Chapter 6
Soil Microbes and Plant Health

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Abstract Soil microbial community is crucial for plant health. They all represent a second much larger genome associated to plants. Microbes vary in their number and diversity which is in order of tens of thousands species in fertile agricultural soils. In general, soil microbial communities include bacteria, fungi, algae, protozoa, nematodes, and microarthropods. Most of them are neutral in relation to their effects on plants. They are important players of the food web as they utilize most of the carbon released by roots as rhizodeposits. Less than ten percent of the total rhizosphere microbes exert beneficial or harmful effects on plants. Pathogenic microorganisms in soil include fungi, oomycetes, bacteria, and nematodes while the beneficial microbial community consists of symbiotic, associative symbiotic and free-living plant growth promoting bacteria (PGPB), arbuscular mycorrhizal fungi and algae. Recent research in plant-microbe interactions showed that host specific microbial species are associated with different plant species in the same soil. The number and diversity of beneficial and deleterious microorganisms depend on the quality and quantity of root exudates which, along with soil physico-chemical properties, give shape to the rhizosphere microbial community structure. This chapter highlights the importance of rhizosphere microbial communities in relation to plant growth. Recent advances on soil-plant-microbe interactions in a balanced and optimized manner are discussed.

Keywords Biocontrol · Mycorrhizal inoculation · Plant microbe interaction · Microbial diversity · Soil microbes

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6.1 Introduction

To meet the food requirement of rapidly growing world population it is very difficult to develop new high yielding crop varieties, having resistance to biotic and abiotic stresses. Our crops still require fertilizers because nutrients may become inaccessible or may be insufficient in soil. Recent work clearly revealed that microorganisms reduce the use of agricultural inputs regarding inorganic fertilizers. Microorganisms, due to their excessive gene pool, are very useful for soil reactions, i.e. by recycling nutrients needed for plant growth (Li et al. 2017).

Microbial communities of diverse groups are important for agricultural productivity (Sharma et al. 2008). Microorganisms from different genera such as *Bacillus, Pseudomonas*, *Rhizobium*, *Azospirillum*, have been reported for their potential in enhancing both above and belowground plant biomass, being useful tools for sustainable agriculture (Igiehon and Babalola 2018).

The rhizosphere is the region of the soil environment that is maintained by border cells and exudates released by roots (Moe 2013; Igiehon and Babalola 2017). Plants produced mucilages, rhizodeposits, nutrients, and exudates which attract and serve as food sources for microorganisms living in the rhizosphere. Plants different developmental stages control and shape the structure of rhizosphere communities (Hou and Babalola 2013; Chaparro et al. 2013). The difference in rhizosphere microbial community structure is induced by the changes in nature and chemistry of metabolites exuded by roots, at different growth stages.

Plants release exudates that have an effect on the diversity of microorganisms and invertebrates living in the rhizosphere. Root exudates are responsible for increasing their populations in the rhizophere by increasing availability of C as a source of food and energy (Aira et al. 2010) These microorganisms in turn can also affect plants by releasing growth regulatory substances. In this view, the rhizosphere organisms are considered as an external environment for plants (Philippot et al. 2013; Spence et al. 2014).

The physical, chemical and biological properties of rhizospheric soil differ with those of the surrounding soil (Kim et al. 2010), as the number of microorganisms and invertebrates found in the rhizosphere are greater compared to bulk soil. The rhizosphere communities are the second set of genome present in plants and perform several roles for growth and development (Nihorimbere et al. 2011). Soil and rhizosphere microorganisms are affected by many factors such as type of soil, climate, plant species and management practices (Jeffrey et al. 2010).

6.2 Rhizosphere and Root Exudates

Soil is sometimes considered just as a source of nutrients. However, it is a complex ecosystem holding bacteria, protists, fungi, and animals (Muller et al. 2016). The rhizosphere area varies with plant species and soil. The term rhizosphere was first

used by Lorentz Hiltner (Hartmann et al. 2008) for the immediate area of soil influenced by the plant roots. It generally covers a 2 mm distance from the root surface, known as the rhizoplane. However, its influence can be found up to 10 mm (Hartmann et al. 2008; Niu et al. 2012). The microbial population in the rhizosphere may vary from thousands to million cells (Nihorimbere et al. 2011). The plant nutrients and exudates are the principle component that changes the microclimate of the rhizosphere (Shukla et al. 2013). Soil microorganisms are C dependent, so they grow well in soil having high amounts of amino acids, organic acids, sugars that are exuded by the plants (Bais et al. 2006).

