Microbial Interactions and Plant Health

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Abstract

With augmented population, hasty industrialization, and urbanization worldwide, land for agricultural production is declining faster, and there is a huge demand for ecologically viable and environmentally affable techniques in agriculture, competent of providing adequate sustenance for the increasing human inhabitants and of improving the quality as well as quantity of certain agricultural harvests. A great deal of endeavor focusing on soil biology and the agroecosystem as a whole is required, enabling better perception of the complex processes and communications governing the stability of agricultural lands and plant kingdom. The scientific advances in modern times, researching biodiversity, have revealed that microbial miscellany is of massive potential that can be explored through careful assortment of the same and their booming use may solve critical agricultural and environmental issues. Here, we promote the thought that considering the mechanism by which plants select and interact with their microbiomes may have a direct or indirect effect on plant health that further may lead to establishment of novel microbiome-driven strategies that can embark upon the development of a more sustainable agriculture.

Keywords

Association • Biofertilizers • Crop production • Inoculation • Microorganisms • PGPR • Phyllosphere • Rhizosphere • Symbiosis

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4.1 Introduction

The ultimate threats of the twenty-first century have become quite comprehensible in the last few decades. Climate change due to the enormous increase in the production of greenhouse gases is real (Crowley 2000). A typical characteristic of modern intensive agriculture worldwide, i.e., application of synthetic chemicals like fertilizers, fungicides, herbicides, and pesticides, has been reported as non-sustainable and having multiple harmful impacts on both human or animal and plant health as well as environmental well-being (Franks et al. 2006; Glick 2014). There is a legitimate need for renewable energy supplies (Cook et al. 1991; Jackson 1999). Under such circumstances, prospective alternatives to the use of chemical or synthetic inputs are microbial inoculants, environment-friendly microbial formulations that act as biofertilizers, phyto-stimulants, and/or microbial biocontrol agents (Olubukola et al. 2012).

Surplus microbes are there in each gram of soil, and microbial cells are found extensively in plant and animal tissues (Andreote et al. 2014). Microorganisms execute various metabolic activities indispensable for their own survival (Sengupta and Gunri 2015), and useful properties of such microbial inoculants could be manifested either by direct endorsement of plant growth through nutrient recycling or indirectly by defending plants from phytopathogens, or by invigorating tolerance to some of the abiotic strain in plants, which grow under nonoptimal ecological factors including soil, higher or lower temperature, acidity, salinity, drought, and heavy metals as well (Penrose and Glick 2003; Kang et al. 2014) .The varied community of microbes develop a metagenome of information that also extends to both outside and inside of the human body (Ahmed et al. 2011). Microbes are also capable of playing major roles in the development of soil aggregates that help in stabilization of the topsoil (van Veen et al. 1997) and improvement of soil health and can help in ecological detoxification, wastewater treatment, etc. (Ahmad et al. 2011). The mechanisms governed by microbes in the regulation of physiological processes of their hosts have been comprehensively studied in the light of latest findings on microbiomes. Even though there is no lucid depiction of the overall function of the plant microbiome, there is considerable confirmation that these communities are involved in infection control, enhanced nutrient attainment, and influence stress tolerance. Thus, currently, noteworthy venture is being exerted on research to build up such microbial inoculants which have positive plant growth properties in environmentally responsive sustainable cultivation (Barriuso et al. 2008a, b).

A large portion of favorable soil microorganisms are still undiscovered, and their environmental functions are pretty indefinite till date. Thus, enormous assays of microbial activities are the fundamental steps toward progress in innovative technologies for proficient exploitation of microorganisms for realization of sustainability in agriculture. Microbial involvement in combination with advancements in digital imaging, nanotechnology, and electronics may play a key role in solving universal challenges of the twenty-first century together with climate change (Ahmad et al. 2011).

This book chapter sums up features of microbial community that make up the plant microbiome and further presents a chain of studies recounting the underneath factors that contour the phylogenetic and useful plant-associated communities.

4.2 Microbial Interactions

Microbial populations interrelate and establish relations with each other and with higher organisms. Usually the relationship is nutritional, though other benefits may accrue, and the association can turn essential to the survival of one or both partners. There are several sorts of associations, viz., amensalism and competition, mutualism, parasitism protocooperation, synergism and commensalism, etc., between the organisms.

Odum (1971) has proposed the following relations:

(a) *Neutralism*, where the two microorganisms perform entirely autonomously
(b) *Symbiosis*, the two symbionts relying upon one another and mutually benefiting the affiliation
(c) *Protocooperation*, a relationship of reciprocal advantage to the two species but devoid of the cooperation being mandatory for their survival or for performance of some response
(d) *Commensalism*, in which only one species derives profit while the other is unaltered
(e) *Competition*, a situation in which there is a repression of one organism as the two species fight for restraining quantities of O_2, space, nutrients, or other common necessities
(f) *Amensalism*, in which one species is covered up while the following is not affected, often the result of toxin production
(g) *Parasitism* and *Predation*, the direct assault of one individual upon another
(h) *Synergism*, in field conditions the probable synergistic effect in the plant between inducing virus and other non-linked viruses which could be brought to those plants from outside sources

4.3 Microbe–Plant Interactions

Plants are exposed to huge numbers of microorganisms that are present in the topsoil and are found on leaves and stems. Plants are the major resource of nutrients for microorganisms being the prime source of organic carbon. Plants provide nutrients through shedding of leaves, pollen, etc., or through exudates or dead tissues in an indirect manner (Sivakumar and Thamizhiniyan 2012). In few instances, nutrients are provided straightway to microbes that form close relations with plants. Associations with plants can vary from those that are tremendously damaging to the plant, such as those with dangerous pathogens, through exchanges, which do not come out to influence plant growth, to advantageous ones such as those formed with

