Chapter 18
Relationship Between Arbuscular Mycorrhizas and Plant Growth: Improvement or Depression?

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18.1 Introduction

Arbuscular mycorrhizal fungi (AMF) are a type of soil fungi belonging to phylum *Glomeromycota* and can associate with the roots of most plants, in which fungal hyphae penetrate the root cortical cells to form inner structures known as arbuscules, hyphae, and/or vesicles (Fig. 18.1a) and outer structures known as extraradical hyphae and entry points (Fig. 18.1b). In the symbiosis system, host plants provide necessary carbon source and energy for mycorrhizal fungi. In return, mycorrhizas form well-developed extraradical hyphae to enlarge the absorption range of plant roots, resulting in the nutrient enhancement of host plants (Zhang et al. 2012b). Hence, arbuscular mycorrhizas play an important role in nutrient acquisition of the host plant (Mohammad et al. 2004; Li et al. 2011). AMF not only senses the signals secreted by the host plant roots but also guides the hyphae into the “presymbiotic growth stage.” AMF also secretes certain factors that are identified by the root system. These mycorrhizal factors can be recognized by plants. Earlier studies had shown that mycorrhizas improved the utilization of nutrients for plants in soils (Wu and Tan 2005; Wu and Zou 2009; Zhang et al. 2012a, b).

Symbiosis between legumes and *Rhizobium* can be described as a typical model. *Rhizobium* absorbs nitrogen from the air and some of which are used for their own consumption; the rest is provided for hosts. The vast majority of legumes can be used to become nitrogenous nutrients, while leguminous plants are also not stingy and produce nonnitrogenous carbohydrate nutrients for the use of rhizobia openly, which is typical of mutualistic association (Simms and Taylor 2002). Arbuscular mycorrhizas as mutualistic symbiosis can help host plants to absorb nutrient and water from the soil to the plant partner, resist the effects of adverse environments, and

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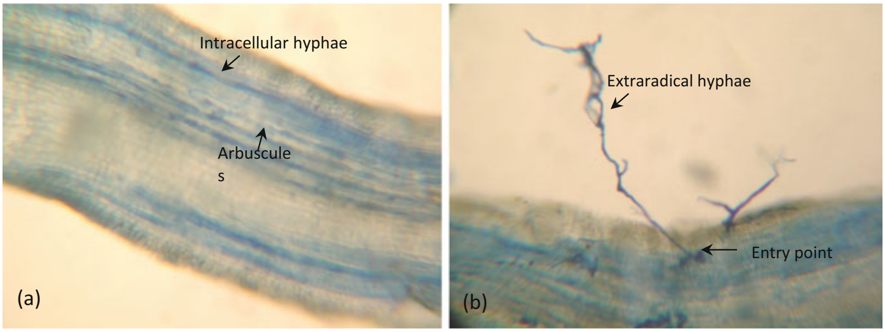

Fig. 18.1 Root colonization [(**a**) intracellular hyphae and arbuscules; (**b**) extraradical hyphae and entry point] of trifoliate orange by an arbuscular mycorrhizal fungus, *Funneliformis mosseae*

improve soil environment, thereby promoting plant growth and development (Deshmukh et al. 2006; Purin and Rillig 2007). In addition, AMF also stimulates endogenous phytohormone synthesis of host plants to increase total biomass and improve stress resistance. Excreta of AMF has a positive effect on soil aggregates that effect on soil stability and soil physical–chemical traits (Bever et al. 2001; Wu et al. 2016b). Based on individual level of plants, studies indicated that the maintenance of the AMF–plant symbiosis system depends on the two-way reciprocal mechanism and that the plant can identify the AMF that is beneficial to it and give the photosynthetic product priority to such AMF. On the contrary, AMF tends to deliver soil nutrients to plants that provide the most photosynthetic products, and this two-way reciprocal mechanism ensures the stability of the symbiotic system (Kiers et al. 2011).

