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Plant-Microbiome Interactions in Agroecosystem: An Application

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Abstract

Global food security is the major challenge for agricultural scientists, but it should not be on the cost of depletion of nonrenewable resources such as soil. Due to the decrease in agricultural land, the use of synthetic chemical fertilizers to increase crop productivity has placed extra strain on fragile agroecosystem, thereby deteriorating its health. Plant-associated microbial communities interact with plants positively or negatively. These interactions are affected by the quality of root exudates and physicochemical properties of soil. Beneficial soil microbes have a number of plant development and growth-endorsing characteristics including biological nitrogen fixation, phytohormone production, nutrient mobilization and solubilization, biocontrol activity, production of hydrolytic enzymes, and stress tolerance induction. These traits of beneficial microbes can be harnessed with better soil health, improved plant growth and productivity, and improved stress tolerance of crop plants. Improvement in beneficial microbial populations through rhizosphere engineering or use of microbial inoculants and/or their metabolites can be helpful to modify the soil microbiome, leading to increased productivity of agroecosystem. Present review highlights the significance of soil microbiome with special reference to plant health. The symbiotic plant microbial communications and the most prominent plant growth-promoting mechanisms used by soil microbes are discussed. The potential applications of plant-microbe interactions for improving crop productivity under natural as well

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as stressful situations to maintain the sustainability of agroecosystem have been explained with examples, followed by their future prospects.

Keywords
Agroecosystem · Microbes · Plant · Crop production · Nutrients · Stress

12.1 Plant-Microbe Interactions: Introduction

Structural community of microbes and their diversity in the rhizospheric regions of plants are essential for plant development, growth, and health. Owing to critical role in plant health, the scientists termed the microbial community associated with plant as second genome of plants (Berendsen et al. 2012) that is much larger than that of plant. Microbes vary in their number and diversity which constitute in order of tens of thousands of species in fertile agricultural soils. In general, soil microbial communities include algae, protozoa, nematodes, fungi, bacteria, and microarthropods (Lynch 1990; Raaijmakers 2001). Most of these microbes have neutral effects on plants, but they are considered as important players of the food web as they utilize most of the carbon released by plant roots as rhizodeposits. The remaining less than 10% of the total rhizosphere microbes exert beneficial or harmful effects on plants. The pathogenic microorganisms in soil include pathogenic fungi and bacteria, oomycetes, and nematodes, while the beneficial microbial community may consist of free-living, associative symbiotic and symbiotic plant growth-endorsing bacterial genera, endophytic AM fungi, and algae. Recent research in plant-microbe interactions shows that host-specific microbial species are associated with dissimilar species of plant growing in the same environment (Berendsen et al. 2012). The number and diversity of beneficial and deleterious microorganisms depend upon the amount and characteristic of exudates from roots (Somers et al. 2004) as these root exudates along with soil physicochemical properties shape the rhizosphere microbial community structure and thus overall health of the plant.

Among beneficial soil-plant-microbe interactions, symbiotic plant-microbe interactions are most important which involve dynamic changes in the genome of interacting partners, through establishment of metabolic and signaling network. In plant-microbe interactions, two symbiotic associations, i.e., root nodule (RN) symbiosis and arbuscular mycorrhizal fungi (AMF) association, have been extensively studied during previous two decades (Kawaguchi and Minamisawa 2010). A third type of microorganisms called endophytes has also been recognized in this regard during recent years. The endophytes reside within tissues of plant without triggering any symptoms of disease and are called as “endosymbionts.” They provide novel bioactive metabolites including phenolic acids, alkaloids, terpenoids, tannins, saponins, steroids, and quinones (Gouda et al. 2016). All these associations are significant for better plant development and growth.

Soil microbes have different plant growth-promoting mechanisms through which they are indirectly or directly implicated in improving plant development and growth. Some mechanisms are very usual and conventional among the culturable microorganisms; however, other microbes are strain-specific. Under natural agroecosystems, vegetation cover, plant species, temperature, and soil moisture regimes, environmental and soil physicochemical conditions induce large fluctuations in microbial population. The fluctuations in growth conditions cause the induction or suppression of plant development and growth-fostering characters of microorganisms. The most common plant development and growth-endorsing features include fixation of biological nitrogen, phytohormone manufacture, solubilization of nutrients, biocontrol activity, excretion of hydrolytic enzymes, and stress tolerance induction. The application of beneficial soil microbes for increasing soil health and crop production is vital for agroecological systems due to their environment-friendly nature, cost-effectiveness, and minimization of the dependence on nonrenewable resources (Sathya et al. 2017).

Plant-microbe synergism in the rhizospheric region is modulated by edaphic features. Such synergism might be valuable, advantageous, or detrimental for one or both of the partners. These interactions can be harnessed with better soil health, improved plant productivity and growth, and induced stress tolerance in crop plants. Improvement in beneficial microbial populations through rhizosphere engineering or use of microbial inoculants and/or their metabolites can be helpful to modify the soil microbiome (Velmourougane et al. 2017), leading to increased crop productivity and agroecosystem sustainability. The use of these beneficial microbes can not only enable plants to maintain their growth and productivity under various kinds of environments but also improve soil health that can be beneficial in maintaining agroecosystem sustainability.

12.2 Soil Microbiome and Plant Health

Soil microbial communities constitute the diverse populations which carry out key functions in ecosystem vital for human, plant, and animal health. Pathogenic microbes can have severe negative impact on plant growth; however, beneficial plant-soil-microbe interactions are vital for sustainable agriculture. Unfortunately, most of the beneficial functions carried out by soil microbes are threatened by climate change, land degradation, and poor management practices (Amundson et al. 2015). The manipulation of soil microbiome is critical to restore ecosystem function (Calderon et al. 2017) for agriculture sustainability. A comprehensive study of soil microbiome interactions under different conditions can create an opportunity to manage ecosystem services and soil microbial metabolism. In rhizosphere, soil microbes interact directly with plant roots and have significant influence on plant health. Rhizosphere is the thin zone of soil around roots that is manipulated and persuaded by root exudates and may harbor up to 10^{11} microbial cells/g of roots (Egamberdieva et al. 2008) or rhizosphere soil. Disease-suppressive soils have more distinct evidence of impact of soil microbiomes on plant health, where beneficial soil microbes are involved directly in the pathogenic microorganism's suppression.

In general, all soils naturally have some ability to suppress pathogenic microorganisms depending upon the number and diversity of beneficial microbes present in the soil. This phenomenon is termed as general disease suppression. The general disease suppression in a soil can be enhanced through stimulation of beneficial microbial community using organic amendments (Hoitink and Boehm 1999). However, soils can also have the ability to suppress specific kinds of pathogens termed "specific suppression" (Raaijmakers et al. 2009) that is attributed to the production of metabolites by beneficial microorganisms which are toxic to certain kind of pathogens while not to the others. In addition to inhibition of pathogens, beneficial microbes can also modulate and boost the defensive mechanism of plants' aboveground parts (Zamioudis and Pieterse 2012) that is known as induced systemic resistance (ISR). The ISR response is associated with priming to accelerate defense-related gene expression (Van der Ent et al. 2009). Although specific microorganisms protect plants against pathogens through direct or indirect mechanisms, the effectiveness of these microbes is mainly manipulated and induced by rest of the community microbes. To be effective against pathogens, these microbes should be there in appropriately good population (Raaijmakers et al. 1995). Most of these microorganisms live as commensals since they neither harm nor directly help the plant; however, they effectively compete with pathogens, thus suppressing them.

Root microbiome is shaped by plant species as plants excrete up to 40% of their photosynthates in the rhizospheric zone (Bais et al. 2006) which directly influences the microbial growth. Rhizosphere soil has much more microbial number than bulk soil (Costa et al. 2006); however, in general, there is less diversity of microbes in rhizosphere than bulk soil that might be attributed to the presence of specific kinds of metabolites in host root exudates which ultimately favor the growth of certain kinds of microbes while suppressing the others. There can be suppression effect of these metabolites on certain microbial species that favors the growth of other microbes. For example, Wang et al. (2018a, b) compared the rhizospheric microorganism's population of four *Ferula* species at different soil depths. They reported that rhizosphere bacteria vary with depth of soil Ferula therapeutic value. The specific rhizosphere bacterial population increased with the medicinal value of *Ferula* species, while soil depth showed negative effect on bacterial abundance. Microbial communities of diverse species of plants growing in the same ground are different (Garbeva et al. 2008; Berg and Smalla 2009), while the same species of plants can induce same communities of microbes in diverse soils (Miethling et al. 2000) even within plant species, there is also genotypic variation in inducing the rhizosphere microbial community (Micallef et al. 2009), suggesting that microbial community structure is shaped by root exudates. As plants can induce the microbial community, it can be concluded that rhizosphere microbial community is host specific that contributes substantially to plant health through suppression of pathogens, provision of growth hormones, and solubilization of nutrients along with performing other important functions.

