

Chapter 14

Mighty Microbes: Plant Growth Promoting Microbes in Soil Health and Sustainable Agriculture



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Abstract Plants undergo a variety of biotic and abiotic stresses and to cope with such stresses, they have developed different direct and indirect mechanisms. Soil contains a diverse microbial community that have a diverse functional niche. For maximum growth and protection benefits, plants establish partnership with a variety of different beneficial microbes such as bacteria and fungi. These microbes can live inside and outside of plant tissue and have a broad host range. Microbes can modulate plant defense signaling pathways in the presence of stress conditions. Beneficial microbes can antagonize stresses and improve plant growth and fitness. We need to better understand the ecology and biology of the microbes associated with plants to exploit maximum services associated with beneficial microbes. For environmentally friendly and sustainable agriculture, we should reduce input of chemical fertilizers, pesticides, and fungicides and in this regard, use of beneficial plant-associated microbes is a promising alternative.

Keywords Beneficial microbes · Sustainable agriculture · Soil health · Symbiosis · PGPR · Fungi · Biotic and abiotic stresses

14.1 Introduction

In the past 50 years, a tremendous increase in the food production has been observed which is usually the outcome of widespread agriculture system called conventional or industrial farming system. According to an estimation of World Bank this system has risen the food production between 70% and 90%. However, for the enhancement

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of food production, this agriculture system relies on various chemicals and artificial enhancements such as fertilizers, pesticides, genetically modified organisms and external energy inputs like fossil fuels, large-scale farms and use of large machine for their management. Although intensive agricultural production is the need of the time, the massive utilization of the natural resources that are nonrenewable such as soil, water, fossil fuels and rock mineral reserves etc. and energy-intensive industrial processes for the fertilizers production and the runoff of the soluble nutrients into the aquatic systems are the sources of environmental contamination (Browne et al. 2013). In addition, intensive agriculture is also affecting the stability of biosphere by increasing the production of greenhouse gases and therefore rising the earth's temperature. This is ultimately generating various types of stress conditions such as salinity, drought, nutrient deficiency, soil erosion, contamination, pest and disease etc. which are affecting both agricultural system and natural ecosystems. Despite enhanced food production by the industrialized agriculture system, due to the negative aspects of this technology, many scientists and farmers are shifting toward sustainable agriculture which is environmentally, economically, and socially more sustainable.

14.2 Sustainable Agriculture

The word “sustain” comes from the Latin word *sustinere* (*sus* means “from below” and *tinere* means “to hold”), implying for long-term support. With respect to agriculture, the term sustainable means a farming system that for an indefinite time can maintain its productivity and efficacy to a society that is socially supportive, commercially competitive, resource conserving, and environmentally sound. So sustainable agriculture mainly emphasizes on long-term production of crops with minimum effects on the environment. In addition to food, it also helps in lessening the utilization of fertilizers and pesticides, water conservation and promoting crops biodiversity. In addition, this system assists in the maintenance of economic stability and assists the farmers in improving their quality of life by using better techniques. In accordance to Food, Agriculture, Conservation and Trade Act (FACTA) of 1990, sustainable agriculture is an integrated system that in the long run will satisfy the needs of human food and fiber, promote agricultural economy by enhancing the quality of natural resources and environment, efficiently utilize nonrenewable resources, and improve the life quality of farmers and society as a whole. In agriculture, environmental sustainability means good stewardship of the natural system and the resources on which farms depend upon. This includes the maintenance of healthy soil, management of water, reduction of pollution, and enhancement of plant biodiversity.

14.3 Benefits of Sustainable Agriculture

The various benefits of sustainable agriculture can be divided into human health benefits and environmental benefits. With respect to human health, in sustainable agricultural crops, people are not being exposed to chemicals, i.e., fertilizers and pesticides, so these crops ensure consumer safety as it reduces their chances of illness after exposure to these chemicals. Additionally, these crops could be more nutritious being more natural and healthier than the crops grown through industrialized agriculture. It also benefits the environment through saving soil water, decreasing soil erosion, and by the maintenance of soil quality. Moreover, it also contributes for enhancing the biodiversity by the provision of natural and healthy environment to a variety of the organisms. One of the major benefits for the environment is the 30% less energy consumption for one unit of crop yield. This reduces the dependence on fossil fuels, and consequently environment is less polluted.

14.4 Sustainable Agricultural Practices

World population is expected to reach 10 billion in 2050 and almost all this growth increase is expected to take place in the developing countries. This will generate many challenges, increasing the demand of more food, fiber and bioenergy and the demand for the preservation of the biosphere. Researchers are aware to address their research efforts for satisfying the food demands of a growing and urbanized world population. In this regard, agricultural practices are basic to fulfill the future agricultural demands of the world (Altieri 2004). Some of the most common techniques include crops rotation, planting cover crops, reduction or elimination of tillage, application of integrated pest management, integration of livestock and crops and adoption of agroforestry practices. Besides traditional solutions, a recommended approach is the use of beneficial native soil microbes as biocontrol agents, which is a strategic technique for the achievement of sustainable agricultural production. These microbes play fundamental role to produce healthy and sustainable crops and preserve the biosphere. They improve the plant nutrition and health and improve the quality of soil (Lugtenberg 2015).