Besides improved plant growth, mycorrhizal inoculation also has the inhibited effects on plant growth. For example, mycorrhizal presence significantly inhibited lemon growth under high phosphorus (5 mmol/L KH_2PO_4) supply (Peng et al. 1993). At high CO_2 concentrations, inoculation with *Glomus intraradices* heavily inhibited plant growth of *Citrus aurantium* (Jifon et al. 2002). It seems that mycorrhiza-modulated responses of host plant growth are a complex issue. In fact, the AMF responses of plant growth may be related to the changes in mutualism, commensalism, and parasitism. In this chapter, we simply discussed the promoted and inhibited effects of AMF on host plant growth and outlined the relevant mechanisms.

18.2 Improvement of Plant Growth by Mycorrhiza

As stated above, mycorrhizal workers often find the promoted effects of AMF inoculation on plant growth (Fig. 18.2). Here, we simply outlined the relevant mechanisms.

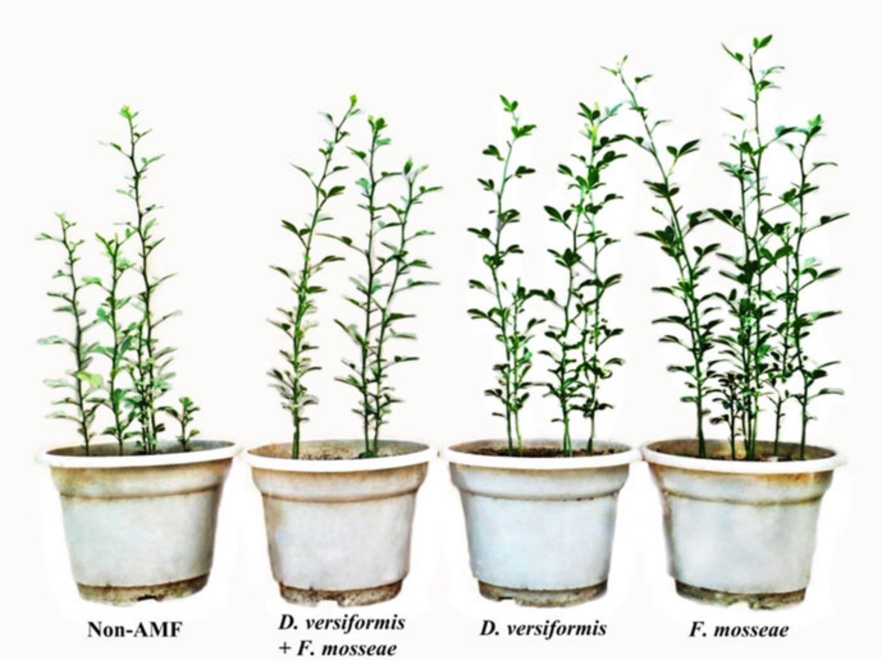

Fig. 18.2 The effect of inoculation with different AMF on growth of trifoliate orange seedlings

18.2.1 Increasing Nutrient Acquisition

It is well known that AMF-promoted growth of host plants is associated with AMF-increased nutrient acquisition. AMF is regarded as an "organ" of the nutrient absorption of plants. It has been estimated that about 75–90% P and 5–80% N in plants are contributed by AMF (Li et al. 1991; van Der Heijden et al. 2008). AMF also increases the absorption of K, Fe, Zn, Cu, and Mo from the soil to the fungal partner. Marschner and Dell (1994) estimated that mycorrhizas contributed 80% of P, 25% of N, 10% of K, 25% of Zn, and 60% of Cu, respectively. In the study of N, it was found that N species affected the absorption efficiency of AMF. The results of Tanaka and Yano (2005) indicated the nitrogen uptake of plants from $(NH_4)_2SO_4$ was ten times as much as $NaNO_3$ after inoculating with *Glomus aggregatum*. Besides, extraradical hyphae of AMF also take part in the metabolic process of N. Meanwhile, AMF can make plants assimilate more available P, leading to improved P nutrition. The study of Graham and Timmer (1985) showed that citrus mycorrhizal seedlings could take in more P nutrition from insoluble P fertilizer after applying soluble and insoluble P fertilizer into citrus mycorrhizal seedlings severally. Mycorrhiza-promoted P acquisition is related to plant status. For example, irrespective of inoculation with *Glomus mosseae* to citrus seedlings, there was no significant difference between P level in shoot and root of mycorrhizal seedlings versus non-mycorrhizal seedlings due to narrow phloem (Koch and Johnson 1984).

