C H A P T E R

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Mycorrhizas in fruit nutrition: Important breakthroughs

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O U T L I N E

1 Introduction

The main symbiotic organisms in the rhizosphere are mycorrhizae, N_2-fixing bacteria, phosphorus-solubilizing bacteria, and phytostimulator hormone–producer bacteria. This beneficial symbiosis including mycorrhizae has significant benefits to plant health and soil quality (Table 24.1). In terrestrial ecosystem, mycorrhizal fungi are surrounded by a number of complex microbial communities such as bacteria and actinomycetes. Possibly, the other rhizosphere organisms may modulate the mycorrhizal symbioses in the rhizosphere area as well.

It is estimated from the fossil record, approximately 480 million years ago, arbuscular mycorrhiza (AM) has an associations in the earliest land plant fossils (Delaux, 2017). The majority of plant species are naturally arbuscular mycorrhiza (AM) dependent. It is obvious that many plant species depend on these symbionts for growth and survival under several different soil and climate conditions. Nearly 90% of plants have symbiotic relation arbuscular mycorrhiza, and this soil fungus belongs to *Glomeromycota* (Schussler et al., 2001).Arbuscular mycorrhizal fungi (AMF) are obligate symbionts of many plants that biotrophically colonize the root cortex and develop an extramatrical mycelium, which helps the plant to acquire water and mineral nutrients from the soil (Elsen et al., 2003; Marschner, 1995) and increases plant resistance against stress factors. Mycorrhizae are providing a critical linkage between the plant root and soil particles. AM fungi provide a range of important ecological services, in particular by improving

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TABLE 24.1 Type of microorganisms and their role on plant and rhizosphere soil systems.

Type of microorganisms	Effects of interaction on plant life
N_2-fixing bacteria (biofertilizers)	N_2 fixation, N cycling for some fruit trees
Mycorrhiza fungi (biofertilizers)	Nutrient and water uptake and improved soil quality for nearly 90% of plant species
Phosphorus solubilizes (biofertilizers)	P cycling, use of rock and organic phosphates
Rhizobacteria (PGPR)	Plant growth and health promotion and regulation of diversity of the microbial population in the rhizosphere
Plant hormone producers (phytostimulators)	Rooting and establishment of seedlings
Biological control agents of plant diseases (bioprotectors and biopesticides)	Increased resistance/tolerance to root diseases and soilborne disease

stress resistance and tolerance, soil structure, and fertility. According to Rouphael et al. (2015), AMF interfere with the phytohormone balance of host plants, thereby influencing plant development (bioregulators) and inducing tolerance to soil and environmental stresses (bioprotector) factors.

2 Facultative and obligatory mycorrhizal plants

The microorganisms play an important role in the plant, soil, and environmental sustainability. Most plant species are facultative symbionts, and they get to benefit from AM fungi. Also, numerous microorganisms including AMF cannot survive without plant roots. Some plant species cannot grow without undergoing association with friendly AMF. Also, some at the same time can survive without AMF. Plant taxa such as *Brassicaceae* and *Chenopodiaceae* are symbiotic, and they lost the capacity to interact with AM fungi (Table 24.2). Those group of taxa devolved an alternative strategy to get their mineral nutrient demands (Brundrett, 2004).

Some plant species cannot grow without mycorrhizal associations, but others do not because they have other strategies for accessing nutrients (Lambers et al., 2011). Plants benefit from AMF associations only in some of the least fertile soils in which they naturally occur (Janos, 1980, 2007). In ecosystem, some herbaceous plant species has low levels of AMF colonization (less than 25%) (Brundrett and Kendrick, 1988). Plants with coarsely branched roots

TABLE 24.2 Plant species and their relation with mycorrhizal symbioses.

Mycorrhizal type	Plants	Number of plant species hosting mycorrhizal fungi	Fungi	Fungal colonization	Total estimated number of fungal taxa
Arbuscular mycorrhiza (AM)	Most herbs, grasses, many flowering plants and several trees (mainly fruit tree), shrublands, hornworts and liverworts	200,000	*Glomeromycota*	Endo	300–1600
Ectomycorrhiza	*Pinaceae* and angiosperms (mostly shrubs and trees, mostly temperate), tropical forests, tundra, and agroforestry	6000	*Basidiomycota* and *Ascomycota*	Ecto	20,000
Orchid mycorrhiza	Orchids species	20,000–35,000	*Basidiomycota*	Endo	25,000
Ericoid mycorrhiza	Members of the *Ericaceae* family	3900	Mainly *Ascomycota*, some *Basidiomycota*	Endo	>150
Nonmycorrhizal plant species	*Brassicaceae*, *Crassulaceae*, *Orobanchaceae*, *Proteaceae*, etc.	51,500			0

Reproduced with based on Brundrett, M., 1991. Mycorrhizas in natural ecosystems. Advances in Ecological Research. Elsevier, pp. 171–313; Brundrett, M.C., 2009. Mycorrhizal associations and other means of nutrition of vascular plants: understanding the global diversity of host plants by resolving conflicting information and developing reliable means of diagnosis. Plant Soil 320, 37–77; Van Der Heijden, M.G., Martin, F.M., Selosse, M.A., Sanders, I.R., 2015. Mycorrhizal ecology and evolution: the past, the present, and the future. New Phytol. 205, 1406–1423.

and with few or no root hairs are expected to be more dependent on AMF than plants with finely branched or fibrous roots (Smith and Read, 2008).