14.5 Plant-Associated Soil Microbiome and Sustainable Agriculture

A goal of sustainability is to look for competent methods of nutrient recycling, pathogens and pest control and the alleviation of negative effects of abiotic stress factors. Microbes offer many services to plants and soil (Ray et al. 2016; Zolla et al.

2013). Various types of organisms are found in the soil microbiome, but among those bacteria and fungi received much attention (Spence and Bais 2013). Several factors affect the recruitment and maintenance of the microbiome in the rhizosphere (a thin layer of soil encircling the plant roots). Plant morphology as well as the rhizodeposition of the plant give rise to distinct microbial population (Rosier et al. 2016). Along with other environmental factors, the chief traits of soil such as micro- and macronutrients, pH, redox and water potential, play a vital role in shaping composition and activity of microbiome. Most of these microbes are found in the rhizosphere and few of them reside inside the plant tissues, known as endophytes (Mercado-Blanco 2015). About 90–100 million bacteria and 200,000 fungi are usually found in a gram of soil. The exudates of plant roots containing a large amount of photosynthetically fixed carbon is the one of the major sources of attraction for these microbes. The relationship between plants and microbes may be beneficial, harmful, or neutral for the plants. Rhizobacteria and fungi that play beneficial role for plant growth and development are known as plant growth promoting rhizobacteria (PGPR) and plant growth promoting fungi (PGPF), respectively. Presently, based on successful interaction of PGPR and PGPF with plants, scientists are now utilizing these in agriculture, horticulture and for other environment services (Gamalero and Glick 2011). Hence understanding the diversity in structure and key function of the microbiome can play important role in sustainability of agriculture.

14.6 Role of Soil Microbes for Stress Tolerance in Crops

Meta-analysis of the plants under various stresses simultaneously show a complex regulation of plant growth and immunity. It is fundamental to understand the phytohormonal interaction in the signaling network, in order to understand the survival of plant microbiome systems under stressed conditions, which will be useful for designing biotechnological strategies to optimize the plants stress adaptive mechanisms and to improve microbes' ability to ameliorate stress situations in crops (Pozo et al. 2015). Although under stress situations the mechanisms involved in plant–microbe interactions are not well understood. However, various ongoing researches are showing evidences of the microbes induced alterations in the plant excreted root exudates, activities of transporters and in the plant morphology and physiology, changes that enable plants to recruit stress alleviating microbes, a strategy that helps in enhancing crop yield under stress environments (Zolla et al. 2013). As the environmental stress factors badly affect the agriculture productions, so rhizosphere microbes play a vital role in assisting plants to survive under such harmful conditions (Barea et al. 2013). Applications of the stress-tolerant PGPR and Arbuscular mycorrhiza (AM) fungi help in plant growth and survival under severe conditions (Nadeem et al. 2014). During stress, various direct and indirect mechanisms are utilized by these microbes to combat the adverse effects (Ahmad et al. 2019). Under unfavorable circumstances, microbes use various biochemical and

molecular mechanisms to promote the plant growth and development. For instance, PGPR regulate hormonal and nutritional balance, produce phytohormones, induce systemic resistance against phytopathogens, produce certain metabolites like siderophores that help in reducing the phytopathogens population around the plants (Spence and Bais 2015; Złoch et al. 2016). Similarly, they can also fix atmospheric nitrogen and solubilize phosphate that facilitate plant growth (Ahmad et al. 2011). In addition, mobilization of nutrients and production of exopolysaccharide and rhizobitoxine, etc. are other mechanisms used by the PGPR (Vardharajula et al. 2011). Rhizobitoxine by inhibiting the ethylene production helps the plant to cope stress situation (Kumar et al. 2009). Besides certain key enzymes such as ACC deaminase, glucanase and chitinase are also produced by these microbes to overcome adverse conditions (Farooq et al. 2009b). Some bacteria also possess sigma factors to alter the gene expression in order to overcome negative effects of stress situations (Gupta et al. 2013). Besides PGPR, fungi also play an important role in the growth and development of plants. Arbuscular mycorrhiza is the most widespread mycorrhizal association present in the agriculture field, which plays an important role in nutrient cycling. So, by utilizing these various mechanisms, microbes assist the plants in maintaining their original growth under the stress conditions as shown in Fig. 14.1. As PGPR are the potential alternate of fertilizers and pesticides, so they are essential for sustainable agriculture production and to deal with future food security concerns. Use of the stress-tolerant microbes in the sustainable agriculture practices can help in enhancing the nutritional values and yields of food grains under the changing environment and can save 20–25% cost of the chemical fertilizers and pesticides. Further utilization of these practices can also assist the farmers in enhancing their financial income by producing organic foods and vegetables. We will focus on the role of PGPR and PGPF in plant growth promotion and protection (Fig. 14.1).

