Chapter 3
Interactions Between Arbuscular Mycorrhizal Fungi and Other Microorganisms in the Rhizosphere and Hyphosphere

Deepak Kumar, Sandeep Kour, Mohd Ali, Roohi Sharma, Parkirti, Vikram, Harish Changotra, Rajesh Kumari Manhas, and Puja Ohri

Abstract The ecosystem of the earth is fascinating and intricate. The interactions that occur in the soil affect its characteristics as a substrate for development and activity of soil microorganisms and plants. The majority of terrestrial plants have a symbiotic, mutually beneficial interaction with the soil fungi known as arbuscular mycorrhizal fungi (AMF). These microorganisms expand the root's absorption region, which improves the plant's ability to absorb nutrients. The symbiont gets plant carbohydrates in return for accomplishing its life cycle. Additionally, AMF aids in the adaptation of plants to biotic and abiotic challenges including salt, drought, extremely high or low temperatures, heavy metals, diseases and infections. AMF are constantly interacting with ample variety of microbes, including endobacteria, rhizobacteria that encourage plant growth and mycorrhiza helper bacteria, plant parasitic nematodes, fungi and other microbes inhabiting the rhizosphere and hyphosphere. Their interactions may be of utmost significance and might affect agriculture. The present chapter summarizes the main microbial community groups and their interaction with AMF in the rhizosphere and hyphosphere along with the advantageous effects of AMF on plants.

Keywords AMF · Mycorrhiza helper bacteria · Rhizobacteria · Rhizosphere · Interorganismal cross-talk

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D. Kumar · S. Kour · M. Ali · R. Sharma · Parkirti · Vikram · P. Ohri (✉)
Department of Zoology, Guru Nanak Dev University, Amritsar, Punjab, India
e-mail: puja.zoology@gndu.ac.in

H. Changotra
Department of Molecular Biology and Biochemistry, Guru Nanak Dev University, Amritsar, Punjab, India

R. K. Manhas
Department of Microbiology, Guru Nanak Dev University, Amritsar, Punjab, India

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3.1 Introduction

Understanding the dynamic processes that occur during the plant-soil interactions requires an intense study of various functional groups of the soil microflora. Among these, the interaction of arbuscular mycorrhizal fungi (AMF) with other microbes is especially interesting because they serve as a living connection between the soil and the roots. AMF are soil microorganisms that interact with 80–90% of vascular plant species and 90% of agricultural plants such as vegetables, cereals and horticultural plants (Chen et al. 2018; Diagne et al. 2020). This symbiosis predates the earliest appearance of terrestrial plants by 400–450 million years, according to fossil records and molecular evidence (Diagne et al. 2020). AMF are widely distributed in various ecosystems, which are essentially determined by the distribution of recognized plant hosts worldwide (Yang et al. 2012). AMF belongs to the phylum *Glomeromycota* and subkingdom *Mucoromyceta*, which includes three classes (*Archaeosporomycetes*, *Glomeromycetes* and *Paraglomeromycetes*) (Tedersoo et al. 2018; Sangwan and Prasanna 2022), consisting of 25 genera, 11 families and over 250 species (Husna et al. 2022). *Glomeromycota* are obligatory symbionts that derive around 20% of carbon from their host plants and, in return, favour host plant's delivery of water and nutrients like phosphorous and nitrogen through root apoplast, arbuscules and intraradical and extraradical hyphae. Arbuscular mycorrhizal symbiosis is undoubtedly one of the most familiar and advantageous relationships between plants and microbes. According to various investigations, they are crucial for plant nutrition and development under stress, and they also improve a variety of crucial ecological functions (Parihar et al. 2019; Chandrasekaran et al. 2021; Dowarah et al. 2021; Yang et al. 2023).

Arbuscular mycorrhizal symbiotic association was once thought to have a bipartite relationship. It is now understood that under normal circumstances, several microorganisms including bacteria, fungi, nematodes and arthropods interact with this fungal-plant symbiotic association and have an impact on the metabolic process of both AMF and host plant (Lu et al. 2023; Szili-Kovács and Takács 2023) (Fig. 3.1). For instance, the interaction of AMF and several bacterial genera including plant growth- promoting rhizobacteria (PGPR) and mycorrhiza helper bacteria (MHB) have been shown to support the health of AMF symbiosis, development of hyphae, germination of spore, colonization of root and the metabolous efficiency of AMF (Chen et al. 2023c). Some of the noteworthy interactions between AMF and bacteria include the binding of bacteria to the fungal spore, production of volatiles by bacteria, transfer of chemicals inside the fungal spore by bacteria and disintegration of the fungal cellular wall (Miransari 2011). It is also believed that some microbial communities in the hyphosphere help AMF acquire organic resources by breaking down complex organic molecules that AMF cannot break down on their own. In exchange, the AMF offers a hyphal exudate- and energy-rich microhabitat that promotes microbial proliferation and motility in the hyphosphere (Wang et al. 2022, 2023a; Faghihinia et al. 2023). This AMF-bacterial interaction can be exploited to increase crop output in sustainable and environmentally friendly way

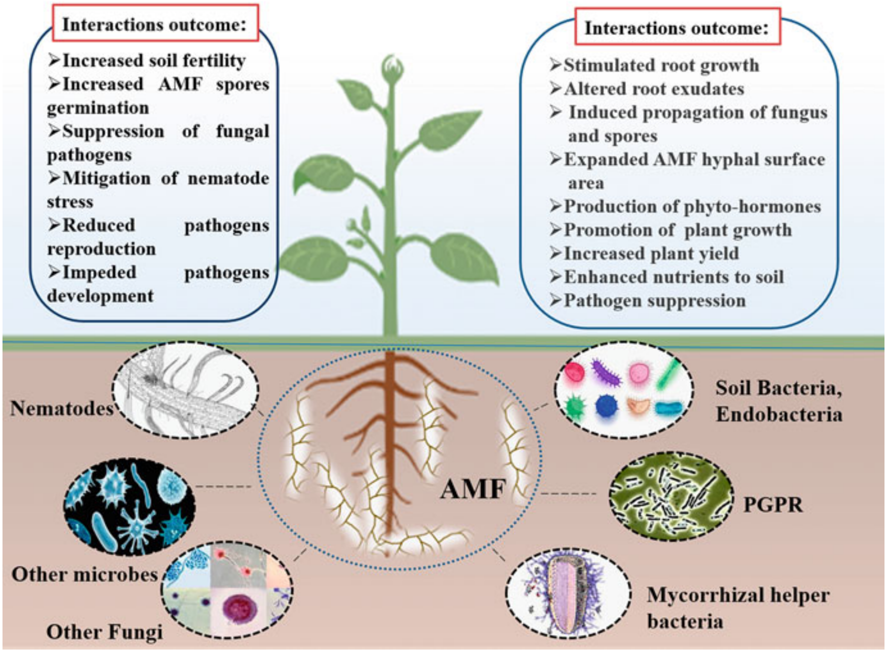

Fig. 3.1 Interaction of arbuscular mycorrhizal fungi (AMF) with other microorganisms in the rhizosphere and hyphosphere