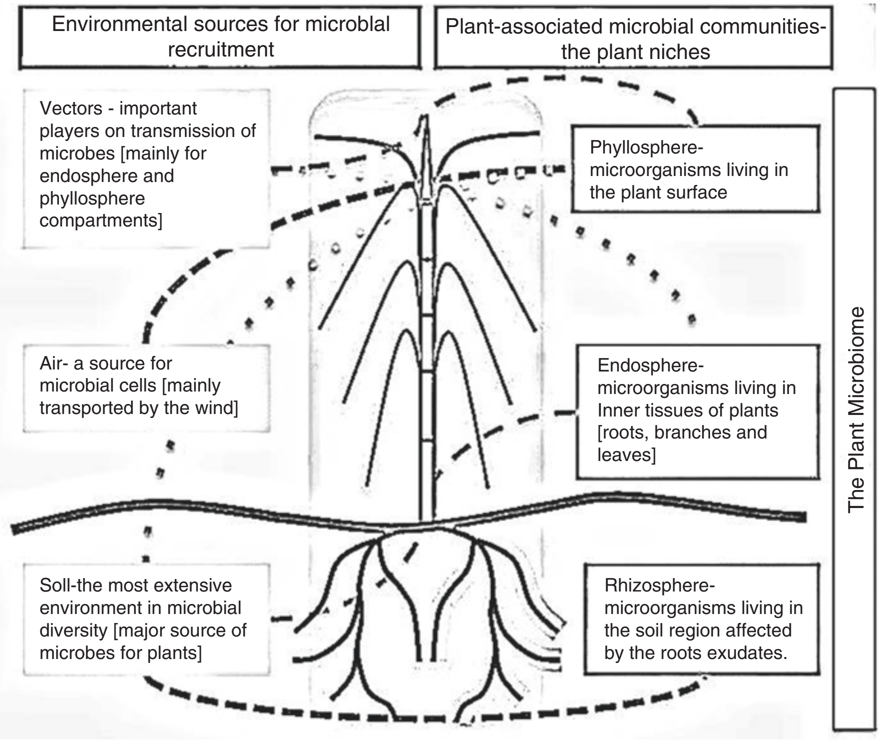

Fig. 4.1 Schematic depiction of the key sources for microbes that compose the plant-associated communities: the rhizosphere, endosphere, and phyllosphere. Width and fill of connections point out the role of ecological sources for the composition of microbial communities in plant-harboring niches

mycorrhizal fungi or nitrogen-fixing bacteria. For most microorganisms, exchanges with growing plants expand no further than the colonization of the surfaces of stems, leaves, and roots because these are regions where exudates are accessible.

Such microbiomes in plants may form divergent communities, like the ones from the rhizosphere, endosphere, or the phyllosphere (Hirsch and Mauchline 2012; Hardoim et al. 2008) (Fig. 4.1). In each of these niches, the “microbial tissue” is established by, and responds to, specific selective pressures (Andreote et al. 2014).

4.3.1 Rhizosphere and Root Exudates

The rhizosphere is the frontier between plant roots and soil where communications among numerous invertebrates as well as microbes influence plant growth, biogeochemical cycles, and indulgence to biotic and abiotic strain (Philippot et al. 2013).

In rhizosphere microbial action is generally high. Hiltner (1904) observed the zone of extreme microbial commotion around the roots and named it as rhizosphere (as cited by Hartmann et al. 2008). Roots emit considerable amounts of sugars, amino acids, hormones, and vitamins, which promote such a widespread growth of fungi and bacteria that these organisms often form microcolonies on the surface of the roots. Primarily roots contain little or no microbial colonization but with advancement in plant growth, in the soil, root exudates, comprising a combination of 10 sugars, 10 organic acids, about 18 amino acids, mucilage, etc., along with other cell exerts or root caps that influence on microbial colonization (Griffin et al. 1976). The chemicals in the forms of root exudates, released in the proximity of plant rhizosphere, are known to belong from the vital group of carbohydrates, phenols, organic acids, protein, and lipid along with other cellular components (Nguyen 2003; Dini-Andreote and Elsas 2013). Root exudates have been grouped and are primarily classified into two major classes, viz., compounds of high molecular weight like polysaccharides and proteins and that of low molecular weight like amino acids, organic acids, sugars, phenolic compounds, and other secondary metabolites (Bais et al. 2006; Badri and Vivanco 2009; Narasimhan et al. 2003). From these molecules, few are linked with establishment of key portions of the microbial community (generally metabolized by a good number of soil organisms, e.g., glucose), but other compounds released are capable of activating precise groups of organisms (those related to signaling and chemo taxis, e.g., flavonoids) (Nguyen 2003; Jones et al. 2004).

Quantitative and qualitative compositions of exudes from plant roots are generally determined by the plant species, plant developmental stage, cultivar, and various environmental factors, including soil pH, temperature, type of soil, as well as presence of microorganisms in soil (Badri and Vivanco 2009; Uren 2000). These differences fabricate microbial communities in the rhizosphere that have a definite degree of specificity for each plant species.

