

Chapter 1

Mycorrhizae Resource Allocation in Root Development and Root Morphology



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Abstract Plant root systems are influenced by genetics and environmental conditions which are leading to varied root system architectures. Different plant species have diverse root system architectures, and mineral nutrient availability is mainly determined by the root system. Also, the availability of mineral nutrient uptake is played by the role of mycorrhizal fungi. In this chapter, the role of plant root development, root architecture, and mycorrhizal inoculation on mineral nutrition was reviewed. The root development, mainly the physiological, morphological, and molecular responses of plant roots to diverse nutrient uptake in assistance to the mycorrhizal fungi, is one of the hot research areas for plant scientists and plant nutritionists. Keeping in mind the importance of this subject, the present chapter is compiled which covers the importance of nutrient uptake in plant growth and development. Moreover, the importance of roots in nutrient uptake and establishing the symbiotic relationship is essential. Underground relations are set up by the plant roots in coordination with different soil microorganisms. Arbuscular mycorrhizal fungi (AMF) as a major soil organism participate in symbiotic relationship and facilitate the plant in growth and root development. Moreover, it shapes the plant roots for the better cooperation with AMF in nutrient and water uptake facilitation. It may change the root morphology, physiology, and molecular behavior which may vary plant to plant.

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1.1 Introduction: Plant Nutrients and Their Requirements

Each plant species has its own root systems. Plant roots are the main source for nutrient uptake. The plant root systems are the basic nutrient absorbing area of the plants. At the same time, plant roots can alter their close environment (in the root-soil interface), called the rhizosphere, by absorbing nutrients and liberating exudate (Shrivastava et al. 2014). This limited area around the root surface (0–20 mm region) is biologically active. The rhizosphere dynamics of any plants, namely, the rhizosphere physics, chemistry, and biology, are completely different than the bulk soil (Marschner 2012; Ortaş 1997). Each plant species root structure and rhizosphere differed significantly on plant nutrition acquisition systems. In addition, plant roots develop symbiotic relationship with mycorrhizae fungi and rhizospheric bacteria to improve nutrients uptake (Barea et al. 2005). Nutrient and water uptake, root respiration, root exudate, and pH changes (either increases or decreases) can occur at this thin soil layer.

Mainly most of the plant nutrient uptake mechanisms recently in the late 1970s were recognized by plant and soil chemistry scientists. During 1900 most of the nutrient elements were determined to be special (Epstein 1997; Marschner 1996). All plant species need to have essential plant nutrients. The essentiality was proposed to consider an element as “essential” when it accomplishes three basic principles: (1) in its absence, plants must be incapable of continuing normal growth, (2) its biological functions cannot be carried out by any other element, and (3) it must be directly involved in plant metabolism. Reports of diverse research groups in the early 1970s perfectly illustrated the rhizospheric processes to understand the effects of nutrient availability in root system development. Marschner’s group since the early 1970s clarified several nutrient uptake mechanisms by root and mycorrhizal fungi (Marschner 2012). However, some nutrients which are less mobile in soil, such as P, K, Zn, Cu, Fe, and $\text{NH}_4\text{-N}$, are more efficiently taken up (Smith and Read 2010).

1.2 Effect of Nutrient Availability in Root System Development

The evolution of root systems such as root branching, root hair development, and mycorrhizal symbiosis with root processes is still under evaluation process. According to Hemsley and Poole (2004), evolution of root system is a notable process that has led to a progressive transformation from the very simple root systems of early land plants to the diverse and complex root systems of the modern plants. Cruz-Ramirez et al. (2009) indicated the ancient plants did not have to face obstacles to acquire water and obtain nutrients efficiently under moist climatic conditions. In drier environments, the plant root system was developed, availability of nutrients increased, and roots become a vigorous anchor for the establishment in

soils with diverse physical and chemical characteristics. Dicotyledonous and monocotyledonous plants have a diverse root system development, and their nutrient and water uptake are determined by root systems. In fibrous root systems, most stem-borne roots develop underground, but in some species, such as maize (*Zea mays*) (Cruz-Ramirez et al. 2009) and sorghum, roots are produced from aboveground structures. Generally, aboveground roots are called aerial roots. It has been reported by Hochholdinger et al. (2004) that prop roots stabilize the main stem and are also capable of branching and taking up mineral nutrients and water.

Lynch (1995) indicated that plant root geometry and morphology are very important for maximizing nutrient uptake because root systems that have higher ratios of surface area to the volume will more effectively explore a larger volume of soil. Several root parameters such as root length, root diameter, root surface area, and root hair density are important for enhanced nutrient uptake by plants. Consequently, changes that arbuscular mycorrhizal fungi (AMF) bring about on root morphology, such as root branching and root elongation, could constitute an additional mechanism by which the fungi enhance P uptake. Adaptive changes of root growth and architecture under P starvation are related to altered carbohydrate distribution between root and shoot, and these changes may be caused by plant hormones (Nacry et al. 2005; Neumann et al. 1999), sugar signaling (Karthikeyan et al. 2007; Vance 2010), and nitric oxide in the case of cluster-root formation in white lupin (Wang et al. 2010).

When soil nutrient concentration is low, root systems of some plant species expanded the capacity by branching thorough this way roots interact with soil organisms and explore the soil. Especially in a low amount of P availability, plant species changed their root branching patterns. Some non-mycorrhizal plants, for example, *Lupinus albus*, a legume plant have special root systems such as cluster roots have a high capacity to uptake P from soil (Marschner et al. 1986; Neumann and Martinoia 2002). The plant species do not establish symbiosis with mycorrhizae in order to get sufficient orthophosphate (Pi) uptake, although their root hairs can contribute with up to 80% of the surface area of the root (Jungk 2001).

Plant root epidermal cells including root hairs (the direct pathway) uptake Pi by leads to lowering of Pi concentrations in the rhizosphere which is called depletion zone. Usually, Pi depletion replacement does not easily keep pace with uptake (Fig. 1.1) (Smith et al. 2011). Plant roots and mycorrhizal fungi that take up P as negatively charged Pi ion (H_2PO_4^-) forms (Smith et al. 2011) indicated that P depletion poses an additional problem because the concentration in plant cells is about 1000-fold higher than in the soil solution and the cell membrane has an inside-negative electric potential. According to Bucher (2007) in this case, Pi uptake requires metabolic energy and involves high-affinity transporter proteins in the *Phl1* family. Marschner (1995) indicated that plants had evolved a range of strategies that increase either Pi uptake capacity or availability of Pi in the rhizospheric soil. The most common of these strategies exist for mycorrhizal symbiosis. Some plant species which don't have mycorrhizal symbiosis can produce of dense "cluster roots" that produce organic anions which release Pi from poorly available inorganic

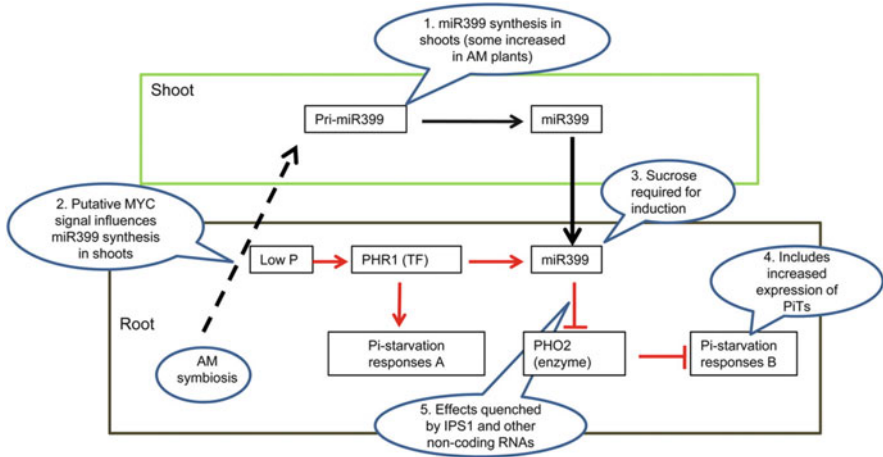


Fig. 1.1 Possible signaling events in AM roots based on studies of Pi starvation in non-mycorrhizal plants and miR399 expression in AM medic. In NM plants, low P increases the activity of the transcription factor (TF) PHR1, which binds to the P1BS element in promoters of several Pi starvation-induced genes (A) and increases their expression. PHR1 also increases the expression of miR399s. miR399s are probably largely synthesized in shoots, where they accumulate more in AM than in NM plants (callout 1); this implies the transfer of (unknown) MYC signals from root to shoot in AM plants (callout 2). miR399s are transferred from shoots to roots. Accumulation in roots is influenced by PHR1 and by such transport from shoots (callout 3). High miR399 levels under low P reduce the activity of the enzyme encoded by PHO2 and hence increase PHO2-dependent Pi-starvation responses, including increased expression of PiTs (callout 4). Effects of miR399s in reducing PHO2 activity can be quenched by noncoding RNAs such as IPS1 (callout 5). PHO2 might then inhibit Pi-starvation responses and reduce the expression of PiTs [modified from Branscheid et al. (2010)]

forms, but these are much less common (Cheng et al. 2011; Lambers et al. 2008, 2010).

