Role of Beneficial Fungi in Sustainable Agricultural Systems

18

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Abstract

Sustainable agriculture is a farming technique on the basis of knowledge of ecosystem services, the study of relationships/interactions between organisms and their physical environment. In sustainable agricultural systems, the inhabitant soil microflora is more crucial for ecosystem processes including nutrient availability and pest/disease suppression.

The rising demand for environmental friendly, organic, and sustainable agricultural practices are driving the application of fertilizers based on beneficial biological products. The use of beneficial fungi in agriculture sector is potentially useful for improved plant health and growth, water uptake, nutrient availability, stress tolerance, and biocontrol. Fungi also play a fundamental role in multifarious physiological processes including mineral and water uptake, photosynthesis, stomatal movement, and biosynthesis of compounds termed biostimulants, auxins, lignan, and ethylene to enhance the ability of plants to establish and cope environmental stresses such as drought, salinity, heat, cold, and heavy metals. This chapter describes the mechanisms underlying beneficial impacts of fungi on growth promotion of the host plant.

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18.1 Introduction

Many of the world's ecosystems are in different moods of decline affirmed by erosion, low fertility and productivity, poor water quality, etc. caused by forest clearing, high-input agricultural production, and stay using land resources for multiple purposes that are not sustainable. However, sustainable agriculture prepares high yields without causing weakness or damages the natural systems and resources that productivity depends on. This kind of agriculture utilizes a special cultivation technique wherein the environmental resources may be entirely used and at the same time guarantee that no injury was executed to it. Therefore, the method of performance is environmental friendly and assures safe and healthy agricultural crops and products. In low-input organic and sustainable agroecosystems, the natural function of microorganisms in supporting soil fertility and/or control of plant pathogens may be more important than in conventional agriculture practices where their importance has been marginalized using high inputs of chemical fertilizers and other agrochemicals.

The status of soil microbial populations is beneficial to vital processes that compel fertility, productivity, and stability of agricultural systems. Several investigations are directed to enhancing knowledge of the diversity, structure, dynamics, and significance of soil microbial communities and their advantageous and cooperative actions in soil fertility and crop productivity.

There is a growing body of evidence that exhibits the potential of different microorganisms to improve plant growth and productivity in agricultural systems. Understanding the potential of soil-beneficial microorganisms needs comprehension of the action of microorganisms in growth enhancement, especially in terms of nutrient supplement and disease suppression, the underlying mechanisms, and the challenges in implementation and commercialization of plant growth-promoting (PGP) microorganisms (Johansson et al. 2004; Pereg and McMillan 2015).

Soil microorganisms possess a close, symbiotic (reciprocal) relationship with plants. They are the most plentiful of all the biota in soil and responsible for promoting nutrition and organic matter cycling, soil fertilization and restoration, and plant health and growth as well as ecosystem primary production. Two examples include rhizobia and mycorrhizae. Mycorrhizae are known as very host-specific fungi that create symbiotic associations with roots of host plant. The beneficial fungi play an important role in improving plant growth and increasing plant yield and also involved in biotic and abiotic stress tolerance, hazardous materials remediation, sustainable crop production, and food safety (Borde et al. 2009). Some of the fungi do not permit the deleterious fungi to colonize the root surface area and are beneficial as biocontrol agents (Ha 2010). In this chapter, we explain the mechanisms behind the positive role of symbionts to host partners.

18.2 General Mechanisms Involved in Plant Growth Promotion Elicited by Microorganisms

Plant growth and performance is remarkably affected by the interactions between plant roots and the surrounding relative soil involving the microbial community inside the soil. The rhizosphere supports microorganisms that may have both positive and negative or inconsequential impact on plant growth and productivity. Although most rhizospheric microorganisms seem to be desirable, harmful microbes such as pathogens and microorganisms generate toxins that prevent root growth or those that eliminate essential substances from the soil. In contrary, the major mechanisms for promoting plant growth include improvement of nutrient availability (biofertilization), suppression of parasitic and nonparasitic pathogens (biocontrol), and production of plant hormones/and or plant growth-promoting substances (phytostimulation) (Martinez-Viveros et al. 2010; Bhattacharyya and Jha 2012).

Many factors are affecting the population of the indigenous rhizospheric microbes including agricultural practices (e.g., soil cultivation, stubble maintenance, burning, season, and so on), plant species, variety/cultivar and genotype, and soil type (Berg and Smalla 2009; Reeve et al. 2010). Plant exudates may cause alterations to soil characteristics including carbon availability and pH, influencing the diversity and activity of microbial communities (Haichar et al. 2008). It is acknowledged that the addition of microorganisms to cropping systems and agricultural soils (bioaugmentation) exhibit an important action on soil microbial processes. The application of agrochemicals such as chemical fertilizers and pesticides/and or fungicides caused concerns about their potential risks to living organisms and pathogen resistance, imposing continuous expansion of novel agents (Fernando et al. 2006). Rhizospheric microorganisms that prevent plant pathogens could be applied as biocontrol agents and may be considered as efficient and alternative to chemical pesticides. Some of the mechanisms for suppression of plant pathogen are direct inhibition of pathogen growth via production of antibiotics, hydrogen cyanide (HCN), and toxins and activation of hydrolytic enzymes (e.g., lipases, proteases, and chitinases) that degrade toxicity agents or pathogen cell-wall components (Whipps 2001; Compant et al. 2005).