14.7 Plant Growth Promoting Rhizobacteria

Among the plant-associated microbiome, PGPR are the potential microbes having ability to colonize the plant roots and stimulate plant growth (Goswami et al. 2016). These soil bacteria belong to various genera such as *Pseudomonas*, *Bacillus*, *Rhizobium*, *Azospirillum*, *Azotobacter*, *Azoarcus*, *Clostridium*, *Enterobacter*, and *Serratia* (Arora et al. 2015). PGPR are also potential microbes that provide plant protection against various environmental stresses (Kang et al. 2014). The effective role of PGPR in sustainable agriculture has been described by an ample literature (Ahmad and Kibret 2014; Arora and Mishra 2016). Initially PGPR's role was explored only for the enhancement of crop productivity, but according to several recent studies they are also important for the proper functioning of agroecosystems (Cheng 2009). PGPR can assist in restoring the degraded land, reducing the environmental pollutants from the soil and improving the soil quality and combating changes in the climate (Kuiper et al. 2004) by a variety of mechanisms.

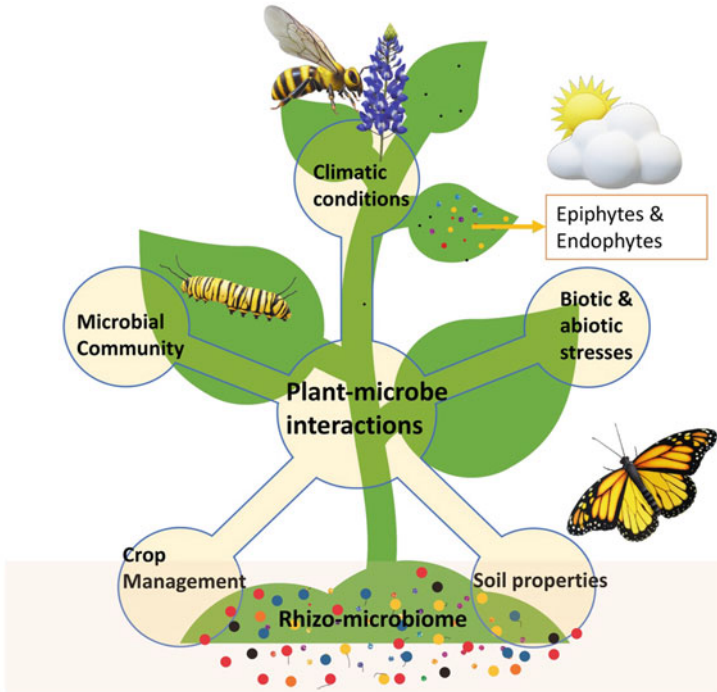


Fig. 14.1 Role of soilborne microbes in plant growth promotion and protection against stresses. PGPR, PGPF and other rhizospheric and endophytic soilborne microbes with a diverse host range help plants in combating several environmental stresses

14.7.1 Mechanisms of Plant–PGPR Interactions

The in-depth understanding of the interactions at the soil–root nexus will help in unlocking the potential of the microbes for agriculture. During recent past, extensive research has been conducted to reveal the mechanisms of plant–microbe interactions (Beneduzi et al. 2012). PGPR usually facilitate the plant growth either directly or indirectly as shown in Fig. 14.2.

14.7.2 Direct Mechanisms

As the availability of the mineral nutrients in the rhizosphere is important for the plant growth, the improvement of mineral nutrition in plants by PGPR is one of the best mechanisms studied among the direct mechanisms (Pii et al. 2015b). Biological nitrogen fixation, siderophores production, phosphorus solubilization, and the manipulation of biochemical and molecular pathways for nutrient acquisition are

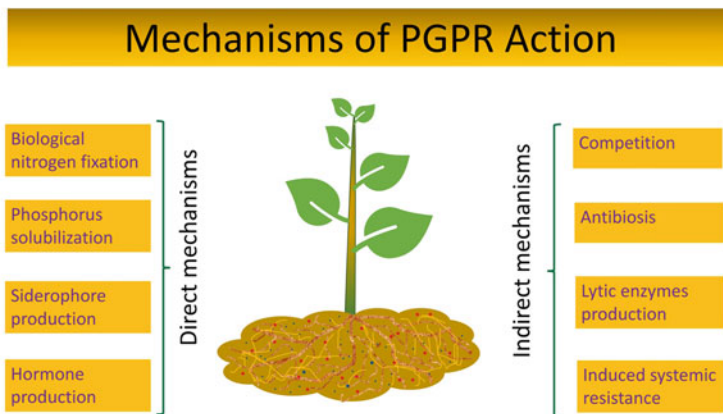


Fig. 14.2 Mechanisms of plant growth promotion by PGPR. PGPR can promote growth and their mutualistic or symbiotic plant hosts from different biotic and abiotic stresses by multimechanistic approach

the various ways utilized by PGPR for mineral nutrients acquisition (Terrazas et al. 2016).