Lambers et al. (2008) indicated that in many cases cluster-root formation might be an alternative strategy to AM formation. Phosphorus is involved in several biochemical mechanisms such as the formation of cell membranes, carbohydrate metabolism, protein synthesis, photosynthesis, respiration sugar metabolism, energy storage, and transfer. Schachtman et al. (1998) indicated that since P is a component of key molecules such as nucleic acids, phospholipids, and ATP, consequently, plants cannot grow without a reliable supply of this nutrient. Soil P concentration may be large; however, most of it is not available or less mobile because of the very low solubility of phosphates of iron, ammonium, and calcium, leading the soil solution P concentration of 10 μm or less (Schachtman et al. 1998). The AM hyphae extend plant root system's capacity to explore more nutrient and water in the soil to cope the stress situations (Fig. 1.2) (Manoharan et al. 2010).

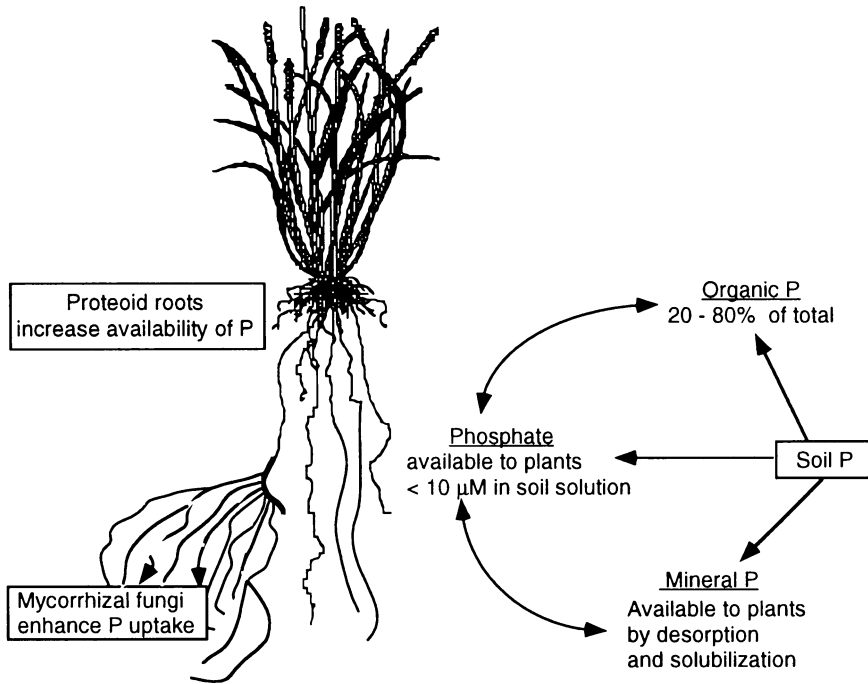


Fig. 1.2 Proteoid roots increase the availability of P. Mycorrhizal fungi enhance P uptake

1.3 Mycorrhizas Alter Root Architecture System

Smith and De Smet (2012) postulated that plant roots involve several varieties of biological processes, such as nutrient uptake, nutrient storage, and mechanical support. In general, root system architecture (RSA) of plants is very dependent on plant species and soil environment (Giri et al. 2018). Root growth is controlled genetically, but it is also influenced by environmental factors (Fageria and Moreira 2011) such as soil quality, mineral nutrient, and soil management. Most tree plants species have short and rare root hairs, and such kinds of plants are dependent on AM colonization. Wu et al. (2010) reported that root architectural alteration in the AM-colonized citrus plant could increase root functioning to explore more water and nutrients under stress conditions. AM mycelia constitute of morphologically different types of hyphae. Relatively coarse and thick-walled hyphae with a diameter between 5 and 20 μm appear to function mainly in nutrient transport and extension of the fungal colony. In general, when plants have a low root-shoot biomass ratio, slow root growth rates, and/or poor root hair development, plant roots demand mycorrhizal symbiosis. If a high amount of total soil P is poorly available, plant demands from mycorrhizal symbiosis and in that case mycorrhizal symbiotic plants uptake more P and grow over the non-mycorrhizal plant (Bolan 1991). Mycorrhizal fungi

are important through the following mechanisms in the rehabilitation of decertified ecosystems (Khan et al. 2017; Sharma et al. 2017; Teotia et al. 2017):

- Enhancing establishment and growth of plants by increasing nutrient uptake
- Contributing to the efficient recycling of nutrients and thus to long-term stability
- Stabilizing the soil structure and quality. Since mycorrhizae fungi:
 - Can access greater soil volume
 - Can break molecules down into usable forms
 - Can turn inorganic phosphorus and nitrogen into forms usable by plants

Mycorrhizae also play a key role in soil aggregate formation, and aggregates can keep carbon in soil (Prasad et al. 2017). Recent research suggests that mycorrhizal fungi might be an important component of the soil organic carbon (SOC) pool, in addition to facilitating carbon sequestration by stabilizing soil aggregates. In an ecosystem, the flow of carbon to the soil-mediated by mycorrhizae serves several important functions such as getting nutrients and water from the soil. Measurements of plant carbon allocation to mycorrhizal fungi have been estimated to be 5–20% of total plant carbon uptake (Pearson and Jakobsen 1993), and in some ecosystems, the biomass of mycorrhizal fungi can be comparable to the biomass of fine roots.

The association of roots with AMF is a very widespread strategy by which plants facilitate their acquisition of mineral elements from the soil (Marschner 1995). In addition to element uptake via mycorrhizal mycelia, AMF has also been shown to affect root morphology and functioning, as well as mycorrhizosphere soil properties. This may lead to indirect effects of the AM association on plant nutrient availability and uptake (Smith and Read 2010). With their thin diameter, 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 like plant root systems, AM hyphae seem to differ considerably in their architecture and physiological activities depending on their genotype. Mycorrhizal hyphae length is also controlled by nutrient level mainly by soil phosphorus levels.

1.4 Mycorrhizae Role on Nutrient Uptake

Mycorrhizal symbioses can increase the spatial availability of P, extending the nutrient absorptive surface by formation of mycorrhizal hyphae. In the symbioses, nutrients are transferred by AMF via their extensive mycorrhizal mycelium to plants, while in return the fungi receive carbon from the plant. The AMF not only influence plant growth through increased uptake of nutrients (P, Zn, and Cu) but may also have no nutritional effects in terms of stabilization of soil aggregates and alleviation of plant stresses caused by biotic and abiotic factors (Smith and Read 2010) .

A primary benefit of AMF is the improved P uptake conferred on symbiotic plants. In low-P soils, mycorrhizal plants usually grow better than non-mycorrhizal plants as a consequence of enhanced direct P uptake of plant roots via the AM

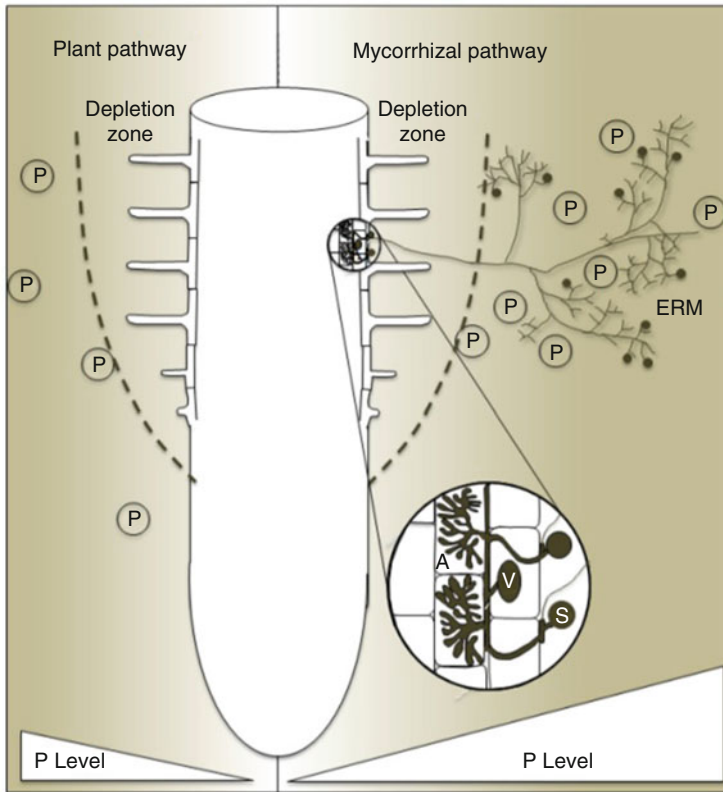


Fig. 1.3 Mycorrhizal effect on nutrient uptake and phosphorus depletion (Bucher 2007; Bücking and Kafle 2015)

pathway. However, plant growth can be suppressed even though the AM pathway contributes greatly to plant P uptake (Smith and Read 2010). The growth inhibitions might be caused by the downregulation of the direct root P uptake pathway. Recent gene expression study (Feddermann et al. 2010) shows that plants induce a common set of mycorrhiza-induced genes, but there is also variability, indicating that there exists functional diversity in AM symbioses. The differential expression of symbiosis-associated genes among different AM associations is related to the fungal species, plant genotypes, and environmental factors. Therefore, regulation of direct uptake pathways through the epidermis, root hairs, and AM pathways require further investigation (Fig. 1.3) (Bucher 2007; Smith et al. 2010). In the case of mycorrhizae, the area exploited more volume of soil as well. As the plants get more mycorrhizal colonization in roots, it will facilitate in nutrients acquisition and reduced chemical fertilizer requirement (Varma et al. 2017).