Furthermore, AMF can form enormous extraradical hyphae networks, extending to 11.7 cm from the root and thus expanding the nutrient uptake range (Effendy and Wijayani 2008). In addition, the transmission rate of soil nutrients in the mycelia network is much higher than that of the nutrient directly in the soil (Zhang et al. 2010). The hyphae bridges are established between different host plants, which increase the substance (carbohydrates, mineral nutrients, water) exchange among plants, thereby, reducing nutrient loss and accelerating nutrient cyclic utilization (Hart and Reader 2005). As a result, such enhancement of nutrient acquisition by mycorrhization is closely associated with growth improvement of host plants.

18.2.2 Enhancing Water Absorption from Soils

Mycorrhizas expanded the absorption area of the root system of the host plant, and the number and length of mycorrhizal hyphae were more than the host plant roots. Developed hyphae in the roots can form loose mycelium, whilst parts of the hyphae also invaded the root, forming a huge composite network (Simard et al. 2012; Wu et al. 2009). Studies in the past showed that the mycorrhizal hyphae and hyphal network had the functioning on absorbing and transferring water in various ecosystems. Extraradical hyphae of AMF enter into the tiny soil pores that plant roots do not pass to take in capillary water, in favor of AMF relief and lower plants wilting coefficient (Bolgiano et al. 1983). Meanwhile, Marulanda et al. (2003) argued that the efficiency of enhanced water uptake by different AMF species against lettuce (*Lactuca sativa*) is closely related to the biomass of extraradical hyphae. Levy and Krikun (1980) showed that mycorrhizas could enhance the transpiration and stomatal conductance of host plants, making the water transport more smooth and fast during water stress and normal water after inoculating *G. fasciculatus* on citrus. This suggests that mycorrhizas may provide a special water channel that reduces the transport distance and resistance of water. Allen (2006) through the analysis has found that extraradical hyphae were directly involved in water transportation; the diaphragm resistance to water flow resulted in limiting the ability of hyphae to transport water. And thus, it is estimated to be 25 cm/h, 131 nL/h, or 100 nL/h from different inference conclusion. Therefore, mycorrhizal hyphae have positive effects on water absorption of host plants irrespective of any water conditions.

AMF inoculation has an indirect influence on water metabolism of host plants under normal water condition, which have been confirmed on various plants, such as onion (Nelsen and Safir 1982), apple (Liu 1989), sunflower (Morte et al. 2000), and citrus (Wu et al. 2007). In low phosphorus soils, AMF can improve the water status of hosts by changing the physiological condition, but the similar effect does not appear in high phosphorus soils. Nelsen and Safir (1982) first reported that onion had higher leaf water potential and transpiration rate inoculated with *G. etunicatum*

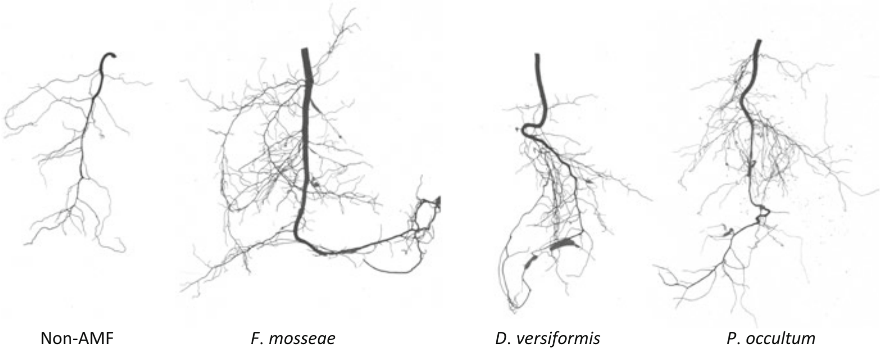

Fig. 18.3 The effect of inoculation with different AMF on root morphology of trifoliate orange seedlings