18.2.1 Mechanisms of Biofertilization

"Biofertilizers" are beneficial microbes that improve nutrient uptake and availability to inoculated plants, contributing to plant nutrition through increasing nutrient uptake and/or through accelerating primary nutrient availability in the rhizosphere. Also, they could be applied for improving crop yield when used complementary to, or as alternative for, synthetic fertilizers.

Nitrogen (N) is an important plant macronutrient that is frequently limited in agricultural soils because of high losses through leaching and emission. Biological nitrogen fixation can be performed by nonsymbiotic bacteria including *Azospirillum*, *Gluconacetobacter*, *Burkholderia*, and *Pseudomonas* species (Dobbelaere et al.

2003) and may be employed in biofertilization of nonleguminous plants including wheat (Egamberdiyeva and Hoflich 2002), rice (Mirza et al. 2006; Muthukumarasamy et al. 2007), maize (Estrada et al. 2005), and sugarcane (Suman et al. 2005). Also, the *Azotobacter* Azo-8 strain was introduced as an efficient bio-inoculant for wheat plant grown under water scarcity conditions along with urea and manure (Singh et al. 2013).

Although agricultural soils usually have considerable total phosphorus, available phosphorus is frequently exhausted from the rhizosphere (Richardson et al. 2009). Soil microorganisms play an essential role in the phosphorus cycle and, therefore, in facilitating phosphorus availability to plants, improving the capacity of plants to obtain phosphorus from the soil through solubilizing and mineralizing inorganic phosphorus, or via accelerating the mobility of organic phosphorus by microbial turnover and/or extending the root system of crop species (Richardson and Simpson 2011). A great number of soil microorganisms with the ability of solubilizing inorganic phosphorus have been isolated, such as *Actinomycetes*, *Pseudomonas*, *Rhizobium*, and *Bacillus* spp. (Richardson et al. 2009; Richardson and Simpson 2011; Bhattacharyya and Jha 2012). Moreover, some fungal from the *Penicillium* genus excrete compounds (organic acids) that expedite the conversion of immobilized phosphorus into soluble forms available for root uptake and plants (Wakelin et al. 2004).

The response of root growth and the flexibility of root system architecture along with the expansion of the rhizosphere, via either root growth or root hair development, are obviously significant for impressive exploration of soil environment and interruption of nutrients. Root hair may form up to 70 % of root volume and can take up to 80 % of phosphorus in non-mycorrhizal inoculated plants (Fohse et al. 1991). Mycorrhizal fungi generally colonize the root cortex of plant and enlarge exteriorly, joining the roots with soil environment and enhancing efficacy of phosphorus absorption by mycorrhizal inoculated plants (Barea et al. 2008).

Mycorrhizal symbiosis can increase plant growth by improvement of plant establishment, protection against different types of stress, and enhanced soil structure and nutrient uptake, especially as fundamental macronutrients (e.g., P, Mg, Ca, K) and micronutrients (e.g., Zn, Cu,) depend on soil pH (Clark and Zeto 2000; Richardson et al. 2009).

It has been reported that enhanced absorptive surface area of the inoculated plant-root systems caused increased area for interactions with other soil microorganisms through formation of hyphae of these symbiotic fungi which also act as a significant route for the translocation of energy-rich plant assimilates to the soil (Johansson et al. 2004). Generally, the effect of plant assimilates on microbial populations has been described in relation to the rhizosphere (Hiltner 1904). The rhizosphere (the narrow region of soil surrounding living plant roots) is characterized by improved microbial activity stimulated by root exudates (Grayston et al. 1997). However, since plant roots in natural habitats are prevalently mycorrhizal, the concept of rhizosphere has been broadened to comprise the fungal component of the symbiosis, causing the term “mycorrhizosphere” (Rambelli 1973; Johansson et al. 2004) (Fig. 18.1).