Rhizosphere soil of the many plants revealed the presence of many species of mycorrhizal fungi. Anand and Reenu (2009) reported that in the rhizosphere of two medicinal plants (*Centella asiatica* and *Ocimum sanctum*) have 16–17 different species of AM fungi. In another study, the results of Shi et al. (2013) shown that 31 AM fungus species belonging to 3 genera (*Glomus* [21], *Acaulospora* [7], and *Scutellospora* [3]) were identified in the rhizospheric soil. In the same rhizosphere soils, other soil beneficial organism richness is supposed to be higher than noninoculated plants.

3 Mycorrhizal dependency

3.1 Mycorrhizal dependency and dependent plant species

Baylis (1975) hypothesized that mycorrhizal dependency is largely controlled by the root system architecture. It was defined mycorrhiza dependency "host inability for growth without AMF at given soil fertility." Mycorrhizal dependency (MD) of the host crop is dependent on soil fertility and fertilizer levels (Ortas, 2012a,c). So far, many hypotheses were suggested to measure the mycorrhizal response on plant growth and nutrient uptake. Gerdemann (1975) and Baylis (1975) were the first researchers who defined the mycorrhizal dependency as the degree to which a plant is dependent on AMF to produce maximum growth or yield at a given level of soil fertility. Baylis (1975) also postulated that magnolioid roots were most dependent upon an AMF for phosphorus uptake, indicating the existence of species differences in the changes in P uptake associated with mycorrhizal colonization. Later on, Plenchette et al. (1983) have determined the "relative mycorrhizal dependency (RMD)" by expressing the difference between the dry weight of the mycorrhizal plant and the dry weight of the nonmycorrhizal plant as a percentage of the dry weight of the mycorrhizal inoculated plant.

Plant benefits from AM fungal colonization in large degree depend on the environmental conditions (Chen et al., 2018a) such as nutrient concentrations and other stress factors (Azcón et al., 2003). Plants will not survive to reproductive maturity without being associated with AMF in the soils (or at the fertility levels) of their natural habitats (Janos, 1980). Graham et al. (2017) reported that some plant species have turned to obligate parasites on the AM fungus and they became fully dependent on fungal nutrition and most probably they lost their photosynthetic capacity. The orchid plant is an example. In different studies, the positive influence of the AM symbiosis on horticultural production was provided by many researchers (Gianinazzi et al., 1989; Lovato et al., 1999). Almost all fruit tree plant species are mycorrhizae dependent for growth and nutrient uptake (Fitter et al., 2011; Kungu et al., 2008). Some species are strongly mycorrhizal dependent than others. The AMF also have many advantages on inducing plant that can tolerate biotic stress (Barea et al., 1996) and abiotic stress factors. Species variation in AMF may cause a difference in the crop growth due to the mycorrhiza effect on certain key processes of plant physiology. AMF influence on optimizing the uptake of mineral nutrients in the rhizosphere is one of a very important regulator of plant development.

In this context, it is natural that many plant species and genus are AMF obligate with good infection. Mycorrhiza species may be selectively preferred by some plant species than the others. For citrus plant, it has been clearly shown that *Glomus clarium* inoculum significantly inoculated sour orange seedling better than the other mycorrhiza species (Ortas, 2012b). It has been reported that some efficient AMF species such as *Glomus aggregatum* are helping plant growth than nonefficient AMF species such as *Glomus intraradices* (Ba et al., 2000; Guissou et al., 1998). Since AMF are obligate symbionts, they may have preferred plant species and ecologically growth conditions.

4 Advantages of mycorrhizal dependency on plant

Mycorrhizal dependency and mineral nutrition potential have been focused by many researchers, and it has been indicated that the benefits of AM fungi on plant growth could vary widely among plant species and even among cultivars or species from different geographic locations (Ortas, 2012b; Plenchette et al., 2005; da Sousa et al., 2013).

The degree of plant dependence is of great practical and ecological interest for plant nutrition. Fungi are better than plants at acquiring mineral nutrition (P, K, N, Zn, Cu, and Ca) from the soil. AMF improve a plant's access to water. Guissou et al. (2016) indicated that AM inoculation significantly improved the N, P, and K absorption compared with non-AM fruit trees. They indicated that AM-inoculated plant leaves have more P concentration than noninoculated tree plants. Plant gets nutrients P, Zn, Cu, N, and water, and the fungus gets carbohydrates. Carbohydrates are moved from the leaves to the rhizosphere the benefit of both sides. The most efficient method of carbon mitigation is photosynthesis mechanism, which can pull the atmospheric carbon to the rhizosphere soil. However, still unknown mechanisms are regulating AMF colonizing such as carbon expenditure, the toxic effect of high P, nutrients, and different other ecological factors. The benefit is provided by AMF, and plant will depend on the relative contribution of root and mycorrhizal mediated nutrient uptake to plants (Janos, 2007). Mycorrhizal dependency has often been quantified by calculating the yield between mycorrhizal and nonmycorrhizal control plants grown in a particular soil at a single soil P level (Hetrick et al., 1992; Koide, 1991; Manjunath and Habte, 1991).