Rouphael et al. (2015) reported that AMF symbiosis could induce changes in secondary plant metabolism leading to the enhanced biosynthesis of phytochemicals with health-promoting properties. It has been reported that AMF can secrete

phosphatases to hydrolyze phosphate from organic P compounds (Koide and Kabir 2000; Marschner 2011), thus improving crop productivity under low input conditions (Smith et al. 2011).

The extraradical hyphae of the AMF are also important to increase the uptake of ammonium, immobile micronutrients such as Cu and Zn, and other soil-derived mineral cations (K^+ , Ca^{2+} , Mg^{2+} , and Fe^{3+}) (Smith and Read 2010). The absences of AMF differ in the total amount of external hyphae length which is the main power for more nutrient uptake. The magnitude of plant growth enhancing effects varies with the nutrient's status of the soil. At the same time, plant rhizosphere mechanisms such as mycorrhizae help the plant to get a high quantity of nutrient mainly P. In most plants, P requirements for growth in the soil are controlled by the mycorrhizal dependences. Also, plant species mycorrhizal dependence can vary with available soil P concentration (Hetrick et al. 1996). The AMF itself cannot stimulate plant growth on very P-deficient soils. Mycorrhizae can utilize soil nutrient efficiently. The AMF affect plant growth only via an increased nutrient supply under well-inoculated conditions. Li et al. (1991) reported that in the non-mycorrhizal plants, the depletion of $NaHCO_3$ -extractable P extended about 1 cm into the outer compartment, but in the mycorrhizal plants, a uniform P depletion zone extended up to 11.7 cm (the length of the hyphae compartment) from the root surface. Also in the same experiment, they found that in the outer compartment, the mycorrhizal hyphae length density was high ($2.5\text{--}7\text{ m cm}^{-3}$ soil) at the various distances (0–11.7 cm) from the root surface (Li et al. 1991). The uptake rate of P by mycorrhizal hyphae was in the range of $3.3\text{--}4.3 \times 10^{-15}\text{ mol s}^{-1}\text{ cm}^{-1}$. Recovery of P is low as it is less mobile mineral which moves mainly by diffusion. Since the rate of diffusion of P is very slow (10^{-12} to $10^{-15}\text{ m}^2\text{ s}^{-1}$), high plant uptake rates create a zone around the root that is depleted of P (Schachtman et al. 1998).

The external hyphae of AM fungi extend well beyond the depletion zone, accessing supplies of nutrient at a distance and in narrow soil pores. Since the hyphae develop around the root distributed beyond the root area, nutrient uptake is high, and the nutrient depletion zone is expanded. When nutrients are removed from the soil solution more rapidly, a nutrient depletion zone develops and that nutrient can be replaced by diffusion (Li et al. 1997). For a poorly mobile ion such as phosphate and potassium, a sharp and narrow depletion zone develops close to the root. AMF can secrete phosphatases to hydrolyze phosphate from organic P compounds (Koide and Kabir 2000; Marschner 2012) and thus improve crop productivity under low input conditions (i.e., phosphorus deficiency) (Smith and Smith 2011). Douds and Millner (1999) indicated that the extraradical hyphae of the AMF could develop up to 8 cm beyond the root-growing zone and act as extensions of the root system in acquiring nutrients from the soil. The extent of depletion zone makes AM-inoculated plant grows better than a non-mycorrhizal plant. These differences depend on the plant root system, including numbers and extent of root hairs.

1.5 Horticultural Plants Root Development and Mycorrhizae

With the current state of soil technology, inoculation is most feasible for transplanted crops and in areas where soil disturbance has greatly reduced the native inoculum potential. The especially pro-inoculated seedling can get benefit from mycorrhiza to penetrate root and hyphae in the soil. Although for citrus seedling changes in the management of the soil-plant system can be sufficient to optimize the mycorrhizal symbiosis, in horticulture the inoculation of seedlings prior to transplant has given the best results (Ortas 2012).

Roots are surrounded by a matrix of soil organisms, in addition to mycorrhizal fungi, that might influence root function and survivorship in complex ways. The effects of global atmospheric and climatic change on roots might be profound, but are difficult to predict. Some of the expected effects of global change on roots will be mediated indirectly through changes in shoot physiology. Increased C gain under elevated CO₂ might increase root length density, promote shallower root systems by stimulating lateral root production over primary root elongation, increase mycorrhizal colonization, and decrease tissue N concentrations, while at the same time, whole-plant nutrient acquisition is increasing (Pritchard and Rogers 2000; Rogers et al. 1999; Tingey et al. 2000).

Plants are able to respond to P starvation by changing their root architecture, including root morphology, topology, and distribution patterns. Increases in root/shoot ratio, root branching, root elongation, root topsoil foraging, and root hairs are commonly observed in P-deficient plants, while the formation of specialized roots such as cluster roots occurs in a limited number of species (Lynch 1995; Vance 2010). P deficiency has been shown to reduce the growth of primary roots and enhance length and density of root hairs and lateral roots in many plant species (Desnos 2008; López-Bucio et al. 2003). Some plant species, for example, white lupin (*Lupinus albus*), can develop cluster roots with dense and determinative lateral roots, which are covered by a large number of root hairs (Lambers et al. 2006; Vance 2010). Therefore, root architecture plays an important role in maximizing P acquisition because root systems with the higher surface area are able to explore a given volume of soil more effectively (Lynch 1995).

Mycorrhizal fungi using external hypha changed root morphology, increased root absorption, and transport of nutrients to roots (Kungu et al. 2008). The results of Hoshyar et al. (2017) showed that sweet cherry rootstock plantlets inoculated with *Diversispora epigaea* gave the highest leaf area, root diameter, root surface, and phosphorus concentration. The work of Wu et al. (2017b) showed that mycorrhizal species are significantly affecting root morphology (Fig. 1.4).

Biopriming of micropropagated plantlets (horticultural) with AMF helps in the development of a superior and stronger root system (Ponton et al. 1990) by increasing the rooting intensity and surface area of existing roots (Puthur et al. 1998). Colonization of a plant root by AMF can alter the morphology of a root system in a structural, spatial, quantitative, and temporal manner (Atkinson 1992; Atkinson et al.

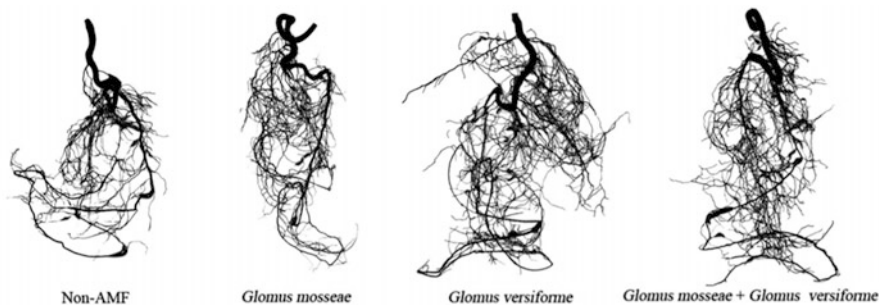


Fig. 1.4 Root system morphology of trifoliolate orange (*Poncirus trifoliata*) infected by *Glomus mosseae*, *G. versiforme*, a mixture of *G. mosseae* and *G. versiforme*, and non-AMF (Wu et al. 2017a)

1994; Berta et al. 1993; Norman et al. 1996). The AMF-colonized roots are highly branched, i.e., the root system contains shorter, more branched, adventitious roots of larger diameters and lower specific root lengths (Atkinson et al. 1994; Berta et al. 1993). As a direct consequence, mycorrhizal inoculation stimulates rooting and growth and thereby transplant survival of cuttings and seedlings raised in the nutrient media.