4.3.1.1 Mechanism of Root Exudation

Plants communities employ a variety of transportation mechanisms to export and exude compounds in the soil rhizosphere (Badri and Vivanco 2009; Weston et al. 2012). Usually, roots can release root exudates through active or passive mechanisms by means of secretion or diffusions, respectively. Majority of low-molecular-weight organic compounds are released from plants through a passive process. Small polar and uncharged molecules are elated by direct passive diffusion, a procedure that depends on membrane permeability, the polarization of the exuded compounds, and cytosolic pH (Badri and Vivanco 2009). Plant root cells release additional substances, like resultant polysaccharides, proteins, and other metabolic derivatives, with the help of various membrane-bound proteins (Weston et al. 2012). These carrier proteins comprise the ATP-binding cassette (ABC) transporters (Badri et al. 2008, 2009a; Loyola-Vargas et al. 2007; Sugiyama et al. 2008), multidrug and toxic compound extrusion (MATE) family (Yazaki 2005), the key facilitator super family (Reddy et al. 2012), and the aluminum-activated malate transporter family (Weston et al. 2012). Though the detailed functions of these membrane-bound transport proteins are not well stated, they have been connected with the transfer of a wide range of compounds into the rhizosphere. Badri et al. (2008, 2009a) found that 25 ABC transporter genes were notably overexpressed in the *Arabidopsis thaliana* (L.) Heynh. roots and played significant roles in these discharge processes. Adding up to ABC transporters, MATEs are also dynamic transporters that export a large variety of substrates across membranes by using the electrochemical gradient of other ions (Weston et al. 2012). Many MATE genes play important role in exporting different compounds, such as plant-derived alkaloids, toxic compounds, antibiotics, citrate anions, and phenolic compounds, out of the cells of plant roots, which have been identified as well as characterized in *Arabidopsis* (Diener et al. 2001; Li et al. 2002; Liu et al. 2009), sorghum (Magalhaes et al. 2007), barley (Furukawa et al. 2007), and rice (Ishimaru et al. 2011).

4.3.1.2 Rhizosphere Microbes Influence Plant Root Exudation

Plant root exudation is also influenced by the microbes (fungi and bacteria), colonized in the rhizosphere (Jones et al. 2004; Leyval and Berthelin 1993; Matilla et al. 2010a, b). Several studies have shown that the arbuscular mycorrhizal fungi colonization can alter plant root exudation qualitatively, e.g., augmenting secretions of N, phenolics, and gibberellins and minimizing secretions of total sugars, potassium ions, and phosphorus (Jones et al. 2004).

Preceding studies have revealed that various ectomycorrhizal fungal taxa have discrete influence on profusion and specifications root exudes of plants (Fransson and Johansson 2010; Rosling et al. 2004). The inoculation with ectomycorrhizal fungus and/or rhizobacteria can modify root exudation in both quantitative and qualitative aspects (Leyval and Berthelin 1993). Another latest research has revealed that both the profusion and individuality of root-associated fungi influence plant root exudation rates (Meier et al. 2013). Furthermore, in reaction to pathogen attack, plants discharge compounds as root exudates, such as oxalic acids, phytoalexins, proteins, and other unknown substances (Nelson 1990; Steinkellner et al. 2007). In addition to fungi, bacteria influence plant root exudation too. For instance, *A. thaliana* was found to produce distinct root exudation profiles when cultured with *Pseudomonas putida* KT2440 compared with the plant without *P. putida*, suggesting that bacteria are also modulating plant root exudation (Matilla et al. 2010a, b). In addition to plant root exudation, the soil microbiome may also influence the plant metabolome (Badri et al. 2013b). Distinct soil microbiomes were applied to *A. thaliana*, and this not only affected plant growth but also influenced the leaf metabolome, which in turn influenced the feeding behavior of the larvae of the herbivore *Trichoplusia ni* (Badri et al. 2013b). Similarly, inoculation of *Arabidopsis* plants under drought stress with distinct microbial communities originating from pine, corn, and *Arabidopsis* soils demonstrated that a sympatric microbiome, with a history of *Arabidopsis* growth, was able to alter the plant's ability to detect drought stress and increased its biomass production compared with the pine and corn microbial communities (Zolla et al. 2013). This may be due to the ability of soil microbes to modulate ethylene levels by degrading the ethylene precursor 1-aminocyclopropane-1-carboxylic acid (ACC) using the enzyme ACC deaminase (Glick 2005). The plant hormone ethylene is involved in a large number of plant responses particularly related to plant stress, and its production is synchronized by nutrition, light, temperature, and even the status and levels of other plant hormones (Glick 2005). High levels of ethylene aggravate stress responses and even weaken plant root growth (Argueso et al. 2007). A large number of soil microbes are able to ease plant stress responses to ethylene production by catalyzing the cleavage of ACC, the direct precursor to ethylene, into α-ketobutyrate and ammonia (Glick 2005; Stearns et al. 2012). Thus, lowering plant ethylene levels improves the plants' capacity to defend against a variety of abiotic and biotic stresses. ACC deaminase activity helps in ameliorating drought stress (Arshad et al. 2008), water stress, salinity stress (Mayak et al. 2004), and overall abiotic stress and also helps in growth promotion function of plants (Glick et al. 2007; Yang et al. 2009). For example, the soil bacterium *Achromobacter piechaudii* ARV8 that has ACC deaminase activity was able to increase tomato and pepper seedling biomass (Mayak et al. 2004). Recently, Stearns et al. (2012) studied the response of *Brassica napus* to ACC deaminase bacteria and showed that genes involved in auxin production were upregulated in the plant, while genes involved in ethylene stress response were downregulated. This provides a clear signal to the benefits ACC deaminase-containing bacteria have on the plant. Determining how the overall bacterial community is involved in mediating and reducing ethylene-mediated stress could create technologies to help the plant deal with abiotic stress.

4.3.1.3 Rhizospheric Interactions

4.3.1.3.1 Root Exudates and Plant–Microbe Interactions

In the last decade, the means by which root exudates mediate rhizospheric interactions have been extensively studied (Fig. 4.2) (Badri et al. 2013a; Broeckling et al. 2008; Chaparro et al. 2013; Doornbos et al. 2012; Micallef et al. 2009a, b).

Plant root-exuded phytochemicals can intervene a number of connections, such as plant–plant, plant–microbe, and plant–faunal. These interactions differ from neutral to advantageous or harmful (Mercado-Blanco and Bakker 2007; Raaijmakers et al. 2009). In few cases, microbes can change from pathogenic to symbiotic depending upon the environmental conditions (Newton et al. 2010). For example, rhizobia, symbiotic nitrogen (N)-fixing bacteria, range from a symbiotic to a neutral interaction with plants based on nitrogen levels in soils (Davidson and Robson 1986; Zahran 1999). Furthermore, under N-limiting conditions, legumes exude more flavones and flavonols to attract and initiate legume–rhizobia symbiosis (Coronado et al. 1995; Zhang et al. 2009).