under low phosphorus soil conditions. Subsequently, Morte et al. (2000) also obtained similar results that inoculation with the AMF on sunflower significantly improved stomatal conductance of host plants and reduced stomatal resistance and natural saturation deficiencies, thereby enhancing water transport and promoting plant growth. Wu et al. (2007) also confirmed that the effects of AMF on the red tangerine seedlings under normal water and *G. mosseae* and *G. geosporum* could significantly increase transpiration rate.

18.2.3 Greater Root Morphology

AMF-promoted plant vegetative growth is related with increased root growth, which is conducive to use and store deep water in the soil for plants, thereby maintaining good water (Subrammanian and Charest 1999). In trifoliate orange seedlings, inoculation with *Glomus mosseae*, *Paraglomus occultum*, and *Glomus versiforme* significantly increased root total length, total projected area, surface area, and volume but decreased root diameter (Wu et al. 2011) (Fig. 18.3). In white clover, *Rhizoglomus intraradices*, *Diversispora versiformis*, and *Paraglomus occultum* significantly induced greater root total length, projected area, and volume (Lü and Wu 2017). The AMF effects were heavily dependent on AMF species used. Yao et al. (2009) found more fine roots and less coarse roots in AM plants. In addition, mycorrhizal colonization also increased root branches of *Vitis vinifera* (Schellenbaum et al. 1991). Greater root morphology of AM plants can ensure host plants to explore more water and nutrients, thereby, keeping a kind of greater plant growth behavior. AMF-improved root morphology is closely related with mycorrhiza-induced IAA production and mycorrhiza-regulated polyamine metabolism (Wu et al. 2012; Liu and Wu 2017)

The root–shoot ratio of inoculated AMF plants is bigger in comparison with non-AMF plants, which has an advantage in nutrient acquisition. And, AMF can change root architecture of host plants to resist the tolerance of drought (White 1992). Greater root morphology under drought stress is the critical role in enhancing water absorption of mycorrhizal plants, relative to non-mycorrhizal plants (Zou et al. 2017).

18.2.4 Regulating Phytohormone Levels

Endogenous hormones are the vital importance for plant growth. Auxin, cytokinin (CTK), gibberellic acid (GA), ethylene (ET), and abscisic acid (ABA) can regulate the growth and development of plants, control plant morphology and physiological metabolism, and also stimulate mutual recognition and mycorrhizal formation between mycorrhizal fungi and plants (Yu et al. 2009). The effects of *Gigaspora rosea*, *Glomus mosseae*, and *Glomus versghrme* on endogenous hormones in maize and cotton plants were studied by Liu et al. (1999) under the pot conditions of greenhouse. They found that AMF could significantly increase the contents of zeatin, auxin, and GA and decrease content of ABA under well-watered and drought conditions. A significantly higher putrescine (Put) and spermidine (Spd) level was found in *Citrus tangerina* seedlings inoculated with *F. mosseae* (Wu et al. 2012). As a result, with the increase of endogenous hormone levels of mycorrhizal plants, plant biomass and growth vigor were also significantly increased. Dugassa et al. (1996) found that AMF increased the contents of auxin, GA, ethylene, CTK, and ABA in stems and leaves. Moreover, Barea and Azcón-Aguilar (1982) had proven that hyphae of AMF could produce auxin, CTK, and GA. These phytohormones may be the initiating factor of plant growth and development and stress resistance gene expression, which can regulate gene expression and protein synthesis (Yu et al. 2009). It demonstrates that mycorrhizal symbiosis can induce and modulate the phytohormone production to stimulate growth and development of host plants, as well AMF.