The presence of microbes in the rhizosphere depends on number of factors such as: (1) plant genotype (Bulgarelli et al. 2012), (2) plant developmental stage (Chaparro et al. 2013), (3) plant hormones (Carvalhais et al. 2013), (4) composition of root exudates (Badri et al. 2013), (5) exposure to disease-suppressive soils (Mendes et al. 2011).

Plant roots release in the rhizosphere a wide variety of chemical compounds that attract soil microorganisms (Huang et al. 2014), that are known as exudates. Root exudates are the products of photosynthesis (Hayat et al. 2017), and include amino acids, organic acids, sugars, enzymes, hormones, mucilage, root cells and C (Dennis et al. 2010). Uren described that about 50% of C fixed by plant is devoted to the root, with 15% respired by the plant and 10% released by the roots as debris (exudates) including border cells (Jones et al. 2009). The compounds released by roots are not organic in nature and may be classified according to their functions such as excretions (H^+, CO_2, HCO_3, ethylene) involved in internal metabolism and secretions (siderophores, enzymes, mucilage, H^+, electrons) required for external processes (Uren 2007).

The rhizosphere is an area of high microbial activity. Several studies reported the effects of roots on microbial process (Kaiser et al. 2010). The roots release higher organic compounds in the rhizosphere due to the microbial biomass whose activities are higher in the rhizosphere than in bulk soil (Jones et al. 2009).

Studies on the microbiome of different plant species revealed that specific exudates perform specific functions, shaping the plant-microbe interaction (Hartmann et al. 2009). They include flavonoids involved in the process of symbiosis between rhizobia and legumes (Abdel-Lateif et al. 2012), sugars and amino acids acting as chemoattractants for microorganisms (Somers et al. 2004) and strigolactones, that enhance branching of mycorrhizal hyphae (Akiyama et al. 2005). Plants attract nematodes, which carry rhizobia toward roots thus contributing to the nodulation process (Horiuchi et al. 2005). The exudates have both positive and negative effects on plants, however, depending on which type of microorganisms are attracted (Hayat et al. 2017).

6.3 Microbial Number and Diversity

In the rhizosphere, there is more cycling of nutrients as well as availability. The solubility of toxic metals also makes it a different microenvironment from bulk soil (Neumann et al. 2009). The type and composition of organic compounds released by roots, i.e. sugars, carbohydrates, nucleotides, vitamins, flavonoids, and stimulators, strongly affect the diversity of species proliferating in the rhizosphere (Dotaniya et al. 2013; Ueno et al. 2007).

The rhizosphere higher amount of nutrients as compared to bulk soil, confer biological and chemical properties due to a large number of macro- and microorganisms which develop a variety of interactions among each other and with roots (Kapoor and Sachdeva 2013). The relationship between plant and microorganisms may be classified as mutualistic, commensalistic or parasitic (Aira et al. 2010; Schirawski and Perlin 2018).

The microbial diversity decreases as the distance from the rhizoplane increases (Chowdhury et al. 2009). It also decreases after long term exposure to older roots, as compared to bulk soil. In general, the bacterial diversity follows the following trend: bulk soil < apical region < basal region (Dennis et al. 2008). According to Hartmann et al. (2009), the root secretions exert both stimulatory as well as inhibitory effects on the microbial community structure and composition. Exudates such as amino acids, organic acids, and carbohydrates have positive effects on chemotactic responses of bacteria. On the other hand roots also release secondary metabolites that inhibit the growth of bacterial and fungal pathogens such as chitosans, jasmonic and salicylic acids (Walker et al. 2003). Plants also release different antibacterial compounds such as ellagic acid, chebulagic acid and norwogonin, that decrease the bacterial number (Miyasaki et al. 2013).

6.4 Plant Microbe Interactions

As agricultural production needs to be doubled in coming year to feed the increasing population of the world, there is also need to reduce the use of chemical fertilizers. To achieve this goal, it is necessary to explore the interaction between plants and microbes, so that microorganisms can be used as biofertilizers, biopesticides as well as bioherbicides (Igiehon and Babalola 2017).

