase in the yield, growth and nutrition level of raspberry plants (Orhan et al. 2006). In the total population of bacteria isolated from the root-free soil, rhizosphere and rhizoplane of *Prosopis juliflora*, the number of phosphate-solubilizing bacteria is high (Rivas et al. 2006). Arbuscular mycorrhizal (AM) fungi are also known for its phosphate-solubilizing capacity. The application of phosphate-solubilizing microbes in the soil may increase the availability of phosphorous to plants. The utilization of soluble phosphorous enhances vegetative growth and fruit quality in plants. The plant-associated microbes or mixed microbial population exhibiting plant-growth-promoting properties including phosphate solubilization, IAA and siderophore production may have potential in the development of efficient biofertilizer to improve crop yield in agriculture.

10 Nitrogen Fixation

The interaction of nitrogen-fixing bacteria with plant roots is one of the most extensively studied symbiotic associations. Plants of the *Fabaceae* family have been known for root symbiosis with *Rhizobium* spp. or *Bradyrhizobium* spp. (Wu et al. 2009; Kawaguchi and Minamisawa 2010). The bacteria penetrate the host plant via the root hair. The root exudates comprising of various flavonoid and isoflavonoid molecules induce expression of *nod* (nodulation) genes by bacteria in rhizobia (Mandal et al. 2010). The root cells form bacterial cells containing root nodule upon induction by bacterial cells released in the cytoplasm. The bacteria utilize nutrient from the

nodules, and in return, they fix atmospheric N_2 to the NH_4^+ . NH_4^+ further converts into amides and are transported via vascular tissues to the plant (Kawaguchi and Minamisawa 2010; Saharan and Nehra 2011). Along with *Rhizobium* spp. or *Bradyrhizobium* spp., other bacterial strains such as *Ralstonia*, *Burkholderia* and *Methylobacterium* also have been reported for their ability to fix nitrogen in the tropical *Fabaceae* plants (Kawaguchi and Minamisawa 2010). The use of nitrogen-fixing bacteria as biofertilizer and bioenhancer in nitrogen-poor soil may reduce the use of costly chemical fertilizers. The use of biofertilizer also reduces the accumulation of unwanted residues of chemical fertilizer which affects soil fertility.

11 Biological Control

Plant-associated symbiotic microbes protect plant from the pathogens by several means. The microbial symbionts prevent the entry of pathogens by competing for shelter and food. This competitive colonization of microbial symbionts provides protection to the host plants. Certain microbes are known to produce antibiotics which have growth-inhibitory activity against the pathogens. The antibiotic production ability also exerts protection to the plant from deleterious effects of plant pathogens. The plant-associated bacterial species of genera *Bacillus*, *Pseudomonas*, *Serratia* and *Streptomyces* are known for their ability to produce fungal cell wall lytic enzymes, antifungals and antibacterial compounds (Lindow 1985; Lindow et al. 1996; Whipps 2001; Mercier and Lindow 2001; Pusey 2002; reviewed by Ryan et al. 2008). The banyan endophytic strains belonging to *B. subtilis* and *B. amyloliquefaciens* exhibited broad-spectrum antifungal activity against phytopathogenic fungi including *Aspergillus niger*, *A. parasiticus*, *A. flavus*, *F. oxysporum*, *Alternaria burnsii*, *Sclerotia rolfsii*, *Chrysosporium indicum* and *Lasiodiplodia theobromae* (Pathak et al. 2012). The banyan endophytic *B. subtilis* K1 strain has been reported for the production of surfactin, iturin and fengycin types of lipopeptides with antifungal, biosurfactant, antimicrobial and antiviral