In a similar way, mycorrhizal symbiotic relationships are governed by an equal exchange of nutrients and benefits for each member (Kiers et al. 2011). As, for example, in experiments on *Medicago truncatula* Gaertn., it was found that as more carbon was given to the mycorrhizal partner, the mycorrhiza in turn provided the plant with more phosphorous (Kiers et al. 2011).

4.3.1.4 Functions of Rhizosphere Microbiome

Microorganisms from the rhizosphere play significant roles in ecological vigor of the plant hosts. Significant microbial processes that are likely to take place in the

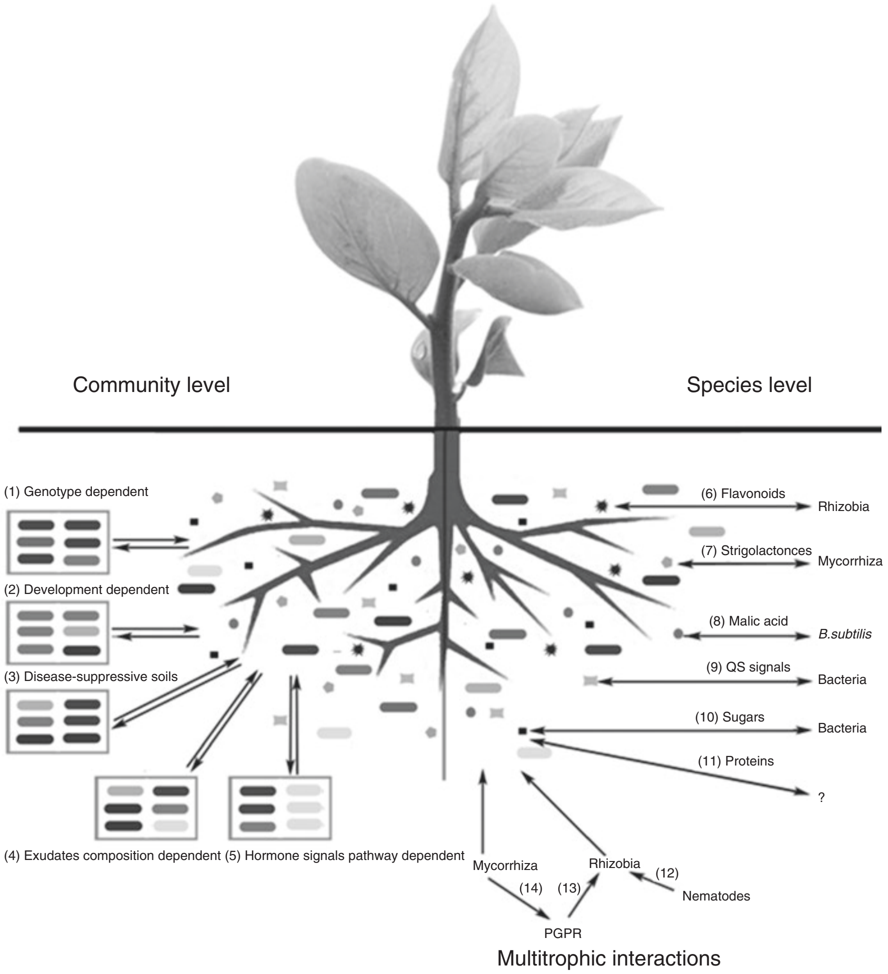

Fig. 4.2 Root exudates intervene a large number of rhizospheric interactions: at the species level (*right* side), multitrophic interactions (*bottom*), and at the community level (*left* side)

rhizosphere consist of pathogenesis and its counterpart, plant protection/growth promotion, along with synthesis of antibiotics, colonization of plants, and recycling of natural resources (Kent and Triplett 2002). Plant–microbe interactions may thus be considered as advantageous, neutral, or detrimental to the plant, depending on the specific microorganisms and plants concerned and on the existing environmental situation (Bais et al. 2006). Exploring the microbes, through sorting out their probable interactions with plant communities, has opened up a new interesting area for experimentations in rhizosphere research.

4.3.1.4.1 Beneficial Functions

Plant beneficial microbial interactions can be more or less divided into three categories. Firstly, microorganisms those, in association with plants, are accountable for its nutrition (i.e., microorganisms that augment the supply of mineral nutrients to the plant). In this case, though majority of microorganisms may not intermingle directly with the plant, their impact on soil abiotic and biotic factor undoubtedly has impacts on plant growth. Again, there are group of microbes, documented as biocontrol agents, which can stimulate plant growth and development in an indirect manner, by prevention of activities of pathogens. The third group comprising microbes, known to produce phytohormones, is responsible for direct plant growth promotion. On the other hand, it seems that neutral connections are found broadly in the rhizosphere of all crop plants. Saprophytes are accountable for different crucial soil processes, like mineralization of associated soil nutrient or turnover processes and decomposition of organic residues in soil. While such organisms neither benefit nor harm the plants straightway, absence of such microbes would undoubtedly influence plant health and productivity, and their presence is evidently essential for soil dynamics (Brimecombe et al. 2007).