12.3 Symbiotic Plant-Microbe Interactions

Symbiosis is the biological association between two organisms that involves dynamic changes in the genome of both partners, through establishment of metabolic and signaling network. In plant-microbe interactions, two symbiotic associations, i.e., root nodule (RN) symbiosis and arbuscular mycorrhizal (AM) symbiosis, have been extensively studied during previous two decades (Kawaguchi and Minamisawa 2010). A third type of microorganisms called endophytes has also been recognized in this regard during recent years. The endophytes reside within the tissues of plant without instigating any disease and are called as "endosymbionts." They provide novel bioactive metabolites including phenolic acids, alkaloids, terpenoids, tannins, saponins, steroids, and quinones (Gouda et al. 2016). All these associations are significant for better development and growth of plants. A list of microbes showing plant growth promotion has been presented in Table 12.1.

12.4 Rhizobial Associations

The root nodule symbiosis involves the development of specialized structures called as root nodules formed through communication between plants and atmospheric nitrogen-fixing bacteria. The "rhizobia" are motile, Gram-negative, rods, do not form spores, and generally belong to the order *Rhizobiales* of class *Alphaproteobacteria*, but several bacteria occur in the order *Burkholderiales* of the class *Betaproteobacteria*. These mutual N_2-fixing bacterial genera include mostly *Allorhizobium*, *Rhizobium*, *Mesorhizobium*, *Bradyrhizobium*, *Azorhizobium*, and *Sinorhizobium*. Most plant species from legume family have the capability to fix N_2 through RN symbiosis (Andrews and Andrews 2017) that gives them competitive advantage under low-nitrogen conditions (Andrews et al. 2013). The atmospheric nitrogen fixed by leguminous plants shares a major proportion of available nitrogen pool in agricultural ecosystems (Andrews et al. 2011).

For the initiation of nodulation process, the host plant produces a number of organic components, mostly flavonoids, which in turn encourage the biosynthesis of protein *NodD* by rhizobial species (Wang et al. 2012; Downie 2014). The amount and type of organic compounds produced by host plants depend upon the legume species. The protein *NodD* induces the transcription of other important genes implicated in the nodulation process and production of Nod factors (*nodABC* genes). The Nod factors such as lipopolysaccharides, lipochito-oligosaccharides, and exopolysaccharides are produced by the rhizobia as signal molecules for plants to initiate the process of nodulation (Jones et al. 2007; Oldroyd and Downie 2008). The basic structure of Nod factors released by different rhizobia is the same but differs in length (Wang et al. 2012) and is modified by species-specific proteins. The Nod factor receptors in legume host perceive the signal and respond accordingly (Wang et al. 2012; Downie 2014). The rhizobia enter the host roots through root hair infection (Sprent et al. 2013) and the host root cell wall material grows and infection thread is formed. In general, rhizobia are attached to the tip of root infection thread

Table 12.1 Effective strains of bacteria (associative and endophytic) and fungi that form association with plant and promote plant growth

Species	Crop	References
Associative bacteria		
Azospirillum spp.	Sorghum (*Sorghum bicolor*)	Pereira et al. (1988)
Azospirillum brasilense		Dobbelaere et al. (2001)
Azospirillum brasilense strain *Sp7*		Molla et al. (2001)
Azospirillum spp.	Grass	Moreira et al. (2008)
Azospirillum brasilense	Wheat (*Triticum aestivum*)	Dobbelaere et al. (2001)
Bacillus subtilis SU47, Arthrobacter sp.		Upadhyay et al. (2012)
Azospirillum brasilense strain *Sp7*	Banana (*Musa acuminata*)	Mia et al. (2007)
Bacillus sphaericus strain UPMB10		Mia et al. (2007)
Herbaspirillum spp.	Sugarcane (*Saccharum officinarum*)	Weber et al. (1999)
Gluconacetobacter diazotrophicus		Suman et al. (2005)
Nitrospirillum amazonense		Schwab et al. (2018)
Bacillus vietnamensis MG43		Govindarajan et al. (2008)
Bacillus japonicum SEMIA 5079 and Azospirillum brasilense Ab-V5	Soybean (*Glycine max*)	Hungria et al. (2013)
Bradyrhizobium elkanii		Kuykendall et al. (1992)
Rhizobium faba	Faba bean (*Vicia faba*)	Tian et al. (2008)
Rhizobium leguminosarum	Pea (*Pisum sativum*)	Frank (1889)
Rhizobium alamii	*Medicago ruthenica*	Berge et al. (2009)
Rhizobium endophyticum	Common bean (*Phaseolus vulgaris*)	Lopez-Lopez et al. (2010)
Mesorhizobium opportunistum	Chickpea (*Cicer arietinum*)	Nandasena et al. (2009)
Azospirillum lipoferum	Rice (*Oryza sativa*)	Ladha et al. (1982)
Gluconacetobacter diazotrophicus		Muthukumarasamy et al. (2005)
Azospirillum sp. *B510*		Bao et al. (2013)
Halobacillus spp.		Rima et al. (2018)
Gluconacetobacter diazotrophicus	Maize (*Zea mays*)	Tian et al. (2009)
Bacillus spp.		Calvo et al. (2017)
Agrobacterium tumefaciens	Cucumber (*Cucumis sativus*)	My et al. (2015)
Azotobacter chroococcum 76A	Tomato (*Solanum lycopersicum*)	Van Oosten et al. (2018)
Pseudomonas putida	Safflower (*Carthamus tinctorius*)	Nosheen et al. (2018)
Rhizobium sp.		Saghafi et al.(2018)
Endophytic bacteria		
Rhizobium leguminosarum bv. Trifolii	Rice (*Oryza sativa*)	Yanni et al. (1997)
Serratia marcescens		Gyaneshwar et al. (2001)
Bacillus pumilus		Bacilico-Jimenz et al. (2003)
Trichoderma spp.		Doni et al. (2014)

(continued)

Table 12.1 (continued)

Species	Crop	References
Bacillus sphaericus	Banana (*Musa acuminata*)	Mia et al. (2007)
Bacillus sp.	Rose (*Rosa damascena trigintipetala*)	El-Deeb et al. (2012)
Paenibacillus polymyxa	Wheat (*Triticum aestivum*)	Beck et al. (2003)
Klebsiella pneumoniae 342		Fouts et al. (2008)
Enterobacter sp.		Tian et al. (2017)
Achromobacter sp. and *Acinetobacter* sp.		Patel and Archana (2017)
Azospirillum sp.		Singh et al. (2017)
Burkholderia phytofirmans PsJN	Tomato (*Solanum lycopersicum*)	Weilharter et al. (2011)
Burkholderia phytofirmans PsJN	Maize (*Zea mays*)	Weilharter et al. (2011)
Klebsiella pneumoniae 342		Fouts et al. (2008)
Klebsiella, *Enterobacter*, and *Pantoea* sp.		Rodrigues and Forzani (2016)
Serratia proteamaculans 568	Soybean (*Glycine max*)	Taghavi et al. (2009)
Gluconacetobacter diazotrophicus	Sugarcane (*Saccharum officinarum*)	Rouws et al. (2010)
Burkholderia phytofirmans	Onion (*Allium cepa*)	Zuniga et al. (2013)
Bacillus, *Pantoea* and *Serratia* genus	Pistachio trees (*Pistacia vera*)	Etminani and Harighi (2018)
Bacillus sp.	*Wedelia trilobata*	Dai et al. (2016)
Enterobacter sp. *Cronobacter* sp.	*Withania coagulans*	Ullah et al. (2018)
Bacillus sp.	*Ammodendron bifolium*	Zhu and She (2018)
Bacillus Pseudomonas sp.	Jerusalem artichoke (*Helianthus tuberosus* L.)	Khamwan et al. (2018)
Fungi		
Glomus versiforme	Chickpea (*Cicer arietinum*)	Alloush et al. (2000)
Glomus intraradices	Pepper (*Capsicum annuum*)	Martin and Stutz (2004) and Beltrano et al. (2013)
Dive versiformis	White clover (*Trifolium repens)*	Lu and Wu (2017)
Glomus intraradices	Rangpur lime (*Citrus limonia*)	Nogueira and Cordoso (2006)
Glomus caledonium	Cucumber (*Cucumis sativus*)	Ortas (2010)
Glomus mosseae, *Glomus intraradices*, *or Glomus versiforme*		Wang et al. (2008)
Rhizophagus irregularis	Wheat (*Triticum aestivum*)	Perez-de-Luque et al. (2017)
Glomus mosseae	Garlic (*Allium sativum)*	Sari et al. (2002)
Glomus intraradices and *Glomus mosseae.*	Maize (*Zea mays*)	Lone et al. (2015)

(continued)

Table 12.1 (continued)

Species	Crop	References
Glomus intraradices and *Glomus mosseae*	Potato (*Solanum tuberosum*)	Lone et al. (2015)
Glomus sp.	Onion (*Allium cepa*)	Shuab et al. (2014)
Glomus mosseae, *Glomus versiforme*, and *Paraglomus occultum*	Peach (*Prunus persica* L. Batsch)	Wu et al. (2010)
Rhizophagus irregularis	Tomato (*Solanum lycopersicum* L.)	Khalloufi et al. (2017)

and moves inside where they multiply and differentiate into pleomorphic forms known as bacteroids, the N_2-fixing form. The whole nodulation process includes initiation of nodule, infection of rhizobia, organogenesis, fixation of atmospheric nitrogen, senescence, and feedback regulation (Oldroyd and Downie 2008; Kouchi et al. 2010). All this process, from the release of chemical signals to the start of N_2 fixation, takes about 6–15 days depending upon crop species.