In addition, AMF-improved plant growth can be regulated by exogenous phytohormones. In trifoliate orange seedlings inoculated with *Glomus versiforme*, exogenous Put, Spd, and spermine (Spm) were applied into rhizosphere (Wu et al. 2010b). The results showed that Put application, but not Spd and Spm, heavily stimulated root mycorrhizal colonization and numbers of entry points, arbuscules, and vesicles, which further magnified AMF-improved plant growth and root morphology. In another study conducted by Liu et al. (2016), trifoliate orange seedlings were grown in a two-chambered root box separated by 37 μm mesh, where trifoliate orange plants were planted in root+hyphae chamber, and indole butyric acid (IBA), ABA, and JA (each at 0.1 μM concentration) were applied into hyphae chamber. The study showed that exogenous phytohormones, especially IBA, magnified the mycorrhiza-stimulated growth responses. In a word, exogenous phytohormones can stimulate greater mycorrhizal growth of host plants, thereby, further magnifying the AMF-improved growth responses.

18.2.5 Regulating Soil Physicochemical Properties

AMF can improve soil structure and contribute to maintain soil fertility, which indirectly affects plant growth (Jeffries et al. 2003; Wu et al. 2014). Glomalin, secreted by AMF, can glue small soil particles into a diameter of >0.25 mm macroaggregates, further forming the large polymers (Lovelock et al. 2004). The formation of soil aggregate is good at improving soil physical condition and increasing soil stability (Bever et al. 2001; Chaudhary et al. 2009). Long-term fields monitoring experiments showed that the soil hyphal density was positively correlated with soil aggregates and carbon–nitrogen fixation (Wilson et al. 2009; Peng et al. 2012). A potted experiment showed that AMF inoculation decreased the loss of P and NH_4^+ in the soil by 6.0% and 7.5%, respectively (Van Der Heijden 2010), which is the critical factor in maintaining greater soil nutrient status, beneficial to growth of host plants. What's more, glomalin can glue and chelate soil toxic substances to ameliorate soil toxic environments and serve as a carbon source to increase plant biomass (Rillig et al. 2002). As a result, mycorrhizal soils generally possess better soil structure and permeability and thus provide a lot of oxygen for respiration and further enhance carbon accumulation in soil. Therefore, this is no doubt that AMF has a significant effect on improving soil structure, thereby, promoting growth of host plants.

18.2.6 Greater Plant Growth Derived from Osmotic Regulation and Early Warning Under Abiotic and Biotic Stresses

Osmotic solute changes such as soluble sugar, amino acids, and glycine betaines directly affect the absorption ratio to mineral nutrients in plants (Duke et al. 1986; Feng et al. 2002; Sharifi et al. 2007). The growth of AMF consumes host carbohydrates, leading to less accumulation of low-molecular organic substances in root cells. As a result, the intracellular osmotic potential is increased, resulting in the enhanced ability of plants to fight against osmotic stress, further stimulating plant growth (Ruiz-Lozano and Azcón 1995). Mycorrhizal plants can absorb more P, Cu, and Mg and reduce the absorption of Na and Cl, thereby alleviating toxic effects on plant growth (Evelin et al. 2009; Wu et al. 2010a). Sannazzaro et al. (2006) also confirmed that inoculation with *Glomus intraradices* significantly increased the ratio of K^+/Na^+ under salt stress in leguminous (*Lotus glaber*). In addition, the ability of different AMF has different resistance to salt stress. *Glomus intraradices* isolated from plants with higher salt tolerance was more effective to alleviate salt damage in the salt-tolerant plants than in non-salt-tolerant plants, which may be due to the long-term adaptability (Estrada et al. 2013). In addition, mycorrhizal plants could induce the roots releasing more H^+ into mycorrhizosphere, as observed higher root H^+ efflux rates in *F. mosseae*-colonized trifoliate orange versus in non-AMF plants under soil salinity (Wu et al. 2013). The acidic rhizosphere caused by mycorrhiza is important to secondary active transporter of organic and inorganic nutrients, turgor regulation, and in the regulation of cell wall plasticity, as suggested in "acid-growth theory" (Wu and Zou 2013).