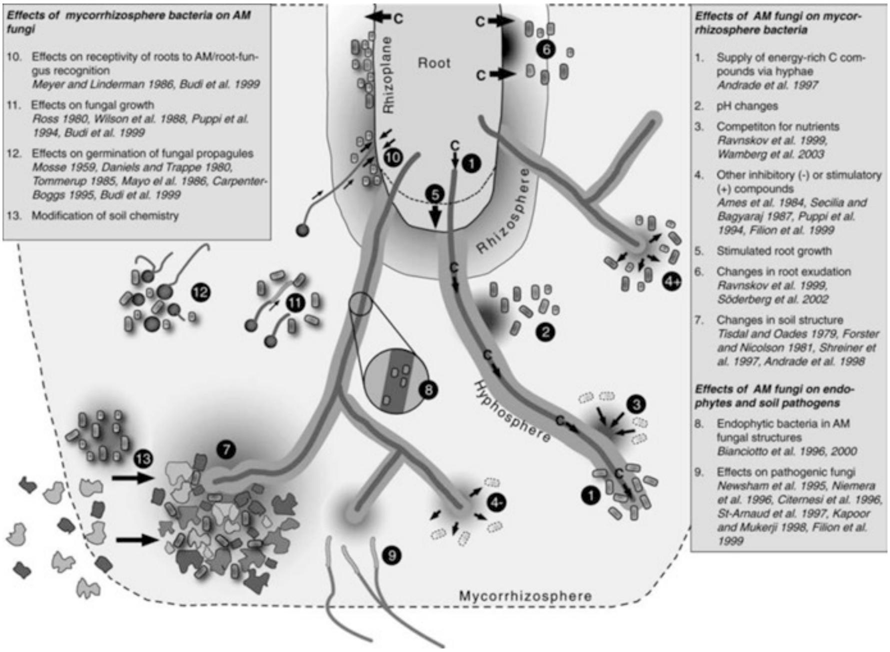

Fig. 18.1 Schematic model of possible interactions between various components of the mycorrhizosphere (Johansson et al. 2004)

18.2.2 Mechanisms of Disease Suppression

Generally, protection of plant growth is consecutively challenged through emerging, reemerging, and indigenous plant pathogens (Miller et al. 2009). As mentioned above, there are a number of mechanisms for plant-pathogen suppression including direct inhibition of pathogen growth by production of antibiotics and other toxins (Whipps 2001; Compant et al. 2005).

Antibiotics are a common section of the self-protective arsenals of bacteria, including *Pseudomonas* species (e.g., *Pseudomonas fluorescens* strains) (Haas and Defago 2005) and *Bacillus* species (e.g., *Bacillus subtilis*) (Kim et al. 2003), as well as fungal species including *Trichoderma*, *Gliocladium*, *Ampelomyces*, and *Chaetomium* (Kaewchai et al. 2009); therefore, these living organisms have great potential for soil conditioning process.

Multifunctional microorganisms including *Trichoderma harzianum* Rifai appear to improve plant growth through solubilizing phosphate and essential micronutrients required for plants, including iron (Fe) and manganese (Mn), and suppress plant pathogens (Altomare et al. 1999). Hydrogen cyanide production inhibits microbial growth and may suppress pathogens including root-knot, black rot, and bacterial canker in tobacco and tomato plants (Lanteigne et al. 2012; Voisard et al. 1989; Siddiqui et al. 2006). However, it has been reported that HCN might be injurious to plants through reducing energy metabolism and inhibiting root growth (Siddiqui et al. 2006). Many various bacterial genera produce HCN, such as *Rhizobium*, *Alcaligenes*, *Bacillus*, *Aeromonas*, and *Pseudomonas* spp. (Ahmad et al. 2008). Also, pathogen suppression may take place competitively by indirect inhibition. There is evidence that a number of bacteria and fungi produce siderophores as iron-chelating sources particularly in times of iron deficiency (Sharma and Johri 2003), such as *Azospirillum*, *Pseudomonas*, *Bradyrhizobium*, *Rhizobium*, *Serratia*, and *Streptomyces* (Martinez-Viveros et al. 2010). Their ability to reduce iron from their surrounding environment makes it unavailable form to pathogenic fungi, resulting in a competitive benefit (Loper and Henkels 1999; O'Sullivan and O'Gara 1992).

Carrillo-Castaneda et al. (2002) reported that inoculation of alfalfa (*Medicago sativa*) with siderophore-producing bacteria grown under iron-limiting conditions resulted in a positive effect on plant growth; however, the possible role for a combination of several growth-promoting mechanisms and not siderophore generation alone cannot be ignored. Moreover, activation of the plant's own defense system, termed induced systemic resistance (ISR), may be considered as another mechanism that is involved in disease suppression. Release of a blend of volatile organic compounds by plant growth-promoting bacteria and fungi may initiate ISR, causing enhanced expression of defense-related genes in the inoculated plants (Naznin et al. 2014).

18.2.3 Mechanisms of Phytostimulation

One of the most important mechanisms involved in plant growth enhancement through some rhizospheric living microorganisms is the production of plant hormones, or phytostimulation; plant growth-promoting microbes stimulate plant growth by producing growth hormones, including auxins, gibberellins, and cytokinins in the adjacency of the roots, or by regulating the levels of ethylene produced by plants. Root characteristics, size, and depth affect the capacity of plants to effectively entrap nutrients from soil environment and vice versa; root elongation and morphology can alter in response to soil nutrient availability (Wijesinghe et al. 2001). Plants bearing both deep and shallow root systems are able to acquire mineralized nitrogen available in top of soils and leached nitrogen in the subsoils (Ho et al. 2005). Therefore, application of phytostimulation for improving plant-root growth could play an important role in facilitating nutrient uptake, particularly if employed in combination with biofertilization.