Generally, the legume species are highly restricted in nature with respect to their plant host symbionts (Liu et al. 2012), in some cases; however, in grain legumes, rhizobial strains from distinctive genera in *Alphaproteobacteria* and *Betaproteobacteria* can nodulate the same legume host (Guimaraes et al. 2012). It is well documented that lateral gene transfer of specific symbiosis genes within rhizobial genera is crucial to allow leguminous plants to form symbiotic association with rhizobial genera under specific soil conditions that sustain symbiosis genes' specificity between rhizobia and legume species (Andrews and Andrews 2017). The nodulation and N_2-fixation process consumes high amount of metabolic energy from the host plant, thus legumes strictly control the number of nodules and nitrogen fixation. The RN symbiosis is not the only process that benefits the legume crop during growth under field conditions. Diverse microbes are associated with legumes as endophytes and epiphytes under natural environments which help in plant development and growth enhancement under dissimilar fertility level and soil physicochemical conditions.

12.5 Plant-Fungi Associations

The AM symbiosis has been recognized as the most common and widely spread ecological synergism between microbes and plants. The endophytic AM fungi are a heterogeneous fungal group of the phylum *Glomeromycota* which make symbiotic relationship with more than 90% of all higher plant families (Bonfante and Genre 2010). The AM fungi synergism is the base of all plant root endosymbioses that originated roughly about 400 million years ago, in the early period of Devonian (Parniske 2008). The AM fungi are a heterogeneous group of diverse fungal taxa, which are associated with the plant roots of over 90% species. They can colonize a wide range of environments including croplands, grasslands, tropical forests, and alpine and boreal zones. These fungi play a significant role in cycling of nutrients and help plants in the absorption of these nutrients, including nitrogen and phosphorous, using their extra radical hyphae and arbuscules (Parniske 2008; Selosse and Roy 2009). The arbuscules are branched structures which are enveloped in the periarbuscular membrane. The phosphate in plants is absorbed through mycorrhizae-induced phosphorous transporter gene such as MtPT4; these genes are upregulated in arbuscules of plant root cells. Some of these transporter genes are essential for establishment of AM fungi symbiosis and also acquisition of phosphate from the surroundings (Javot et al. 2007).

In case of AM fungi symbiosis, both the partners (plant and fungi) get benefited from the association as the AM fungi improve host plants' growth through manipulating water absorption, mineral uptake, and inducing resistance against diseases while the host plants' presence is compulsory for growth and reproduction of the fungi (Smith and Read 2008). In natural ecosystems, the mycorrhizal fungi help plants to survive better by improving the overall plant growth and fitness. It has been a well-known fact that mycorrhizal fungal genera significantly improve the uptake of nutrients, induce abiotic and biotic stresses mitigation in host plants, and increase plant biomass as compared to artificially induced nonsymbiotic conditions; the AM host plant can survive without AM fungal partner (Smith and Read 2008). Contrariwise, the AM fungal symbionts are obligate biotrophs which cannot grow without host plant, showing that these fungi strictly depend on host plants for their growth and reproduction. The AM fungi are important in ecosystems establishment and play a critical role in early stages of the life cycle of host plant (Knappova et al. 2016). In addition to helping in phosphorus acquisition, the mycorrhizal fungi also aid in the uptake and transfer of considerable amount of nitrogenous compound to host plant via fungal hyphae.

12.6 Endophytes

Endophytes, called as endosymbionts, are a group of endosymbiotic microorganisms colonizing plant tissues. The bacterial endophytes were first reported by Darnel in 1904 in plants, which can also provide a number of novel bioactive compounds including phenolic acids, alkaloids, terpenoids, tannins, saponins, steroids, and quinones (Gouda et al. 2016). A huge number of bacterial and fungal genera colonizing the intercellular and/or intracellular locations of plants have been identified (Singh and Dubey 2015). They complete all or part of their life cycle within tissues of host plant without producing any obvious symptom of disease. The endophytes improve the plant growth and nutrient concentration and have the capability to persuade stress tolerance against various types of biotic and abiotic stresses in addition to fixation of N_2, as in case of rhizobia (Beneduzi et al. 2013).

With almost every plant species, the endosymbionts are associated and have integral role in life of plant. The endosymbiosis is considered crucial for plant's survival. It is documented that from per gram of fresh shoot and root weight, about 10^5 cfu of endophytic bacteria can be isolated, and they are so diverse in nature that around 70–80% of them are still waiting for their identification despite advancement in the sciences. Among the important functions of endosymbionts are defense from plant pathogens, communication with other associated microbes, involvement in stimulating the plant defense processes against abiotic and biotic ecological stresses, and volatile compound production. Bacterial endophytes are also reported to produce allelopathic compounds, and these compounds act as natural biocontrol for diverse pests (González and Lopez 2013) in addition to fixation of N_2, as in case of rhizobia. The blend of all these growth-enhancing properties augments immunity level of plant against pests and diseases (Hayat et al. 2010). In addition to symbiotic fungi and rhizobia, roots of plants are also inhabited by a diverse variety of bacterial species from other genera of bacteria, such as *Azotobacter*, *Paenibacillus*, *Pseudomonas*, *Bacillus*, *Burkholderia*, *Rhizobium*, and many more, which consecutively function together and mutually promote plant development and growth (Maheshwari 2013) as endosymbionts. The endophytic fungi have been classified into nonclavicipitaceous and clavicipitaceous endophytes and belong to the *Ascomycota* or *Basidiomycota* group (Jalgaonwala et al. 2011). These endophytic fungi have the ability to produce a number of bioactive compounds including antibiotics and can be a good bioresource to develop biopesticides. Among the soil-inhabiting microorganisms, nonsymbiotic endophytic bacteria are less studied for their potential roles and plant growth-promoting aspects (Rosenblueth and Martinez-Romero 2006). The endosymbiont inhabitants in plant species differs with developmental stage of host plant, host crop species, and environmental conditions (Dudeja and Giri 2014).

12.7 Plant Growth-Promoting Mechanisms of Soil Microbes

Soil is heterogeneous in nature and has diversity of microorganisms. Soil-plant-microbe interactions are important for ecosystem sustainability. About 5% of the total microorganisms in soil have beneficial impact on plant growth. These beneficial microbes have different plant growth-promoting mechanisms through which they are indirectly or directly intricate in improving plant development and growth (Nadeem et al. 2013). Some mechanisms are very usual and customary among the microbes which are cultured in labs, while others are strain-specific. Under natural agroecosystems, vegetation cover, plant species, temperature and soil moisture regimes, and environmental and soil physicochemical conditions induce large fluctuations in microbial population. The fluctuations in growth conditions cause the induction or suppression of plant growth-enhancing phenomenon of microorganisms. The most conventional plant growth-enhancing characteristics include fixation of atmospheric nitrogen, production of phytohormones, solubilization of nutrients, biocontrol activity, making hydrolytic enzymes, and stress tolerance induction. The schematic view of plant growth-enhancing mechanism by soil microbes is presented in Fig. 12.1.