by producing inoculum comprising the fungus and bacteria, also known as AMF bio-enhancers (Sangwan and Prasanna 2022).

Further, AMF also interacts with plant parasitic nematodes as they share the plant roots as source of food and habitat in the rhizosphere. AMF may promote resistance and plant tolerance by inhibiting the development of nematodes. The possibility of greater nematode tolerance or resistance of AMF-infected plants has sparked research in AMF-nematode interactions (Patel et al. 2022; Vishwakarma et al. 2022). Furthermore, the interaction of AMF with other fungi and various other microorganisms in rhizosphere and hyphosphere has also been studied and is being utilized for the sustainable management of plant pathogens (Bao et al. 2022). Consequently, it is crucial to carefully assess such interactions and take into account their application in agronomy. This may lead to some novel perceptions for future research, hastening the development of the discipline and yielding more effective agricultural strategies. Therefore, considering the outcomes of AMF interactions, the present chapter focuses on the interaction of AMF with other microorganisms inhabiting the rhizosphere and hyphosphere.

3.2 AMF and Plants

Plant roots are inhabited by numerous microbes that also include AMF, which are beneficial for plant health in many ways. They modify morphology and physiology of plant roots, affect their growth, influence their nutrient status and resist various plant stresses (Sharma et al. 2023; Thangavel et al. 2022). AMF interact with their wide range of hosts by penetrating into their root epidermis using their own fungal hyphae. In roots, they colonize in cortical cells and form arbuscules. Arbuscules consist of fungal hyphae enveloped in peri-arbuscular membrane, which is a modification of cortical cell plasma membrane. This interaction provides better use of soil nutrients and better resistance to variable stresses (Wipf et al. 2019).

The AMF colonization involves reciprocal recognition between two partners mediated by symbiotic molecules before they both come in contact with each other, resulting in the pre-symbiotic stage. During their interaction, both partners recognize each other via cross-talk of signal molecules synthesized by both individuals. As soon as the fungal hyphae make contact with root epidermis, they form hyphopodia, an adhesion structure. The introduction of hyphae in roots initiates the symbiotic phase, and the latter is followed by the formation of pre-penetration apparatus, which leads hyphae to the inner root tissue. From there, hyphae grow into the deep cortical cells and form arbuscules. Thus, root colonization proceeds, and extensive hyphal network explores more soil by forming extraradical hyphae. This extraradical mycelium extends to form common mycorrhizal networks to make contacts among root systems of two or more than two host plants (Lanfranco et al. 2016; Sarkar and Sadhukhan 2023).

At the time of colonization, the interaction between both partners is facilitated mainly by regulated signalling and carotenoid pathways. After establishing colonies, the AMF provides the host plant with ion and nutrient uptake in return for receiving photosynthates (such as carbohydrates). This carbon supply in AMF thus transports sugars from aerial parts of the plants to their roots. Along with nutrient exchange, AMF also strengthen defence response in plants by modifying biosynthesis of secondary metabolites. Thus, AMF modify signalling pathways and nutritional state of host plants, which enhance the production of protective compounds in plants for defence (Kaur and Suseela 2020; Sarkar and Sadhukhan 2023). However, during the interaction of AMF with non-host plants, the pattern-recognition receptors presenting on plasma membrane of plant act as a part of the innate immune system. Their function is to recognize conserved molecular patterns linked with pathogens or microbes as well as molecular patterns associated with damage and ultimately to activate pattern-triggered immunity in plants. Thus, when AMF come in contact with a non-host plant, the danger-associated peptide signalling pathway is activated; consequently, the trading of carbon and phosphorus between AMF and host plant does not occur, which negatively affects nutrient availability, causing photosynthetic suppression, oxidative stress and cell wall lignification, which eventually subdue the growth of the non-host plant (Wang et al. 2023b). In contrast to it, the symbiosis between AMF and host plant acquires numerous benefits, as the plant provides photosynthates to fungi in a controlled way, and the fungi also help in better survival of the host plant under stressful conditions. AMF colony provides a feedback mechanism for regulated transport of mineral nutrients in root cortical cells, thus, improving availability of all essential nutrients (Thangavel et al. 2022). AMF also modulates immunity of plants against plant pathogens by providing more nutrient to the plant to produce more metabolites by modulating plant metabolites (Sarkar and Sadhukhan 2023). AMF may modify plant physiological functions under various stresses to increase plant tolerance by altering various morphological features (Zhang et al. 2022; Jiménez-Pérez et al. 2022). AMF inoculation may also enhance expression of certain defensive genes in plants to elevate its immunity (Stratton et al. 2022). The spores, vesicles as well as the extra- and intra-radical mycelia of AMF also act as a sink in case of heavy metal accumulation in plants; thus, it also helps in detoxification (Adeyemi et al. 2021). Conclusively, more insight into the role of AMF in enhancing plant resistance toward various environmental stress along with its widespread use in agricultural field can minimize the use of chemical pesticides and fertilizers, thus promoting soil and plant health. Table 3.1 summarizes interaction between AMF and their host plants during various stress conditions.