1.5.1 Potato

Potato relies heavily on fertilizer input (Davies et al. 2005) and responds well to mycorrhizal symbiosis. In addition, the potato is a globally plated crop in a wide range of habitats and climate condition. Several reports in controlled environments and field inoculation trials have shown that mycorrhizal inoculants benefit potato production. The first successful study on field inoculation has been reported by Black and Tinker (1977), followed by numerous studies using different potato cultivars and different mycorrhizal inoculants (reviewed by Wu et al. 2013). The results of these studies depended on potato cultivars, inoculants used, phosphorus concentrations, amendment, and tuber size category of interest (Douds Jr et al. 2007). Overall, trial inoculation studies resulted in higher yields and larger tubers than treatments using conventional chemical fertilizers (Douds Jr et al. 2007; Wu et al. 2013; Upadhyaya et al. 2013).

Hijri (2016) analyzed the data set containing 231 field trials conducted by farmers over a 4-year period in Europe and northeast America through an incentive program that was set up by the inoculant industry in 2011 to promote the application of mycorrhizal-based inoculants in agriculture. This data set was unique, in that farmers themselves performed the experiments using their conventional practices under authentic field conditions. In contrast to experiments that are conducted in greenhouses and controlled field trials with many replicates and randomized blocks, the

experimental design of this study was simplified in order to encourage farmer involvement. There are no replicates per field trial, but this is compensated by the large sample size. The inoculant used in the present study contains a single strain of one AMF species, *R. irregularis* (synonym *G. irregulare*) DAOM 197198, which exhibits substantial plasticity and an ability to adapt to different environmental conditions. However, *R. irregularis* DAOM 197198 may still be limited to specific agricultural environments, particularly in P-rich soils and under highly stressful conditions. The host plant can influence AM fungal community composition directly, by regulating carbon allocation to roots, by producing secondary metabolites, or by changing the soil environment.

Different mycorrhizal fungi used in the horticultural plants are listed in Table 1.1.

1.6 Role of Mycorrhizae on Field Crops (Mainly Cereal Crop) Root Morphology and Growth

Cereals plants such as maize, wheat, and rice are the main food supply for the majority of world population. Nearly 40% of daily food intake are from cereals. Cereal seed nutrient concentration is very important. It is well known that plant species nutrient acquisition capacity depends on soil and ecological conditions. So, plant root capacity and relation with mycorrhizal fungi are important for sufficient nutrient uptake from soils. It is known that cereal plant has very extensive root systems and long root hairs have high natural ability to take up nutrients from the soil. Mycorrhiza also has a positive effect on various cereal crop root morphologies as well. However, the effect of mycorrhizae on several cereal crops varies from plant to plant. Here, we discussed the effect of mycorrhizae on maize, wheat, and rice plant root morphology.

1.6.1 Maize

During different stages of root development, maize root system consists of different root types (Hochholdinger 2009). In crop species, such as maize, Pi starvation significantly affects the total root length of both primary and lateral roots (He et al. 2003).

Maize is well known as a host plant for spore propagation. There are several maize genotypes, and the genotypes are significantly different in terms of nutrient efficiency through root development. Also, maize plant gives a high response to mycorrhizal inoculation as well. Ortas and Akpınar (2011) showed that several maize genotypes and mycorrhizal inoculation have a diverse response to plant root growth (Fig. 1.5). Compared to the non-inoculated ones, root dry weight tended to be higher with mycorrhizal inoculation.

Table 1.1 Some examples of successful applications of mycorrhization in micropropagation

Name of the plant species	AMF species	References
<i>Actinidia deliciosa</i> (kiwi)	<i>Glomus</i> sp. strain E3	Schubert et al. (1992)
<i>Allium cepa</i>	<i>Gigaspora rosea</i> , <i>Glomus mosseae</i>	Rancillac et al. (1996)
<i>Annona cherimoya</i>	<i>G. deserticola</i>	Azcon-Aguilar et al. (1996)
Apple and peach rootstocks	<i>Glomus</i> sp. strain A6	Sbrana et al. (1992)
Apple (M9, M26, Golden)	<i>G. fasciculatum</i> , <i>G. mosseae</i> , <i>G. intraradices</i>	Branzanti et al. (1992)
Banana cv. Grade Naine	<i>G. manihotis</i>	Rodríguez-Romero et al. (2005)
Banana dwarf cavendish	<i>Glomus caledonium</i> and <i>G. macrocarpum</i>	Ortas et al. (2017)
<i>Capsicum annuum</i> L. (Chile ancho pepper) cv. San Luis	<i>G. albidum</i> , <i>G. claroides</i> , <i>G. diaphanum</i>	Estrada-Luna and Davies (2003)
<i>Citrus limon</i> L. Burm. “Zagara Bianca”	<i>G. mosseae</i> (BEG 116), <i>Glomus</i> sp.	Quatrini et al. (2003)
Crab apple cv. Marjatta	<i>G. claroideum</i> , <i>G. fistulosum</i>	Uosukainen and Vestberg (1997)
<i>Diospyros kaki</i> “Rajo”	<i>G. intraradices</i> , <i>G. mosseae</i>	Marin et al. (2003)
<i>Fragaria vesca</i> (strawberry)	<i>G. fistulosum</i>	Cassells et al. (1996)
<i>Fragaria X ananassa</i> cv. Elvira G. clarum	<i>G. etunicatum</i> , <i>G. intraradices</i> , <i>Gi. rosea</i> , <i>Gi. gigantea</i> , <i>G. margarita</i> , <i>Scutellospora calospora</i> , <i>S. heterogama</i> , <i>S. persica</i>	Taylor and Harrier (2001)
<i>Juglans regia</i> (Walnut)	<i>G. mosseae</i> , <i>G. intraradices</i>	Dolcet-Sanjuan et al. (1996)
<i>Musa</i> spp. cv. Pacovan <i>Acaulospora scrobiculata</i>	<i>G. clarum</i> , <i>G. etunicatum</i>	Yao et al. (2002)
<i>Musa</i> spp. cv. Grande Naine	<i>G. proliferum</i> , <i>G. versiforme</i> , <i>G. intraradices</i>	Jaizme-Vega et al. (2003)
<i>Musa</i> spp. cv. Grande Naine	<i>G. intraradices</i>	Declerck et al. (2002)
<i>Persea americana</i> (avocado)	<i>G. fasciculatum</i>	Vidal et al. (1992)
<i>Persea americana</i>	<i>G. deserticola</i> , <i>G. mosseae</i>	Azcón-Aguilar et al. (1992)
Potato cv. Goldrush	<i>G. etunicatum</i>	Yao et al. (2002)
<i>Prunus avium</i> , <i>Syringa japonica</i>	<i>G. aggregatum</i> , <i>G. deserticola</i>	Arines and Ballester (1992)
<i>Phoenix dactylifera</i>	<i>G. fasciculatum</i> , <i>G. intraradices</i> (LPA8), <i>Glomus isolate</i> (LPA21)	Bouhired et al. (1992)
<i>Pyrus communis</i>	<i>Glomus</i> sp.	Rapparini et al. (1996)

(continued)

Table 1.1 (continued)

Name of the plant species	AMF species	References
<i>Rosa hybrida</i> L., cv. New Dawn	<i>G. intraradices</i>	Pinior et al. (2005)
<i>Vitis vinifera</i> L.	<i>G. mosseae</i> , <i>G. manihotis</i> , <i>G. deserticola</i> , <i>Gigaspora gigantea</i> , <i>Acaulospora laevis</i>	Singh et al. (2003)
<i>Vitis vinifera</i> L.	<i>G. mosseae</i> , <i>G. manihotis</i> , <i>Scutellospora heterogama</i> , <i>Gigaspora gigantea</i> , <i>Entrophospora colombiana</i> , <i>Acaulospora laevis</i> , <i>A. sorbiculata</i>	Krishna et al. (2006)

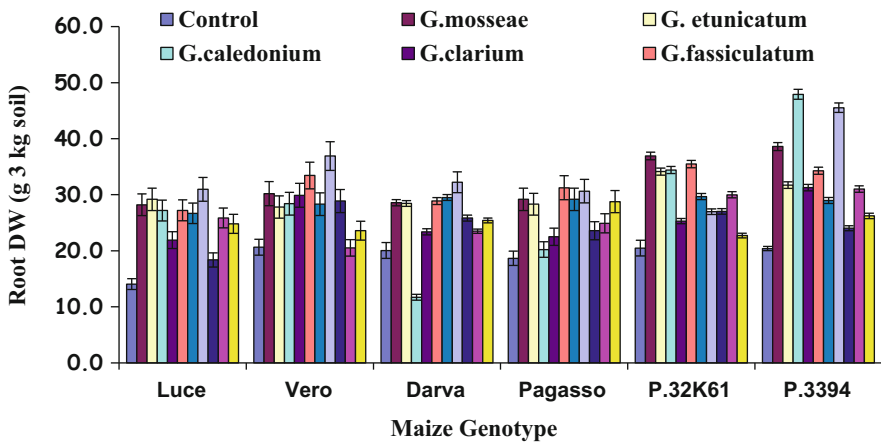


Fig. 1.5 Different maize genotypes response to different mycorrhizae species on root growth

Maize plant root development is also strongly affected by soil ecological conditions such as soil fertility, and soil microbial conditions are very important. Under sterile and non-sterile soil conditions, root attributes significantly affected maize plant growth (Table 1.2) (Ortas 2015). It has been found that under sterile soil conditions, maize plant root length is nearly twice bigger than non-sterile soil conditions. Since with soil sterilization, soil microorganisms especially mycorrhizae spore eliminated plant root growth has become greater. Also, shoot and root ratio was affected under sterile and non-sterile conditions as well. And it is well known that maize plant is responding to mycorrhiza inoculation.