6.4.1 Beneficial Interactions

Plant-associated microorganisms use different mechanisms for influencing and modulating the plant health (Huang et al. 2014). The PGPB *Bacillus amyloliquefaciens* can successfully be used to enhance drought resistance of plants (Su et al.

2017). PGPB isolated from plants growing in metal contaminated soil have the ability to survive at high concentration of zinc and cadmium and can be used for phytoremediation of contaminated sites (Montalbán et al. 2017). Some PGPB protect plants from soil borne diseases by producing toxic compounds (Muller et al. 2013).

Under water deficient conditions, arbuscular mycorrhizal (AM) fungi change the plant water relationship and improve their resistance to water stress (Birhane et al. 2012). AM fungi are well known for their potential to facilitate nutrient uptake, particularly phosphorus, by crops growing in phosphorus deficient soils (Mohammadi et al. 2011), i.e. *Phragmites australis* (Liang et al. 2018) or the AM *Rhizophagus irregularis* that improves plant growth enhancing Verticillium wilt resistance in cotton (Zhang et al. 2018).

Algae enhance soil fertility and promote plant growth by supplying growth promoting substances. The application of algal extract *Oscillatoria* sp. and *Spirogyra* sp. increased seed germination, seedling growth, and number of leaves, and height of *Medicago sativa* (Brahmbhatt and Kalasariya 2015). In another study, Shariatmadari et al. (2013) reported that improvement in plant growth parameters by the application of algal extract was due to the presence of growth promoting substances such as phytohormones.

Actinomycetes are also important soil microorganism contributing a higher proportion of soil biomass. They are capable of producing large quantities of antibiotics, extracellular enzymes, organic acids, bioactive compounds, phytohormones and other secondary metabolites. Several isolates of actinomycetes have been found to promote plant growth via direct and indirect mechanisms (Singh et al. 2018). Sreevidya et al. (2016) reported that four isolates of actinomycetes significantly increased the yield of chickpea. The PGPB *Streptomyces* spp. can be used as biofertilizers, as they help to release nutrients from the complex organic compounds (Vurukonda et al. 2018).

Soil protozoa also affect plant growth by influencing the beneficial potential of PGPB (Weidner et al. 2017).

6.4.2 Negative Interactions

Microorganisms regulate host populations everywhere in the soil environment. They may be pathogenic and may cause diseases in plants. In such interactions, pathogens grow and multiply inside the plant by causing various kind of diseases, and can also move from diseased to healthy plants (Abdul-Kareem 2012).

The pathogenic fungi feed on plant tissues and weaken their defense systems. One of the mechanisms exploited to survive in the host plant is the secretion of effector proteins which interact with plant proteins thereby disturbing their normal function. Recently, effector proteins were identified in fungal pathogens important for Indian agriculture, such as *Microbotryum lychnidis-dioicae* (Kuppireddy et al. 2017) and *Fusarium proliferatum* (Gao et al. 2018). These effector proteins cause destructive tomato diseases by producing dark brown necrotic spots leading to death

of the entire plant. The infection on wheat during different growth stages by *Fusarium culmorum* has also been reported by Spanic et al. (2018). Fungal phytopathogens reduce the plant yield although their abundance may decrease in suppressive soils (Lobmann et al. 2016).

Viral infections in plants have also been reported in species of *Chenopodium* and *Nicotiana* grown in common gardens. Viral infections develop necrotic spots and cause reduction in above ground biomass (Kollmann et al. 2007). Changes in the growth and physiological parameters of pepper as affected by *Tobacco mosaic virus* have also been studied. The viral infection causes stunting, necrosis, deformation and defoliation in plants which resulted in reduction of fruit production (Pazarlar et al. 2013). In another study, incidence of Cucumber green mottle mosaic virus, Squash mosaic virus and melon necrotic spot virus was observed which resulted in 10–15% yield reduction (Ling et al. 2014). Cucumber green mottle mosaic virus is a virus disease of cucurbits which can be transmitted via pollen to healthy plants (Liu et al. 2013). Viral diseases in cotton are major cause of yield reduction. According to an estimate, about 30% reduction in cotton is due to cotton leaf curl virus (Hassan et al. 2016).