5 Mycorrhiza-dependent horticultural plant species

As can be seen in Table 24.3, many horticultural tree plants are mycorrhiza dependents. Jaizmevega and Azcon (1995) indicated that RMD of tropical horticultural fruit crops such as avocado, papaya citrus, banana, vineyard, cherry, fig, pistachio, and pineapple is highly responsive to AMF when the inoculum consists of *Glomus* spp. Plant species give different response to the different mycorrhiza species. Under similar growth conditions, by using the data of Fig. 24.1, mycorrhizal dependency (MD) of horticultural plant was calculated. Plant species mycorrhiza dependency was significantly differed without considering the growth mediums. It seems that citrus plant is strongly mycorrhizal dependent than the other plant species (Table 24.3). So far in our different research works, it has been observed that sour orange seedlings are a strongly mycorrhizal dependent under several soil and nutrition conditions (Ortas, 2012b). After soil sterilization, without mycorrhizal inoculation, sour orange seedlings are nearly not grown (Ortas et al., 2018). On the other hand, mycorrhiza-inoculated seedling is grown in several times bigger than noninoculated one (Fig. 24.2).

Many studies have been done to determine mycorrhizal dependency by using Plenchette et al. (1983) equation. Hetrick et al. (1996) indicated that, when the soil available phosphate concentration is the growth-limiting factor of the plant, MD is positively correlated with the MD in phosphorus uptake. The degree of AMF dependency varied according to phosphorus levels and fungal inoculum (Cardoso et al., 2008). The results of Costa et al. (2005) shown that the mycorrhizal dependency varied according to the AMF and soil condition. In another research, Sharma et al. (2001) reported that the values of MD were negatively correlated with soil P levels. Host plants' phosphate acquisition ability and phosphate utilization efficiency can determine the dependency of mycorrhizae. Plant ability of phosphate acquisition mainly depends on morphological and physiological characteristics of plant roots (Koide, 1991; Schachtman et al., 1998).

AMF must be considered a necessary factor for promoting horticulture plant productivity and health. Since horticultural plants are produced in nursery beds, containers, or by tissue culture, AM biotechnology or soil biotechnology is feasible and rewarding mainly for crops, which involve a transplant stage application. With efficient AMF species and a careful selection of compatible host/fungus/substrate combinations, maximum benefits can be obtained from AMF inoculation. In general, the earlier AMF inoculation or seedling produced with AMF infection at the appropriate stage of seedling production can provide better yield and benefit.

Under greenhouse conditions with similar growth medium, different mycorrhizal species were used. Generally, in comparison with noninoculation, mycorrhizal inoculation increased banana, vineyard, cherry, citrus, fig, and pistachio plant total dry weight (Fig. 24.1). In general, selected mycorrhiza species produce more total dry weight than

TABLE 24.3 Effects of several mycorrhiza species on different plant mycorrhiza dependencies.

Treatments	Banana	Vineyard	Cherry	Citrus	Fig	Pistachio	Mean
G. mosseae	32	27	59	91	24	48	47
G. intraradices	28	27	40	89	38	34	43
G. caledonium	33	25	24	92	39	31	41
G. clarium	36	23	37	82	38	41	43
G. etunicatum	34	27	24	81	33	38	40
Cocktail	25	26	10	91	28	30	35
Indigenous Myco.	28	23	37	49	17	36	32
Mean	31	26	33	82	31	37	40

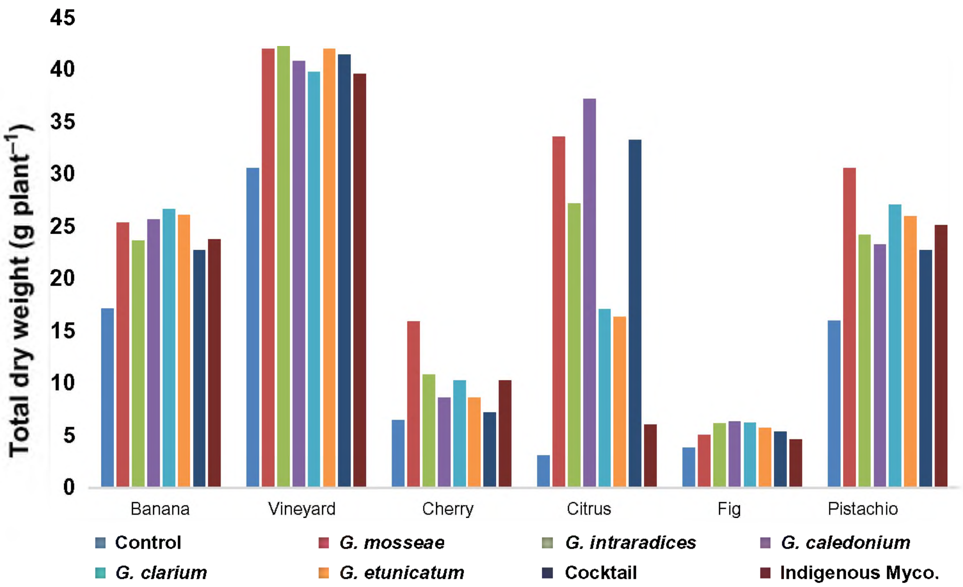

FIG. 24.1 Effect of different mycorrhizal species on plant growth.