Ortas (2003) reported that indigenous and exartite mycorrhizal fungi strains significantly improved plant growth in maize. In a similar work, maize plant root growth significantly enhanced with mycorrhizal inoculation and also increased with P fertilizer increases under sterile and non-sterilized treatments (Table 1.3). In non-inoculated plants, the root growth was higher in non-sterile treatments; however, in selected mycorrhizal inoculated treatments, the root growth was higher in sterile treatments than non-sterile treatments. With increasing P fertilizer application

Table 1.2 Effect of sterile and non-sterile soil treatments on maize plant parameters, phosphorus, and zinc concentration (Ortas 2015)

Soils treatments		Shoot		Root		S/R	Root length		Root colonization (%)	
		DW		DW			(m pot ⁻¹)			
		(g pot ⁻¹)		(g pot ⁻¹)						
Sultanönü	S	3.87	±0.22c	3.49	±0.27cd	1.11	102	±7c	3	±1d
	NS	3.75	±0.13c	2.96	±0.35d	1.27	60	±5c	11	±3c
Harran	S	4.75	±0.32b	4.18	±0.39ab	1.14	124	±3b	4	±1d
	NS	5.14	±0.39ab	3.74	±0.48bc	1.37	83	±11c	24	±7b
Menzilat	S	5.02	±0.46b	4.63	±0.21a	1.08	222	±12a	3	±1d
	NS	5.74	±0.47a	4.61	±0.02a	1.25	138	±22b	36	±5a

Table 1.3 Effect of mycorrhizal inoculation and P fertilizer on maize root growth under sterile and non-sterile soil conditions

Mycorrhizal species	P Application	Root dry weight (g/plant)			
		Sterile		Non-sterile	
Control	P0	1.25	±0.53ef	0.65	±1.00f
	P1	1.74	±0.60d-e	1.13	±0.52ef
	P2	2.59	±1.01a-e	2.28	±0.69a-e
<i>G. etunicatum</i>	P1	1.99	±0.41d-e	3.53	±0.40a-e
	P2	1.83	±0.93d-e	2.23	±1.87c-e
	P3	3.54	±1.25a-e	4.87	±1.30ab
<i>G. caledonium</i>	P1	2.47	±0.45a-e	4.79	±0.20a-c
	P2	3.72	±2.24a-e	5.49	±4.00a
	P3	4.15	±1.52a-d	5.78	±1.34a
<i>G. mosseae</i>	P1	1.83	±0.84d-e	3.94	±0.84a-d
	P2	3.54	±0.47a-e	4.17	±0.75a-d
	P3	3.97	±0.72a-d	4.71	±1.82a-c

P1 0, P2, 25, and P3 125 mg P₂O₅ kg⁻¹

in both sterile and non-sterile soils, the root dry weight increased. In generally *G. caledonum* inoculation significantly increased maize root growth better than other mycorrhizal species.

1.6.2 Wheat

Wheat inoculated by AMF strengthened root systems in comparison to non-inoculated plants. The AMF-inoculated wheat plant promotes optimization of root morphological characteristics than non-AMF-inoculated wheat plants. This results in longer root length, greater root surface area, smaller root average diameter, and heavier fresh and dry root weights of the wheat plant. Wheat root surface area can also be enhanced through mycorrhizal association (Marschener 1998). Root average diameter was also of great importance in the evaluation of the function of mycorrhizal symbiosis. A glasshouse pot experiment found that root length of the mycorrhizal wheat plant was $674.3 \text{ cm plant}^{-1}$, whereas non-mycorrhizal wheat plant root length was $646.8 \text{ cm plant}^{-1}$. Likewise, root surface area of the mycorrhizal wheat plant was $95.3 \text{ cm}^2 \text{ plant}^{-1}$, and the non-mycorrhizal wheat plant was $70.9 \text{ cm}^2 \text{ plant}^{-1}$ (Mohammad and Malkawi 2004). Generally, the stronger the root systems are, the smaller the average root diameter should be, which is partly due to the fibrous root system of mycorrhizae-inoculated wheat plant. Thus, AMF has the ability to increase root density of wheat plant.

Wheat spends first into root development during early growth stages and then enters into AMF biomass. The wheat plant also involved in root biomass production before photosynthetic products were used for AM fungal development and AM fungal biomass in roots (Castillo et al. 2012). More than 50% of root segments of wheat were mycorrhizal in a month after seeding. Root colonization patterns of AMF in wheat are highly variable. The root colonization of wheat by AMF is shown in Fig. 1.6. Wheat plant physiology is a major determinant of the levels of colonization.

Wheat plant roots can be classified into several categories according to their ontogenesis and functions. Two root types are distinguished in wheat—the seminal roots (also called primary roots), which develop at the scutellar and epiblast nodes of the embryonic hypocotyls of the germinating caryopsis, and adventitious roots (also called shoot-borne, nodal secondary, or crown roots), which subsequently emerge from the coleoptilar nodes at the base of the apical and tillers. The AMF-inoculated wheat roots extracted water at the fastest rate from the upper soil layers when soil water contents were higher and later extracted water primarily from deeper depths as water in the upper soil layers was depleted. The wheat root dry matter, total root length, and AM colonization were higher under well-watered condition than under dry condition.

Root characteristics and AMF infection of wheat plant influenced by phosphorus (P) supply. Wheat has an extensive root system which makes it responsive to AMF. The AMF infect the root cortex of wheat plants while producing a network of hyphae in the soil. AM symbiosis improves wheat plant growth at vegetative stages through

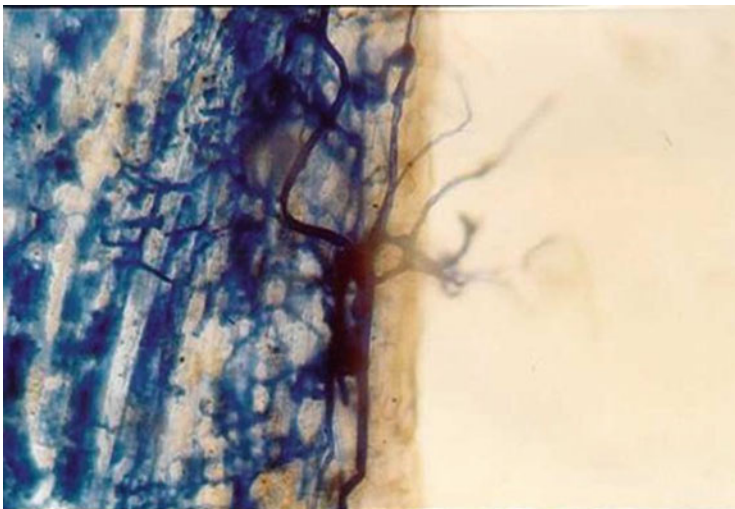


Fig. 1.6 Colonization of wheat root by AMF where mycorrhizal arbuscules and hyphae are visible (Ortas 2000 unpublished pictures)

increasing stomatal conductance, enhancing nutrient use efficiency (NUE), accumulating soluble sugar, and improving ion homeostasis (Zhu et al. 2016). Usually, roots with smaller average diameter result from a high proportion of root hairs, which help roots get into small pores in soil easier and therefore increase soil volume roots are exposed to and finally get chances to absorb more P from the soil solution. The increased absorption and utilization of P element in wheat plants then attribute to bigger root system with heavier root biomass. Mycorrhizal dependence on the symbiosis has a coarser wheat root system and develops fewer root hairs in low fertility soils. Likewise, wheat yield was increased by AMF at low P levels.

Growth rates of mycorrhizal fungi in and around roots probably play a major part in replacement of some mycorrhizal fungi by other types. Wheat varieties (Snowbird and 13Nqw1265) responded positively to the inoculation of fungi strain *R. irregularis* (DAOM240442), resulting in a significantly heavier root fresh weight as compared to non-inoculated controls. A comparison between wheat colonized by mycorrhizal strains *F. mosseae*, *F. caledonius*, and *R. irregularis* and non-mycorrhizal controls demonstrated that mycorrhiza inoculation significantly improved root dry weight. Colonization of mycorrhizal strain *R. irregularis* positively benefited wheat root development, represented by a significantly smaller root average diameter than controls and Myke-inoculated wheat. Inoculation of mycorrhizal fungus Myke, without significant differences from non-inoculated control wheat, had no obvious influence on host root average diameter. Colonization with *R. irregularis* fungus contributed to stronger root systems, as evidenced by longer roots, larger root surface area, and smaller root average diameter in *R. irregularis* wheat than in non-mycorrhizal controls. Likewise, AMF strain *R. irregularis* significantly promoted hosts' root growth and development, with longer roots than the

non-inoculated controls. Thus, the AMF has genus or even species-specific requirements for successful establishment of the symbiosis. This could be reflected in different accumulation patterns of secondary compounds in roots colonized by different AMF. A small protein, designated Myk15, was found to be strongly induced in wheat (*Triticum aestivum* L.) roots colonized by the AMF *Glomus intraradices*. This protein, which is most abundant in root fractions characterized by strong mycorrhizal colonization, has been characterized using two-dimensional polyacrylamide gel electrophoresis and microsequencing (Fester et al. 2002).