Yellow vein mosaic disease (YVMD) caused by begomoviruses is the most devastating disease of okra affecting both quality and yield of crops (Sanwal et al. 2016; Venkataravanappa et al. 2017). Another important problem in tomato production caused by a virus is the tomato leaf curl, whose causal agent also belongs to the begomovirus group (Moriones et al. 2017). Microorganisms responsible for food spoilage such are yeasts, moulds and bacteria (Rawat 2015).

6.4.3 Plants as Habitat for Microbial Population

The rhizosphere contains beneficial microorganisms, i.e. rhizobia and AM fungi, which establish associations with the roots, provide fixed nitrogen and nutrients and get in exchange carbon-based compounds. On the other hand, the plants exposed to a wide range of pathogens, such as bacteria, fungi and viruses, evolved several defense mechanisms (Biswas et al. 2016). The roots are covered by layers of microbes in the rhizosphere, and even seed may also contain microorganisms. These complex communities modulate the plant growth, health and development, seed germination, plant ecology and productivity (Chen et al. 2018).

The microorganisms found in association with medicinal plants might be involved in release of secondary metabolite from medicinal plant (Chen et al. 2018). In another study Sanchez-Lopez et al. (2018) investigated whether microorganisms can be transmitted from one generation to another. They isolated *Methylobacterium* sp. from seeds of pioneer *Crotalaria pumila* growing in metal contaminated soil. The seeds associated microbial isolates were capable to colonize the plant up to three generations, including root cortical cells as well as xylem. In another study,

the bacterial diversity, plant exudates and physico-chemical properties of rhizosphere soil from young and old tea plants were compared. Although the physico-chemical properties remained similar, changes were observed in catechin and microbial distribution (Arafat et al. 2017).

6.5 Microbes and Plants Growth

Plants affect microbial diversity as the microbiome lives in close association with roots, xylem, stems and leaves. On the other hand, these microorganisms also influence plant health and productivity (Bogino et al. 2013). Microorganisms have been used to enhance crop productivity and soil health as well as for bioremediation of contaminated soils, wastewater treatment and recycling of industrial waste (Ahmad et al. 2011). They play a vital role in nutrients mobility and uptake by plants, promoting growth and protecting plants from diseases (Table 6.1). Fundamental processes include phosphate and sulphate solubilization, nitrogen fixation, denitrification, siderophore production, signal transduction, immune modulation, pathogens control (Prakash et al. 2015). Microorganisms also decompose organic matter and get C and energy for their own growth (Rillig et al. 2007). In anaerobic conditions, microbes immobilize 20–40% of C in the substrate, the remaining being released into the atmosphere (Zak et al. 2000; Rajendiran et al. 2012). Studies recommended the use of microbial-based fertilizers for sustainable agriculture and environment safety, instead of chemical fertilizers alone (Prakash et al. 2015).

Microorganisms-based fertilizers, along with compost, decrease the negative effect of chemical fertilizers and further enhance the quality of crops, as suggested by the enhancement of β-carotene, Brix degrees and vitamin C content reported in tomatoes (El Kiyum 2017). The PGPB colonize roots influencing the plant growth and development (Hayat et al. 2017). The interaction of PGPB with their rhizobial counterparts could result in the enhancement of nodulation efficiency (Guiñazú et al. 2010). Plants release amino acids, carbohydrates, vitamins and lipids, through roots thus enhancing microbial activities in soil. PGPB enhance geochemical cycling of essential nutrients, particularly nitrogen, phosphorus and micronutrients such as copper, zinc, iron, manganese in soil for plant growth and development (Dotaniya and Vasudev 2015). Plant growth promotion by addition of microorganisms in soil i.e., *Pseudomonads* as well as phytohormones productions have been documented (Nassal et al. 2018).

PGPB promote plant growth and crop yields by producing growth hormones, increasing plant nutrient availability, and of microbes that can act as biocontrol agent against pathogens (Dotaniya and Vasudev 2015; Jacoby et al. 2017). Inoculation of plants with AM increased efficiency of water use, plant biomass and chlorophyll content, even under metal stress (Andrade et al. 2015).