3.3 Interaction of AMF with Bacteria

Populations of bacterial species in the rhizosphere have a remarkable effect on plant growth and productivity (Liu et al. 2020). PGPR, endobacteria, MHB, detrimental bacteria and other kinds of soil-based bacteria have been found to have interactions with AMF (Olsson et al. 2017). Enhancing the tripartite interaction of AMF, bacteria and plants that host it necessitates an understanding of how they interact (Noceto et al. 2021; Chang et al. 2017). Both types of bacterial species present in the rhizosphere and cell matric of some fungal strains are included in this group of bacteria (Miransari 2011). Positive, neutral or adverse associations can occur with the mycorrhizal association or other rhizospheric microbes, but AMF association with bacteria is predominantly based on their constructive outcomes (Hassani et al. 2018).

The root metabolites influence the biochemicals produced by microbes (bacteria); however, these soil microbes are also capable of releasing chemicals that increase the concentration of root exudates activating AM hyphae and expanding the degree of root inhabitation (Olanrewaju et al. 2019). In addition, plant hormones produced by soil microorganisms can affect spore and hyphae development as well as AM establishment (Miransari et al. 2014). Various elements exert an impact on the interaction between soil bacteria and AMF (Rillig et al. 2018). In fact, bacterial species have different capacities for adhering to AM hyphae, which is also influenced by the physiological stage of the hyphae. The research on bacterial attachment is scarce; however, information regarding other linked features including AM race and strains of bacteria, plant genera, rhizosphere and climatic parameters is available in the literature (Artursson et al. 2006; Sanon et al. 2009). Forthcoming

Table 3.1 Effect of arbuscular mycorrhizal fungi (AMF) on plants

AMF	Host plant	Stress condition	Reported effects	References
Rhizophagus irregularis	Pistachio (*Pistacia vera*)	Salinity stress	Enhanced activities of catalase, superoxide dismutase and glutathione reductase and increased content of tocopherol and carotenoid	Afshar and Abbaspour (2023)
R. irregularis	Soybean (*Glycine max*)	Drought stress	Increased root activity, plant biomass and photosynthesis, decreased ROS activity and increased membrane index stability	Begum et al. (2023)
F. mosseae	Shisham (*Dalbergia sissoo*)	Entisol soil	Enhanced stomatal conductance and photosynthesis rate and plant growth and biomass	Bhardwaj et al. (2023)
R. intraradices	Manchurian catalpa (*Catalpa bungei)*	Low, medium and high nitrogen levels	Enhanced growth of seedlings and N and P levels	Chen et al. (2023a)
F. mosseae and *C. etunicatum*	Camel grass (*Alhagi sparsifolia*)	Salt or drought stress	Enhanced root growth, phosphorus nutrient uptake, activated antioxidant enzymes and balanced hormonal levels	Chen et al. (2023b)
F. mosseae	Milkvetch (*Astragalus adsurgens*)	Cadmium-consisting saline soil	Improved phosphorus uptake and improved sodium/potassium ratio in shoot, also elevated shoot biomass observed	Jia et al. (2023)
R. irregularis	Flooded gum (*Eucalyptus grandis*)	Cadmium stress	AMF helped retaining Cd in fungal structure	Kuang et al. (2023)
F. mosseae	Milkvetch (*A. adsurgens*)	Cadmium- and lead-contaminated soil	Increased root mass and shoot mass, elevated rhizospheral bacterial community	Li et al. (2023a)

(continued)

Table 3.1 (continued)

AMF	Host plant	Stress condition	Reported effects	References
			thus enhancing phytoremediation efficiency	
G. mosseae	Barrelclover (*Medicago truncatula*)	Cadmium stress	Enhanced photosynthetic efficiency, increased plant biomass, decreased heavy metal contamination and increased phytohormone synthesis	Li et al. (2023b)
C. etunicatum	Green tea (*Camellia sinensis*)	Drought stress	Increased plant height, plant biomass and plant mineral content in roots	Liu et al. (2023a)
Paraglomus occultum	Tomato (*Solanum lycopersicum*)	Salt stress	Enhanced plant growth performance and gas exchange rate	Liu et al. (2023b)
Paraglomus species	Indian shot (*Canna indica*)	Flooding and lead stress	Alleviated Pb toxicity, alleviated flooding stress and enhanced growth of host plant	Lv et al. (2023)
Funneliformis sp., *Glomus* sp., *Rhizophagus* sp., *Claroideoglomus* sp. and *Acaulospora* sp.	Rice (*Oryza sativa*)	Phosphorus deficiency	Increased plant phosphorus uptake, increased plant growth, enhanced soil enzyme activities	Mitra et al. (2023)
R. intraradices and *F. mosseae*	Sunflower (*Helianthus annuus*)	Water stress	Elevated chlorophyll content and declined MDA and shoot proline content	Noroozi et al. (2023)
Funneliformis mosseae, *R. intraradices*, *F. geosporus*, *Claroideoglomus etunicatum*, *Glomus aggregatum* and *R. irregularis*	Wheat (*Triticum durum*)	Water deficiency	Increased height of aerial part, length of internodes, length of ear, plant dry weight and chlorophyll content	Ould et al. (2023)
R. irregularis		Salt stress	Salt stress was alleviated by	Wang et al. (2023c)

(continued)

Table 3.1 (continued)

AMF	Host plant	Stress condition	Reported effects	References
	Swamp oak (*Casuarina glauca*)		increasing plant biomass and accumulation of chlorine in roots; also salt exclusion process observed	
G. versiforme *F. mosseae*	*Snapdragon (Antirrhinum majus)*	Low temperature and weak light	Increased stomatal conductance, photosynthetic rate, transpiration rate and water use efficiency	Wei et al. (2023a)
R. intraradices	Sweet flag (*Acorus calamus*)	Chromium toxicity	Altered rhizospheric bacterial community, increased tolerance toward heavy metal and enhanced nutrient uptake and also the soil carbon input	Wei et al. (2023b)
P. brasilianum, *G. deserticola*, *G. monosporum*, *F. mosseae*, *R. irregularis*, *G. clarum*, *G. etunicatum*, *Gigaspora margarita* and *G. aggregatum*	Tulsi (*Ocimum sanctum*)	Saline stress	Enhanced plant growth and antioxidant enzymes	Yilmaz et al. (2023)
F. mosseae, *Acaulospora foveata* and *C. etunicatum*	Rice (*O. sativa*)	Water deficit	Increased phosphorus content and osmotic potential in plants	Yooyongwech et al. (2023)
F. mosseae (Fm) along with *Agrobacterium rhizogenes* and *Piriformis mosseae*	Rice (*O. sativa*)	Salt stress	Increased biomass, improved osmoregulation ability and maintained high ratio of K^+/Na^+	Zhang et al. (2023a)
R. intraradices and *C. etunicatum*	Maize (*Zea mays*)	Molybdenum stress	Localized heavy metals in root, enhanced nutrient uptake, plant biomass and photosynthetic pigments	Zhang et al. (2023b)

(continued)

Table 3.1 (continued)

AMF	Host plant	Stress condition	Reported effects	References
Glomus sp. consisting AMF complex	Tomato (*S. lycopersicum*)	Drought stress	Stimulated growth of plant in terms of increased length, greater number of leaves and more dry and fresh weight	Slimani et al. (2022)

investigation therefore needs to note this impact and explore whether such connections can affect crop yields commercially.