Bacteria, living in the rhizosphere, exert their favor on growth of the plants globally and are referred as PGPR, i.e., plant growth-promoting rhizobacteria (Kloepper and Schroth 1978). The number of bacteria, recognized as PGPR, has been found to increase on a recent time, due to various advanced studies in bacterial taxonomy and better understanding regarding mechanisms of actions of various PGPR, covering a broader collection of plant species as well. Presently, PGPR comprise members from varied bacterial taxonomic classes (Lucy et al. 2004), and we are going to discuss a few instances in order to illustrate the mode of functioning and biodiversity of such bacterial community. A wide range of beneficial PGPR have been utilized profitably for inoculation of crop plants that include members from the genera *Azospirillum* (Cassán and García Salamone 2008), *Pseudomonas* (Loper and Gross 2007), *Bacillus* (Jacobsen et al. 2004), *Stenotrophomonas* (Ryan et al. 2009), *Serratia* (De Vleeschauwer and Höfte 2007), *Streptomyces* (Schrey and Tarkka 2008), and *Rhizobium* (Long 2001). *Rhizobium* (Long 2001) and some fungi from the genera *Trichoderma*, *Coniothyrium*, and *Ampelomyces* have also been described to be beneficial for the host plant (Harman et al. 2004). The mode of functioning of these PGPR has complex mechanisms to promote plant growth, development, and protection. Important among them are biofertilization (improving nutrient availability to plants), phytostimulation (plant growth promotion through production of phytohormones), and biocontrol (control of diseases, primarily through production of various antibiotic as well as antifungal metabolites and lytic enzymes and induction of plant defense responses). The genera *Bacillus* and *Pseudomonas* are known to be the predominant ones among PGPR groups from the rhizosphere (Morgan 2005). It is mentioned that in several instances regarding individual benevolent connections between plants and microbes, a wide range of mechanisms are actually implicated therein (Muller et al. 2009). The direct plant growth promotion functions are complicated enough to discriminate from disease control, and the comparative significance on a specific method can differ within dissimilar pathogen systems (Chet and Chernin 2002).

4.3.1.4.2 Pathogen Inhibition

Bacteria and fungi live in the region of roots and get nourished on root exudates and dead root cells. Competition amid microbial species in this region is rigid. In the fight for perseverance and establishment in the niche, bacteria use a number of strategies.

4.3.1.4.3 Antagonism

Root colonization not only results in high PGPR inhabitant densities in the root system, it also delivers antagonistic metabolites that are concerned in straight inhibition of plant pathogens (Shoda 2000; Raaijmakers et al. 2002). This includes inhibitions of growth of microbes, i.e., antibiosis, by use of diffusible antibiotics or organic volatile compounds, biosurfactants, and toxins and the mechanism of parasitism, which perhaps could involve synthesis of extracellular enzymes that can degrade cell walls, such as chitinase and β1,3-glucanase (Compant et al. 2005; Haas and Défago 2005). Degradation of the pathogenicity factors for the pathogens, like toxic substances released by favorable organisms, has also been recorded as mechanism for protection (Haas and Défago 2005). To exhibit the function of antibiotics in the process of biocontrol, the mutants impaired in the process of biosynthesis or mutants with overproducing habit have been utilized together with, in few cases, reporter genes, or probes have been used to explain efficient production of the compound in rhizosphere. For example, *Bacillus subtilis* strains were found to develop a number of strong antifungal metabolites, viz., kanosamine, zwittermicin A, and lipopeptides from fengycin, iturin, and surfactin families (Emmert and Handelsman 1999; Ongena and Thonart 2006). Excess synthesis of the extracellular protease in *Stenotrophomonas maltophilia* W81, a mutant strain, has been reported to exert improved biocontrol of *Pythium ultimum* (Dunne et al. 2000). Release of glucanase and chitinase by *Streptomyces* and *Trichoderma* species has been reported to play a pivotal role in myco-parasitism of phytopathogenic fungi (Whipps 2001).

4.3.1.4.4 Colonization

For all thriving plant–microbe connections, the capability to colonize plant habitats is vital (Lugtenberg et al. 2002; Kamilova et al. 2005). Distinct bacterial cells can affix to surfaces and, after cell division and propagation, form dense aggregates normally referred to as macro-colonies or biofilms. Steps of colonization comprise of attraction, detection, adherence, incursion (pathogenic microbes and endophytes only), followed by colonization and growth, along with some other strategies for establishment of connections. Roots start cross talk with soil microbes by generation of signals that are accepted by the microbes, which in turn produce signals that set off colonization (Berg 2009). PGPR get to surfaces of the root through active motility using flagella and are guided by chemotactic responses (Pinton et al. 2007). This proves that ability of PGPR highly depends upon their capacity to take benefit of a precise situation or on their abilities to become accustomed to varying conditions or plant species. In the majority cases, after 2–3 weeks, the population of PGPR declines progressively with time after inoculation from 107,109 cells per gram dry soil to 105,106 cells per gram dry soil (DeFlaun and Gerba 1993). However such population threshold remains adequate to provide positive effects (Raaijmakers et al. 2002). As a result, the rhizosphere proficiency of the biocontrol agents involves successful root colonization along with the aptitude to live and proliferate by the side of growing plant roots over a long period, in presence of native microflora (Weller 1988; Lugtenberg and Dekkers 1999).

4.3.1.4.5 Competition

Competition for resources such as oxygen and nutrients occurs generally between soil-inhabiting organisms. For biocontrol, competition occurs, while antagonists compete straightway with the pathogenic microbes for various resources. Root-inhabiting microorganisms compete for appropriate sites at the surfaces of roots. Competition for nutrient elements, such as carbon, is considered to be accountable for the incidence of fungistasis, leading toward suppression of germination of fungal spore (Alabouvette et al. 2006). Given, the comparative profusion of substrates from the rhizosphere, the efficacies of uptake of nutrients, and catabolism by the bacterial community are a major factor for competitiveness (Chin-A-Woeng et al. 2003). The capacity for rapid growth when substrates are encountered is not the only factor affecting rhizosphere competence, as rhizobacteria deploy many other metabolic strategies. As, for example, the capacity for extracellular conversion of glucose to gluconic acid and 2-ketogluconic acid enables some bacteria, together with quite a few species from the genera *Pseudomonas*, in order to impound glucose successfully and gives some aggressive advantage over microbes that lack the capability to utilize these compounds (Gottschalk 1986).