The topology analysis revealed differences in root architecture not detected by any of the other measures of root morphology. This might be due to the fact that wheat plants especially mycorrhizal plants could increase the ability to withstand adversity by delaying protein degradation and maintaining normal metabolism of proteins. In this study, the enzyme activity results showed that AM symbiosis significantly influenced these enzymes to different degrees to respond to the invasion from the environment, which might be the result of a complex interaction between the AMF and plants.

Wheat plant colonized by AMF shows to deplete soil water thoroughly than non-mycorrhizal plants. Because shoot of the wheat plant with AMF usually has larger biomass (more evaporative leaf surface area) than non-AMF wheat plants. Also, the root systems of the wheat plant with AMF inoculation often finely divided and thus have a more absorptive surface area for water and nutrient absorption. The AMF enhances the function of the wheat plant's root hairs and acts as an extension of the root systems allowing the mycorrhizal plants to explore and capture nutrients and water from a larger volume of soil compared to non-AMF plants. Mycorrhizal root colonization increase nutrients absorption, their effective utilization in stress condition, and retaining nutrients for a longer time which ultimately reduces leaching losses. Mycorrhizal wheat plants produce more root dry matter in comparison to non-mycorrhizal plants.

Mycorrhizal wheat plants maintained higher transpiration and shoot water potential than a non-mycorrhizal plant. Wheat plant leaf expansion is more severely reduced when drought affects seminal rather than nodal roots (Volkmar 1997). Wheat plant root signals enhance the fluxes of ions and growth hormones capable of regulating stomatal activity and enzyme biosynthesis, photosynthetic capacity and activity, as well as transpiration. Root tip meristematic activities initiate changes in root distribution, resulting in the synthesis of plant growth regulators, and apparently sense and signal information regarding the soil supply of water and nutrients. The AMF increased the capability of the root system to scavenge water in the drier soil, resulting in less strain to foliage and hence higher stomatal conductance and shoot water potential at particular low soil water content (Duan et al. 1996).

The hyphae of AMF penetrate roots and grow extensively between and within living cortical cells, forming a very large and dynamic interface between symbionts. Root hairs and extrametrical hyphae of vesicular-arbuscular and AMF enlarge the effective absorbing surface area considerably. Root hairs have a diameter of 0.003–0.007 mm, a length of 3–13 mm, and a normal life span of a few days. Wheat roots are usually infected by soilborne vesicular-arbuscular and AMF. The

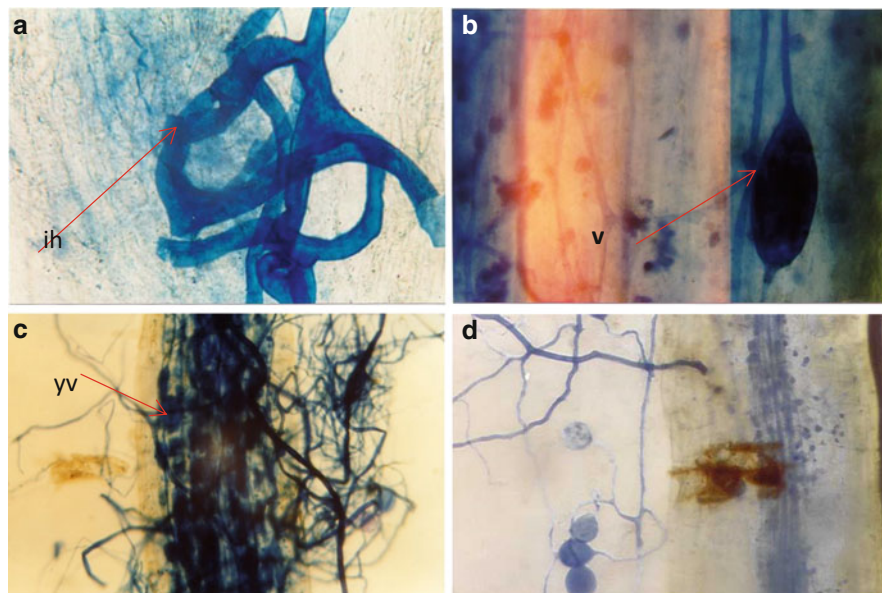


Fig. 1.7 Mycorrhizal structures in wheat roots (*Triticum aestivum*) after artificial inoculation with *G. mosseae*. Roots showed (a) intraradical intercellular hyphae (indicated by “ih” and arrow), (b) vesicles (indicated by “v” and arrow), (c) young vesicles and numerous hyphae (indicated by “yv” and arrow), and (d) segments indicated external hyphae and spores. Fungal structures were stained with trypan blue. Bars, 50 μ m (Ortas 2000 unpublished pictures)

AMF extrametrical hyphae, which also extend several centimeters away outside of the roots into the soil rhizosphere, are 5–10 times thinner than the root hairs and explore an area around the root, which exceeds the zone of nutrient depletion around uninfected roots. Mycorrhizal structures in wheat roots are shown in Fig. 1.7.

1.6.3 Rice

Rice is mostly cultivated in an anaerobic or flooded condition, where AMF inoculums are reported to decline. The occurrence of AMF colonization of rice roots under the anaerobic condition is still under debate. Anaerobic or flooded condition inhibits root colonization of rice plant due to the anoxic environment (where O_2 is completely absent). The amount of O_2 in anaerobic soil disappears a few hours after flooded condition. When the soil is flooded, water creates a barrier limiting O_2 movement into the soil. The O_2 moves slowly through the water layer and creates a thin surface layer of aerobic soil. Lack of O_2 in the flooded soil causes a shift from aerobic to anaerobic organisms. In this situation, O_2 moves through the stem and roots of water adapted plants like rice via aerenchyma tissue. Thus, the rice root system is affected by an anaerobic condition that resulted in a low percentage of

AMF root colonization. The AMF colonization of rice roots is commonly present at the early growth stages and decline with the age of the plant under anaerobic condition (Ilag et al. 1987). Continuous flooding may exert stress to the rice plant roots and disrupts the morphological and physiological functions of the plant. It decreases root surface area for mycorrhizal colonization. These root changes which become more pronounced over time may explain why in conventional flooded fields, AMF colonization in rice roots diminishes with the age of plant (Lumini et al. 2011; Solaiman and Hirata 1998).

There were several reasons involved to reduce AMF colonization of rice plant under anaerobic condition. It may be possible that due to the oxygen level by itself, the specific chemistry and microenvironment of flooded soils might cause a decrease in AMF colonization. Another reason may be that AMF cannot tolerate microaerophilic condition (Wirsel 2004). Thus, the reduction of AMF under flooded conditions is a consequence not only of a modification of root morphology but also an anatomical change, which leads to the disappearance of the cortical cells that required for intercellular hyphae and arbuscules (Vallino et al. 2014). The whole process on how AMF declines in rice plant under the anaerobic condition is shown in Fig. 1.8.