There are numerous instances of better communication between various bacterial strains such as *Bacillus*, *Paenibacillus*, *Pseudomonas* and *Rhizobia* and various AMF species like *G. clarum*, *G. intraradices*, *G. mosseae* and *G. versiforme* (Artursson et al. 2006). These encouraging responses encompass pathogenic suppression, phosphate solubilization, root colonization by AMF and development and propagation of fungus and spores (Singh et al. 2013; Emmanuel and Babalola 2020).

3.3.1 Endobacteria

The closest interaction occurs when bacteria exist as endobacteria inside the cells of fungus. Regardless of their genomic and functional differences, the communities of bacteria that are associated with fungi make up a brand-new form of microbiome called the fungal microbiome (Desirò et al. 2015). The relationship that exists between AMF and endosymbiotic bacteria can affect how well they function and how well they interact with microbes that are pathogenic as well as how effectively plants grow and develop (Nanjundappa et al. 2019). An endobacterial symbiosis improves a mycorrhizal fungus' viability and boosts its bioenergetic potential (Salvioli et al. 2016). There are several ways or mechanisms that depict that the bacteria anchored to a fungal spore can impair the activity of fungal organism, through release of chemicals that influence the expression of fungal genes or by introduction of chemicals in fungal spore or by adherence to the fungal exterior through the release of lectins and probably by the breakdown of the fungal cell wall and generation of volatile compounds that alter expression of fungal genes (Bonfante and Venice 2020).

Endobacteria have been found in a variety of fungal groups in numerous recent investigations (Olsson et al. 2017). The bacterial endosymbiont that has been studied most extensively is the *Glomeromycota* endobacteria (Bonfante and Desirò 2017). There are two different kinds of endosymbionts in *Glomeromycota*: (1) a gram-negative, rod-shaped beta-proteobacterium and such notable species of the *Gigasporaceae* family including Candidatus *Glomeribactergigasporarum* and (2) a homogeneous gram-positive, coccoid- shaped bacteria distributed among

Glomeromycota family that includes *Mollicutes*-related endobacteria (MRE) (Alabid et al. 2019; Naito et al. 2017). For instance, MRE was found in two species of liverwort, *Conocephalum conicum* and *Lunularia cruciata*, which was hosted by AMF in the order *Glomerales* (Desirò et al. 2013).

Some endobacteria found inside the cytoplasm of AMF are also thought to be PGPR, creating a close relationship with AMF such as actinobacteria (Qin et al. 2017). The results from Lasudee et al. (2018) demonstrated that rice crops cultivated in soil supplemented with PGPR, *Streptomyces thermocarboxydus* strain S3 stimulated growth in low-nutrient soil facing distress from a drought. Similarly, growth was enhanced, and growth parameters were eased with association of endobacteria *Bacillus pumilus* as PGPR and AMF *Glomus deserticola* (Medina et al. 2003). Endobacteria played a significant function in the pre-symbiotic phase of fungus by boosting its bioenergetic capability, according to an examination of RNA-seq data from the AMF *Gigaspora margarita* having endobacterium or in its absence.

Besides some reports that suggest interrelationship between endosymbiotic bacteria and *Glomus* species, majority of the studies focus on the relationship between endosymbiotic bacterium and mycorrhizal fungi *Gigaspora margarita* (Bennett and Groten 2022; Bonfante and Venice 2020). *Gammaproteobacteria* were found to be present in *Ascomycota* and *Basidiomycota* accordingly (Kramer et al. 2016; Liu et al. 2023c). Further reports showed that the presence of endobacterium *Mycoavidus cysteinexigens* may substantially impact *M. elongata*'s metabolic processes where the non-mutant strain having endobacteria displayed a slower rate of development in comparison to the strain that was lacking endobacteria, indicating that the fungus encounters a metabolic cost for dealing with *Mycoavidus* (Uehling et al. 2017).

3.3.2 Plant Growth-Promoting Rhizobacteria

Plant growth- promoting rhizobacteria improve plant growth while interacting with root systems. PGPRs are advantageous microbes that stimulate plant growth using various processes, such as (1) the creation of plant hormones like jasmonic acid, (2) improved solubility of mineral phosphate in soil, (3) pathogenic management, (4) mitigation of plant stress and (5) interacting with beneficial microbes like AMF, bacteria, etc. (Aalipour et al. 2020; Vocciante et al. 2022). AMF and PGPR also interact and modify plant growth, development and stress management. By influencing root colonization and boosting the absorption of nitrogen and phosphorus, PGPR have the power to promote AM fungal growth (Sagar et al. 2021). Although some PGPR have been shown to flawlessly inoculate plant roots, information regarding the treatment intensity of AMF hyphae by PGPR is scarce (Hartmann et al. 2008).

There are various microbial strains of PGPR and AMF variety combinations that could encourage rice establishment and growth in paddy fields. They have combinatorial stimulating effects that boosted grain yield, phosphate solubilization, nitrogen fixation, plant growth and pathogen suppression (Artursson et al. 2006). *Bacillus*, *Pseudomonas*, *Azospirillum* and *Herbaspirillum* are among the bacterial strains, whereas *Rhizophagus irregularis* (formerly known as *G. intraradices*) and *Funneliformis mosseae* are AMF species (Hoseinzade et al. 2016; Premkumari and Prabina 2017; Lasudee et al. 2018; Norouzinia et al. 2020; Beura et al. 2020). For instance, Beura et al. (2020) observed that the interaction of AMF (*F. mosseae*) with PGPR *A. brasilense* and *B. cepacia* together with rock phosphate-enriched compost was found to boost root length and dry root biomass due to hyphal extensions that expanded the surface size and growth of rice. Similarly, the pairing of urea and triple super phosphate nutrients with AMF (*F. mosseae*) and bacteria that fix nitrogen (*Herbaspirillum seropedicae*) enhanced the development of rice (Hoseinzade et al. 2016). According to Norouzinia et al. (2020), the treatment of *Pseudomonas putida* strain S34 and *Pseudomonas fluorescens* strain R167 together with AMF *R. irregularis* considerably boosted rice grain production while reducing the adverse effects of salinity stress.