Competition for tracer elements, like as iron, zinc, manganese, copper, etc., too occurs in soils. As, for instance, iron is an indispensable element for growth of all existing organisms and the lack of its bioavailable form in soil habitats results in an enraged competition (Loper and Henkels 1997). Siderophores, the compounds with lower molecular weight and higher affinity for iron, are synthesized by some of the microbes or mostly biocontrol agents in order to solubilize and obtain the ferric ions competitively under iron-restraining conditions that further render the very element unavailable to other microbes from soil that are unable to thrive without iron (Loper and Henkels 1997; Haas and Défago 2005). The microbes, having properties of siderophore production, on the contrary, can take up iron–siderophore complex by means of using a particular receptor located in the outer cell membrane. Suppression of the soilborne pathogens of various plants, by *Pseudomonas*, through siderophore production has also been reported by many authors (Loper 1988; Weger et al. 1988; Buysens et al. 1996).

4.3.1.4.6 Induced Resistance

Bacteria, associated with plants, reduce the actions of pathogens by means of microbial antagonism along with by activating the plant to better defense mechanism, a phenomenon termed “induced systemic resistance (ISR)” (Shoda 2000; Van Loon 2007).

Sometimes, the methods of induced systemic resistance, elicited by plant growth-promoting rhizobacteria, overlap to some extent to that of systemic acquired resistance, i.e., SAR of pathogens. Both of the mechanisms stand for a condition of improved basal confrontation of the plant, which depends upon signaling compounds such as jasmonic acid, ethylene, and salicylic acid (Van Loon 2007). Natural defense response against stresses from biotic or abiotic origin such as physical stresses (heat or frost), inoculation by pathogenic or nonpathogenic organisms, and chemical molecules from natural or synthetic origins is exhibited by all plants (Alabouvette et al. 2006).

4.3.1.4.7 Plant Growth Promotion

Biofertilization

The system of escalating the performance of crop plants by PGPR is not finely comprehended yet. A number of PGPR inoculants are commercialized at present that appear to support augmentation in plant growth, through one of the following mechanisms:

1. Production of bio-stimulants or phytohormones
2. Inhibition of plant infection as bioprotectant
3. Enhancement of nutrient acquirement as biofertilizers

PGPR as biofertilizer perform both directly and indirectly by serving to make nutrient available to the host plant and influencing growth of plant root and morphology positively or by additional favorable symbiotic interactions (Vessey 2003). The major instance of such kind of relationship is fixation of nitrogen by bacteria. The symbiosis between legume host and rhizobia is one of the significant examples of plant growth-promoting rhizobacteria (PGPR). Bacteria from this cluster can metabolize root exudates that are mainly carbohydrates and supply nitrogen to the host plant in return for production of amino acids. The free-living bacteria like *Azospirillum*, *Burkholderia*, and *Stenotrophomonas* have nitrogen-fixing ability as well (Dobbelare et al. 2003). One more nutrient element that can be provided to the crop plants through oxidation by bacteria is sulfate (Banerjee and Yesmin 2002). Bacteria can also supply plant nutrition by releasing phosphorous from organic sources like phytates and hence help in plant growth promotion indirectly (Unno et al. 2005). Use of *Azospirillum* resulted in augmentation of root growth and activities that increase uptake of phosphorous along with other macro- and microelements (Dobbelaere and Okon 2007). *Pseudomonas fluorescens* CHA0 has capability of acidification of its surroundings and solubilization of mineral phosphate, which strongly depends on its aptitude of gluconic acid production (De Werra et al. 2009).

4.3.1.4.8 Phytostimulation

Phytostimulation enhances plant growth in a direct way. Phytohormones [e.g., production of indole-3-acetic acid (IAA), auxins, cytokinins, and gibberellins] play an important role in processes of plant growth. Such phytohormones can be produced by the plants themselves as well as by their allied microbes, as, for example, *Azospirillum* spp., in addition to its capacity of fixing the atmospheric nitrogen

(Steenhoudt and Vanderleyden 2000). Species from the genera *Bacillus* and *Pseudomonas* can synthesize the plant growth regulators or phytohormones that help crops in having greater amount of fine roots which have the effect of increasing the absorptive surface of plant roots for uptake of water and nutrients. They can produce phytohormones like gibberellins, cytokinins, indoleacetic acid, and ethylene production inhibitors. Indole-3-acetic acid is a phytohormone that is involved in cell division, root initiation, as well as enlargement of plant cells (Salisbury 1994). Auxins are most plentiful phytohormones quantitatively, which are exuded by *Azospirillum* spp., and their synthesis, more willingly than fixation of nitrogen, is the prime factor that is accountable for the encouragement of profuse rooting of plants and, thereby, enhanced plant growth (Bloemberg and Lugtenberg 2001). Furthermore, plant-associated bacteria can influence the hormonal balance of the plant. Ethylene is the significant instance to illustrate the fact that the stability is most imperative for the result of hormones: at lower level, it can endorse growth of plant in quite a few species together with *Arabidopsis thaliana*, whereas it is generally considered as an inhibitor toward plant development and known as a senescence hormone (Pierik et al. 2006). The general effect on the plant can be direct, that is, through plant growth promotion, or indirect, that is, through improving plant nutrition via the better development of the roots, and it is hard to differentiate between them. The increase in root IAA level for plantlets of lodgepole pine, infected with *Paenibacillus polymyxa*, as well as root concentration of dihydroxyzeatin riboside in case of plants inoculated using *Pseudomonas fluorescens* (Fuentes-Ramirez and Caballero-Mellado 2005), may be accredited to the orientation of plant hormone synthesis by the bacterial species. However, the uptake of bacterial synthesized phytohormones cannot be excluded, since both *P. polymyxa* and *Pseudomonas* produce IAA and cytokinins in vitro (Fuentes-Ramirez and Caballero-Mellado 2005).