The main phytohormone, auxin (IAA), promotes root growth and root architecture attributes such as root hair cluster positioning, lateral root extension, and root vascular tissue development (Aloni et al. 2006). Many rhizobacteria, such as beneficial, pathogenic, associative, and free living, are potentially proficient to produce IAA (Tsavkelova et al. 2006). These include *Azospirillum*, *Azotobacter*, *Aeromonas*, *Bacillus*, *Burkholderia*, *Enterobacter*, *Rhizobium*, and *Pseudomonas* (Spaepen et al. 2006; Martinez-Viveros et al. 2010). Cytokinins promote plant cell division and regulate root growth and development through reducing primary root elongation and lateral root formation and stimulating root hair formation (Werner et al. 2003; Riefler et al. 2006). These substances are produced by some plant growth-promoting rhizobacteria, including *Arthrobacter*, *Azospirillum*, *Pseudomonas*, and *Paenibacillus* species, but their participation in plant growth promotion is not well known (Richardson et al. 2009).

Likewise, gibberellins induce the development of stem tissue, root growth, and lateral root branching and are produced by different species of plant growth-promoting rhizobacteria, including *Azotobacter*, *Azospirillum*, *Bacillus*, *Herbaspirillum*, *Rhizobium*, and *Gluconobacter* (MacMillan 2002; Bottini et al. 2004).

Another important hormone involved in plant growth and development is ethylene, although it may have distinctive impacts on plant growth depending on its doses in plant roots (Pierik et al. 2006). Ethylene synthesis is necessary for the initiation of systemic resistance during interaction with associative microorganisms, and higher doses are mediated in plant defense against a range of stresses and upon pathogen infection (Broekaert et al. 2006). Certain growth-promoting bacteria, including *Azospirillum brasilense*, may produce lower levels of ethylene, which may enhance root hair formation (Ribaudo et al. 2006). In plants, ethylene has previously been found to be produced from the precursor 1-aminocyclopropane-1-carboxylate (ACC), which is released by roots within the rhizosphere during stress and reabsorbed through the roots, which is in turn converted to ethylene. However, accumulation of ethylene in the roots causes decreased root growth, aggravating plant stress (Babalola 2010). Rhizospheric plant growth-promoting fungi and bacteria that can break down ethylene precursor ACC diminish the adsorption of ethylene through the root tissues and permit the plant to reestablish a healthy root and cope with environmental biotic and abiotic stresses (Glick 2005). Plant growth enhancement by ACC (a source of nitrogen) degrading microorganisms seems to be specifically significant under stress conditions including drought, cold, salinity, or heavy metal stress (Mayak et al. 2004; Grichko and Glick 2001). Root zone microorganisms are able to degrade ACC including *Azospirillum*, *Achromobacter*, *Enterobacter*, *Bacillus*, *Pseudomonas*, and *Rhizobium* strains (Martinez-Viveros et al. 2010).

18.3 The Arbuscular Mycorrhizal Symbiosis

The oldest (>460 million years BP) and the most popular kind of mycorrhizal association is *arbuscular mycorrhizal* (AM) symbiosis. Many terrestrial plants (~250,000 species of plants worldwide) are capable of forming the symbiosis (Smith and Read 1997).

According to Schussler et al. (2001), almost 160 fungal taxa of the order *Glomales* (*Glomeromycota*) have been explained in terms of their spore morphology, although new molecular technique exhibit that the real number of AM taxa may be much higher (Daniell et al. 2001; Vandenkoornhuyse et al. 2002).

It has been reported that in time of AM symbiosis formation, the fungus permeates the cell walls of root cortical and constitutes haustoria-like structures that interact with the host cytoplasm (Smith and Read 1997). These fungal structures and highly branched arbuscules in particular prepare an improved surface area for metabolic conversions between the fungus and the plant. Moreover, production of certain structures, vesicles, by some of the AM believed to act as storage tissues (Smith and Read 1997). According to Johnson et al. (2002), plants in natural terrestrial ecosystems colonized with AM may instate about 10–20 % of the fixed carbon through photosynthetic process in their fungal confederate. Obviously, this exhibits an important input of energy to the soil environment, and this source of carbon may be vital to living microbes associated with the mycorrhizosphere.