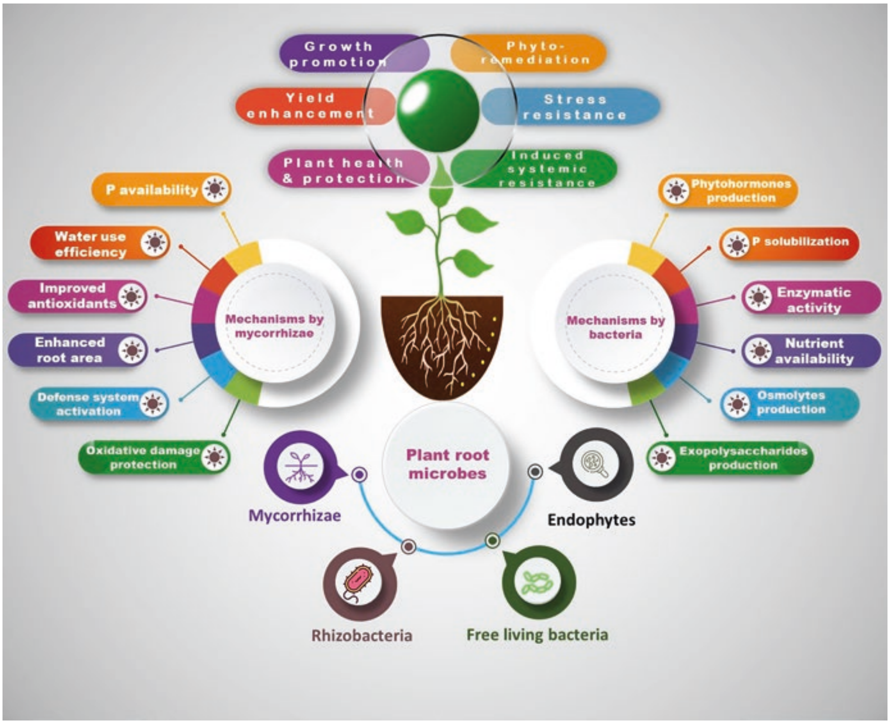

Fig. 12.1 Common plant growth-enhancing mechanism by soil microbes

12.7.1 Biological Nitrogen Fixation

The atmospheric nitrogen shares the major proportion of its total contents on earth that is not directly available to plants. It needs to be reduced artificially to NH_3 (ammonia gas) by Haber-Bosch procedure (Rubio and Ludden 2008) or through natural means such as thunderstorms and biological nitrogen fixation (BNF). During BNF, atmospheric N_2 is reduced to NH_3 by N_2-fixing microorganisms through nitrogenase activity (Kim and Rees 1994). This biologically fixed N_2 accounts for around 66% of the total fixed N_2 through all means worldwide. Biologically, N_2 is fixed by nitrogen-fixing bacteria called as rhizobia. The bacteria involved in BNF are categorized into free-living, associate, and symbiotic bacteria. Although free-living N_2 fixers such as *Gluconacetobacter*, *Azospirillum*, and *Azotobacter* spp. abundantly exist in natural ecosystem (Bashan and Levanony 1990), the contribution of these bacteria is negligible when compared with total BNF. The symbiotic nitrogen-fixing bacteria called as “rhizobia” contribute the highest proportion of BNF (Zahran 2001).

In addition to rhizobia, other plant growth-promoting rhizobacteria (PGPR) such as diazotrophs also have the nitrogenase complex which fix N_2 in nonleguminous plants. These diazotrophs form nonobligate interactions with their host plants (Glick et al. 1998) other than legumes and fix nitrogen. Nitrogenase complex is a metalloenzyme that has two components (Dean and Jacobson 1992; Bottomley and Myrold 2015). The first component is an iron (Fe) protein (dinitrogenase reductase) and the second one is molybdenum (Mo)-Fe protein (dinitrogenase). Nitrogenase complex has three biochemically distinct forms depending on their requirements for either molybdenum (Mo), vanadium (V), or iron (Fe) as a critical metallic component of the cofactor associated with the catalytic site (Bottomley and Myrold 2015). Nitrogen fixation is a complex process that consists of series of oxidation and reduction reactions and consumes high amount of metabolic energy during reduction of dinitrogen to ammonia. The nitrogen-fixing genes (*nif* genes) are of several distinct forms which are present both in symbiotic and free-living nitrogen-fixing bacteria (Kim and Rees 1994), Archaea and *Proteobacteria* (Bottomley and Myrold 2015). The BNF has significant contribution in agroecosystem sustainability that is considered as the second most important process on earth for plants after photosynthesis.

12.7.2 Phytohormone Production

Phytohormones are produced by plants for proper growth and productivity. These phytohormones such as plant growth regulators and complex organic molecules need a considerable amount of metabolic energy and nutrients for their synthesis. Bacteria have the ability to synthesize significant quantities of phytohormones. The bacterially synthesized phytohormones are released into plant body which results in significant positive effects on plant growth and development. It is well documented in literature that bacteria can produce up to 60 times higher amount of plant growth regulators as compared to plants (Camerini et al. 2008).

The important phytohormones which are produced by soil microbes include auxins, gibberellins, abscisic acid, ethylene, and cytokinins. These phytohormones help in plant growth during cell division, cell enlargement, seed germination, root formation, and stem elongation (Taiz and Zeiger 2000; Khalid et al. 2006; Kang et al. 2010). These microbially produced phytohormones meet the plant's hormonal requirements and save much needed plant's metabolic energy, thus improve crop growth and productivity (Zahir et al. 2010; Jamil et al. 2018).

Auxins are effective under stress but some plants are unable to produce enough auxins to cope with adverse conditions, resulting in failure to alleviate stress conditions. Under such conditions, exogenous application of auxins or inoculation with microbes having ability to produce auxins can help for resumption of normal metabolic functions (Ahmad et al. 2013c). Jamil et al. (2018) evaluated the exogenous application of L-tryptophan in combination with *Pseudomonas fluorescens* under drought conditions that resulted in significant increase in physiological parameters and yield.

Abscisic acid (ABA) is also a stress hormone (Zhang et al. 2006) and plays a critical role in photoperiodic induction of flowering (Wilmowicz et al. 2008). Gibberellins (GA) are involved in leaf expansion and stem elongation of plants. Exogenously applied GA promotes parthenocarpy in fruits, bolting of the plants, breaks tuber dormancy, and increases the number of buds and fruit size. A number of soil microorganisms have been reported to produce GA which can have positive or negative effects on plant growth and nodulation. They have the ability to induce nodule organogenesis but can inhibit nodulation at infection stage (McAdam et al. 2018). Cytokinin has been reported to be involved in plant cell division, root development, root hair formation, and chloroplast development, shoot growth, and leaf senescence. It also controls cell division in plants (Arkhipova et al. 2007; Oldroyd 2007) and regulates nodulation and nitrogen fixation (Kisiala et al. 2013). Ethylene is a stress hormone produced in plants that regulates plant physiological processes and induces stress tolerance in plants (Arshad and Frankenberger 2002). The higher concentration of ethylene under stress negatively affects plant growth (Zahir et al. 2008). Bacterial strains have been reported to regulate ethylene production in plants through 1-aminocyclopropane-1-carboxylic acid (ACC) deaminase activity (Ahmad et al. 2011; Khan et al. 2013; Singh et al. 2015).

Literature reports the production of phytohormones such as auxins, ABA, cytokinins, and gibberellins by *Rhizobium*, *Sinorhizobium*, *Bradyrhizobium*, *Azospirillum*, *Bacillus*, *Paenibacillus*, and *Pseudomonas* (Bottini et al. 2004; Boiero et al. 2007; Afzal et al. 2010; Zahir et al. 2010; Gamalero and Glick 2011; Ahmad et al. 2011; Mumtaz et al. 2017) which improve plant growth and productivity under natural conditions (Ahmad et al. 2015, 2016; Mumtaz et al. 2018).

12.7.3 Nutrient Solubilization

Nutrient cycling is the major function of soil microorganisms. Crop residues when incorporated into the soil are attacked by microorganisms for carbon, energy, and nutrient source. The mineral nutrients from decomposed crop residues enter in to the soil while carbon is released as CO_2 into the atmosphere. Moreover, microbes also solubilize chemically fixed nutrients such as potassium (K), phosphorus (P), iron (Fe), and zinc (Zn). Microorganisms release extracellular enzymes such as phosphatases which solubilize the inorganic phosphate in soil. Microorganisms also produce organic acids which lower the soil pH in microclimate, thus causing the solubilization of nutrients such as P, K, Fe, and Zn (Jennings 1994; Ahmad et al. 2016). It has been well documented that bacteria produce gluconic acid and its derivatives which solubilize the Zn and inorganic phosphate in soil (Gadd and Sayer 2000; Saravanan et al. 2007). Soil microbes also secrete low-molecular-mass iron-chelating compounds, siderophores, which can solubilize iron thus making it bioavailable (Machuca et al. 2007).

Scientists around the globe are working to identify the microbial strains responsible for the solubilization of insoluble nutrients in soil. For example, *Bacillus aryabhattai* and *Bacillus* sp. (AZ6) have been recognized as potential candidates for Zn solubilization from insoluble Zn resources (Ramesh et al. 2014; Hussain et al. 2015). Similarly, Mumtaz et al. (2017) screened 70 isolates and reported that 4 isolates can be the potential strains for solubilization of insoluble Zn in soil. They reported these strains as *Bacillus aryabhattai* S10, *Bacillus* sp. ZM20, *B.*

aryabhattai ZM31, and *B. subtilis* ZM63 after identification through 16S rDNA sequencing. In addition to *Bacillus*, the strains from other genera can also solubilize inorganic Zn compounds. For example, *Acinetobacter* sp. (AGM3), *Gluconacetobacter diazotrophicus*, and *Exiguobacterium aurantiacum* have been reported to solubilize inorganic Zn and Fe compounds, thus increasing Zn and Fe contents in grain crops (Ramesh et al. 2014; Gandhi and Muralidharan 2016; Shaikh and Saraf 2017). Secretion of chelating ligands, amino acids, organic acids, phytohormones, and vitamins by microbial strains can be the possible mechanisms for solubilization of inorganic compounds in addition to oxidoreductive systems and proton extrusion (Wakatsuki 1995; Saravanan et al. 2007).