FIG. 24.2 Effects of mycorrhizal inoculation on sour orange citrus seedling growth.

cocktail and indigenous inoculation. Indigenous mycorrhiza-inoculated citrus seedlings produce less DW than other mycorrhiza species inoculation.

Generally, indigenous mycorrhizal inoculation effect on mycorrhiza dependency is less than selected mycorrhiza species. Cocktail mycorrhiza inoculation also has fewer effects on MD. This may be related to with a number of mycorrhizal propagules and mycorrhizal spore quality.

6 Mycorrhizae and plant nutrition

6.1 Mycorrhizae reduce the nutrient deficiency stress

Increased nutrient uptake made possible by the AM symbiosis results in more vigorous plants. When AMF-inoculated young plantlets raised in nurseries are planted in field, they quickly adapt to the dry climate conditions (Chen et al., 2018b). Similarly, Sellal et al. (2017) reported that AMF inoculation significantly increases the growth and health of young argan trees, and they indicated that inoculated seedlings increase their fitness and survival after planting. Mycorrhizal symbiosis results in reduced nutrient stress and also can reduce other environmental stresses such as soil drought; they can benefit plant growth.

These fungi can benefit plants by enhancing the nutrient-absorbing ability of roots especially important in facilitating uptake of phosphorus. In addition to element uptake via mycorrhizal mycelia, AMF has also shown to affect root morphology and functioning, as well as mycorrhizosphere soil properties. With their thin diameter ($<10\,\mu m$), AM hyphae might be able to access smaller soil pores and better compete with soil microbes for nutrient resources, compared with plant roots. Neumann and George (2010) indicated that just like plant root systems, AM hyphae seem to differ considerably in their architecture and physiological activities depending on their genotype. This enhancement of nutrient uptake is a result of the extensive system of hyphae and mycelia that pervade soils. Mycorrhizal hypha length is also controlled by nutrient level mainly by soil phosphorus levels. Recent works are strongly indicating that phosphate delivery is among the most important benefits for the host in AM symbiosis (Karandashov and Bucher, 2005), and all results showed that the arbuscules are the site of transfer of phosphate from the fungus to the plant cells (MacLean et al., 2017).

All physiological evidence indicates that the P uptake pathway by AM is often accompanied by reduction in P absorbed directly by root hairs and epidermis (Smith and Read, 2008). The reduction is usually related to the depletion of P in the rhizosphere area. Also, the operation of AM P uptake pathway is believed to be under the reduced expression of Pht1 transporters in root epidermal cells. Also, mycorrhizal inoculation may transfer the nutrient elements such as nitrogen, sulfur, and microminerals such as copper and zinc via the arbuscules as well. The relationship of this fungus with plants is a mutually beneficial one, with the fungi receiving energy in the form of carbohydrates from the host plant. One of the most dramatic effects of mycorrhizal inoculation on the host plant is the increase in P uptake and Zn mainly due to the capacity of the AMF to absorb phosphate from soil and transfer it to the host roots. Even under abiotic stress conditions, mycorrhizal inoculation increases the nutrient concentration.

7 Contribution of mycorrhizae on P uptake and plant growth

The AMF can utilize soil nutrient efficiently. Mycorrhizal fungi may be making significant contributions to ecosystem nutrient cycling in a large scale on mineral nutrients. AM fungi affect plant growth only via an increased nutrient supply under a well-inoculated condition. AMF can secrete phosphatases to hydrolyze phosphate from organic P compounds (Marschner, 2012), thus improving crop productivity under low input conditions (Smith et al., 2011). The extensive hyphal network of mycorrhizal fungi and extension of mycorrhizosphere influence the physicochemical and biochemical properties of the soil and directly or indirectly contribute to the release of phosphate from inorganic complexes of low solubility (Parniske, 2008). Phosphorus exists in the natural soil ecosystems as inorganic orthophosphate, primarily involved in inert complexes with cations such as iron phosphate ($FePO_4$), aluminum phosphate ($AlPO_4$), and calcium phosphate ($CaPO_4$) and in organic molecules such as lecithin and phytate, the latter of which can account up to 50% of total soil organic phosphate. P uptake mechanisms in between plant species are so complex. Since P is highly immobile in the soil, its acquisition by the roots generates a depletion zone surrounding the epidermis and the root hairs of rhizosphere.