AMF can activate defense reactions of host plants and increase defensive enzyme activities to protect host plants escaping pathogens like viruses and bacteria, which is beneficial to plant growth under pathogens conditions. Earlier studies had shown that higher chitinase activities in the roots of mycorrhizal plants limited the growth and development of root pathogens (Gianinazzi-Pearson et al. 1996; Dumas-Gaudot et al. 1996; Elsharkawy et al. 2012). AMF reduces the harm of nematodes by altering plant root exudates, and roots secrete abundant substances to regulate growth of AM symbiosis (Buwalda et al. 1984). Inoculation with AMF can increase the production of secondary metabolites such as jasmonic acid and the metabolism of carbon and nitrogen, thereby enhancing plant resistance to fungal diseases (Li et al. 2013). In addition, mycorrhizal hyphal networks can communicate the signals of intruders like *Acyrthosiphon pisum* among different plants for early warning (Babikova et al. 2013).

18.3 No or Depressed Effects of Mycorrhiza on Plant Growth

Besides growth promotion under mycorrhization, we also occasionally found no positive effect or inhibited effect on plant growth (Fig. 18.4). Possibly, the negative effect of mycorrhiza on plant growth is not reported by researchers. In general, the negative effect of mycorrhizas occurs in high phosphorus conditions, especially

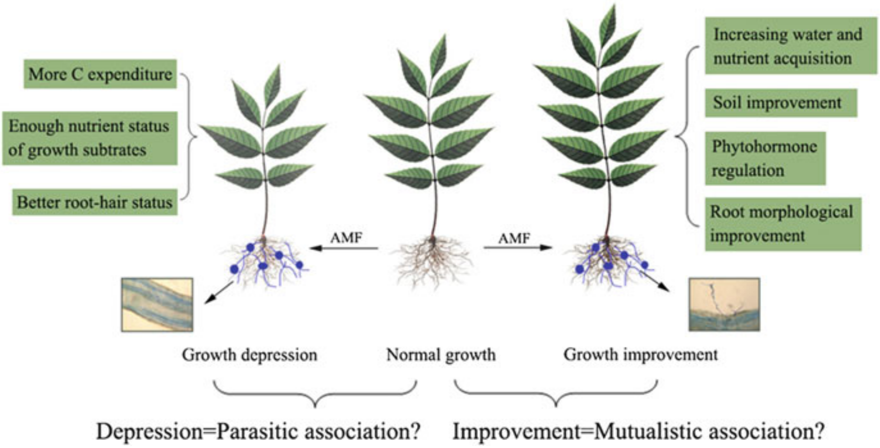

Fig. 18.4 The schematic diagram of mycorrhizal effects on growth of host plants

when photosynthate or light level is limited, such as young plants (Reynolds et al. 2005). Earlier study by Bethlenfalvay et al. (1983) showed that, in soybean grown in 0, 25, 50, 100, or 200 mg hydroxyapatite [HAP, $Ca_{10}(PO_4)_6(OH)_2$] per pot, *Glomus fasciculatum*-colonized plants showed 20, 25, and 38% growth retardation under 0, 100, and 200 mg HAP, relative to non-colonized controls. At 50 mg HAP, growth of mycorrhizal plant was significantly enhanced. The study of Peng et al. (1993) showed that lemon growth under mycorrhization was inhibited under high phosphorus supply. The growth of *C. aurantium* was inhibited by 18% with *Glomus intraradices* inoculation at high CO_2 concentrations, while at normal CO_2 concentration, the growth of *C. aurantium* was promoted by 15% under mycorrhization (Jifon et al. 2002). Studies of *Citrus tangerina* seedlings inoculated with AMF showed that *Glomus versiforme* inhibited the plant height, stem diameter, dry weight of shoots and roots, and dry weight of plants.