Table 6.1 Impact of microbial inoculation on crop growth

Growth condition	Crop	Response	Reference
(a) Impact of bacterial inoculation on crop growth			
Lab studies	Rice (*Oryza sativa*)	Inoculation significantly increased germination, root and shoot length, and plant vigor	Vandana et al. (2018)
Lab studies		Inoculation suppressed economically important crop pathogens	Shakeel et al. (2015)
Field experiment		Improved all quality parameters	Choudhary et al. (2013)
Pot study	Maize (*Zea mays*)	Enhanced plant growth and yield parameters by suppressing fungal pathogens	Akhtar et al. (2018)
Lab and field conditions		Significantly affected root-system architecture	Vacheron et al. (2018)
Greenhouse and field conditions		Inoculation increased plant height and dry weight	Jarak et al. (2012)
Field and pot experiment		Improved shoot and root length, root dry weight, yield cob weight and P uptake	Baig et al. (2014)
Field experiments	Wheat (*Triticum aestivum*)	significantly increased macro and micro nutrients and grain total biomass yields	Turan et al. (2018)
Greenhouse conditions		Inoculation significantly increased plant biomass, at all stages	Nguyen et al. (2019)
Field experiment		Improved plant height, number of spikelets per spike and grain yield	Sial et al. (2018)
Lab conditions	Tomato (*Solanum lycopersicum*)	Significantly increased stem height and root mass	Cendales et al. (2017)
Growth chamber		Suppressed soil-borne diseases and promoted plant growth	Qiano et al. (2017)
Pot experiments		Improved fruit quality by increasing carbohydrates, sugar and ascorbic acid	Pishchik et al. (2018)
Field experiment under salt stress	Cotton *(Gossypium hirsutum* L.)	Increased seed germination, total shoot, root dry weight and yield under salt stress	Pulatov et al. (2016)
Field experiment		Enhanced yield	Alavo et al. (2015)
Field experiment		Improved plant growth by increasing phytohormone production	Pindi et al. (2014)

(continued)

Table 6.1 (continued)

Growth condition	Crop	Response	Reference
Pot study	Chickpea (*Cicer arietinum* L.)	Enhanced plant height, leaf area leaf and stem weight, pod number and weight	Gopalakrishnan et al. (2015)
Pot study		Increased fresh and dry biomass	Goswami et al. (2013)
Field study	Hungarian vetch (*Vicia pannonica*)	Increased dry matter, crude protein ADF, NDF macro and micro nutrients	Yolcu et al. (2012)
Greenhouse conditions	Radish (*Raphanus sativus*)	Increased photosynthetic pigments, free amino acids, proline, phytohormones and N, P, K^+ content	Mohamed and Gomaa (2012)
Culture media	Banana (*Musa acuminate*)	Enhanced fresh and dry weight, plant height, stem thickness and modified roots architecture	Martin et al. (2015)
Field study	Strawberry *(Fragaria ananassa)*	Increased yield per plant	Pirlak and Murat (2009)
Glass house conditions	Sorghum (*Sorghum bicolor*)	Bacterial strains showed enhanced plant growth parameters, chlorophyll, carbohydrates, phosphorus nitrogen and other nutrients	Kumar et al. (2012)
Control conditions	Thale cress (*Arabidopsis thaliana*)	Improved shoot length and rosette diameter	Schwachtje et al. (2012)
Pots study	Poinsettia (*Euphorbia pulcherrima*)	Increased number of leaves, leaf area and volume of roots	Zulueta-Rodriguez et al. (2014)
Field study	Castor (*Ricinus communis* L.)	Significantly increased leaf biomass, number of leaves, root and shoot length, stem base diameter and leaf moisture content	Sandilya et al. (2017)
(b) Impact of mycorrhizal inoculation on crop growth.			
Metal stress (Pot experiment)	Rice (*Oryza sativa*)	Decreased metal uptake	Zhang et al. (2011)
Pot experiment	Carrot *(Daucus* carota) sorghum (*Sorghum bicolor*)	Improved plant growth	Kim et al. (2017)
Field conditions	Artichoke (*Cynara cardunculus*)	Improved yield	Colonna et al. (2015)
Pot study	Red amaranth (*Amaranthus cruentus*) and spinach (*Spinacia oleracea*)	Improved growth and yield	Ghosh et al. (2017a, b)