Some plant increases the root-soil interface to maximize access to available P in rhizosphere (Fig. 24.3). Some plants are using root secrete organic acids such as malate and citrate to compete with P cation binding. Nearly 90% of plant species get an important part of P thorough mycorrhizal external hyphae (fungal hyphae grow up to 100 times longer than root hairs).

As shown in Fig. 24.3, the depletion zone around roots is very narrow, and depletion zone of AM-inoculated root area is much larger than root alone. At the same time, AM fungal colonization induces expression and secretion of a plant-derived acid phosphatase in the rhizosphere, which further liberates Pi (Ezawa et al., 2005). The characterization of a high-affinity Pi transporter (PT) through extraradical hyphae is a milestone in the definition of AM fungi as biofertilizers. All research work data showed that Pi, taken up by the extraradical mycelium from soil solutions, is translocated through the AM fungal hyphae as polyphosphate (poly-Pi). Also, research clearly shows that Pi uptake is under gene control. Benedetto et al. (2005) have reported that tomato Pi transporter genes are consistently expressed

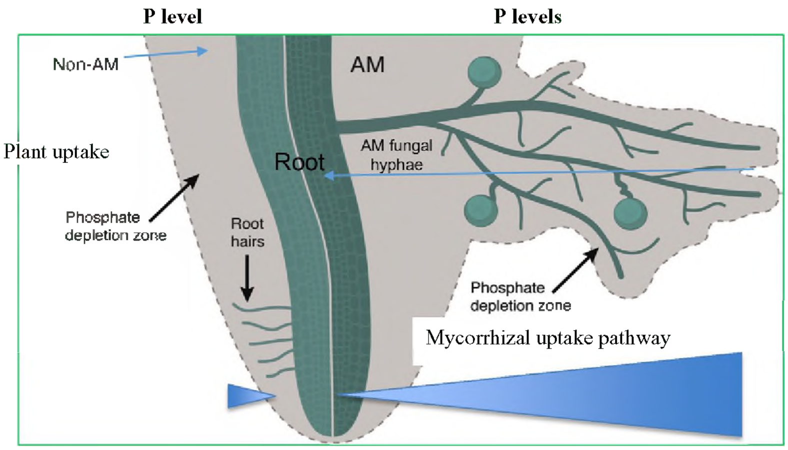

FIG. 24.3 Phosphate depletion zones that develop around a nonmycorrhizal root hairs and the root colonized by AM fungi. Plant P and other nutrient uptake and mycorrhizal inoculation uptake pathways are completely different from each other. *Modified from Hodge, A., 2017. Accessibility of inorganic and organic nutrients for mycorrhizas. Mycorrhizal Mediation of Soil. Elsevier, pp. 129–148.*

inside the arbusculated cells, suggesting that plants guarantee maximum Pi uptake through the activation of the whole gene family. According to Javot et al. (2007) after poly-Pi hydrolysis in the arbuscule, the phosphorous is then released as Pi into the periarbuscular space. Mycorrhiza-specific Pi transporters are responsible for plant Pi uptake in arbuscule-containing cells to plant tissue.

8 Contribution of mycorrhizae on other nutrient uptake

In both major inorganic N sources, nitrate and ammonium are regarded as relatively mobile in soil, transported to roots by mass flow in the soil solution. Since ammonium is less mobile than nitrate AMF, mainly ectomycorrhizae absorb ammonium from the soil solution. The results of Chalot et al. (2006) indicated that NH_3/NH_4^+ is thought to be the preferential form of N released by the fungus and uptake by the plant. Guether et al. (2009) reported that a mycorrhizal-specific lotus AMT gene has recently been identified to be responsible for N uptake. It seems that nitrogen is then transferred from the fungus to the plant as ammonium form. Govindarajulu et al. (2005) indicated that with isotope-labeling experiments in combination with gene expression data have demonstrated that inorganic N (nitrate and ammonium) is taken up by the extraradical mycelium, incorporated into amino acids, and translocated to the intraradical mycelium, mainly as arginine. Van Der Heijden et al. (2015) indicated that, up to 80% of plant, N and P are provided by mycorrhizal fungi.

Nutrient deficiency is a common nutritional problem in crop production in many arid and semiarid soil conditions. Under such soil conditions, also, there are salt and alkalization problems. Latef and Chaoxing's (2011) results show that mycorrhiza-inoculated tomato plants grown under nonsaline and saline conditions have higher P and K concentrations than compared with non-AM-inoculated plants. Mycorrhizal inoculation or indigenous potential of mycorrhizae in such soil is a critical factor in crop production for P, Cu, and Zn. The results of Navarro and Morte (2019) showed that, under lower P supply conditions, Zn or Fe increased more in the mycorrhiza inoculation of *Citrus macrophylla* Wester seedling plants. In addition, mycorrhizal infection results in an increase in the uptake of other macro- and micronutrient and water uptake. The results of Grimaldo-Pantoja et al. (2017) revealed that, under salt conditions, mycorrhiza inoculation significantly increases pepper plant P concentration.