Phosphate solubilization in soil depends upon the organic and inorganic nature of phosphate complexes that can be catalyzed by organic acid secretion and proton discharge. The P availability in soil depends upon pH and amount and nature of soil minerals. Under acidic conditions, P makes complexes with Fe and aluminum (Al), while at alkaline pH, it makes complexes with calcium (Goldstein 2000). The phosphate-solubilizing bacteria (PSB) solubilize Fe/Al-phosphate complexes by releasing proton, altering the negative charge at exchange sites, and thus facilitating the release of phosphate ions from complexes. The decreased adsorption of phosphates facilitates the release of primary and secondary orthophosphates (Henri et al. 2008). Moreover, the PSB can secrete carboxylic acid that releases carboxyl ions, thus replacing P in precipitated complexes through ligand exchange. Under alkaline conditions, PSB solubilize calcium phosphate complexes through secreting the organic acids thus acidifying the surrounding environment. The calcareous soils have high buffering capacity that can reduce the efficiency of PSB in releasing P (Stephen and Jisha 2009). From organic complexes, PSB release P through secretion of extracellular enzymes such as phosphatases (Dodor and Tabatabai 2003).

12.7.4 Biocontrol Activity

Soil microorganisms are effectively involved in the suppression of soil pathogens. The production of siderophores, antibiotics, hydrolytic enzymes, and competition for nutrients along with triggering the ISR in plants are important biocontrol mechanisms which soil microbes employ to improve plant productivity (Lugtenberg and Kamilova 2009; Kotan et al. 2009; Glick 2012). Moreover, degradation of fungal cell wall through hydrolytic enzymes is also used by soil microorganisms (Ramyasmruthi et al. 2012). The cell wall-degrading enzymes are important weapons to control phytopathogenic fungi in soil (Picard et al. 2000). The well-known fungal cell wall-degrading enzymes include chitinase, lyase, and cellulase (Nadeem et al. 2013). These enzymes are important for suppression of diseases. For example, inoculation with *Pseudomonas* sp. containing chitinase can inhibit the growth of *Rhizoctonia solani* through degradation of cell wall (Nielsen et al. 2000).

The antibiotics produced by soil microbes are mostly effective to control fungal pathogens (Glick 2012). A number of important antibiotics and antifungal metabolites are produced by soil microorganisms. These include 2,4-diacetyphlaroglucinol, phenazines, tensin, pyoluteorin, viscosinamide, pyrrolnitrin, and hydrogen cyanide (Haas and Keel 2003; Mazurier et al. 2009; Bhattacharyya and Jha 2012; Glick 2012). Hydrogen cyanide (HCN) is a volatile antibiotic produced by bacteria that works synergistically with other antibiotics to improve their efficiency for the suppression of plant diseases. It has been observed that inoculation with *Pseudomonas* strain having ability to produce HCN can suppress black rot of tobacco (Voisard et al. 1981).

Siderophores are Fe-chelating compounds which bind the available Fe in soil thus making it unavailable for use by soilborne pathogens. Siderophore-producing bacteria have been recognized as useful tools for biocontrol, as plant Fe requirement is much lower than most of the microorganisms (O'Sullivan and O'Gara 1992). Moreover, many plant species have the potential uptake Fe complexed with siderophores (Wang et al. 1993) that is not available to pathogen. These siderophore-producing bacteria reduce the availability of iron to fungi (Sayyed et al. 2008), thus suppressing its growth (Arora et al. 2001). It has been observed by Matthijs et al. (2007) that inoculation with *Pseudomonas* strain having ability to produce siderophores suppressed the disease caused by *Pythium* sp. by decreasing iron availability for fungal growth. It has been well documented that fungi are unable to use Fe complexed with siderophores (Solano et al. 2009). It might be due to high affinity of siderophores for Fe that limits its availability for fungal growth (Glick 2012).

Soil microbes can induce resistance in plants against pathogens, leading to induced systemic resistance (ISR). The ISR is phenotypically similar to the systemic acquired resistance (SAR) that is plant's internal mechanism to respond to infection by pathogens (Pieterse et al. 2009). Siderophore-producing bacteria are also involved in ISR, thus enhancing plant's defensive mechanism against pathogenic microorganisms. Literature reports the effectiveness of siderophores producing PGPR to enhance ISR against fungal and viral diseases (Saravanakumar et al. 2007). In addition to siderophores, jasmonate and ethylene signaling also stimulate the host plant's defense mechanisms against pathogens (Verhagen et al. 2004). Other ISR compounds released by soil microbes include lactones, homoserine, cyclic lipopeptides, 2,4-diacetylphloroglucinol, lipopolysaccharides (LPS), and some other volatile compounds (Lugtenberg and Kamilova 2009). Some antibiotics produced by soil microbes are also directly involved in ISR that can enhance the efficiency of antibiotics, thus increasing resistance against pathogens (Jha et al. 2011). From above discussion, it can be concluded that in addition to other plant growth-promoting mechanisms, soil microorganisms can also be effective in protecting plants against pathogens by suppressing their growth.

12.7.5 Enzymatic Activity

Production of enzymes by soil microorganisms is an important aspect that has been extensively explored by scientist during recent years. A number of bacterial strains have been documented which produce certain enzymes such as ACC-deaminase, catalase, cellulase, phosphatase, and chitinase. These enzymes can help plants to withstand different kinds of biotic and abiotic stresses. For example, ethylene is one of the phytohormones that has specific role in plant senescence and maturity. It is required for plant metabolism during normal growth and development, but in lesser amount (Khalid et al. 2006). It is also produced under stress (Saleem et al. 2007) that causes the change in normal metabolic processes of plants leading to its rescue from stressed conditions. Higher level of ethylene is produced under stresses that decreases the root and shoot growth of plants. For example, Ahmad et al. (2011) reported a decrease in root and shoot length and increase in stem diameter of mung bean under salinity stress, and they linked it to increase in ethylene concentrations. The ACC-deaminase has been reported in a number of bacterial strains belonging to genera *Pseudomonas*, *Bacillus*, and *Enterobacter* (Nadeem et al. 2010b; Ahmad et al. 2011). The improvement in plant growth due to inoculation with ACC-deaminase-containing bacteria under stressful environments has been well documented (Mayak et al. 2004; Zahir et al. 2010; Ahmad et al. 2012; Glick 2012). ACC is the immediate precursor of ethylene and cleaves it into α-ketobutyrate and NH_3 (Glick et al. 1998).

Chitinase is also an important enzyme that is produced by soil microbes and has the potential to suppress plant diseases (Glick et al. 2007). Similarly, another microbial enzyme cellulase can help in the penetration of rhizobia into root hairs during nodulation, thus increasing the nitrogen fixation in legumes (Sindhu and Dadarwal 2001). Phosphatases are also produced by phosphate-solubilizing soil microbes which help in the release of inorganic P from complexes, thus increasing P availability to plants (Dodor and Tabatabai 2003). The hydrolytic enzymes, such as chitinases, proteases, lipases, and glucanases, are also produced by soil microbes which are effective in biocontrol of pathogens. These enzymes are involved in fungal cell wall dissolution, thus suppressing their growth. The effectiveness of biocontrol mechanism of soil bacteria has been well documented against different pathogens (Kim et al. 2008; Glick 2012).

12.7.6 Stress Tolerance Induction

Soil microbes have adapted to a wide range of environments, thus can tolerate higher degree of environmental stresses. For example, *Rhizobium* can tolerate up to 64 dS m^{-1} salinity in solution culture (Forawi 1994) that enables these bacteria to develop successful symbiosis with legume crops, thus increasing nodulation under salt-stressed conditions (Ahmad et al. 2011). It has been reported that rhizobia are more tolerant to environmental stresses than their host plants (Elsheikh 1992). The PGPR also have remarkable tolerance against different stresses such as drought and salinity (Sandhya et al. 2009; Ahmad et al. 2011). Fungi can also be used as good tool to induce stress tolerance. For example, endophytic fungi including *Rhizodermea veluwensis*, *Phialocephala fortinii*, and *Rhizoscyphus* sp. enhanced the heavy metal stress tolerance in *Clethra barbinervis* by increasing the K uptake and decreasing the heavy metal concentrations in plant parts, thus enabling it to grow naturally at mine sites (Yamaji et al. 2016). The exact mechanisms of higher levels of stress tolerance of soil microbes have not yet been explored (Spaepen et al. 2009); however, these might be the production of exopolysaccharides (EPS) by soil bacteria that protect them against stresses, thus enhancing their survival (Upadhyay et al. 2011). Literature also reports the accumulation of poly-β-hydroxybutyrate, proline, and ectoine in bacterial body as protective measures for their survival under stress conditions (Bernard et al. 1993; Arora et al. 2006). The ACC-deaminase activity of soil bacteria and fungi has also been well documented as a mechanism for stress tolerance induction in crop plants (Glick et al. 2007; Nadeem et al. 2010a, b; Ahmad et al. 2011; Aban et al. 2017; Saravanakumar et al. 2018). The use of these stress-tolerant strains can be effective to improve soil fertility and crop growth (Egamberdieva and Kucharova 2009; Ahmad et al. 2013). It is evident from the above literature that beneficial soil microbes can withstand variable soil and environmental conditions that enable them to live better in competitive environment. These mechanisms make beneficial soil microbes a useful tool to maintain soil fertility and increase crop productivity and agroecosystem sustainability.