It has been acknowledged that AM fungi also interact directly with the soil through producing extra radical hyphae that may spread out several centimeters within the soil (Rhodes and Gerdemann 1975). The extra radical hyphae structures constitute a greater total surface area than that of roots solely, which enhances the potential for nutrient and water uptake (Auge 2001; Rhodes and Gerdemann 1975). Besides, the extra radical hyphae structures seem to be significant to the plants for phosphorus acquisition efficiency and other mineral nutrients uptake (Read and Perez-Moreno 2003). Also, Hodge et al. (2001) suggested that the extra radical mycelium of AM fungi may improve mobilization of organic nitrogen forms from plant residue. It was previously believed that mycorrhizal symbiosis may also mitigate adverse effects of plant pathogens (Newsham et al. 1995; Niemira et al. 1996; St-Arnaud et al. 1997; Azcon-Aguilar and Barea 1996) and negative role of metals (Khan et al. 2000). Moreover, the extra radical hyphae may interface with other soil microbes either directly through physically and/or metabolically interfacing with other soil-living organisms in the mycorrhizosphere or indirectly through altering host plant physiology (e.g., root morphogenesis and patterns of exudation within the mycorrhizosphere) (Johansson et al. 2004).

18.3.1 Effects of AM Fungi on Fungal Pathogens

Arbuscular mycorrhizal fungi may interact with other root-associated microbes, like pathogenic fungi. The potential mechanisms of interaction are similar as those mentioned above. The differential impacts of a crude extract from the growth medium of the AM fungus *Glomus intraradices* were studied on spore formation of two pathogenic fungi and on the growth of two bacterial species (Filion et al. 1999). Conidial germination of *Fusarium oxysporum* (a plant-root pathogen) was inhibited, while conidial germination of *Trichoderma harzianum* (a mycoparasitic fungus) and the growth of *Pseudomonas chlororaphis* were promoted, and *Clavibacter michiganensis* growth was uninfluenced. The assayed impacts were correlated with extract dose, and no significant effect of pH on germination or growth was found. They concluded that the unspecified substances released by the AM fungus to the growth medium were the major factor describing the differential growth of the employed microbes.

Citernesi et al. (1996) screened bacteria separated from 17-year-old *Glomus mosseae* pot culture. They reported that many of the bacterial strains within the various zones of the mycorrhizosphere were vigorously antagonistic against in vitro growth of *Fusarium* and *Phytophthora*. Their findings also suggest the probability of integrated application of AM fungi and their associated bacteria in biocontrol of soilborne pathogenic fungi. Many researchers have mentioned that the ability of AM-inoculated plants to better stand up to an attack from root pathogens may be described to an improved nutritional status in the host plant because of the attendance of the AM fungus. However, there are contradictory reports on this theory. In a field experiment, Newsham et al. (1995) transplanted *Glomus* sp.-treated and *Glomus* sp.-non-treated seedlings of *Vulpia ciliata* into a natural ecosystem and found that inoculation of AM did not influence phosphorous content in the plants. However, the AM protected the plants from the adverse impacts of *Fusarium oxysporum* attack on root and shoot growth. Obviously, the AM inhibited pathogen development in the root tissues. The results also showed that root-infecting mycofloras of AM plants had fewer naturally occurring infections of *F. oxysporum* and *Embellisia chlamydospora* compared to AM plants following transplantation (Newsham et al. 1995). They suggested that the main advantage granted by AM fungi to *V. ciliata* seedlings is the protection from deleterious fungi, rather than enhanced phosphorous acquire. In a study, Niemira et al. (1996) employed a peat-based medium containing *Glomus intraradices* to test whether it could inhibit *Fusarium sambucinum* (a common tuber dry rot) in minitubers of potato plants. Results revealed less (20–90 %) tuber dry rot for minitubers grown in this medium. Furthermore, St-Arnaud et al. (1997) reported that the presence of *Tagetes patula* plants inoculated with AM fungus *G. intraradices* may suppress root pathogen development in soil and by means of that decrease severity of disease in cocultured non-mycorrhizal carnation (*Dianthus caryophyllus*). In other study, Caron (1989) found significant decrease in Fusarium populations in the soil surrounding mycorrhizal tomato (*Lycopersicon esculentum*) roots and subsequently proposed a possible role for AM fungi in biocontrol of the soilborne pathogens.

18.3.2 Soil Fungal Communities Confer Agroecosystem Stability

Beneficial soil microorganisms such as AM fungi are key component in natural agroecosystem through providing crucial ecosystem services including nutrient uptake, organic matter recycling, and antagonism versus plant pests/disease (Borie et al. 2010; Pozo et al. 2009; Ramos-Zapata et al. 2012). *Arbuscular mycorrhizal* fungi, saprophytes, use up the destroyed organic materials in soil and are definitely innocuous and often beneficial for mobilization of mineral nutrients (Hodge et al. 2001; Lopez-Roez and Pozo 2013).

The ecological importance of *Perisporiopsis lateritia*, *Phanerochaete velutina*, and *Pleurotus* sp. can be described by their function in dead vegetation recycling process through converting hard wood to usable forms (Chaverri and Gazis 2010; Wells et al. 1998; Cohen et al. 2002). Some fungi (e.g., *Navisporus floccosus*), characterized in digesting the secondary compounds such as lignin, tannin, and cellulose in soils; preparing nutrients availability for offspring of the present plant generation

(Parihar et al. 2012). It has been reported that soil AM fungi may be considered as an essential component of an ecosystem to help the carbon and nitrogen recycling in soil environment (Phillips et al. 2012).