(continued)

Table 6.1 (continued)

Growth condition	Crop	Response	Reference
Poly bags	Chilli (*Capsicum* annuum)	Increased plant growth and yield parameters, chlorophyll, and nutrient uptake	Elahi et al. (2012)
Field experiments	Melon (*Cucumis melo*) watermelon (*Citrullus lanatus*)	Significantly increased plant growth with higher nutrient content	Ortas (2012)
Green house	Finger millet (*Eleusine coracana*)	Highest growth parameters were observed.	Patil et al. (2013)
In vitro experiments	Banana (*Musa acuminata*)	Superior biocontrol potential for disease management	Ganesan et al. (2009)
In vivo experiment	Mango (*Mangifera indica)*	Inoculation significantly control stem end rot disease	Suhanna et al. (2013)
Field conditions	Brazilian fern tree (*Schizolobium parahyba*)	Increased wood yield	Cely et al. (2016)
Greenhouse and field conditions	Red sage (*Salvia miltiorrhiza*)	Improved root growth and boosts the secondary metabolism	Zhou et al. (2018)
Field study	Gum trees (*Eucalyptus sp*.)	Inoculation positively affected stem diameter, stem length, and the fresh and dry biomass	Vitorino et al. (2016)
Pot experiment	Cucumber (*Cucumis sativus*)	increased plant height, stem diameter, dry weight, and macro and micro nutrient	Chen et al. (2017)

6.6 Soil Microbes as Biocontrol Agent

Soil microorganisms act as biopesticides and protect plants from pathogens by producing a range of different metabolites (Table 6.2). They possess several mode of actions such as the production of antibiotics, biosurfactants, cell wall degrading enzymes, chitinase, glucanase, toxins, siderophores and induction of systemic resistance in plants (Perez-Montano et al. 2014; Kumar and Singh 2015). Disease-causing organisms including bacteria, fungi, and nematodes causing severe soil borne diseases negatively affect all crops. Among pathogenic microbes, fungi are responsible for huge losses in economically important crops (Perez-Montano et al. 2014).

In these conditions (PGPB) and fungi interact in a complex system. Bacterial strains often encountered in the rhizosphere that can act as biocontrol agents belong to different genera such as *Acetobacter*, *Azotobacter*, *Bacillus*, *Pseudomonas*, *Paenibacillus*, *Streptomyces* (Berg and Smalla 2009; Kumar and Singh 2015). Some strains such as *Pseudomonas aeruginosa*, *Ochrobactrum lupine*, *Novosphingobium* and *Pentaromativorans* spp. have shown a disease management capacity vs Tomato Cucumber mosaic and bacterial spot (Dashti et al. 2012; Hahm et al. 2012).

Table 6.2 Metabolites used in biocontrol produced by microbial strains

Species	Biocontrol potential	Reference
Bacteria		
Acinetobacter	Chitinase	Krithika and Chellaram (2016)
Achromobacter sp. *Achromobacter xylosoxidans, Achromobacter xylosoxidans*	HCN production	Ngoma et al. (2013)
Alcaligenes sp.	Siderophores	Patel et al. (2018)
Alcaligenes sp.	Siderophores	Sayyed and Patel (2011)
Pseudomonas strains	HCN, siderophores	Sandilya et al. (2017)
Pseudomonas sp.	Siderophores, HCN, lipase, protease	Ghodsalavi et al. (2013)
Pseudomonas sp.	Antibiotics 2,4 DAPG	Asadhi et al. (2013)
Pseudomonas aeruginosa	Antibiotic, siderophores, HCN production	Uzair et al. (2018)
Pseudomonas putida	HCN production, siderophores production	Vandana et al. (2018)
Bacillus cereus		
Pseudomonas brassicacearum	Secondary metabolites	Andersson (2012)
Pseudomonas fluorescens	Protease, chitinase, glucanases	Ruchi et al. (2012)
Pseudomonas fluorescens	Antibiotics 2,4-diacetylphloroglucinol	Weller et al. (2012)
Pseudomonas aureofaciens	Siderophores	Chaiharn et al. (2009)
Bacillus firmus		
Bacillus subtilis	Chitinase and HCN	Shakeela et al. (2017)
Bacillus cereus	Chitinase	Ajayi et al. (2016)
Bacillus anthracis	Siderophores, pectinase, chitinase	Pandya et al. (2015)
Paenibacillus taichungensis		
Paenibacillus xylanilyticus		
Bacillus thuringiensis	Siderophores, phenols, HCN production chitinase activity	Ahmed et al. (2014)
Pseudomonas fluorescens		
Pseudomonas poae		
Bacillus sp.	Chitinase activity	Han et al. (2014)
Paenibacillus sp.		
Bacillus cereus	Surfactin type lipopeptide	Jourdan et al. (2009)
Pseudomonas, *Bacillus*, *Pantoea* and *Serratia*	Siderophores production, protease, HCN production	Etminani and Harighi (2018)
Pseudomonas, Bacillus, Brevundimonas, Azotobacter, Enterobacter	HCN, Lipase, protease	Patel and Desai (2015)
Pseudomonas, Bacillus subtilis sp.	lipase, amylase, chitinase, HCN	Bhatt and Vyas (2014)
Klebsiella sp.		
Cronobacter malonaticus		