It is well known that 3–20% of plant photosynthates can be expended for mycorrhizal symbiosis. Hence, the improvement and inhibition of plant growth under mycorrhization is due to the competition between host plant and AM fungus for the carbon source (Buwalda and Goh 1982). Mycorrhizal plants need to consume more C sources and accumulate fatty acids in the roots, thereby increasing the root or rhizosphere respiration and reducing the contents of soluble starch in the roots. In the early stage of AMF infection, plant defense systems are activated, and fungal symbiotic consumes part of the energy. Hence, AMF and plant roots have a C competition in the process of pre-symbiosis. As reported by Buwalda and Goh (1982), total oxidizable C, soluble sugar content, and C/N ratio were lower in *Gigaspora margarita*-colonized perennial ryegrass plants, indicating a competition of mycorrhizas with the host for photosynthetically derived C, finally causing growth depression. We conclude that (1) if the expenditure of AM fungus in carbohydrates does not affect the request of host plant in carbohydrates, the establishment of AM symbiosis is mutualistic association, which can stimulate growth performance of host plants and (2) if the C expenditure of AM fungus affects the normal C request of host plants, AM presence may be a parasitic association.

In addition to the C competition between host plants and AM fungus, nutrient status of growth substrates heavily regulates the shift of mutualistic association and parasitic association. As reported by Peng et al. (1993), growth of lemon under mycorrhization was inhibited under high P supply. Similarly, at high CO_2 concentrations, growth of *C. aurantium* was depressed by inoculation with *Glomus intraradices* (Jifon et al. 2002). Possibly, the host plant roots can absorb enough P from growth substrates and do not request AMF functioning on nutrient acquisition from soils. We guess that (1) if growth substrates have adequate soil fertility to fulfil the request of roots, AM functioning will be weak in nutrient acquisition, resulting in no or depressed effects on growth of host plants and (2) if growth substrates have deficient soil fertility and do not fulfil the request of roots, AM functioning will be strengthened in nutrient acquisition, resulting in growth improvement of host plants.

Mycorrhizal hyphae and root hairs of host plants collectively absorb soil nutrients at the root surface (Wu et al. 2016a). In a general rule, the plant species with abundant root hairs are less dependent on mycorrhizal symbiosis for nutrient acquisition (Itoh and Barber 1983). As proposed by Baylis (1975), root hair length and abundance may indicate the degree of mycorrhizal dependence and mycorrhizal responses. Plants with few root hairs are strongly mycorrhiza-dependent, while those with a huge number of root hairs are less dependent on mycorrhizal symbioses (Novero et al. 2008). Typically non-mycorrhizal plants, including rushes, sedges, and grasses, have highly developed root hairs (Hetrick et al. 1988). It concludes that plants with high mycorrhizal dependence and less root hairs have strongly positive responses to mycorrhization, and plants with low mycorrhizal dependence and abundant root hairs have weak responses to mycorrhization.

18.4 Conclusion and Future Prospects

In general, AMF has improved effects on the growth of host plants, which is related to the promotion of water and nutrition absorption, improvement of endogenous hormone levels, enhancement of stressed tolerance, improvement of soil physico-chemical properties, and root morphological modification (Fig. 18.4). Occasionally, AMF represents no or depressed effects on plant growth, which is associated with C expenditure, nutrient status of growth substrates, and root hair status. Essentially, AMF effects on plant growth that is involved in mutualistic or parasitic association (Fig. 18.4). Future prospects in several fields are needed to keep a watchful eye:

1. The relevant mechanisms of mycorrhiza-improved plant growth at the molecular level need to be studied.
2. The critical value of AMF-promoted/inhibited plant growth about the soil fertility level should be clear and definite.
3. Transition between mutualistic and parasitic association will be paid attention to mycorrhizal works.
4. Expect the emergence of negative reports in the literature, and also keep a watchful eye on the underlying mechanisms of AMF-induced negative effects on plant growth.

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