Generally, mycorrhizal fungi include higher value of carbon (10/1 C/N) and less amount of nitrogen (N ¼ 10 %) in their cells than those of bacteria (Hoorman 2011). Mycorrhizal fungi contribute in recycling of both nitrogen and phosphorus to improve availability of mineral nutrients for the plants. Their properties, small size and high surface area, are more efficient in mineral acquisition from the soils when compared to the plant-root hairs (Hoorman 2011). Evidence suggests, however, that plant's roots cultivated with particular species of fungi caused significant nutrient acquisition and higher nutritional levels of crop plants (Yaseen et al. 2011; Albrechtova et al. 2012). In addition to symbiont, free-living soil fungi including *Trichoderma* are established to be responsible for improved plant growth and development, higher biomass production, and lateral root branching via the mechanism mediated by synthesis of auxins (Contreras-Cornejo et al. 2009). Specific fungi, including *Piriformospora indica* and *Trichoderma*, are beneficial in plant-soil systems and act as biocontrol agents (Harman and Mastouri 2010; Serfling et al. 2007) to support agricultural crops from severe injury caused by pathogen attack (Ha 2010). According to Chalot and Brun (1998), ectomycorrhizal fungi can effectively degrade the undesirable phenolic constituents in the forest soils.

The ecto- and endo-AM fungi may prepare definite advantages to host plants through expanding surface area for sufficient water and nutrient uptake, improving stomatal regulation to preserve proper water potential, and increasing twofold the minimal stomatal conductance (Aroca et al. 2008; Arnold and Engelbrecht 2007) for better gaseous exchange which subsequently result in amplified photosynthetic quantum yield (Wu and Xia 2006; Xian-Can et al. 2010) (Table 18.1).

18.3.3 Relevance of Mycorrhizosphere Interactions to Sustainable Agriculture

Soil-beneficial fungi are specifically useful for the plant partner in agriculture and take part in several services including water levels, nutrient improvement, stress tolerance, pest and disease protection, and weed control. Sustainable agroecosystem relies on beneficial fungi due to its contribution in decomposition of soil organic matter, nutrient uptake, organic matter and nutrient recycling, antagonism against plant pathogens/pests, and crop management (Ansari et al. 2013). Generally, two main groups of soil endophytic fungi have been previously recognized, exposing dissimilarity in evolutionary interaction: (1) the clavicipitaceous endophytes (C-endophytes), which associate with grasses and systemically infect their hosts, and (2) the non-clavicipitaceous endophytes (NC-endophytes), which can be reproduced from asymptomatic parts of a broad range of plant (nonvascular) hosts, belonging to angiosperms (Singh et al. 2011).

Mycorrhizal fungi colonizing the plant-root systems (rhizosphere) extend within the rhizosphere and are efficiently involved in enhancing soil fertility and crop

Table 18.1 Soil-beneficial fungi effects on different physiological and catabolic processes in various host plant species

Fungal species/strain	Plant type	Fungi-mediated response/activities	Beneficial effects on plant species	References
AM fungi	Dead vegetation in soil	Degrade of dead organic	Nutrient mobilization	Hodge et al. (2001)
Phanerochaete velutina	Wood	Decomposing wood	Phosphorus translocation	Wells et al. (1998)
Pleurotus sp.	Wood	Wood decay	Nutrient mobilization	Cohen et al. (2002)
Perisporiopsis lateritia	Leaves of *Hevea* sp.	Leaves decay	Nutrient mobilization	Chaverri and Gazis (2010)
Navisporus floccosus	Wood	Wood decay	Nutrient mobilization	Phillips et al. (2012)
M fungi	*Pinus taeda*	Decomposing organic matter	Carbon and nitrogen cycling	Hoorman (2011)
AM fungi	*Vigna unguiculata*	Mineral uptake	Improved nutritional status	Yaseen et al. (2011)
M fungi	*Allium cepa*	Plant growth	Improved nutritional status	Albrechtova et al. (2012)
Trichoderma sp.	Arabidopsis sp.	Auxins dependent mechanism	Higher biomass production and increased lateral roots formation	Contreras-Cornejo et al. (2009)
Trichoderma sp.	Agriculturally important crops	Biocontrol	Crop management	Chalot and Brun (1998), Harman and Mastouri (2010), and Serfling et al. (2007)
Ectomycorrhizal fungi	Higher plant species	Phenolic compounds degradation	Plant protection	Ha (2010)
Ectomycorrhizal fungi and AM fungi	Agricultural crops	Stomatal physiology and water relation	Improved water potential status and increased photosynthesis rate	Arnold and Engelbrecht (2007) and Wu and Xia (2006)

productivity in natural and agroecosystems (Bonfante and Genre 2010). It has been reported that mutualistic symbioses (intimate interspecies interactions) contribute to plant's life cycle through supplying micro- and macronutrients, enhanced growth, and improved thermotolerance and resistance from different environmental biotic and abiotic stresses such as drought, salinity, herbivore, and pathogen infection (Lingua et al. 2012; Singh et al. 2011; Rodriguez et al. 2008). A strong growth-promoting activity was found during the symbiosis of *Piriformospora indica*, a plant-root-colonizing basidiomycete fungus, with a broad spectrum of plant species