activity (Pathak et al. 2012). The *Pseudomonas stutzeri* exhibited inhibitory activity against *Fusarium solani* by producing chitinase and laminarinase (Mauch et al. 1988). The fungal antagonists, *Paenibacillus polymyxa* strains, isolated from wheat, lodge pine, green beans and canola have been reported for the production of antifungal compounds, fusaricidin A, fusaricidin B, fusaricidin C and fusaricidin D (Li et al. 2007). Oocydin A produced by the endophyte, *Serratia marcescens*, isolated from *Rhyncholacis penicillata* exhibited antifungal activity (Strobel et al. 2004). The *P. viridiflava* from grass produces antimicrobial compounds, ecomycins B and C (Miller et al. 1998). These antibiotic-producing strains may have a potential role as biocontrol agents in controlling plant disease caused by pathogens. The preinoculation of biocontrol agents can reduce the damage caused by the bacterial, fungal and viral plant pathogens. Various plant-associated microbes exhibiting broad-spectrum microbial antagonistic activity have been studied for their potential use as biocontrol agents in small scale as well as in the field level. The indigenous *Pseudomonas* strains isolated from rice rhizosphere exhibited an antimicrobial-compound-dependent suppression of bacterial leaf blight and sheath blight diseases caused by *Xanthomonas oryzae* and *Rhizoctonia solani*. *B. luciferensis* exerted a protective effect against Phytophthora blight in paper by increasing root colonization along with protease production and enhancing antimicrobial activities (Rangarajan et al. 2001). The antifungal volatiles from the *P. aeruginosa* Sha8 inhibited the growth of *F. oxysporum* and *Helminthosporium* sp. (Hassanein et al. 2009). Along with the production of antifungal compounds, plant-associated microbes confer protection to the plant by eliciting the plant defence system. This strategy is known as induced systemic resistance (ISR). In the ISR, the inducing bacterium does not exert any apparent damages to the host plant. Another defence response is systemic acquired resistance which is relatively similar to ISR response. In SAR, primary infection of pathogens activates their defence mechanism. The plant-associated microbes produce specific molecules known as

elicitors which trigger the plant defence responses. The chitosan from the fungal cell wall, lipopolysaccharides from gram-negative bacteria, elicitors from oomycetes of *Phytophthora cryptogea* and flg22 from bacterial flagellin are examples of microbial elicitors responsible for the induction of systemic resistance in the plant (reviewed by Garcia-Brugger et al. 2006).

12 Improvement in Phytoremediation by Plant-Associated Microbes

The plant has a natural tendency to absorb soil as well as atmospheric pollutants and remediate these environmental pollutants. The plants raise the endophytes harbouring degrading genes when they are grown in contaminated soil. The plant-associated microbes belonging to genera including *Pseudomonas*, *Burkholderia*, *Methylobacter* and *Herbaspirillum* have the ability to degrade a wide range of pollutants including methane, trinitro toluene, chlorinated benzoic acids, nitro aromatics, benzene, toluene, ethylbenzene, xylene, tetrachlorophenol and polychlorinated biphenyl (reviewed by Ryan et al. 2008). The methylobacterium endophyte of the hybrid poplar tree had the capacity to degrade nitro-aromatic compounds including 2,4,6,-trinitro toluene (Van Aken et al. 2004). The inoculation of *Pseudomonas* endophyte along with organochloride herbicide 2,4-dichloro phenoxyacetic acid (2,4-D) in pea plants showed no accumulation of 2,4-D (Germaine et al. 2006). Another experiment of the inoculation of 2,4-D without preinoculation of 2,4-D degrading strain leads to significant detection of herbicide and the signs of phytotoxicity such as reduction in biomass and leaf abscission. This experiment demonstrated the effectiveness of the *Pseudomonas* strain in improving phytoremediation of 2,4-D (Germaine et al. 2006). The phyllosphere and endosphere are the important niches for horizontal gene transfer through plasmid due to the aggregation of diversified microbes carrying degradative genes. The natural transfer of

degradative plasmid, pTOM-Bu61, in the endophytes suggests the importance of plant-associated microbes in increasing the diversity of microbes carrying the degradative genes which have importance in phytoremediation of environmental pollutants (Taghavi et al. 2005).

13 Concluding Remarks

In the universe, microbes seem to have coevolved with the plant system and established close association to perform biological functions. The plant system is an important niche to study microbial ecology and their variety of relationships with the plant. The symbiotic relationship between the plant and microbes confers a wide range of benefits to plant as well as microbial communities. In such interaction, the plant provides a platform for the microbes to perform diversified biological activity and produce bioactive metabolites which can have a positive impact on the plant's health. The beneficial plant-associated microbes can serve for their wide array of applications in agriculture, environmental clean-up and pharmaceutical field. These plant-associated microbes with the ability to produce pathogen-inhibitory activity and plant-growth-promoting potential can be used as potential biocontrol agents and biofertilizers in agriculture industries. The capability of these microbes to synthesize a bioactive metabolite with a diverse range of bioactivity such as antimicrobial, antifungal, antitumour and antiviral can be exploited in the development of a potent therapeutic agent in pharmaceutical industries. The capacity of biotransformation and degradation of toxic environmental pollutant leads to exploitation of plant-associated microbes in microbe-mediated phytoremediation to clean up the environment from the pollutants. Though the plant-associated microbes have been studied extensively, their interactive effects and functions have not been comprehensively understood. In detail an understanding of this plant-microbe interactive relationship may open the door to develop efficient biofertilizers, biocontrol

agents, novel therapeutics, environmental clean-up agents and efficient nutraceuticals and to make disease-resistant plants.

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