In comparison to applying chemical fertilizers alone, dual treatment of *Schizolobium parahyba* with AMF and PGPR enhanced wood output by around 20% (Diagne et al. 2020). AMF and *B. subtilis* in dual treatment of *Acacia gerrardii* Benth (Talh trees) under salinity stress led to a substantially higher dry mass, number of nodules and leghemoglobin level compared to those treated with AMF or *B. subtilis* alone (Hashem et al. 2018). These researchers discovered a beneficial synergistic relationship between AMF and *B. subtilis* in terms of the activities of enzymes such as nitrogenase, nitrate and nitrite reductase enzymes as well as the amounts of total lipids, phenols, fibre and osmoprotectants including betaine and amino acids (glycine and proline).

AMF and phosphate- solubilizing bacteria (PSB) may interact in a beneficial way, as PSB with the aid of AM hyphae converts scarcely accessible phosphorous molecules into orthophosphate (inorganic as well as organic forms of phosphorus) that AMF might take in and transfer to the host plant (Nacoon et al. 2020). Plant treatment with AMF and such bacteria not only enhances phosphorus acquisition from nutrient-poor soils but additionally improves the activity of phosphatase, PSB number and mycorrhization (Wahid et al. 2022). AMF (*Funneliformis mosseae*), *Pseudomonas fluorescens* (PSB) and triple superphosphate addition are efficient and affordable techniques to enhance crop production in maize under salt-stress conditions (Ghorchiani et al. 2018). Inoculation with two local phosphate-solubilizing bacterial strain, *Pseudomonas fluorescens* BAM4 and *Burkholderia cepacia* BAM12, along with AMF (*Glomus etunicatum*) and plants supply with tricalcium phosphate in a phosphorus-poor soil remarkably boosted various growth parameters such as dry shoot and root yield and leaf surface area in wheat (Saxena et al. 2015). Under severe drought conditions, dual treatment with AMF (*Rhizophagus irregularis* or *Funneliformis mosseae* or a mixture of both) and PGPR (*Pseudomonas fluorescens*) enabled *Cupressus arizonica* to mitigate water scarcity damages and improved drought tolerance by means of an improved activity of ascorbate peroxidase and glutathione peroxidase as compared to those treated with a single microbe (Aalipour et al. 2020). Similar effect was observed under drought stress in *Melissa officinalis* L. (Lemon balm) when it was inoculated with PGPR and AMF, which enhanced its photosynthetic pigments; biomass; proline level; nitrogen, phosphorus and potassium content; and relative water content (Eshaghi Gorgi et al. 2022).

3.4 Interaction of AMF with Mycorrhiza Helper Bacteria

The existence of other microbes, notably bacteria in the rhizosphere, often influences mycorrhizal symbiosis. These microbes create mechanisms for discerning interplay with the rhizospheric microbiome, and they influence the growth of mycorrhizal connections in a neutral, unfavourable or advantageous way. The specialization of the bacterial and mycorrhizal (1) strain and species, (2) root of plants, (3) soil structure, (4) abiotic and biotic stressors, (5) nutrient competition and (6) soil microbial diversity all affect the relationship among the AMF and the MHB (Arruda et al. 2021). A group of bacteria known as mycorrhiza helper bacteria affects the symbiotic relationship of AMF with plant roots. These bacteria can assist the growth of hyphae, spores, root colonization and metabolic fitness of AMF, all of which are necessary for the symbiosis to occur (Richardson et al. 2009). They encourage the development of particular AMF symbiotically associated with their non-specific host plant (Bharadwaj et al. 2008). By influencing the spore wall (Boer et al. 2005), generating stimulants like carbon dioxide (Carpenter-Boggs et al. 1995), or influencing the AMF phosphorus uptake (Ruiz-Lozano and Bonfante 2000), they can affect spore germination. The majority of AM spores are colonized by a variety of microorganisms, including fungi, bacteria, actinomycetes and microbes, which alter spore germination and chitin mineralization (Ames et al. 1989).

AMF can also change the composition of microorganisms in the rhizosphere by competing for nutrients in soil. Saprophytes and symbionts are two forms of bacteria that communicate with AM species, a few of which are unfavourable, while others are neutral or even beneficial (Johansson et al. 2004). Although the amount of specificity was not recognized, a number of strains of *Rhizobium* and *Pseudomonas* had different degrees of adherence to germinating spores of AMF and hyphae under aseptic conditions (Bianciotto et al. 1996). The capacity of MHB to generate molecular signals that control and govern the gene networks of fungus having AMF symbiosis was also demonstrated in various investigations (Lies et al. 2018). Table 3.2 enlists some interactive effects of MHB on AMF.

3.5 Interaction of AMF with Plant Parasitic Nematodes

Various biotic stressors including plant parasitic nematodes, in addition to abiotic stresses, have impact on plant growth and development (Kaur et al. 2022; Kumar and Ohri 2023). PPNs are significant agricultural pests commercially, and nematicides that are most effective must be substituted with nematode control methods, which have less adverse effect on non-target organisms since they do not meet the

Table 3.2 Interaction of arbuscular mycorrhizal fungi (AMF) with mycorrhiza helper bacteria (MHB)