Boron deficiency is also common in many soil conditions, especially under semiarid and low-fertile soil conditions. Boron is mainly accumulated in the fruits and upper leaves of plants. And translocation can only occur from other plant parts toward the fruits. Mycorrhizae also have effects on boron uptake of apple seedling (Gastol et al., 2016) and translocation (Shireen et al., 2018; Watts-Williams and Cavagnaro, 2014). Roots and hyphae were the first structure to respond to boron uptake and translocation in plant fruits.

9 Mycorrhizae and other rhizosphere organisms

9.1 Mycorrhiza is an efficient mechanism in rhizosphere for plant health

The physiology of the plant is highly affected by the presence of the fungal symbionts (Smith et al., 1994). The effects of AMF on the growth and development of horticultural plants have been studied and described by many research papers (George and Marschner, 1996; Lovato et al., 1996, 1999, 2006). In general, fruit crops have received more attention than vegetable and ornamental crops. Obviously, the interest of horticulturists in AM technology is due to the easy inoculum application. The ability of AMF to increase the uptake of phosphorus and other nutrients and to increase resistance to biotic and abiotic stress. Fruit tree plants are having benefit through AMF by increasing uptake of P and other nutrients and also increasing resistance to biotic and abiotic stresses. Plant species, which can use organic phosphate by root exudation of phosphatase, may not need to depend on mycorrhizal colonization, and they are known as nonmycorrhizal plants. The AM fungi can alter rhizosphere of plant through the profile of volatile organic carbon released by roots that can affect the number and richness of rhizosphere organisms. Also with mycorrhizal inoculation, the root morphology of plants can increase, and root morphology increases the plant adaption to the soil environments. Flasinski and Rogozinska (1988) reported that root exudation increases for phosphatase under P-deficient condition in no host plant species.

9.2 Relationship between plant-bacteria-mycorrhizae

Rhizobacteria, referred as plant growth–promoting rhizobacteria (PGPR), are agronomically useful and active root-colonizing microbes that are involved in N fixation, nutrient solubilization, water and nutrient uptake, salinity and drought tolerance, enzyme production against soilborne pathogens, and phytohormone production. Bacteria are the most abundant microorganisms in the rhizosphere. Bacteria mostly collaborate with mycorrhiza fungi in the rhizosphere. Both mycorrhizae and PGPR can influence the plant physiology to a greater extent, especially considering their collaboration or competitiveness in root colonization; PGPRs act as biofertilizers having efficient symbiotic relationship with mycorrhiza species on many plant roots and promote plant growth. AMF and PGPR have potential to increase plant growth and also control soilborne diseases including plant-parasitic organisms. Numerous plant growth–promoting rhizobacteria are well known to exhibit beneficial effects with mycorrhizal inoculation on plenty of horticultural crops. The results of Sharma and Sharma (2017) showed that tomato plants treated with dual or individual inoculation of AMF and PGPR showed significantly enhanced plant growth.

When plant-bacteria-mycorrhizae work together, it is termed as tripartite relationship, which can promote plant growth, nutrients, and water uptake and make plant defense system stronger against stress factors. The establishment of tripartite relationship depends on plant-soil-microorganism feedback system, and all the contributors are involved in multidirectional exchange of goods and services, which induce changes in the aboveground and belowground interactions (Ortaş et al., 2017). Positive and negative interaction between tripartite organisms mainly depends on energy resource limitation. There are several different models to explain the way of tripartite interaction where the optimal resource allocation model is emphasize under resource-limited condition (Revillini et al., 2016) (Fig. 24.4).

The interaction between mycorrhiza and plant root has several benefits irrespective of their contribution to host plant growth and nutrient uptake. Also, mycorrhizal inoculation is a strong sink for photosynthesis. Mycorrhizae demand more carbon from plant to survive and consequently leeched more carbon to the rhizosphere. Finally, when there is a good infection, mycorrhizal fungi compensate the carbon drainage and carbon use.

It is believed that AM fungi and *Rhizobium* stimulate the photosynthetic process in their host plant as a C sink. The calculation of Miransari (2014) indicated that the amounts of plant photosynthesized C supplied to AM fungi and *Rhizobium* range from 4% to 16% of the total fixed C.

10 Compatibility and collaboration of AMs with other rhizosphere microbes

In the rhizosphere, the complex relationship between mycorrhiza and other organisms is still under extensive search by several advance laboratory conditions. Recently, the use of DNA-based research methods has increased our understanding of the specificity of mycorrhizal fungi toward their host plants and interaction with other soil rhizosphere organisms.