12.8 Application of Plant-Microbe Interactions in Agroecosystem

Plant-microbe interactions in the rhizosphere are modulated by edaphic factors. Rhizosphere is the zone of maximum biological activity, and plant roots and soil microbes communicate with each other. These interactions might be beneficial or harmful for one or both of the partners.

The beneficial plant-microbe interactions can be harnessed with better soil health, improved plant growth and productivity, and induced stress tolerance in crop plants. Improvement in beneficial microbial populations through rhizosphere engineering or use of microbial inoculants and/or their metabolites can be helpful to modify the soil microbiome (Velmourougane et al. 2017), leading to increased crop productivity and agroecosystem sustainability. Crop improvement through inoculation with beneficial soil microbes under normal and stressful environments has been widely studied and reviewed by many scientists (Glick et al. 2007; Singh et al. 2013; Nadeem et al. 2011, 2013, 2014, 2015; Ahmad et al. 2016). However, application of modern techniques to improve performance of soil microbes can be a key to agriculture sustainability by improving crop productivity, balanced nutrition, soil fertility, and plant stress tolerance (Gouda et al. 2018). Some selected examples of plant growth promotion by mycorrhizae and PGPR are presented in Table 12.2.

12.9 Plant Growth Promotion under Normal Conditions

Soil microbiome can effectively be exploited for improving the productivity of agroecosystems. Previous section reports the important plant growth-promoting mechanisms which directly or indirectly improve crop yield and soil health, thus overall productivity of the system. Manipulation of rhizosphere microbiome

Table 12.2 Effectiveness of microbes for promoting plant growth

Growth condition	Crop	Response	References
(a) the impact of bacterial inoculation on crop growth under normal and stress conditions			
Normal (field trial)	Chickpea (*Cicer arietinum*)	Dual inoculation of bacteria enhanced nodule number, nodule fresh weight, shoot N content, and yield	Valverde et al. (2006)
Normal (pot and field condition)		Inoculation improved nodulation and yield of chickpea	Elkoca et al. (2008)
Drought stress (pot trial)	Pea (*Pisum sativum*)	Rhizobacteria containing ACC-deaminase enhanced the growth of pea plant by reducing the negative impact of drought	Zahir et al. (2008)
Normal (field trial)	Rice (*Oryza sativa*)	Significant increase in growth due to improving number of tillers and shoot length	Bao et al. (2013)
Normal (field trial)		Inoculation with phosphate-solubilizing bacteria enhanced the growth and yield parameters, and significant increase in yield parameters was observed	Chamani et al. (2015)
Normal (pot and field condition)		Significant increase in number of tiller and seed yield	Isawa et al. (2010)
Normal (pot and field condition)	Maize (*Zea mays*)	Significant increase in growth was observed in pot and field trials	Ferreira et al. (2013)
Normal (pot trial)		Endophytic and rhizobacteria associated with sugarcane enhanced the maize growth and indole acetic acid content	Rodrigues and Forzani (2016)
Normal (pot trial)		Nitrogen-fixing *Gluconacetobacter diazotrophicus* colonized the inbred grain corn lines and sweet corn varieties. A positive correlation was observed between plant sucrose content and colonization efficiency	Tian et al. (2009)
Nutrient deficiency (pot trial)		Multistrain bacterial consortium significantly improved the growth of maize by enhancing the availability of P and K	Abou-el-Seoud and Abdel-Megeed (2012)
Drought stress (pot study)		Inoculation with *Azospirillum* helped maize seedling tolerate drought stress to a higher level as compared to uninoculated plants	Garcia et al. (2017)

(continued)

Table 12.2 (continued)

Growth condition	Crop	Response	References
Salinity stress (pot trial)	Wheat (*Triticum aestivum*)	Inoculation reduced sodium uptake and improved plant growth, sugar, and proline content	Upadhyay et al. (2012)
Normal (field trial)		Endophyte inoculation significantly increase the root length, root fresh weight, and root dry weight	Singh et al. (2017)
Normal (field trial)		Inoculation of wheat with bacteria in the biofertilizer enhanced the growth and productivity	Hussain (2016)
Drought stress (pot trial)		Under drought stress, endophytic *Burkholderia phytofirmans* PsJN improved the growth of wheat by maintaining ion balance	Naveed et al. (2014)
Salt and drought stress (hydroponic study)		*Arthrobacter protophormiae* (SA3) and *Dietzia natronolimnaea* (STR1) improved salt tolerance, while *Bacillus subtilis* (LDR2) provide protection against drought tolerance	Barnawal et al. (2017)
Normal (field trial)	Sugarcane (*Saccharum officinarum*)	Inoculation enhanced germination, growth, and sugarcane juice content	Beneduzi et al. (2013)
Normal (field trial)	Soybean (*Glycine max*)	Rhizobium inoculation enhanced the soybean yield compared to uninoculated	Hungria et al. (2013)
Abiotic stress (lab study)	Carrot (*Daucus carota*)	Inoculated bacteria showed biocontrol potential and significantly enhanced and promoted root formation on carrot slices	Etminani and Harighi (2018)
Normal (lab study in glass vial)	Cucumber (*Cucumis sativus*)	Nitrogen-fixing bacteria showed nitrogen-fixing ability and caused positive effect on plant growth	My et al. (2015)
Salinity stress (lab study)		Improved the growth of cucumber by reducing the impact of salinity. Inoculated plant showed better growth compared to inoculated plants	Nadeem et al. (2016)
Normal (lab study)	*Wedelia trilobata*	Endophytic *Bacillus* significantly enhanced the growth of inoculated plant. Effect of endophyte was different in case of invasive and native clonal plants	Dai et al. (2016)

(continued)

Table 12.2 (continued)

Growth condition	Crop	Response	References
Normal (pot study)	Potato *Solanum tuberosum*	The rhizobacterial strains showed variable response and caused significant positive impact on potato growth	Dawwam et al. (2013)
Nutrient stress (pot study)	*Okra(Abelmoschus esculentus)*	Inoculation enhanced the root and shoot growth of okra compared to no inoculation	Prajapati et al. (2013)
Normal (pot study)	Century plant *Agave americana* L.	Significant increase in plant growth and sugar content was observed due to phytohormone production and nutrient-solubilizing ability of bacteria	Torre-Ruiz et al. (2016)
Metal stress (pot study)	Mustard greens (*Brassica juncea*)	Inoculation enhanced the phytoremediation efficiency of plant and improved growth compared to uninoculated one	Qiu et al. (2014)
Normal and metal stress (pot study)	Pearl millet *Pennisetum glaucum*	Mitigate the negative impact of temperature and salinity stress and improve growth by the production of phytohormones and phosphorus availability	Misra et al. (2012)
Salinity stress (pot trial)	Barley (*Hordeum vulgare* L) and pearl millet (*Pennisetum glaucum*)	Inoculation improved the phytoremediation activity of the plant. Less electrolyte leakage and more membrane stability was observed in inoculated plants	Jodeh et al. (2015)
Salt and drought stress	Tomato (*Solanum lycopersicum*)	*Azotobacter* strains showed high tolerance to salt and drought stresses and alleviated the negative effects exerted by stress on tomato plants	Viscardi et al. (2016)
Salt stress (pot study)	Camelina (*Camelina sativa*)	Improved salinity tolerance of inoculated plant was due to several mechanisms. Salinity tolerance and presence of ACC-deaminase enzyme is responsible for reducing stress-induced ethylene	Heydarian et al. (2018)
Salinity stress (pot trial)	Oat seedlings (*Avena sativa*)	Inoculation modulated the expression profile of *rbcL* and *WRKY1* genes and enhanced plant's stress tolerance against salinity	Sapre et al. (2018)

(continued)

Table 12.2 (continued)