(Verma et al. 1998). The *P. indica* produces thin-walled, white color, and hyaline hyphae throughout the life cycle which exhibits multinucleated character. Following to anastomosis between various types of hyphae, the formation of certain chlamydospores (thick-walled big resting spore) occurs either separately or in clusters at their tip. The released chlamydospores then trigger germination in the soil and subsequently infect other host through creating intra- and intercellular hyphal network (Das et al. 2012). Moreover, *P. indica* imitate the potentiality of specific AM fungi in different morphological, functional, and growth promotional points of view (Das et al. 2013) with supplemental profit that it can grown axenically. Tsimilli-Michael and Strasser (2013) confirmed that the *P. indica* may be a novel candidate symbiont for supplying immense growth-promoting activity with a broad spectrum of plants species. This symbiotic interaction caused in higher biomass production of the shoots and floral parts of the plant which can be used for biologically active compounds in pharmaceutical industries (Kumar et al. 2011; Oelmuller et al. 2009). *P. indica* (the growth-promoting endophyte) in many cases acts as a biofertilizer, bioregulator, and bioprotector both in mono- and dicotyledonous plant species (Das et al. 2012). The mutually beneficial relations between *P. indica* and roots are valuable being its wide spectrum of uses in farming systems (Franken 2012). It is acknowledged that specific biochemical and/or genetic processes are involved in biosynthesis of ethylene and signaling to maintain an interaction between the symbionts and host plants (Khatabi et al. 2012).

18.3.4 Sustainable Nutrient Supply

It has been well known that AM may improve phosphorous level, enhance nitrogen uptake, or increase disease resistance in their host partners. Other soil microorganisms, such as nitrogen fixing and or phosphate solubilizing bacteria, can synergistically interact with AM fungi and stimulate plant growth through a range of mechanisms (Puppi et al. 1994). The symbiotic association between fungi and host plants becomes even more important in low sustainable input and organic agricultural systems. Under these situations, AM mycelium may act an influential role in nutrient mobilization from plants litter (Johansson et al. 2004).

Hodge et al. (2001) suggested that the inoculation with AM *Glomus hoi* improved decomposition of plant litter in soil and caused increased nitrogen acquisition from the litter as well. Hyphal growth of the fungal symbiont was also improved in the presence of the complex organic material in soil (Fig. 18.2). Bacteria associated with the AM may assist the nutrient cycling in soil. Several examples of this kind of association are available from bacterial-AM fungal-legume tripartite symbiosis, where diazotrophic bacteria prepare fixed nitrogen for both the plant and the fungus. Interestingly, legume nodulation by nitrogen-fixing bacteria and AM establishment often take place synchronously and synergistically.

The presence of nitrogen fixation genes in endosymbiotic bacteria (*Burkholderia*) in AM hyphae has been previously showed by Minerdi et al. (2001) who suggest that there may be a potential for enhanced nitrogen source to mycorrhizal infected

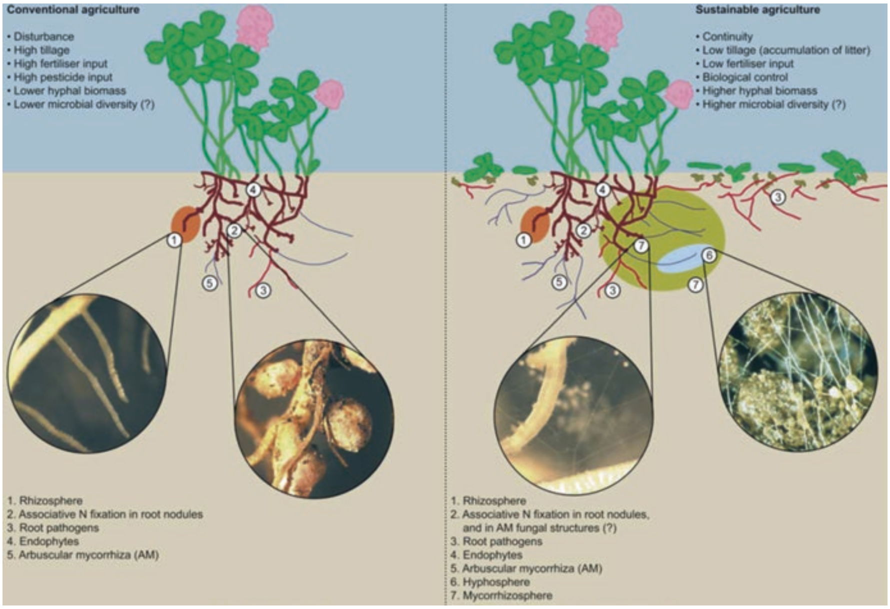

Fig. 18.2 Schematic model of the mycorrhizosphere concept compared to the rhizosphere concept: characteristics of conventionally managed agricultural soils (*left*) in contrast to sustainably managed agricultural soils (*right*) (Johansson et al. 2004)