14.7.2.1 Biological Nitrogen Fixation

Nitrogen (N) is the most vital element for plant growth and development. Although 78% of N is available in atmosphere, plants are unable to use this molecular nitrogen directly. Biological nitrogen fixation helps in providing this important nutrient to plants in a usable form. In this process, N is converted into ammonia (NH_3) using ATP, which is catalyzed by the nitrogenase enzyme. Various microbial genera such as *Pseudomonas*, *Bacillus*, *Azospirillum*, *Erwinia*, and *Rhizobium* can fix atmospheric nitrogen (Silva et al. 2016). Both symbiotic and nonsymbiotic bacteria can fix the atmospheric nitrogen (Bhat et al. 2015). The nonsymbiotic bacteria include *diazotrophicus*, *Azospirillum*, *Azotobacter*, and *cyanobacteria*. The symbiotic nitrogen fixation is carried out by the members of *Rhizobia* genera through forming symbiotic association with leguminous plants and most of the atmospheric nitrogen is fixed through this process. However free-living *diazotrophs* contribute very less for the bioavailability of N to the plants (Jones et al. 2007). Biological nitrogen fixation is economically viable and environmentally safe alternative of chemical fertilizers. Some of these bacteria-forming root nodules also play an important role in interaction between plants and bacteria (Yan et al. 2008). Different abiotic stresses like salinity and drought inhibit the root nodulation. Nitrogenase enzyme is very sensitive to salt stress and its activity is severely hampered under salt stress condition, which ultimately inhibits nitrogen fixation. PGPR help plants in combating these stress conditions and offer great services to promote and protect plant growth.

14.7.2.2 Solubilization of Phosphorus

Like nitrogen, phosphorus (P) is also an essential nutrient important for plant growth and development. It is important for root growth and for various physiological processes of plants. Plants usually acquire P from the soil in the form of phosphate ions. Phosphorus in the soil is present in excess both in the organic and inorganic forms but less than 1% is readily available for plants (Terrazas et al. 2016). So, in order to ensure the availability of immobilized P to plants, solubilization of inorganic forms and the enzymatic mineralization of organic P is required (Gerke 2015). PGPR make it available to plants through mineralization and solubilization. The plant-microbe association in soil helps in enhancing the mobility of phosphorus and its availability to plants. The phosphate solubilizing rhizobacteria are very common in nature and their numbers differ from soil to soil. They govern biogeochemical cycle in natural agriculture system and usually mobilize phosphate by producing organic acids and phosphatase. The phosphate solubilization may result either due to decrease in pH or due to cation chelation. Various genera of PGPR and fungi are able to solubilize phosphate (Yadav et al. 2014). Most of the plant-associated PGPR improve phosphorus uptake in plants from soil under the P deficient condition possibly through production of organic acids and phosphatases and by lowering pH. These organic acids compete for binding sites on soil and make the availability of P to plants. The organic acids decrease the surrounding pH and release phosphate from the H^+ ions. Among the various organic acids, 2-ketogluconic acid is the effective acid. Moreover, cotransport of protons along with exudation process acidify the external medium that promotes acid solubilization of the immobilized P (Terrazas et al. 2016). The phosphatase enzymes of PGPR assist in mineralizing the organic forms of P and releasing orthophosphate groups in soil (Azeem et al. 2015). Several PGPR are reported to have ability of phosphate solubilization, so their use in agriculture may be cost-effective and sustainable.

14.7.2.3 Production of Siderophores

Iron is a micronutrient vital for plant growth playing crucial role in photosynthesis, respiration, DNA synthesis, and nitrogen fixation. Iron in nature exists in ferrous Fe (II) and ferric Fe (III) oxidation states. Under aerobic environment, iron is mostly present as ferric (Fe^{3+}) form which has very less solubility due to formation of insoluble hydroxides and oxyhydroxides that are not available to both plants and microbes (Mimmo et al. 2014). Microbes usually obtain iron by synthesizing and secreting low molecular weight organic compounds usually known as microbial siderophores (Lemanceau et al. 2009), that have high affinity for ferric form of iron (Mishra et al. 2011). These siderophores form stable complexes with Fe^{3+} which through ABC transporters are transported into the microbial cell (Braun and Hantke 2011; Hider and Kong 2010) where they are reduced from Fe^{3+} to soluble Fe^{2+} form (Rajkumar et al. 2010). Siderophores are water soluble and are usually divided into

intracellular and extracellular siderophores. Plants mostly acquire iron through microbial siderophores using various means either by direct uptake or by ligand exchange reaction that helps in enhancing chlorophyll contents of plant leaves. Application of the siderophores producing PGPR in iron deficient plants helps in alleviating the Fe deficiency, showing the possible role of these microbes in assisting the plant roots for nutrients acquisition by making them available to soil (Pii et al. 2015a).