Maybe, more efficient nutrient cycling by mycorrhiza fungi would relieve some plant stress, thereby leading to improved nodulation and N_2 fixation by *Rhizobium*. Under stress conditions, AM and *Rhizobium* may influence the efficiency by improving the nutrient and water uptake, enhance the plant morphology and physiology, and improve hormone signaling between host and microorganism to establish better symbiosis, and AM controls the pathogen and disease factors. In our long-term observation, some plant such as soybeans under sterile soil conditions without mycorrhizal inoculation plant nodulation is not well developed. It seems that still there are several unknown

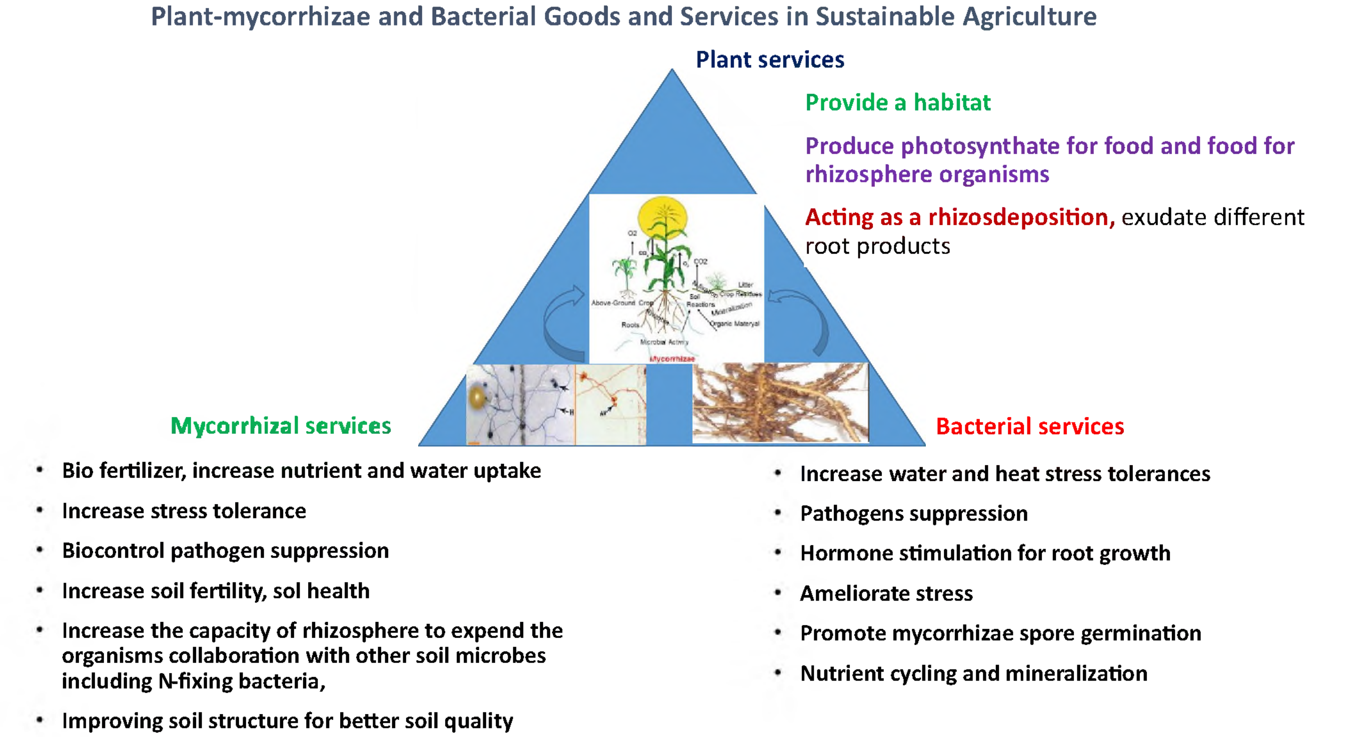

FIG. 24.4 Multidirectional exchanges of goods and services among plants, mycorrhizal fungi, and rhizobacteria relation. Exchanges presented here show mycorrhizae and bacteria include plants benefits to plant growth, mycorrhizal fungi and rhizobacteria in several ways. Bacteria and mycorrhizal inoculation also increase soil fertility and soil quality directly and indirectly.

mechanisms between AM and *Rhizobium* interaction. Also, the N_2-fixing rhizobium bacteria and mycorrhiza fungi are the most relevant representatives of beneficial plant symbionts as well (Barea, 2015), which are directly related to nutrient cycling and uptake. Under different ecological conditions, dual inoculation of both mycorrhizal fungi and N-fixing bacteria can benefit the host plant. Both *Rhizobium* and mycorrhizal fungi are interacting with their host plant like lentils and green bean. It is estimated that *Rhizobium* and mycorrhizal fungus well-infected plant provide up to 80% and 75% of necessary N and P for plant use and growth (Miransari, 2014). Dual inoculation of both AM-plant symbiosis and the bacteria-legume symbiosis is of agricultural and environmental implications, and they can substantially contribute to available P and N production and utilization by plant and decreasing the amount of N and P chemical fertilization. The results of Kuang et al. (2005) indicated that the positive interactions between P and N, which are resulted by mycorrhizal and N-fixing bacterial symbioses, significantly increase plant growth. Also, it has been reported by Smith et al. (2010) that AM species increase the efficiency of legume plants, through enhancing the uptake of nutrients such as P, Cu, and Zn, which are important for nodulation and N fixation (Smith et al., 2010).