Growth condition	Crop	Response	References
Salt stress (pot study)	Citrus (*Citrus macrophylla*)	Both rhizobacterial strains reduce the negative impact of stress, and lower contents of abscisic acid (ABA) and salicylic acid (SA) were observed in inoculated plants under salt stress	Vives-Peris et al. (2018)
(b) the impact of mycorrhizal inoculation on crop growth under normal and stress conditions			
Normal (pot trial)	Onion (*Allium cepa*)	Mycorrhizae enhanced chlorophyll content as well as fresh and dry weight of onion	Shuab et al. (2014)
Normal (pot trial)	White clover (*Trifolium repens)*	Significant increase in nodule number, root length, volume and number of lateral roots, and chlorophyll content	Lu and Wu (2017)
Normal (pot trial)	Lettuce (*Lactuca sativa*)	Rhizophagus intraradices enhanced the Zn uptake of lettuce grown at two P levels; however, *Funneliformis mosseae* did not affect Zn content	Konieczny and Kowalaska (2016)
Abiotic stress (lab studies)	Common milkweed (*Asclepias syriaca*)	Mycorrhizae influenced plant resistance phenotype and a key factor for determining the outcome of plant herbivore	Vannette and Hunter (2013)
Drought stress (pot study)	Lime (*Citrus aurantifolia*)	Improved growth through its significant positive impact on chlorophyll contents and photosynthesis activity of the plant	Shahsavar et al. (2016)
Normal (pot study)	Tomato (*Solanum lycopersicum*)	Enhanced the plant resistance against bacterial wilt and improved its growth	Tahat et al. (2012)
Drought stress (lab study)		Mycorrhizal inoculation positively affects the tomato tolerance to water stress. A group of fungal genes play a key role in the water-transport process	Chitarra et al. (2016)
Normal (pot study)	Tomato (*Solanum lycopersicum*) and pepper (*Capsicum annuum*)	Caused significant impact on plant biomass, P accumulation, and improved fruit yield	Padmavathi et al. (2015)
Normal (pot study)	Sorghum (*Sorghum bicolor*) and chili pepper (*Capsicum annuum)*	Mycorrhizae caused significant differences in the growth of the host plant which shows preference of host plant for fungus.	Lee and Eom (2015)

(continued)

Table 12.2 (continued)

Growth condition	Crop	Response	References
Normal (pot study)	*Melberry (Morus alba)*	Improved growth through its significant positive impact on chlorophyll contents and photosynthesis and stomatal conductance	Shi et al. (2016)
Normal (pot study)	*Chinese Wedelia* (*Wedelia chinensis*)	Among seven indigenous AM fungi, *Glomus fasciculatum* improved plant nutrition and improved plant growth	Nisha and Rajeshkumar (2010)
Salinity stress (pot study)	Hangbaiju *(Chrysanthemum morifolium)*	Inoculation enhanced root length, shoot and root dry weight, and root N content. Nitrogen uptake could be the mechanism responsible for salinity tolerance	Wang et al. (2018a, b)
Drought stress (pot study)	Soybean (*Glycine max*)	Mitigated the impact of water stress. Arbuscule formation was higher in the unimproved than improved genotypes	Salloum et al. (2017)
Drought stress (pot study)	Maize (*Zea mays*)	Mycorrhizae together with rhizobacteria enhanced the vegetative and reproductive traits, root colonization, the grain yield of maize, content of P and N	Ghorchiani et al. (2018)
Salt stress (lab study)	*Acacia gerrardii*	Mycorrhizae alone and in combination with bacteria promoted plant growth by enhancing N, P, K, Mg, and Ca contents and phosphatase activities and reducing Na and Cl concentration	Hashem et al. (2016)

changes the soil microbial diversity and population that improves plant performance through change in water dynamics and enzyme activities in soil (Ahmadi et al. 2018). Rhizosphere engineering through augmentation can help to enhance root colonization that increases the availability of nutrients, reduces the use of chemical fertilizer, and conserves organic systems (Ahemad and Kibret 2014). It has been observed that combined use of rhizobacteria, endophytic bacteria, and arbuscular mycorrhizal fungi (AMF) significantly enhanced crop productivity by less use of chemical fertilizers (Pérez et al. 2007).

The PGPR can enhance crop productivity and nutrient availability through fixing atmospheric N_2, solubilizing inorganic P, production of Fe(III)-specific chelating siderophores, and phytohormones such as cytokinins, auxins, and gibberellins (Fravel 2005). Siderophore-producing bacterial strains *Stenotrophomon aschelatiphaga* and *Myristica yunnanensis* significantly improved plants' zinc and phosphorous contents of canola and maize plants (Ghavami et al. 2016). Results showed a significant increase in root and shoot Zn contents, thus improving crop growth and productivity. They suggested these strains as potential bioinoculant for improving plant productivity that can reduce the use of chemical fertilizers. This can also be a possible option to correct the nutrient deficiency in canola and maize crops, leading to agroecosystem stability (Ghavami et al. 2016).

Solubilization of nutrients is an important mechanism used by soil microbes to improve growth, yield, and quality of crop plants. In alkaline calcareous soils, the decreased efficiency of fertilizers especially Zn and phosphorus is an issue. Especially formation of insoluble zincate complex upon Zn fertilization is considered a serious threat to soil-plant nutrition. The issue can be resolved by inoculation with Zn-solubilizing bacteria. For example, Mumtaz et al. (2018) evaluated four Zn-solubilizing PGPR strains *Bacillus* spp. (ZM20), *B. subtilis* (ZM63), and *B.* aryabhattai (ZM31 and S10) for their effectiveness to improve growth, yield, and quality of maize grains. It was observed that Zn-solubilizing *Bacillus* strains significantly improved the plant growth, yield, and nutrient concentration in maize grains. Use of phosphate-solubilizing bacteria can also be helpful to improve crop productivity and fertilizer efficiency in alkaline calcareous soils. Recently, Ahmad et al. (2018) evaluated the phosphate-solubilizing *Bacillus* strains to improve cotton growth under alkaline conditions. They reported that bacterial strains varied in their growth-promoting traits and they differed in P-solubilization efficiency. Efficient root colonization of these strains in cotton under salt-affected soils helped plants to uptake more phosphorus thus improving cotton growth.

The combined use of PGPR with other soil microbes and/or organic and inorganic sources of nutrients can be effective to improve crop productivity by sustaining soil fertility. Ahmad et al. (2015) evaluated *Pseudomonas fluorescens* in combination with different sources of organic manure and chemical fertilizer for enhancing the productivity of cucumber (*Cucumis sativus* L.). They reported significant improvement in growth, fruit quality, and yield of cucumber by combined application of *P. fluorescens*, organic manure, biogas slurry, and chemical fertilizer. So, the combined use of organic sources and *P. fluorescens* can be used to enhance cucumber productivity that can also sustain soil fertility for future. Similarly, the effectiveness of ACC-deaminase-based biofertilizer consisting of *Rhizobium* and *Pseudomonas* strains was evaluated in combination with P-enriched compost under field conditions to improve the productivity of chickpea on marginal soils in Bahawalpur. The combined use of ACC-deaminase-containing biofertilizer and P-enriched compost effectively improved chickpea productivity on marginal soils under field conditions and can be used as effective strategy to cope with scenario of limited water availability and sustaining agroecological systems (Ahmad et al. 2017).

Mycorrhizal associations use different growth-promoting characteristics (Smith and Read 2008) such as improvement in rhizobial activities for N_2 fixation (Krapp 2015), improvement in photosynthetic rates (Hashem et al. 2015), enhancing phosphatase activity in soil (Liu et al. 2015), producing bioactive substances (Goicoechea et al. 1997), detoxification of heavy metals (Zong et al. 2015), reducing the effect of stresses through osmotic adjustments (Xun et al. 2015), and increase in resistance to abiotic (Hashem et al. 2015) and biotic (Yuan et al. 2016) stresses. Fungi enhanced the nitrogen status of plants when applied in combination with PGPR, rhizobia, or both (Barnawal et al. 2014; Armada et al. 2015; Barrett et al. 2015). The AM fungi enhance surface area of plant roots through symbiotic associations (Kaiser et al. 2015) and help in the exchange of nutrients between soil and plant roots (Buscot 2015), thus enhancing nutrient uptake and plant growth. Rice is the crop with high water requirement and is severely affected by water scarcity and climate change. The AM fungi can establish strong symbiotic associations with roots of rice crop. Rice has been studied as a model for molecular determinants regarding establishment and functioning of AM symbiosis to provide insights into potential breeding target for improving the crop interaction with AMF. There are strong evidences which show the beneficial effects of AM fungi on performance of rice crop under field conditions (Mbodj et al. 2018).

Moreover, multistrain biofertilizers can be more efficient than single-strain inoculants due to their multifarious traits. For example, Zahir et al. (2018) evaluated the effectiveness of multistrain biofertilizer to enhance growth, nodulation, and productivity of ten genotypes of mung bean under field conditions. They also evaluated the effect of biofertilizer on total bacterial DNA in soil and reported increase in nodulation, growth, and yield of mung bean as compared to uninoculated control. The genotypes also varied in their productive potential and responded differently to biofertilizer under field conditions.

12.10 Role of Soil Microbes under Stress

Climate change and anthropogenic activities breed a number of environmental stresses which can seriously affect the productivity of agroecosystems (Vimal et al. 2017). These stresses are classified as abiotic (salinity, drought, flooding, temperature, wounding, and heavy metal stresses) and biotic (insect and pathogenic stresses). These stresses can significantly reduce the productivity of cropping systems. Soil microbes can be successfully used to reduce the effect of these stresses on crop productivity. Mechanisms used by these microbes for reducing the impact of environmental stresses are summarized in above sections. A number of reports are available regarding field application of these mechanisms for inducing stress tolerance in crop plants (Glick et al. 2007; Ahmad et al. 2012; Nadeem et al. 2014), thus enabling plants to maintain normal metabolic processes. This section summarizes some of the selected studies regarding use of soil microbes under abiotic and biotic stresses.