14.7.2.4 Modulation of Biochemical and Molecular Mechanisms

Although plants may have ability of enhancing the mineral uptake by themselves but PGPR basically enhance the availability of the key nutrients in the rhizosphere, which improves the mineral nutrition in the PGPR-associated plants. ATPases in plasma membrane are responsible for the generation and maintenance of H^+ electrochemical gradients across the transmembrane, that is necessary for the transport of numerous nutrients such as phosphate PO_4^{2-} , sulfate SO_4^{2-} and nitrate NO_3^- . Hence PGPR improve the mineral uptake by enhancing H^+ extrusion across the membrane. Concerning the N nutrition, PGPR application induces the expression of various nitrate transporter genes (Kechid et al. 2013). Similarly, PGPR application also enhance the root iron chelate reductase activity that is involved in reducing Fe^{3+} to soluble Fe^{2+} prior to uptake by transporters (Zhao et al. 2014).

14.7.2.5 Production of Phytohormones

Phytohormones play a key role in plant development and growth (Glick et al. 2010) and their activity is mainly associated with the plasticity of the root system (Kloepper et al. 2007). PGPR can also produce auxin, cytokinin, and gibberellins that influence the root architecture (Vacheron et al. 2013). Many PGPR have the ability to synthesize and secrete indole-3-acetic acid (IAA, auxin) as secondary metabolites (Scagliola et al. 2016). Bacterial- and plant-derived IAA play an additive role by enhancing the root length and surface area to provide better access to soil nutrients (Glick 2012). Additionally, IAA have been found to induce the expression of the key genes both in plants and microbes which are required for the better establishment of efficient plant-PGPR interactions (Spaepen and Vanderleyden 2011). PGPR producing 1-aminocyclopropane-1-carboxylate (ACC) deaminase are able to cleave the ethylene precursor (ACC) into 2-oxobutanoate and ammonia and hence facilitate the plant growth improvement by reducing the stress ethylene level (Glick 2014). Under stress, ethylene is produced in two peaks, the first one being much smaller is believed to activate the defense mechanisms whereas the second peak has adverse effects on plant growth. PGPR having ACC deaminase activity act as a sink for ACC, thus mitigating the negative effects of ethylene on plant growth (Glick 2014). As a result, plants applied with ACC deaminase PGPR

show better associations with microbes, enhance nutrients uptake and ultimately improve the plant growth (Nadeem et al. 2014).

14.7.3 Indirect Mechanisms

Indirect mechanisms have basic role in biocontrol and based on the features of the mechanisms, can be further be distinguished into three groups: (1) competition, (2) antibiotic and lytic enzyme production, and (3) induced systemic resistance (Beneduzi et al. 2012).

14.7.3.1 Competition

PGPR compete with pathogenic microbes at two different levels: (1) competition for essential nutrients and (2) competition for niches. Direct competition among PGPR and pathogens help in reducing the incidence and severity of the diseases. Similarly, production of microbial siderophores represents an effective biocontrol mechanism, which due to higher affinity for Fe, reduces its availability to phytopathogens for their proliferation (Lugtenberg and Kamilova 2009).

14.7.3.2 Antibiotic and Lytic Enzymes Production

2,4-Diacetylphloroglucinol, pyrrolnitrin, zwittermicin A, phenazine, tensin, and xanthobaccin are some of the antibiotics produced by the biocontrol PGPR, especially preventing the proliferation of pathogenic fungi (Mazurier et al. 2009). Depending on the induction by various environmental stimuli, more than one kind of antibiotics might be produced by each PGPR strain (Duffy and Défago 1999). Many PGPR acting as biocontrol agents have been commercialized in order to avoid the use of pesticides. Similarly, many biocontrol PGPR strains are able to produce lytic enzymes such as proteases, lipases, chitinases, glucanases and cellulases that help in preventing the infection of various fungi by compromising the integrity of their cell walls (Kim et al. 2008).