AMF	Associated MHB	Host plant	Effect on AMF	References
Rhizophagus irregularis	*Rhizobium tropici*	Bean (*Phaseolus vulgaris* L.)	Increased amount of infectious propagules such as vesicles and arbuscules and improved hyphal growth	Banuelos et al. (2023)
R. irregularis	*Paenibacillus validus*	Carrot (*Daucus carota*)	Improved the mycelium of the fungus, leading to the production of viable spores	Gupta and Chakraborty (2020)
Funneliformis mosseae	*Pseudomonas fluorescens*	Maize (*Zea mays*)	Significantly increased vegetative and reproductive traits, root colonization, yield of maize grain and nutrient content in plant tissue	Ghorchiani et al. (2018)
R. irregularis	*L. fusiformis*	Maize (*Z. mays*)	Enhanced root growth and uptake of nutrients by promoting AMF mycelium growth	Battini et al. (2017)
Gigaspora margarita	*Curtobacterium*, *Ensifer* and *Bacillus* sp.	Alfalfa (*Medicago sativa*)	Improved hyphal growth, solubilized degraded chitin and spore germination	Long et al. (2017)
Rhizophagus irregularis	*Burkholderia anthina*	Chicory (*Cichorium intybus*)	Enhanced the solubilization of phosphate	Taktek et al. (2015)
Gigaspora margarita	*Bacillus megaterium*	Neem (*Azadirachta indica*)	Increased mycorrhization effectiveness	Budi et al. (2012)
Glomus intraradices	*Paenibacillus favisporus*	Tomato (*Solanum lycopersicum*)	Increased IAA production, biomass and root	Bidondo et al. (2011)
Gigaspora rosea	*Pseudomonas putida*	Cucumber (*Cucumis sativus*)	Improved plant tolerance to stressful conditions	Gamalero et al. (2010)
G. geosporum	*Flexibacter*, *Lysobacter*, *Pseudomonas*, *Chondromyces* and *Cellvibrio*	*Plantago lanceolata*	Improved spore germination	Roesti et al. (2005)
F. mosseae	*Pseudomonas fluorescens* 92rk	Tomato (*S. lycopersicum*)	Improved root colonization and hyphal development	Gamalero et al. (2004)
G. clarum	*Bacillus pabuli*	Pea (*Pisum sativum*)	Increased intake of nutrients, AMF	

(continued)

Table 3.2 (continued)

AMF	Associated MHB	Host plant	Effect on AMF	References
			colonization, development of hyphae, spore emergence and root colonization	Xavier and Germida (2003)

requirements of the present environmental conditions (Sharma et al. 2023; Kumar et al. 2023). A possible alternative would be to use AMF to increase host resistance and/or tolerance (Pires et al. 2022). AMF, a subphylum of *Glomeromycotina*-related fungi that symbiotically coexist with over 85% of terrestrial plants, including agricultural or horticultural crops, have the potential to defend plants through biodefense (Malar et al. 2022). Numerous researchers have reported that AMF may act as alternative to pesticides for the growth and development of agricultural plants as well as nematode management (Table 3.3) (Wani et al. 2017; Ryan and Graham 2018; Bagyaraj et al. 2022). AMF found in aerial or underground plant parts have been reported to decrease nematode infection (Schouteden et al. 2015). Similarly, plants with mycorrhizae are more nematode-resistant. Mycorrhizae treatment changes the root metabolites, which has been found to minimize the penetration of nematodes in mycorrhizal plants and transiently paralyze nematodes (Dey and Ghosh 2022). AMF are particularly effective against *Meloidogyne* spp. in several hosts; however, the protective impact depends on the host species, the AMF or other factors (da Silva Campos 2020; Poveda et al. 2020). Additionally, the growth and development of host plants is facilitated by AMF colonization because it increases nutrient uptake in plants from the soil and increases the host plant's resilience or tolerance to root-knot nematode (RKN) infection (Begum et al. 2019; Wang et al. 2023d). In particular, by fostering plant growth and absorption of nutrients and competing with other microbes for photosynthate and infective areas, AMF might, to some extent, boost the host plant's disease resistance (Dowarah et al. 2021). However, host plant, AMF species and RKN species are just a few of the variables that affect AMF and plant RKN interaction. AMF has the potential to boost host plant resistance, particularly to RKN. In addition, interaction between *Pratylenchus* and AMF occurs in host roots, and the control and strength of impact that AMF have on the population densities of *Pratylenchus* spp. can vary depending on the order/genus of AMF and the species of hosts plants. *Pratylenchus* population densities may change due to AMF inhabitation via improved plant nutritional status, enhanced root biomass, resource competition or induced systemic plant responses (Gough et al. 2022; Rodrigues et al. 2021). Further, AMF decreases the amount and size of large cells in roots that have been infected by *Meloidogyne*. As a result, the nematodes lay down fewer eggs since they are smaller and require longer to mature into adults. Additionally, AMF has a positive impact on species that are resistant to *Meloidogyne*, and using AMF along with other microbes or nematicide substances lowers the chance of *Meloidogyne* infection and promotes plant growth (da Silva Campos 2020; da Silva Campos et al. 2013).

Table 3.3 Interaction of arbuscular mycorrhizal fungi (AMF) with plant parasitic nematodes

AMF	Nematode species	Host plant	Effect reported	References
Funneliformis mosseae, *Rhizophagus fasciculatus* and *R. intraradices*	*Meloidogyne graminicola*	Rice (*Oryza sativa*)	Reduced root gall development	Malviya et al. (2023)
Septoglomus deserticola and *F. mosseae*	*M. incognita*	Pepper (*Piper nigrum*)	Reduced egg masses	Udo et al. (2023)
F. mosseae, *R. intraradices* and *Glomus versiforme*	*M. incognita*	Tomato (*S. lycopersicum*)	Reduced density of nematodes in soil	Wang et al. (2023d)
G. mosseae	*M. incognita*	Tomato (*S. lycopersicum*)	Decreased gall index of root	Abo-Korahv and Yassin (2022)
F. mosseae	*M. incognita*	Tomato (*S. lycopersicum*)	Increased juvenile mortality	Alamri et al. (2022)
R. irregularis	*M. incognita*	Tomato (*S. lycopersicum*)	Increased number of galls and egg masses	Detrey et al. (2022)
F. mosseae	*Pratylenchus thornei*	Mung bean (*Vigna radiate*)	Reduced reproduction	Gough et al. (2022)
F. mosseae	*M. javanica*	Tomato (*S. lycopersicum*)	Reduced nematode population	Nafady et al. (2022)
R. irregularis	*M. incognita*	Tomato (*S. lycopersicum*)	Decreased galling index	Sedhupathi et al. (2022)
R. intraradices	*M. graminicola*	Tomato (*S. lycopersicum*)	Reduced egg masses by reducing number of giant cells	Shanthi et al. (2022)
G. mosseae	*M. incognita*	Sweet pepper (*Capsicum annuum*)	Decreased galling and egg mass production	Udo et al. (2022)
F. geosporum	*M. incognita*	Sweet pepper (*Capsicum annuum*)	Reduced galling index and nematode reproduction	Herrera-Parra et al. (2021)
G. mosseae	*M. javanica*	Eggplants (*S. melongela*)	Reduced egg masses and number of galls	Sharma et al. (2021)
R. intraradices	*Meloidogyne* spp.	Coffee (*Coffea arabica*)	Reduced nematode development	Vallejos-Torres et al. (2021)
Dentiscutata heterogama, *F. mosseae* and *Rhizophagus* sp.	*Heterodera glycines*	Soybean (*Glycine max*)	Reduced egg hatching by up to 62%	Pawlowski and Hartman (2020)