plants through atmospheric nitrogen fixation. More study is also required on the possible interactions of mycorrhizal fungi with decomposition processes. There is now a growing consciousness of functional differences among various AM fungi, and as our ability to perceive of their functional capacities raises we may be able to select appropriate species for maximize of nutrient recycling (Johansson et al. 2004).

18.3.5 Biocontrol

Microbial inoculants may be utilized as alternative and efficient tools for suppression of disease and pests in agricultural cropping systems, allowing the decreased application of chemical pesticides that could otherwise display threats to human health and nontargeted living organisms. The biological control agents may influence AM fungi, or be influenced themselves by AM fungi, in the same manner to the interactions as mentioned above. Biocontrol organisms against particular pathogenic fungi may have adverse impacts on nontarget soil AM fungi. Studies have shown that the mechanisms of antagonistic interactions causing biocontrol may involve competition for soil nutrients and colonization sites as well as production of fungistatic compounds. However, few researches have explicitly investigated interactions involving AM fungi (Johansson et al. 2004). Some beneficial impacts of rhizobacteria on AM fungal colonization of roots could be because of antagonistic effects on competing pathogens (Azcon-Aguilar and Barea 1996), as well as direct synergistic effects on mycorrhizal colonization itself (Budi et al. 1999). Different plant-root-colonizing or seed-borne *Pseudomonas* spp. have been reported to be influential microbial control agents in plant-pathogen systems under in vitro (Chin-A-Woeng et al. 2003; Leeman et al. 1996), greenhouse (Knudsen et al. 1999), and field (Johnsson et al. 1998; Knudsen et al. 1997) conditions. Chin-A-Woeng et al. (1998) reported that *Pseudomonas chlororaphis* PCL1391, an effective bacterial strain for colonizer of tomato roots, revealed efficient antagonistic activity against *Fusarium oxysporum*. The aforesaid bacterial strain produced a broad spectrum of antifungal compounds, such as hydrogen cyanide, phenazine-1 carboxamide, proteases, and chitinases (Chin-A-Woeng et al. 1998).

By knocking out the phenazine biosynthetic operon, it was shown that the mutants exhibited significantly lower biocontrol activity, indicating that this substance was an important antifungal factor for suppressing disease in tomato roots. It has been reported that the presence of the biocontrol bacteria caused in 70–80 % reduction of the density of the hyphal network inside part of tomato roots (Bolwerk et al. 2003). However, the effects on AM fungal hyphae were not investigated. Besides producing antifungal substances, the capacity of bacteria to colonize root surfaces and thereby closely interact with pathogens may further promote pathogenic suppression (Lagopodi et al. 2002).

Despite the rising number of studies over the last years, the underlying mechanisms are poorly understood. Some fundamental mechanisms have been previously proposed: enhancement of plant nutrition and competition for photosynthates (Azcon-Aguilar and Barea 1996); however, AM caused suppression of root pathogens and promotion of saprotrophs and plant growth (Kapoor and Mukerji 1998). The other mechanisms that tend to be inconsistent among studies include changes in morphological and anatomical features of root system induced by the AM fungus and triggering plant defense mechanisms by AM fungi (Gianinazzi-Pearson et al. 1994). The combination of AM fungi with growth-promoting rhizobacteria may prefer the inoculum production (Singh 1992).

Many studies have shown that some AM fungi present biocontrol characteristics (Niemira et al. 1996; Caron 1989; Newsham et al. 1995) against plant-root pathogens. Whether AM fungi may be applied as biological control agents virtually or potentially act as vectors for associated bacteria with biocontrol characteristics remains to be further explored.

18.4 Conclusions

Interactions between symbiotic microbial and host plant are prominent to keep the continued existence of both microorganism as well as the host under environmental restrictions. These interactions are important for soil-plant-water relations, mineral uptake, stomatal regulation, gas exchange, and photosynthetic process. Moreover, symbiotic root-associated fungi are critically efficient in enhancing plant growth and conferring plant tolerance to different types of stresses. In view of the fact that process of plant growth and development, which conclude crop yield, cannot be correctly described without possessing idea of microbial interactions. Thus, it is required to study plants from a symbiotic systems attitude to understand the contributions of all organisms in a symbiotic relationship for better plant health, growth, and survival.

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