Rice plant roots form symbiotic associations with AMF under flooded or anaerobic conditions. The AM symbiosis represents the default state of most rice plant root systems and is known to modify root system architecture. This complex root architecture influences AMF colonization. In anaerobic condition, the arbuscular mycorrhizae colonization is regulated by directly influencing rice plant root architecture and anatomy but without the basic AM functionality. The effect of AMF root

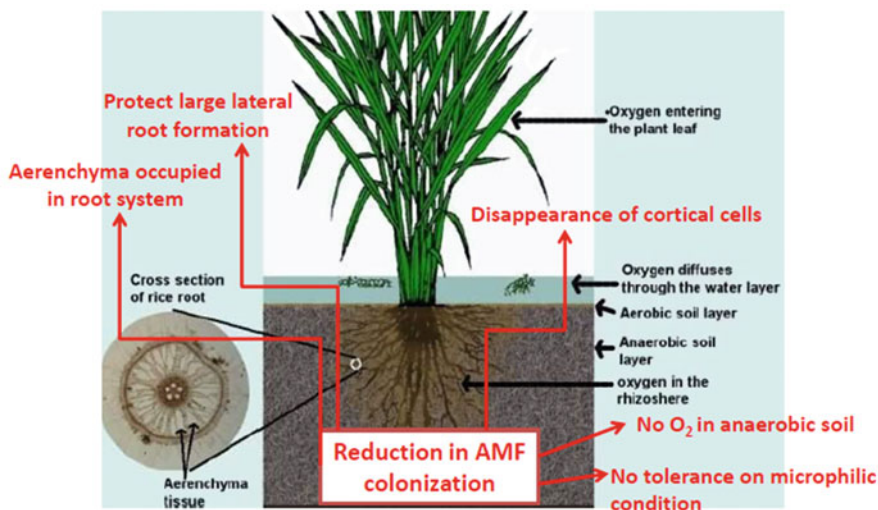


Fig. 1.8 Causes for declining in AMF colonization in rice root system under anaerobic condition

colonization on flooded rice was not symbiotic but rather parasitic under anaerobic condition. Likewise, the effect of AMF on root branching was a consequence of the presence of diffusible signals from the fungus, not of the establishment of the symbiosis (Gutjahr et al. 2009). Similarly, the AMF can grow and colonize rice roots in anaerobic soil while maintaining their signaling properties and functional capacities. The AMF is aerobic microbes, and the occurrence of AM symbiosis in anaerobic condition could be associated with the development of aerenchyma in flooded rice plant roots. The developed aerenchyma allows AMF to obtain atmospheric oxygen under anaerobic condition. It results in a dynamic alteration in the AMF community through different plant physiological changes. This is due to the increase of the aerenchyma tissues, which are not compatible with AMF development.

Rice plant has three types of roots such as (1) crown roots (CR), which emerge from the nodes on the stem and tillers; (2) large lateral roots (LLR), which originate from crown roots and shows indeterminate growth; and (3) fine lateral roots (FLR), which originate both from CR and LLR, whose growth is determinate. The AMF colonization is linked to LLR availability. The LLR has more impact on the success of AM fungal colonization. Rice plant root morphological differences were found between aerobic and anaerobic growth conditions. The branching index (BI) of the rice root apparatus was higher in aerobic condition than the anaerobic condition. The BI is the ratio between the different number of LLR to the length of CR ($BI = nLLR/cm\ CR$), which describes the degree of the root apparatus branching (Gutjahr et al. 2009). The AMF stimulates root branching that occurs from a synergic effect between the fungal presence and the positive impact of aerated soil (Maillet et al. 2011). In contrast, under anaerobic conditions, colonization detects in CR system and LLR system but is absent in the FLR system. The root colonization values are also always higher in LLR than CR under anaerobic condition. The LLR and FLR show opposite responses. The LLR support AM colonization, whereas FLR does not because gibberellic acid signaling expressed less than in FLR in comparison to LLR inhibits AM development in FLR. It is presumed that gibberellic acid has a pleiotropic effect on fine root anatomical traits and, in turn, potentially influences the symbiosis signaling pathway (Fiorilli et al. 2015). Likewise, anaerobic condition influences the root architecture leading to a decrease of the LLR and a proliferation of aerenchyma tissues. Rice root system becomes heterogeneously colonized by AM fungi, with LLR preferentially entering into the association. However, root type-specific transcriptional responses to AMF symbiosis were quantitatively more pronounced for CR despite their modest physical engagement in the interaction. Furthermore, colonized CR adopted an expression profile more related to mycorrhizal large lateral than to non-colonized crown roots despite their modest physical engagement in the interaction. Furthermore, colonized crown roots adopted an expression profile more related to mycorrhizal large lateral than to non-colonized crown roots, suggesting fundamental reprogramming of crown root character. Thus, three types of rice plant root involve AMF root colonization directly or indirectly.

1.7 Conclusion

Plant roots are the primary structure for plants which assist in nutrient and water uptake from growth media to the plants. In achieving the proper plant growth, plant roots make the association with the soil microbes such as bacteria and mycorrhizal fungi, depending on the root morphology. They vary from plant to plant, and shortcoming of nutrient and water uptake by the roots is facilitated in association with mycorrhizal fungi. AMF brings the nutrients to the plant roots through a transportation mechanism at the expense of carbon. Moreover, the symbiotic association further shapes the plant roots for a specific plant root-mycorrhizal association. Further studies on root morphology and root plasticity in mycorrhizal inoculated plants are the need of time for better understanding of resource allocation.

References

- Arines J, Ballester A (1992) Mycorrhization of micropropagated *Prunus avium* L. plantlets. Micropropagation, root regeneration, and mycorrhizas Joint meeting between COST, Dijon, France, p 45
- Atkinson D (1992) Tree root development: the role of models in understanding the consequences of arbuscular endomycorrhizal infection. *Agronomie* 12:817–820
- Atkinson D, Berta G, Hooker J (1994) Impact of mycorrhizal colonisation on root architecture, root longevity and the formation of growth regulators. In: Impact of arbuscular mycorrhizas on sustainable agriculture and natural ecosystems. Springer, Berlin
- Azcón-Aguilar C, Barcelo A, Vidal M, De La Vina G (1992) Further studies on the influence of mycorrhizae on growth and development of micropropagated avocado plants. *Agronomie* 12:837–840
- Azcon-Aguilar C, Padilla I, Encina C, Azcon R, Barea J (1996) Mycorrhizal inoculation (*Glomus deserticola*) enhances plant growth and changes root system morphology in micropropagated *Annona cherimola* Mill. Novel biotechnological approaches to plant production: from sterile root to mycorrhizosphere Joint COST meeting, Pisa, Italy, p 21
- Barea JM, Pozo MJ, Azcon R, Azcon-Aguilar C (2005) Microbial co-operation in the rhizosphere. *J Exp Bot* 56:1761–1778. <https://doi.org/10.1093/jxb/eri197>
- Berta G, Fusconi A, Trotta A (1993) VA mycorrhizal infection and the morphology and function of root systems. *Environ Exp Bot* 33:159–173
- Black R, Tinker P (1977) Interaction between effects of vesicular–arbuscular mycorrhiza and fertiliser phosphorus on yields of potatoes in the field. *Nature* 267:510–511
- Bolan N (1991) A critical review on the role of mycorrhizal fungi in the uptake of phosphorus by plants. *Plant Soil* 134:189–207
- Bouhired L, Gianinazzi S, Gianinazzi-Pearson V (1992) Influence of endomycorrhizal inoculation on the growth of *Phoenix dactylifera*. Micropropagation, root regeneration and mycorrhizas Joint meeting between Cost, Dijon, France, p 53
- Branscheid A, Sieh D, Pant BD, May P, Devers EA, Elkrog A, Schauser L, Scheible W-R, Krajinski F (2010) Expression pattern suggests a role of MiR399 in the regulation of the cellular response to local Pi increase during arbuscular mycorrhizal symbiosis. *Mol Plant-Microbe Interact* 23:915–926
- Branzanti B, Gianinazzi-Pearson V, Gianinazzi S (1992) Influence of phosphate fertilization on the growth and nutrient status of micropropagated apple infected with endomycorrhizal fungi during the weaning stage. *Agronomie* 12:841–845