(continued)

Table 3.3 (continued)

AMF	Nematode species	Host plant	Effect reported	References
F. mosseae	*M. incognita*	Tomato (*S. lycopersicum*)	Decreased the density of nematodes in soil	Pham et al. (2020)
G. mosseae	*M. incognita*	Tomato (*S. lycopersicum*)	Reduced gall index and population of nematode	Shanthi (2019)
R. intraradices and *F. mosseae*	*Nacobbus aberrans*	Tomato (*S. lycopersicum*)	Reduced nematode penetration in root	Marro et al. (2018)
G. fasciculatum	*M. incognita*	Tomato (*S. lycopersicum*)	Reduced reproduction of nematode	Samal et al. (2018)
Gigaspora albida, *Claroideoglomus etunicatum* and *Acaulospora longula*	*M. arenaria*	Red ginger (*Alpinia purpurata*)	Decreased number of galls and egg mass production	da Silva Campos et al. (2017)
R. irregularis	*M. incognita*	Tomato (*S. lycopersicum*)	Reduced egg masses	Sharma and Sharma (2017)
G. mosseae	*M. javanica*	Tomato (*S. lycopersicum*)	Decreased egg number in egg masses	Sohrabi et al. (2017)
Trichoderma harzianum and *G. aggregatum*	*M. incognita*	Basil (*Ocimumbasilicum*)	Increased mortality	Tiwari et al. (2017)
F. geosporum	*M. incognita*	Cucumber (*Cucumis sativus*)	Reduced egg number per egg mass	Wang et al. (2017)
Acaulospora colombiana	*Meloidogyne* spp.	Cassava (*Manihot esculenta*)	Reduced nematode eggs and population density	Séry et al. (2016)

3.6 Interaction of AMF with Other Fungi

Another important group of microorganisms in the mycorrhizosphere is fungi. They help in promotion of plant growth by playing vital role in the ecosystem like the solubilization of phosphorus (P), fixation of atmospheric nitrogen and synthesis of indole-3 acetic acid (IAA) (Mendes et al. 2013). Interaction of AMF with other fungi has been studied in various plants like tomato, oil palm, soyabean, *Brassica juncea*, etc. (Bao et al. 2022). AMF are closely associated with the roots of their host plants, so they are bound to interact with plant pathogens that dwell in the mycorrhizosphere through competition, antibiosis and parasitism (Filion et al. 1999). Several pathogenic fungi affect plant growth and yield. However, it has been seen that mycorrhizal plants are less severely damaged from fungal infection as compared to non-mycorrhizal plants (Dehne 1982; Filion et al. 1999). The infection caused by fungal pathogens like *Ophiobolus*, *Phytophthora*, *Thielaviopsis*, *Fusarium*, *Macrophomina*, *Pyrenochaeta*, *Rhizoctonia*, *Phoma*, *Pythium*, *Sclerotium* and *Cylindrocarpon* in plants like onion, banana, red clover, peach, soyabean, barley, kidney bean, peanut, cotton, citrus, strawberries, tobacco, poplar and ginseng can be ameliorated by the inoculation of AMF like *Glomus margarita*, *G. fasciculatum*, *G. heterogama*, *G. etunicatum*, *G. calospora* and *G. macrocarpum* (Becker 1976; Steinkellner et al. 2012; Bubici et al. 2019; Eke et al. 2020; Aljawasim et al. 2020; Guzman et al. 2021). AMF defends plants from fungal pathogens by increasing the build-up of lignins and non-soluble polysaccharides in plant root cell walls (Jamiołkowska et al. 2017). Also, the mycorrhizal fungal hyphae present in the plant roots create physical barrier for the contagion of pathogenic fungi (Amer and Abou-El-Seoud 2008). Sudhasha et al. (2020) reported the interaction between AMF *G. intraradices* and a pathogenic fungus, *F. oxysporum*, and found that after inoculation with *G. intraradices*, the development of pathogenic fungus was inhibited. It was proposed that the growth and reproduction of fungal pathogen might have been subdued by the chemical balance of the mycorrhizae (Sudhasha et al. 2020).

Another group of fungi that can co-exist with AMF and improve plant growth is ectomycorrhizal fungi (EMF). There are certain plant species called ‘dual mycorrhizal plants’ that are capable of associating with both AMF and EMF, either in the same root system or at a distinct life stage or environment (Teste et al. 2020). In these plants, AMF and EMF compete with each other for root space, which results in vertical segregation with AMF abundance at deep soil and EMF at shallow horizons of soil (Albornoz et al. 2022). The proposed reason behind this vertical segregation is that AMF can only amass inorganic phosphorus that is plentiful at deeper soil horizons, whereas EMF can also obtain organic phosphorus that is abundant at shallow soil (Neville et al. 2002). Association of plants with both AMF and EMF depends on various environmental factors like climatic conditions, availability of nutrients, age of plants, etc. (Teste et al. 2020). Usually, AMF colonization occurs first and succeeded by EMF; however, in certain instances, ectomycorrhizas establish first and decrease AMF colonization by developing a mantle that serves as a barrier to AMF infection (Diagne et al. 2020). Contrastingly, EMF infection is not affected negatively by AMF establishment (Duponnois et al. 2003). Several studies have been conducted, which showed that combined application of AMF and EMF enhanced plant’s growth. For instance, in a study, it was observed that simultaneous application of both AMF and EMF considerably enhanced phosphorus content and biomass of *Casuarina equisetifolia* plants as compared to plants applied solely with either EMF or AMF (Elumalai and Raaman 2009). Combined inoculation of AMF and EMF increased plant growth and improved rhizobial nodulation process in *Acacia crassicarpa* (Lesueur and Duponnois 2005). AMF, EMF and *Rhizobium* application at the same time showed similar results in *Robinia pseudoacacia* plants (Tian et al. 2003). In another study, inoculation of *Eucalyptus grandis* with mixtures of both AMF and EMF species enhanced below-ground dry weight of the plant but had negative effect on its above-ground dry weight (Holste et al. 2017). In dual mycorrhizal plants, different advantages of both AMF and EMF like drought resistance, pathogen defence and aggregation of soil have been hypothesized, but they still need full investigation (Teste et al. 2020).