(continued)

Table 6.2 (continued)

Species	Biocontrol potential	Reference
Rhizobium nepotum	Siderophore	Ghorpade and Gupta (2016)
Rhizobium	Siderophore	Datta and Chakrabartty (2013)
Herbaspirillum seropedicae	Siderophore, chitinase	Trovero et al. (2018), Rosconi et al. (2015)
Streptomyces sp.	Antibiotics, volatile organic Compounds	Vurukonda et al. (2018)
Streptomyces sp.	Secondary metabolite.	Singh et al. (2016)
Streptomyces spp.	Siderophore, cellulase, lipase, protease, chitinase, hydrocyanic acid and β-1,3-glucanase	Sreevidya et al. (2016), Gopalakrishnan et al. (2014, 2015)
Streptomyces, *Bordetella*, *Achromobacter*	Antibiotics	Abbas et al. (2014)
Streptomyces spp.	Siderophores	Franco-Correa et al. (2010); Lee et al. (2012)
Klebsiella, *Enterobacter*, *Pantoea*	HCN, chitinase, ammonia, cellulose, pectinase	Rodrigues et al. (2016)
Fungi		
Trichoderma sp.	Siderophore	Srivastava et al. (2018)
Trichoderma sp.	Activated salicylic acid (SA) and jasmonic acid	Martínez-Medina et al. (2016)
Trichoderma sp.	Harzianic acid	Vinale et al. (2013)
Trichoderma spp.	Siderophore	Ghosh et al. (2017a, b)
Beauveria spp.		
Metarhizium spp.		
Trichoderma harzianum	Activated salicylic and jasmonic acids	Alkooranee et al. (2017)
Trichoderma brevicompactum Trichoderma virens	β-1,3-glucanase and β-1,4- glucanase	Ayoubi et al. (2014)
Trichoderma asperellum	Siderophore	Weizhen and Lei (2013)
Trichoderma harzianum, T. reesei	Siderophore	Lehner et al. (2013)
Trichoderma atroviride	Regulates salicylic and jasmonic acids, and ethylene	Salas-Marina et al. (2011)
Trichoderma virens, *Trichoderma atroviride*	Activate salicylic and jasmonic acids defense signalling pathway	Contreras-Cornejo et al. (2011)
Trichoderma viride, Aspergillus flavus, Curvularia lunata, Rhizopus stolonifer	Antibiotics	Makut and Owolewa (2011)
Penicillium sp.	Endoglucanase, β-glucosidase,	Santa-Rosa et al. (2017)

(continued)

Table 6.2 (continued)

Species	Biocontrol potential	Reference
Penicillium echinulatum	Endoglucanases, xylanases, and β-glucosidases	Schneider et al. (2014)
Penicillium echinulatum	Cellulases, xylanases	Ritter et al. (2013)
Penicillium simplicisssum, *Acremonium* sp.	Chitinase, β-1, 3-glucanase, amylase, Siderophore	Potshangbam et al. (2017)
Aspergillus terreus	Chitinase	Krishnaveni and Ragunathan (2014)
Phoma sp.	Volatile compounds	Naznin et al. (2014)
Cladosporium sp.		
Ampelomyces sp.		
Phoma sp.	Volatile compounds	Naznin et al. (2013)
Ralstonia solanacearum	Volatile compounds	Tahir et al. (2017)
Pseudozyma aphidis	Extracellular metabolites	Barda et al. (2015)
Beauveria Bassiana, *Metarhizium anisopliae, Paecilomyces* sp.	Amylases, cellulases, esterases, lipases, proteases, gelatin, caseinase, pectinase	Fernandes et al. (2012)
Talaromyces wortmannii FS2	Volatile compounds	Yamagiwa et al. (2011)