14.7.3.3 Induced Systemic Resistance

Although plants have many chemical and physical methods to defend against pathogens. Under such circumstances, PGPR colonizing the root surface help plants by activating their defense response against pathogens (Salas-Marina et al. 2011). Plants are usually protected from pathogens by preventing the growth of pathogens through competition for nutrition and space and by reducing symptoms of diseases (Ghazalibiglar et al. 2016). Various mechanisms of defense against biotic stresses

are being used by the PGPR. Systemic acquired resistance (SAR) and induced systemic resistance (ISR) are the two kinds of resistances induced against pathogens. It is basically a physiological state of enhanced defensive capacity elicited by various environmental stimuli, priming innate defenses of the plants which react faster against the future pathogenic attack (Nawrocka and Małolepsza 2013). For the induction of resistance, both SAR and ISR use different signaling mechanisms. ISR consists of jasmonic acid (JA) and ethylene pathways while in SAR, salicylic acid (SA) and pathogenesis-related (PR) proteins accumulate (Dimkpa et al. 2009). PR proteins act synergistically with antioxidant enzymes and provide higher degree of protection against pathogens. SA plays a role in systemic development which acquire resistance. In addition, nonpathogenic bacteria also stimulate ISR in plants (Wani et al. 2016). They enhance the level of peroxidase and chitinase enzymes in plant leaves and roots. Moreover, induced resistance is systemic because in addition to primary infection site, defensive capacity also spread the whole plant, which is mostly due to JA and ET pathways, stimulating the plant defense mechanisms against variety of pathogens (Verhagen et al. 2004). The efficacy of SAR and ISR is widespread and includes bacterial, viral, and fungal pathogens. Their effects vary from plant to plant and also depend on the level of PGPR–plant interactions. Activation of defense system enhances the activity of antioxidant enzymes such as superoxide dismutase, peroxidase, catalase and guaiacol etc. which provide protection against oxidative damage caused by reactive oxygen species (ROS) and pathogen (Ghazalibiglar et al. 2016). Various bacterial components such as flagellar proteins, β -glucans, chitin and lipopeptides also stimulate ISR inside the plants (Annapurna et al. 2013). Various changes in plants are induced due to ISR like alteration in the cell wall, change in the level of chitinase, phenylalanine ammonia lyase and expression of stress-related genes (Choudhary and Johri 2009). *Pseudomonas* and *Bacillus* are well known for their induced systemic and antagonistic effects. Although plants have many chemical and physical methods, use of these PGPR is very cost-effective, beneficial, and sustainable approach for providing protection to plants against pathogens.

14.8 Plant Growth Promoting Fungi

14.8.1 Arbuscular Mycorrhizal Fungi

Arbuscular Mycorrhizal Fungi (AMF) establish symbiotic relationship with a variety of plant species by forming fungal hyphal network and specialized structures called arbuscules. AMF improve plant growth by accruing nutrient absorption that significantly affect the soil health status specifically under stress conditions. AMF can help plants to withstand a variety of biotic and abiotic stresses. One of the important factors for a better crop production is the availability and absorption of nutrients. Under limited nutrients conditions, plants establish symbiotic relationship with AMF to access and utilize the available nutrient resources efficiently for better growth,

photosynthetic efficiency, and enzyme activity. AMF-inoculated plants show increased accumulation and absorption of mineral nutrients by improved nutrient availability, uptake, and assimilation (Hashem et al. 2015). This effect may be due to the hyphal networks that interact with roots under the soil (Muthukumar et al. 2014) and may change the root architecture to ameliorate nutrient deficiency. One of the important and growth limiting environmental stress is water. It can hamper various metabolic functions such as nutrient uptake, nutrient assimilation, protein synthesis, and photosynthesis (Ahmad et al. 2019; Nazar et al. 2015). Water stress accompanied with heat stress can lead to extreme drought stress thereby limiting the plant's ability to grow (Ahanger and Agarwal 2017). Under drought stress, plants produce reactive oxygen species (ROS) that are scavenged by different antioxidant enzymes to minimize the stress symptoms (Hashem et al. 2015; Wu and Zou 2017). However, symbiotic relationship of AMF with roots can offer great services to withstand the water stress by a better uptake of nutrients, osmolyte production, and scavenging of ROS (Hameed et al. 2014; Yooyongwech et al. 2013). AMF can activate the antioxidant system to scavenge free radicals to maintain cellular redox levels (Wu and Zou 2017). Temperature stress (high and low) can halt various plant developmental and metabolic processes thus causing adverse effects on global agricultural productivity as it is often accompanied with drought, salinity, and mineral stresses (Jedmowski et al. 2015; Machado and Paulsen 2001). Temperature stress can damage fruits, cause delays in germination, reduce growth, biomass accumulation and photosynthetic efficiency (Adam and Murthy 2014; Farooq et al. 2009a; Jedmowski et al. 2015; Liu et al. 2013; Paredes and Quiles 2015). AMF inoculation increased the plant growth and productivity by increasing photosynthetic efficiency (Xu et al. 2016; Zhu et al. 2012), accumulation of proline and sugars (Evelin et al. 2009; Xu et al. 2016) and improved water-use efficiency (Elhindi et al. 2017). Water and temperature stresses are usually accompanied with salinity stress that is also a major abiotic stress that can severely affect plant growth and development (Khan et al. 2014). High salinity can affect ionic homeostasis, enzyme activity and nutrient acquisition by disrupting the cellular redox level (Iqbal et al. 2015; Khan et al. 2014). AMF play an important role in improving plant growth, biomass, productivity, and photosynthetic activity under saline conditions (Alqarawi et al. 2014; Aroca et al. 2013; Elhindi et al. 2017; Evelin et al. 2009; Latef and Chaoping 2014). More interestingly, AMF-inoculated plants showed reduced salt-triggered oxidative damage by activating cellular antioxidant and osmoprotectant defense system (Alqarawi et al. 2014; Scagel et al. 2017; Yang et al. 2014). Soil accumulation of toxic heavy metals can affect the crop growth and productivity. Once present in soil, these heavy metals such as lead, arsenic, cadmium, and mercury can transfer easily from soil into plant tissues and can potentially cause several health risks in humans and animals. However, certain plant species can accumulate heavy metals and expel them by volatilization. AMF are found under very high saline conditions in a variety of soils (Ahanger et al. 2014; Hameed et al. 2014). Some plants in association with AMF can help in the phytoremediation of heavy metals from agricultural soil thus can reduce the associated health risks by phytoextraction and