3.7 Interaction of AMF with Other Rhizospheric and Hyphospheric Microorganisms

The zone influenced by root as well as mycorrhizal fungus is referred to as the mycorrhizosphere (Bao et al. 2022). In other words, it comprises the soil region governed by plant roots, i.e. rhizosphere, and the region surrounding, influenced by the individual fungal hyphae, i.e. hyphosphere (Priyadharsini et al. 2016). The organic substances exuded by the roots and mycorrhizae stimulate and enhance the microbial activity in mycorrhizosphere, which differs from the bulk soil (Linderman 1988; Frey-Klett et al. 2005). Apart from fungi and bacteria, AMF also intermingle with protozoa, arthropods and other soil fauna (Zhang et al. 2020; Geisen and Quist 2021) (Fig. 3.2). Soil protozoans and collembola (soil arthropods) are known to coexist and interact with AMF species in the mycorrhizosphere (Innocenti and Sabatini 2018).

Another group of rhizospheric microorganisms that interact with AMF are *Actinomycetes*. The spores of AMF often harbour *Actinomycetes*. The volatile compounds released by these *Actinomycetes* help in the germination of AMF spores

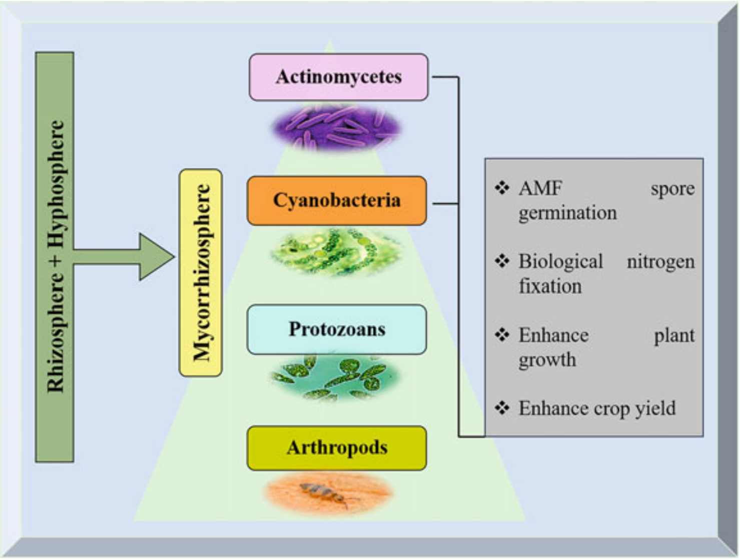

Fig. 3.2 Some other microorganisms that interact with AMF in the mycorrhizosphere

(Gryndler 2000). *Frankia*, a diazotrophic genus of *Actinomycetes*, lives in symbiotic association with roots of plants like *Alnus*, *Casuarina*, *Comptonia*, *Elaeagnus* and *Myrica* and form actinorhiza (specialized nodules) where nitrogen fixation takes place. These plants might also interact with fungi and form arbuscular mycorrhiza (Berliner and Torrey 1989). This tripartite interaction has variable results on plant growth. In an experiment, treatment of *A. cordata* with *Frankia* increased plants growth, but inoculation with *G. mosseae* and *G. fasciculatum* alone had no effect on the growth. However, when both AMF and *Frankia* were applied simultaneously, the plant growth was remarkably enhanced than when *Frankia* was applied alone (Lumini et al. 1994).

AMF also interact with blue-green algae (cyanobacteria) and play a crucial role in enhancing the fertility of agricultural fields. These autotrophic, occasionally motile and mostly filamentous organisms are capable of fixing carbon and feeding it to the soil ecosystem (Gryndler 2000). Cyanobacteria are key constituents of microbial consortia in rice fields (Ashmrita and Radha 2017). In the agricultural ecosystems, AMF-*Cyanobacterium* interaction shows promising effects on nitrogen fixation, growth and productivity of crops (Ojha et al. 2018). For instance, the combined application of cyanobacteria and AMF in paddy fields leads to biological nitrogen fixation by blue-green algae and the production of phytohormones by AMF, which brought favourable results and improved nutrient availability, grain and straw yield and soil structure (Panneerselvam et al. 2017; Bao et al. 2022).

3.8 Conclusion

Interactions of AMF and microorganisms in the rhizosphere and hyposphere are among the most significant and crucial factors affecting soil structure and characteristics, along with plant's growth. In the rhizosphere and hyphosphere, there are numerous kinds of microbial life that interact with AMF, which include bacteria, fungi and other microorganisms. For the tripartite symbiosis of plants, AMF and other microorganisms, nutritional exchange is crucial. The root exudates as well as microbial secretions can support the symbiotic interactions between different plants, AMF and soil microbes. Furthermore, the development of associative symbiosis and colonization are linked to various microbial-mediated proteins, events and pathways. Although some microbial consortia incorporating mycorrhizal inoculum are used in agriculture, our understanding regarding the complicated interaction between AMF and microorganisms in the rhizosphere and hyphosphere is still in its infancy. Therefore, utilizing various molecular approaches, future investigation may focus on the more in-depth exploration of relationship between the host plant, AMF and other microorganisms. This could result in a more effective use of soil microorganisms for crop production, which is also eco-friendly and agriculturally sustainable. New methods for molecular ecology and metagenomic investigations may provide more information about the relationships between various microbes and AMF.

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