4.3.1.4.9 Pathogenic Functions

Root exudates can attract both favorable and pathogenic populations (Schroth and Hildebrand 1964) that may be virulent for a few hosts. Many pathogens, fungi and bacteria, have evolved and exhibited a higher level of host specificity (Raaijmakers et al. 2009). Plants are also not out of defense. In fact, it is found that approximately 2% of the identified fungal species are capable of colonization in plants and thereby can cause infection in plant body (Buchanan et al. 2000). Though plants remain in constant contact with virulent fungal, bacterial, or viral pathogens, successful contamination is hardly recognized. This is because a common confrontation in opposition to most of such pathogens, named as “nonhost resistance” or “horizontal resistance,” is found in plant bodies (Heath 1981). This reinforces the concept that the plants are not always fit targets for infection by a definite group of pathogens owing to reflexive opposition mechanisms ensuing “basic incompatibility.” Such resistance mechanisms consist of configurational barriers and poisonous chemicals that are there in the strong plants, bound triumphant infection to specific pathogens, which have the abilities to conquer these factors and thus reveal “basic compatibility.” However, even if contact is recognized with the plant, pathogenic microbes are frequently confronted with toxic compounds named phytoanticipins (van Etten et al. 1994). This phrase consists of a range of components fashioned by various biosynthetic pathways that obtain antimicrobial characteristics. Such resultant metabolites of low molecular mass are primarily stored in inert forms in the organelles or vacuoles and are exuded upon demolition of the cells. While destruction of the integrity of the host plant tissue is a component of the colonization mechanism by fungal bodies, phytoanticipins symbolize a significant confrontation strategy in opposition to such pathogens. Though, in some cases, pathogenic bodies conquer the preformed hindrances from host plants and may expand virulent contamination leading toward ailment in plant bodies. Plant diseases participate directly in the eradication of ordinary possessions from agriculture. Particularly, soilborne pathogens impart more losses, as fungi remain most hostile from soil. Their detrimental effects range from placid symptoms to catastrophes where entire fields with agricultural produce can be ruined. Consequently, they become persistent and foremost threats toward stability of ecosystem and food production function worldwide. Most common bacterial agents comprise of Gram-positive bacterium *Streptomyces scabies* and the Gram-negative bacteria *Ralstonia* spp., *Erwinia carotovora*, and *Pseudomonas*. The oomycetes and fungal phytopathogens include members from the genus *Rhizoctonia*, *Rhizopus*, *Fusarium*, *Pythium*, *Phytophthora*, and *Verticillium* (Tournas and Katsoudas 2005). Among the woodland pathogens, the significant ones are the filamentous fungi like *Phytophthora* spp. (Rizzo et al. 2005) and *Armillariella* and *Heterobasidion* (Asiegbu and Nahalkova 2005).

4.3.2 Phyllosphere: Plant Community with Microbiome

A second component of plant–microbiome interaction consists of microbes colonizing the aboveground area or exterior of plant tissues, i.e., the phyllosphere. The phyllosphere is a massive ecology that is likely to attain an area of 6.4 × 108 km^2 and is heavily colonized by microbes (Morris and Kinkel 2002). The terminology is generally used to describe the surface of the leaf (Vorholt 2012) though it is applicable to any aerial plant tissue.

The microbial communities from the phyllosphere have indispensable roles in plant growth and development. Protecting plant community from invading pathogens, fixation of atmospheric nitrogen, biosynthesis of phytohormones (Jones 1970; Freiberg 1998; Brandl et al. 2001; Kishore et al. 2005), carbon sequestration (Bulgarelli et al. 2013), etc., are some of such functions that are essential for sustainable agricultural practices.

Lindow and Brandl (2003) reported that community of phyllosphere is mainly comprised of bacteria, algae, fungi, and nematodes or protozoa in a few instances. Bacteria are the most plentiful community among these microbes that are found between 105 and 107 cells per cm^2 (Beattie and Lindow 1995; Andrews and Harris 2000) in phyllosphere. These communities are sometimes to be found far away from the rhizosphere, prime resource of plant-associated microorganisms, and are found to exhibit higher rates of colonization, mostly promoted by the movement of airstream as well as vectors (Bulgarelli et al. 2013). Organisms from the phyllosphere can flourish and survive even under oligotrophic ecological surroundings with ultraviolet radiation, restricted nutrient accessibility, and varied pH, temperature, and moisture conditions (Andrews and Harris 2000). Air along with aerosols, earth, and moisture are the prime sources that frame the communities from the phyllosphere (Bulgarelli et al. 2013). The interaction among different ecological factors can amend the microbial communities from phyllosphere. Genomic structure of plants is one of the key drivers, determining the composition of bacterial communities in the phyllosphere in temperate (Redford et al. 2010) and tropical forests (Lambais et al. 2006). Diverse plant communities anchor different microbes, owing to the creation of precise niche and confined circumstances that are governed by the inherited and the efficient metabolic activities of the plants (Redford et al. 2010). The uniqueness of the phyllosphere was reported in plants of beans, lettuce, cucumber, maize, and grasses with alteration in the profusion and constitution of bacterial community (O'Brien and Lindow 1989; Kinkel et al. 2000; Rastogi et al. 2012). Geological remoteness is also another significant player in configuring microbial communities in the phyllosphere (Bokulich et al. 2014). The diverse bacterial communities anchored by grapevines manipulate superiority of the produced wine. In a more comprehensive outlook, the intraspecific alteration in the composition of the microbial community in the phyllosphere can be noticed, primarily governed by the heterogeneous nutritional condition, found in leaf surfaces, where the heterogeneous carbon sources like glucose, fructose, and sucrose lead to precise microbial colonization on the leaf veins, the regions close to the exterior appendages and stomata (Lindow and Brandl 2003; Vorholt 2012). According to Davey and O'Toole (2000) and Lindow and Brandl (2003), such heterogeneity in few instances is endorsed by the microbial association in biofilms that are general characteristic of organisms from the phyllosphere, functioning as the defender and aggregator of bacterial cells under the regular uncongenial circumstances. Regardless of such instances, it is likely to detect a "core" for the microbial population from the phyllosphere that colonize host plants, from the phyla *Actinobacteria*, *Bacteroidetes*, *Firmicutes*, and *Proteobacteria* (Redford et al. 2010; Vorholt 2012). These phyla consist of the most plentiful and well-examined microbes that signify the fact that additional researches regarding this issue should be planned to assess taxonomic ranks beyond phylum. Consequently, this core is assumed to be made of microbes depicting a coevolving history with the plant communities, along with the host structure that is complementary to the specifications found inside the bacterial cells. Such microbial reserve can be utilized for the benevolence of farming practices that endorse the movement and odd or synergistic associations, which may kindle plant growth and/or defense in opposition to attack of pathogenic communities.