phytostabilization (Latef et al. 2016). AMF have very beneficial effects in stress amelioration and activation of key defense mechanisms. However, extensive research is needed to understand the exact mechanism of amelioration by AMF–plant interactions.

14.8.2 *Entomopathogenic Fungi*

Entomopathogenic fungi or insect pathogenic fungi have been studied very well as microbial control agents in the field and greenhouse experiments (Ahmad et al. 2020; Vega 2018; Vega et al. 2009). When a spore encounters the insect body, it develops infection structures that penetrate the cuticle, cause intoxication and ultimately kill the insect. The killed insect sporulates and produces millions of spores that can start a new infection cycle in a host. Scientists have focused more on insect–fungal interactions than the biology and ecology of plant–fungal interactions. In addition to their negative effects on insect pests, various entomopathogenic fungi have been reported as plant growth promoters and protection agents through rhizospheric and endophytic colonization (Jaber and Enkerli 2016, 2017; Lacey et al. 2015; Vega 2018). Endophytes are the beneficial or mutualistic microbes that reside within plant tissues without causing any harmful symptoms. Research has mainly focused on the rhizospheric colonizers and have not tapped much about the endophytes that is emerging as a great area of research. More than 170 bioformulations have been developed from almost 12 fungal species as inundative biopesticides against insects, mites, and ticks (de Faria and Wraight 2007). Relatively, less research has focused on the potential of fungal entomopathogens such as *Verticillium*, *Metarhizium*, *Beauveria*, *Paecilomyces* etc. as endophytic agents for plant protection and growth promotion (Akutse et al. 2013; Gurulingappa et al. 2010; Lopez et al. 2014). *Beauveria* belongs to the group of entomopathogens that can cause infection in a wide range of insect and plant hosts (Arnold and Lewis 2005; de Faria and Wraight 2007). *Metarhizium* spp. colonize many plant species, including switchgrass, haricot bean, tomato, wheat, and soybean (Akello and Sikora 2012; Behie et al. 2012, 2015; de Faria and Wraight 2007; Elena et al. 2011; Greenfield et al. 2016; Sasan and Bidochka 2012). Another important aspect of fungal entomopathogens, such as *Metarhizium* spp., is their role as nutrient translocator from a killed insect pest to the host plant (Behie et al. 2012, 2017). Moreover, fungal entomopathogens can confer plant protection against plant pathogens (Akello and Sikora 2012; Akutse et al. 2013; Jaber 2015; Lopez et al. 2014; Mantzoukas et al. 2015; Vidal and Jaber 2015; Zhou et al. 2016). Microbial consortia can be facilitated in nature to achieve long-term ecosystem services to benefit plant productivity and sustainable agriculture. In order to achieve better biological control and plant growth promotion, the use of compatible microbes as consortia has gained a great attention. When used as consortia, fungal

entomopathogens and other beneficial microbes, the bioformulations helped plants synergistically and effectively in stress management (Shrivastava et al. 2015). These ecological roles provide opportunities for the multiple use of entomopathogenic fungi in integrated pest management (IPM) strategies for sustainability in agriculture. We need more research to unravel the mechanisms of action of the plant growth promoting and pest suppressive effects of entomopathogenic fungi in soil and their short- and long-term multitrophic interactions. Understanding such interactions will provide answers to complex but important ecological links and molecular cross-talks and may facilitate more exploration and exploitation of biocontrol agents to achieve our sustainability goals in natural and managed agroecosystems. We also need a concerted approach to explore the potential of entomopathogenic fungi in establishing systemic or localized endophytic colonization in naturally occurring biota for improved plant productivity and protection. Future research on such entomopathogenic fungi as endophytes, biocontrol agents, plant growth promoters, and disease antagonists could lead to understand in depth their ecological niches, improved production and formulations and better pest management.