It seems that N-fixing capability of *Rhizobium* may be enhanced when host plant roots are infected with optimum mycorrhizal species. Our early research showed that mycorrhizal inoculation improved soybean nodulation and root morphology (unpublished data). The results of Ames et al. (1987) indicated that preestablishment of mycorrhizae improved cowpea nodule activity and root dry weight. Long time ago, Hayman (1986) reported that the *Rhizobium*-AM-leguminous plant interaction exists, and some legumes grew so poorly without mycorrhizas as to be ecologically obligate mycorrhizae. Many studies also showed that AM fungal communities in legume roots are different from those in no legume roots. This mean mycorrhizae and rhizobia relationship and interaction may be selective depending on host plant. Root colonization of AM may be different with rhizobia inoculation for each host plants. In an experiment, N-fixing plant roots densely mycorrhizae colonized >70%–80% of its root system (Ortas, 2008).

For example, dual inoculation of mycorrhizal fungus and *Thiobacillus* on maize crop with sulfur application on alkaline soil has decreased rhizosphere soil pH, which made nutrients available to the plant roots (Ansori and Gholami, 2015). The symbiotic effectivity of dual and tripartite symbiotic agent bacteria and AM fungi was investigated in two pot culture experiments on different soybean cultivars by Takacs et al. (2018). The results indicated that both

TABLE 24.4 Density of total bacteria, nitrogen-fixing bacteria, and *Actinomycetes* populations in rhizosphere soil inoculated with different AM fungal species (Secilia and Bagyaraj, 1987).

AM species	Rhizosphere soil population density (colony-forming units/g soil)		
	Bacteria (×10^6)	N_2 fixers (×10^5)	Actinomycetes (×10^4)
Control (non-AM)	14.7	12.4	13.4
Glomus fasciculatum	41.9	42.0	26.1
Gigaspora margarita	34.0	87.9	17.7

microbial-inoculated cultivars were better than that of control, proving that even drought-tolerant genotypes. The results of Efthymiou et al. (2018) suggest that AM and phosphate-solubilizing microorganism *Penicillium aculeatum* may possibly act synergistically without showing and antagonistic interactions to improve the uptake of P in wheat. In general, plant-mycorrhizae-bacteria association gets the benefit in terms of three core functions of bacteria, that is, mineral nutrient mobilization from soil minerals, fixation of atmospheric nitrogen, and increased plant resistance against stress factors and pathogens.

Until now, the following bacterial genera have been reported for the association with mycorrhizal fungi such as gram-negative *Proteobacteria* and gram-positive *Firmicutes* and gram-positive *Actinomycetes* (Frey-Klett et al., 2007; Secilia and Bagyaraj, 1987). Since AM spores are obligate in terms of their growth, development, and multiplication, they are grown on host plant root medium. Through mycorrhiza multiplication, also rhizosphere is rich of viable useful bacterial species (Table 24.4). Mycorrhizal spores' application as inoculum is also rich of bacteria medium is applied to the soil medium. As a result of dual inoculation, plants are getting benefit from mycorrhiza spores and bacteria as well in several ways (Fig. 24.3). Also, microbial communities such as the activity of mycorrhizal helper bacteria may increase mycorrhizal activity to uptake less mobile nutrient from soil. The mycorrhizal helper bacteria assist the AM fungi up to 3.8-fold increase in root colonization (Duponnois and Plenchette, 2003). Also, bacteria help plant to increase the number of mycorrhizal spores and mycorrhizal colonization. The results of Secilia and Bagyaraj (1987) showed that different AMF species inoculated plant rhizosphere soil populations of total bacteria, nitrogen-fixing bacteria, and *Actinomycetes* were significantly higher than noninoculated control treatments (Table 24.4). Also, their results clearly suggest that different AMF species affect the physiology of the host in different ways. According to Marschner (2012) effect of rhizosphere microorganisms on root morphology and nutrient availability, this alteration may affect nutrient acquisition and plant growth.

11 Future aspects and concluding remarks

In this review, the role of mycorrhizae in plant growth and nutrient uptake clearly and extensively was determined. It is obvious that mycorrhiza is an important part of plant symbiosis for sustainable life. However, still there is more need to work on the role of mycorrhizae under field conditions for better sustainable ecological agriculture. Under field conditions, several experiments were performed to understand the potential contribution of mycorrhizae on field and horticultural plant growth and nutrient uptake. After long-term evaluation, it is sound to use mycorrhizal inoculation for horticultural plant, and for field crop plant, it is sound to manage the soil and crop systems. Since horticultural plant is grown as a seedling and transplanted to the field conditions, it is sound to produce mycorrhiza-inoculated seedlings. And it is sound to suggested using mycorrhiza for mycorrhizae dependent plant species before transplanting to field conditions. The future challenge of the use of mycorrhizal fungi in the production of horticultural fruit plants will be to optimize combinations of plant species and mycorrhizal fungi species, inoculation methods, and soil or substrate properties for mycorrhizal use and effectiveness. These facts show that mycorrhizal inoculation is necessary for healthy, effective, and well-grown quality seedling production. Mycorrhizal inoculation is going to be the key mechanism for healthy food for plant physiology. To manage indigenous mycorrhizae under greenhouse and field conditions, the effect of soil and crop management will be important. For future, our research direction will be focusing on soil and crop management systems and using mycorrhizal inoculated horticultural seedlings for large agricultural practice.

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