4.3.3 Endosphere: A Forte Meant for Close Friends

The existence of microbial cells in plant inner tissues was explained long ago as the same as plant infection. At that time, the microbes within plant tissues were individuals that are able to contaminate the host plants, leading toward difficulties in growth and development of plants as well as losses in yield. Perhaps, such association was caused due to the accessibility of methods for detection of microbial connections that time that were merely proficient in making out microbes that are easy to cultivate or found in large quantities. The occurrence of nonpathogenic microbes within plant tissues was explained by De Bary (1866) for the first time, who revealed that microbes are present in microscopically examined plant tissues. Such examination remained unknown until the endophytes were defined. The endophytes are generally defined based on the capability to perceive the microbial cells from plant tissues that have been surface sterilized formerly (Hallmann et al. 1997). Petrini (1991) has given a functional description for endophytes as "organisms that at some part of their life cycle colonize internal plant tissues without causing apparent harm to the host." On a more exhaustive examination, endophytes are divided in the subgroups "obligate" and "facultative" by the researchers. Endophytes, which depend on metabolism of host plants for their endurance, and are transmitted among plants through the activity of vectors or by vertical transmission, are classified as obligate ones (Hardoim et al. 2008). Endophytes, those living on the outer surface of the host plants at some point of their life cycle, are known as facultative ones. They are recruited by the host plants from neighboring communities from the soil mass, mainly from the rhizosphere. Endophytes are there in every plant inner tissues (Rosenblueth and Martinez-Romero 2006). The existence of endophytes in plants cultured in vitro has been explained, where such organisms seem to be closely connected with host plants not in by means of colonizing the culture media but preferably living inside the tissues of the plant (Almeida et al. 2009; Abreu-Tarazzi et al. 2010). Mendes et al. (2007) showed that the endophytic *Burkholderia* spp. have the capacity to regulate the growth of the pathogenic *Fusarium moniliforme*. Ferrara et al. (2012) showed that the endophytic diazotrophs from roots of sugarcane are capable of producing substances related to plant growth-promoting functions and can exude greater amount of amino acids that could aid in plant nutrition. Araújo et al. (2002) showed that the whole endophytic community is influenced by the occurrence of the pathogen and incidence of disease like variegated chlorosis in citrus is a consequence of the dealings between the endophytic community and pathogenic *X. fastidiosa* and not with the host only. The capability of genetically customized endophytes that generate the heterologous protein cry1Ac7 can control *Diatraea saccharalis*, a sugarcane pest (Quecine et al. 2014). Though numerous individual abilities have been explained for endophytes, such organisms, as a community, are competent enough for several other functions that cannot be detected from separate case studies on the microbes.

Numerous studies were made to find the origin of endophytic organisms (Hallmann et al. 1997; Saikkonen et al. 1998; Mitter et al. 2013). The origin of microbes, residing in rhizosphere or the seed-borne ones, is firmly associated to the strategy of preservation of the same within the host plants that confirms the diffusion of endophytic microbes between plants. The evidence of the mechanism of transmission as well as survival of specific endophytes and their interaction with plant bodies are indicated through their genomic organization. Dini-Andreote et al. (2012) studied over sizes and origins of numerous endophytic genomes. The scientists related the lifestyle of microbes to the genome size for detection of the deviation in ecological conditions as one of the key drivers of expansion or shrinking of genome. Endosymbionts usually possess more compacted genomes, while bacteria from niches of variable ecological conditions such as rhizosphere need to harbor the complete cache of genes to survive under diverse environmental situations, leading toward dominance of larger genomes. Apparently, endophytes appear to fit in the former portion of the theory since they exist within plant bodies, where the surroundings are more secure in comparison with the rhizosphere. Nevertheless, taking into account the origin and transmissions of endophytes, it is said that probably few endophytes must deal with distinct environments during their course of life cycle when they remain outside host plants. Mitter et al. (2013) showed a greater deviation in the genome size of bacterial endophytes, which suggests that the community of endophytes consist of microbes from various origin. Those with bigger genomes are likely to live in varied environments like soil or rhizosphere, and the ones with smaller genomes are to be transmitted vertically within stable surroundings.

4.4 Conclusion

If microbiome–plant interactions are understood and described in a more improved and detailed manner, such data could be accessible for the invention of newer technologies, concentrating on a superior investigation of the characteristic in agricultural strata, influenced by microbes. Alteration in the configuration of microbial population, for example, by injection of distinct exogenous microbes or by means of influencing ecological circumstances toward benevolence of specific sets of microbiomes, heading toward improved plant opposition or effectiveness in the nutrient uptake could be a reality. In this manner, the progress of “microbiome-driven cropping systems” may effect in the subsequent uprising in agricultural field, offering a further sustained structure for plant production.

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