Pseudomonas spp. have been reported for their potential against *Rhizoctonia solani* and *Phytophthora capsici* (Arora et al. 2008). *Trichoderma* and *Sebacinales* spp. are well known to control foliar, fruit and root pathogens, or even invertebrates such as nematodes (Shoresh et al. 2010). Endophytic fungi also have antimicrobial activities and play an important role in the regulation, or even suppression, of plant diseases, i.e. powdery mildew in wheat (Xiang et al. 2016).

PGPB release different lytic enzymes to compete with pathogens such as chitinases, glucanases, proteases (Viterbo et al. 2002). They produce chitinases and glucanases that degrade the fungal cell wall (Kumar et al. 2010). Fungi from several groups, including *Acremonium* sp. *Hansfordia pulvinata*, *Sarocladium implicatum*, *Simplicillium lanosoniveum* and *Lecanicillium lecanii* are efficient in controlling other phytopathogenic fungi by producing enzymes, proteases, lipases and antifungal metabolites that inhibit the germination of pathogens' propagules.

Soil microbes also produce antibiotics such as guanidylfungin A, nigericin, geldanamycin, controlling other disease-causing species (Trejo-Estrada et al. 1998). They can also produce alkaloids which are highly reactive and active, including alkaloids, festuklavine and elimoklavine (Bekemakhanova and Shemshura 2001) Antibiotics are low molecular weight organic compounds produced by specific groups of microorganisms. Beneficial *Pseudomonas* spp. can inhibit disease development by producing DAPG (diacetyl-phloroglucinol) and HCN (Hydrogen cayanide) (Junaid et al. 2013). Microbes can even produce hydrogen cyanide to protect plants from pathogens, as reported by Martinez-Viveros et al. (2010). Various antibiotics produced by microbes have been reported, such as amphisin A, kanosamine, A, zwittermicin, oomycin A, oligomycin, cyclic lipopeptides, 2,4-diacetyl

phloroglucinol, hydrogen cyanide, pyoluteorin, phenazine, pyrrolnitrin, and xanthobaccin (Hitendra et al. 2017).

Siderophores are iron chelating compounds produced by microorganisms in iron deficient conditions. These siderophores chelate iron by converting it into complexed forms that cannot be used by other microorganisms in Fe deficient conditions. This is an important mechanisms in biological control by microorganisms, as it deprives other competing plant pathogenic fungi and bacteria. There are three different groups of siderophores which have been reported, namely catecholate siderophores, hydroxamate siderophores, and mixed siderophores (Vellasamy et al. 2015).

PGPB also trigger the plant defense mechanisms prior to infection, and in this way reduce the disease incidence. The induction of a systematic resistance results by the modulation of salicylic acid, jasmonic acid and ethylene pathways in the plants. PGPB from several genera including *Pseudomonas*, *B. amyloliquifaciens*, *B. subtilis*, *B. pasteurii*, *B. cereus*, *B. pumilus*, *B. mycoides*, and *B. sphaericus* reduce the severity of various diseases on many plants (Choudhary et al. 2007).

Some cyanobacteria and algal extracts were also found as efficient biocontrol agents because they produce antibacterial and antifungal metabolites. They can be applied to activate plant resistance mechanisms such as induced systematic resistance (Shunmugam et al. 2015).

Finally, also beneficial fungi may improve plant growth and contribute in controlling their diseases. Species from genera *Aspergillus*, *Penicillium*, *Phoma*, *Piriformospora*, *Fusarium*, and *Trichoderma* have been reported for inducing systematic resistance in plants (Hossain et al. 2017), and systematic resistance and suppression of anthracnose in cucumber (Elsharkawy et al. 2015).

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