Soil microbes can reduce the effect of stresses on plant growth by releasing 1-aminocyclopropane-1-carboxylic acid (ACC) deaminase which consumes the ACC; the immediate precursor of ethylene thus suppresses the stress-induced production of ethylene (Abou-Shanab et al. 2006; Glick et al. 1998). Other well-known plant growth-promoting mechanisms used by soil microbes under stress include alteration of root morphology, increase in water uptake, antibiotics production, and induction of plant defense mechanisms (Kidd et al. 2017). The PGPR also influence mobility and phytoavailability of trace metals in soil (Sessitsch et al. 2013).

12.10.1 Abiotic Stress

Abiotic stresses such as drought, salinity, and heavy metals are among the most common problems of our agroecological systems. Many efforts are being made to cope with these stresses. Plants also regulate internal metabolic processes to adapt to the stressed environments, however, by compromising their yield. Higher levels of ethylene production, imbalance of ionic ratios, nutritional imbalance, and production of toxic reactive oxygen species are among the major changes which occur in plants under different kinds of stresses. Beneficial soil microbes can effectively be used to regulate the metabolic processes of plants under stress, thus maintaining their yields (Nadeem et al. 2014). Use of these microbes can be durable, cost-effective, and environment-friendly that not only enhances crop yield but also improves soil health.

Environmental stresses can also affect the growth of beneficial soil microbes; however, they have adapted to a wide range of environments through their particular characteristics such as production of exopolysaccharides and ACC-deaminase activity. For example, *Rhizobium* can tolerate up to 64 dS m^{-1} salinity in solution culture (Forawi 1994) that enables these bacteria to develop successful symbiosis with legume crops, thus increasing nodulation under salt-stressed conditions (Ahmad et al. 2011). The stress-tolerant soil microbes can also be effective to induce tolerance in crop plants against abiotic stresses such as salinity, drought, high temperature, and heavy metal toxicity (Grover et al. 2011). The exopolysaccharides released by soil microbes can also protect plants from desiccation by forming protective layer around soil aggregates (Tisdall and Oades 1982). Exopolysaccharides also increase root colonization of microbes (Santaella et al. 2008) by improving soil aggregation (Sandhya et al. 2009) and improving water and nutrients availability to plants (Tisdall and Oades 1982). The inoculation with ACC-deaminase containing bacteria has the potential to reduce negative effect of ethylene on pepper and tomato plants, thus improving growth of these crops (Mayak et al. 2004). It has been reported that the combined use of *Rhizobium* with PGPR-containing ACC-deaminase minimized the negative effect of ethylene on mung bean, thus improving nodulation under salinity stress (Ahmad et al. 2011).

The use of bacteria with ACC-deaminase activity is helpful in improving crop productivity under stresses, and the efficiency of microbial inoculants can be improved by using them in combination with exogenous plant growth regulators. For example, Jamil et al. (2018) evaluated the effectiveness of using *Pseudomonas fluorescens* strain containing ACC-deaminase in combination with L-tryptophan to reduce the effect of drought stress on wheat crop. They reported that using L tryptophan at 25 ppm along with *P. fluorescens* is more effective than their separate application. They suggested that the approach could be effective to improve productivity of wheat under water scarcity. In another study, Nadeem et al. (2017) reported that *P. fluorescens* in combination with compost and biochar improved the water stress tolerance in cucumber. They conducted a greenhouse experiment for evaluating the effectiveness of integrated use of biochar, compost, and *P. fluorescens* to alleviate the effect of water-deficit stress. They used three levels of water, i.e., field capacity (D0), 75% field capacity (D1), and 50% field capacity (D2), and concluded that integrated use of these sources was an effective strategy to alleviate the deleterious effects of water stress on cucumber growth. They, however, proposed field studies to further investigate the biotechnology for its long-term impact on agroecosystem sustainability.

Soil microbes present in rhizosphere of hyperaccumulating plants are distinct with higher genetic diversity and have high level of resistance to metal stress, which can effectively be used to improve crop performance and phytoremediation of heavy metal-contaminated soils (Thijs et al. 2017; Benizri and Kidd 2018). Recently, Ghasemi et al. (2018) evaluated the effect of bacterial inoculation on plant health, growth, and Ni phytoextraction ability of three Ni-hyper accumulator species, *Odontarrhena inflate*, *O. bracteata*, and *O. serpyllifolia* using five rhizobacterial strains isolated from *O. serpyllifolia*. They reported that bacterial strains effectively enhanced the Ni removal by stimulating plant growth and/or increasing shoot Ni concentration. However, the efficacy of these strains varied with soil type, plant species, and bacterial strain. Antioxidative enzymes and malondialdehyde (MDA) and H_2O_2 concentration was also lower in inoculated plants, indicating protective effect of these strains on plants. In another study, Alvarez-Lopez et al. (2017) evaluated the effect of combined use of composted sewage sludge and bacterial inoculation on the growth and heavy metals (Cd and Zn) accumulation ability of *Salix caprea* and *Nicotiana tabacum* in contaminated mine tailings. Bacterial inoculation improved biomass of tobacco in compost-amended soil, while it did not work so efficiently in unamended soil.

The AM fungi have been reported to improve the carbon and nitrogen cycling in alpine grasslands (Li et al. 2015). The hyphal networks of AM fungi help plants in uptake of water and nutrients in stressed environments and restrict the availability of heavy metals to plant roots (Miransari 2011). The fungal associations can be helpful in the restoration of degraded lands and forests. The use of fungi in combination with organic sources or bacteria has been reported to be helpful in the restoration of soil fertility and organic matter contents in degraded soils (Rashid et al. 2016).

12.10.2 Biotic Stress

The use of soil microbes can also be effective to control pests and diseases of field crops. For example, Prabhukarthikeyan et al. (2014) evaluated the combined use of PGPR and endophytic bacteria (*Bacillus* strains) and reported that the combination was effective in controlling the fusarium wilt and fruit borer in tomatoes in the absence of pesticide. In another report, Bandi and Sivasubramanian (2012) reported the ability of *Pseudomonas fluorescens* to induce systemic resistance against thrips (*Thrips tabaci* L.). He regarded *Pseudomonas fluorescens* as effective biocontrol agent against pests. Soil microbes have the ability to produce allelopathic substances, which are effective against various pests of crop plants (Sessitsch et al. 2004). Different metabolites synthesized by soil microbes suppress growth and prevalence of plant pathogens that indicates their potential to be used as effective biopesticides. It has been reported that beneficial soil microbes can suppress growth of pathogenic fungi, bacteria and viruses, weeds, nematodes, and insect pests through production of antibiotics and hydrolyzing enzymes or ISR (Gao et al. 2015).

The use of soil microbes as biocontrol agent is regarded as an environment-friendly approach as these microbes are very specific to their host pathogens (Kachhawa 2017). The use of soil microbes could decrease agrochemical use, helping to foster environmental sustainability by reducing the harmful effects of toxic chemical compounds. The use of plant growth mechanisms of beneficial soil microbes is economical and ecofriendly approach to protect plants against stress conditions. These plant-microbe interactions are vital for sustainable agriculture because this approach depends upon biological processes and can replace conventional agricultural practices (Kumar and Verma 2018).

The above discussion shows the effectiveness of soil microbes for enhancing crop productivity under normal as well as stressed environments. It is evident from the literature that soil microbes use a number of direct and indirect mechanisms for improving crop productivity. The use of these beneficial microbes can not only enable plants to maintain their growth and productivity under various kinds of environments but also improve soil health that can be beneficial in maintaining agroecosystem sustainability.

12.11 Conclusions and Future Prospects

Above discussed literature indicates that soil microbiome has strong implications on plant growth. Soil-plant-microbe interactions can be harnessed with good crop productivity and ecosystem sustainability. Soil microbes interact with plant roots positively or negatively and thus have significant effects on plant growth and productivity and soil health. Symbiotic plant microbe interactions have been well documented which can significantly improve plant growth. These interactions are affected by quality of root exudates and physicochemical properties of soil.

Beneficial soil microbes have a number of plant growth-promoting mechanisms including biological nitrogen fixation, phytohormone production, and nutrient solubilization. These traits of beneficial microbes can be harnessed for better soil health, improved plant growth and productivity, and improved stress tolerance of crop plants. Improvement in beneficial microbial populations through rhizosphere engineering or use of microbial inoculants and/or their metabolites can be helpful in modifying the soil microbiome, leading to increased productivity of agroecosystem. The soil microbes are equally effective to enhance plant growth under normal as well as stress conditions. Soil microbes also protect plants from biotic and abiotic stresses through ACC deaminase activity, exopolysaccharides production, and production of hydrolytic enzymes and volatile compounds.

Future research should focus on understanding the mechanisms involved in bacterial-induced growth promotion. Research should also be conducted to investigate why the same isolate with specific PGP traits performs differently and could not induce the same plant response under distinct soil conditions. Strategic improvement in plant-microbe interactions through bioinformatics, molecular genetics, and modeling tools should be carried out for improving crop productivity and agroecosystem sustainability.

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