14.8.3 *Trichoderma*

Trichoderma spp. have been used to control and manage plant diseases and plant growth. Historically, *Trichoderma* spp. have been known as an effective biocontrol agent of several phytopathogens. It is ubiquitously available in soil and can be easily isolated and cultured to be used for sustainable agriculture. *Trichoderma* spp. have the potential to control many plant diseases including sheath blight (de França et al. 2015), Fusarium wilt (Al-Ani 2017), bacterial wilt (Yuan et al. 2016), downy mildew (Perazzolli et al. 2012), root-knot nematode (Al-Hazmi and Tariq 2016) etc. *Trichoderma* spp. employ an array of mechanisms that are very useful to improve plant growth, mineral nutrients assimilation, secondary metabolites production, plant defense modulation, and siderophore production. Such mechanisms of action establish *Trichoderma* spp. as suitable candidates for biocontrol of many phytopathogens and can be formulated as biopesticides. The mode of action of *Trichoderma* can be either mycoparasitism or non-mycoparasitism. *Trichoderma* spp. act against fungal phytopathogens mycoparasitically (Elad et al. 1982) that involves development of infection structures, penetration and subsequently killing the opponent fungus thus offering direct biocontrol. The mycoparasitic mechanism of *Trichoderma* spp. is species dependent and is due to the production of cell wall degrading enzymes (Harman et al. 2004; Sivan and Chet 1989). Some *Trichoderma* spp. are not mycoparasites of other fungi and the mechanism of action can be antibiosis, competition and by mediating plant defenses against phytopathogen (Howell 2003).

14.8.4 Other Plant Growth Promoting Fungi

Endophytes from the genus *Epichloë* (Clavicipitaceae: Ascomycota) can establish symbiotic relationships with above ground parts of certain grass species and can be transmitted vertically (Gundel et al. 2011; Schardl 2010). The proportion or prevalence of endophytic colonization depends upon the fitness of host plant and potential of vertical transmission to progeny (Gundel et al. 2011). *Epichloë* spp. protect plants from herbivores by producing defensive compounds such as alkaloids (Saikkonen et al. 2013; Schardl 2010) and get photosynthetic products, protection, nutrients, and reproduction mechanisms (vertical transmission) in return. They can also enhance plant growth, photosynthetic efficiency and tolerance to biotic and abiotic stresses in host (Bao et al. 2015; Saikkonen et al. 2013). The profile of alkaloids depends upon the fungal species and strains, plant species and the environmental conditions (Ryan et al. 2015; Saikkonen et al. 2013). *Epichloë* spp. have been found to modulate SA signaling pathway in plants and protect them from pathogens (Wiewióra et al. 2015).

Fusarium is a genus that is composed of cosmopolitan species with a wide range of host plants. Many *Fusarium* spp. are the causative agents of various diseases in plants whereas some species have been reported as plant growth promoting agents with a wide range of host plants to colonize endophytically (Imazaki and Kadota 2015). They can produce secondary metabolites that are the drivers of steering their biology and ecology (Bills and Gloer 2016; Kaul et al. 2016; Stępień et al. 2018). *Fusarium* spp. can assist the host plant from insects and pathogens (Ji et al. 2009). The potential of *Fusarium* spp. as a symbiont needs a plenty of research to fill the knowledge gaps. There are many other plant-associated epiphytic and endophytic fungi that have the potential to affect the herbivores negatively and plant growth positively and can be promising microbial agents for soil health and sustainable agriculture.

14.9 Concluding Remarks and Future Perspective

Plants have coevolved multifaceted direct (production of toxins) and indirect mechanisms to defend themselves against a multitude of biotic and abiotic stresses. To achieve maximum benefits, plants do partnership with a variety of different beneficial microbes (e.g., bacteria and fungi) through mutualism or symbiosis. Microbes mediate plant defense signaling by modulating and cross-talking and fine-tuning their phytohormone (JA, SA, etc.) signaling pathways in the presence of stresses (Pieterse et al. 2012). These defense mechanisms are mostly associated with costs that can compromise the growth and reproduction. Beneficial microbes can efficiently antagonize stresses and improve plant growth and fitness (Pineda et al. 2017). In order to exploit the maximum benefits associated with beneficial microbes, we need to understand the ecology and biology of the microbes associated with plants for a sustainable agriculture. The ecological roles of plant-associated microbes

remains elusive and needs deeper digging. We should promote the strategies to conserve the beneficial microbes among growers for environmentally friendly and sustainable agriculture while reducing input of chemical fertilizers, pesticides, and fungicides.

Conflict of Interests Authors declare no conflict of interests.

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