- Bucher M (2007) Functional biology of plant phosphate uptake at root and mycorrhiza interfaces. *New Phytol* 173:11–26
- Bücking H, Kafle A (2015) Role of arbuscular mycorrhizal fungi in the nitrogen uptake of plants: current knowledge and research gaps. *Agronomy* 5:587
- Cassells A, Mark G, Periappuram C (1996) Establishment of arbuscular mycorrhizal fungi in autotrophic strawberry cultures in vitro. Comparison with inoculation of microplants in vivo. *Agronomie* 16:625–632
- Castillo C, Puccio F, Morales D, Borie F, Sieverding E (2012) Early arbuscular mycorrhiza colonization of wheat, barley and oats in Andosols of southern Chile. *J Soil Sci Plant Nutr* 12:511–524
- Cheng L, Bucciarelli B, Liu J, Zinn K, Miller S, Patton-Vogt J, Allan D, Shen J, Vance CP (2011) White lupin cluster root acclimation to phosphorus deficiency and root hair development involve unique glycerophosphodiester phosphodiesterases. *Plant Physiol* 156:1131–1148
- Cruz-Ramirez A, Calderon-Vazquez C, Herrera-Estrella L (2009) Effect of nutrient availability on root system development. <https://doi.org/10.1002/9781444310023.ch11>
- Davies FT, Calderón CM, Huaman Z, Gómez R (2005) Influence of a flavonoid (formononetin) on mycorrhizal activity and potato crop productivity in the highlands of Peru. *Sci Hortic* 106:318–329
- Declercq S, Risede J-M, Delvaux B (2002) Greenhouse response of micropropagated bananas inoculated with in vitro monoxenically produced arbuscular mycorrhizal fungi. *Sci Hortic* 93:301–309. [https://doi.org/10.1016/S0304-4238\(01\)00347-8](https://doi.org/10.1016/S0304-4238(01)00347-8)
- Desnos T (2008) Root branching responses to phosphate and nitrate. *Curr Opin Plant Biol* 11:82–87
- Dolcet-Sanjuan R, Claveria E, Camprubi A, Estaun V, Calvet C (1996) Micropropagation of walnut trees (*Juglans regia* L) and response to arbuscular mycorrhizal inoculation. *Agronomie* 16:639–645
- Douds DD Jr, Nagahashi G, Reider C, Hepperly PR (2007) Inoculation with arbuscular mycorrhizal fungi increases the yield of potatoes in a high P soil. *Biol Agric Hortic* 25:67–78
- Douds DD, Millner P (1999) Biodiversity of arbuscular mycorrhizal fungi in agroecosystems. *Agric Ecosyst Environ* 74:77–93. [https://doi.org/10.1016/S0167-8809\(99\)00031-6](https://doi.org/10.1016/S0167-8809(99)00031-6)
- Duan X, Neuman DS, Reiber JM, Green CD, Saxton AM, Augé RM (1996) Mycorrhizal influence on hydraulic and hormonal factors implicated in the control of stomatal conductance during drought. *J Exp Bot* 47:1541–1550
- Epstein E (1997) The science of composting. CRC Press LLC, Boca Raton, FL
- Estrada-Luna AA, Davies FT (2003) Arbuscular mycorrhizal fungi influence water relations, gas exchange, abscisic acid and growth of micropropagated chile ancho pepper (*Capsicum annum*) plantlets during acclimatization and post-acclimatization. *J Plant Physiol* 160:1073–1083
- Fageria NK, Moreira A (2011) The role of mineral nutrition on root growth of crop plants. In: Sparks DL (ed) *Advances in agronomy*, vol 110. Elsevier Academic, San Diego
- Feddermann N, Finlay R, Boller T, Elfstrand M (2010) Functional diversity in arbuscular mycorrhiza—the role of gene expression, phosphorous nutrition and symbiotic efficiency. *Fungal Ecol* 3:1–8
- Fester T, Kiess M, Strack D (2002) A mycorrhiza-responsive protein in wheat roots. *Mycorrhiza* 12:219–222
- Fiorilli V, Vallino M, Biselli C, Faccio A, Bagnaresi P, Bonfante P (2015) Host and non-host roots in rice: cellular and molecular approaches reveal differential responses to arbuscular mycorrhizal fungi. *Front Plant Sci* 6:636
- Giri B, Prasad R, Varma A (2018) *Root biology*. Springer International Publishing (ISBN 978-3-319-75910-4) <https://www.springer.com/us/book/9783319759098>
- Gutjahr C, Casieri L, Paszkowski U (2009) Glomus intraradices induces changes in root system architecture of rice independently of common symbiosis signaling. *New Phytol* 182:829–837
- He Y, Liao H, Yan X (2003) Localized supply of phosphorus induces root morphological and architectural changes of rice in split and stratified soil cultures. *Plant Soil* 248:247–256
- Hemsley AR, Poole I (2004) *The evolution of plant physiology*. Elsevier, London

- Hetrick B, Wilson G, Todd T (1996) Mycorrhizal response in wheat cultivars: relationship to phosphorus. *Can J Bot* 74:19–25
- Hijri M (2016) Analysis of a large dataset of mycorrhiza inoculation field trials on potato shows highly significant increases in yield. *Mycorrhiza* 26:209–214
- Hochholdinger F (2009) The maize root system: morphology, anatomy, and genetics. In: *Handbook of maize: its biology*. Springer, New York
- Hochholdinger F, Woll K, Sauer M, Dembinsky D (2004) Genetic dissection of root formation in maize (*Zea mays*) reveals root-type specific developmental programmes. *Ann Bot* 93:359–368
- Hoshyar Z, Abedi B, Ganji Moghadam E, Davari Nejad G (2017) Effect of arbuscular mycorrhiza on growth and physiological behavior of PHL-C rootstock. *J Plant Physiol Breed* 7:53–60
- Ilag LL, Rosales A, Elazegui F, Mew T (1987) Changes in the population of infective endomycorrhizal fungi in a rice-based cropping system. *Plant Soil* 103:67–73
- Jaizme-Vega M, Rodríguez-Romero A, Hermoso CM, Declerck S (2003) Growth of micropropagated bananas colonized by root-organ culture produced arbuscular mycorrhizal fungi entrapped in Ca-alginate beads. *Plant Soil* 254:329–335
- Jungk A (2001) Root hairs and the acquisition of plant nutrients from soil. *J Plant Nutr Soil Sci* 164:121–129
- Karthikeyan AS, Varadarajan DK, Jain A, Held MA, Carpita NC, Raghothama KG (2007) Phosphate starvation responses are mediated by sugar signaling in Arabidopsis. *Planta* 225:907–918
- Khan MH, Meghvansi M, Prasad K, Siddiqui S, Varma A (2017) Arbuscular mycorrhizal symbiosis and nutrient resource limitation: predicting the linkages and effectiveness of partnership. In: *Mycorrhiza-nutrient uptake, biocontrol, ecorestoration*. Springer, Cham
- Koide RT, Kabir Z (2000) Extraradical hyphae of the mycorrhizal fungus *Glomus intraradices* can hydrolyse organic phosphate. *New Phytol* 148:511–517. <https://doi.org/10.1046/j.1469-8137.2000.00776.x>
- Krishna H, Singh S, Minakshi PV, Khawale R, Deshmukh P, Jindal P (2006) Arbuscular-mycorrhizal fungi alleviate transplantation shock in micropropagated grapevine (*Vitis vinifera* L.). *J Hortic Sci Biotechnol* 81:259–263
- Kungu JB, Lasco RD, Dela Cruz LU, Dela Cruz RE, Husain T (2008) Effect of vesicular arbuscular mycorrhiza (VAM) fungi inoculation on coppicing ability and drought resistance of *senna spectabilis*. *Pak J Bot* 40:2217–2224
- Lambers H, Shane MW, Cramer MD, Pearse SJ, Veneklaas EJ (2006) Root structure and functioning for efficient acquisition of phosphorus: matching morphological and physiological traits. *Ann Bot* 98:693–713
- Lambers H, Raven JA, Shaver GR, Smith SE (2008) Plant nutrient-acquisition strategies change with soil age. *Trends Ecol Evol* 23:95–103. <https://doi.org/10.1016/j.tree.2007.10.008>
- Lambers H, Brundrett MC, Raven JA, Hopper SD (2010) Plant mineral nutrition in ancient landscapes: high plant species diversity on infertile soils is linked to functional diversity for nutritional strategies. *Plant Soil* 334:11–31. <https://doi.org/10.1007/s11104-010-0444-9>
- Li XL, George E, Marschner H (1991) Phosphorus depletion and pH decrease at the root soil and hyphae soil interfaces of VA mycorrhizal white clover fertilized with ammonium. *New Phytol* 119:397–404
- Li XL, George E, Marschner H, Zhang JL (1997) Phosphorus acquisition from compacted soil by hyphae of a mycorrhizal fungus associated with red clover (*Trifolium pratense*). *Can J Bot Revue Canadienne De Botanique* 75:723–729
- López-Bucio J, Cruz-Ramírez A, Herrera-Estrella L (2003) The role of nutrient availability in regulating root architecture. *Curr Opin Plant Biol* 6:280–287
- Lumini E, Vallini M, Alguacil MM, Romani M, Bianciotto V (2011) Different farming and water regimes in Italian rice fields affect arbuscular mycorrhizal fungal soil communities. *Ecol Appl* 21:1696–1707
- Lynch J (1995) Root architecture and plant productivity. *Plant Physiol* 109:7

- Maillet F, Poinot V, Andre O, Puech-Pagès V, Haouy A, Gueunier M, Cromer L, Giraudet D, Formey D, Niebel A (2011) Fungal lipochitooligosaccharide symbiotic signals in arbuscular mycorrhiza. *Nature* 469:58
- Manoharan P, Shanmugaiah V, Balasubramanian N, Gomathinayagam S, Sharma MP, Muthuchelian K (2010) Influence of AM fungi on the growth and physiological status of *Erythrina variegata* Linn. Grown under different water stress conditions. *Eur J Soil Biol* 46:151–156
- Marin M, Mari A, Ibarra M, Garcia-Ferriz L (2003) Arbuscular mycorrhizal inoculation of micropropagated persimmon plantlets. *J Hortic Sci Biotechnol* 78:734–738
- Marschner H (1998) Role of root growth, arbuscular mycorrhiza, and root exudates for the efficiency in nutrient acquisition. *Field Crop Res* 56:203–207
- Marschner H (1995) Mineral nutrition of high plants. Academic, London
- Marschner H (1996) Mineral nutrient acquisition in nonmycorrhizal and mycorrhizal plants. *Phyton Annales Rei Botanicae* 36:61–68
- Marschner H (2011) Marschner's mineral nutrition of higher plants. Academic, London
- Marschner P (2012) Marschner's mineral nutrition of higher plants. Academic, London
- Marschner H, Romheld V, Horst WJ, Martin P (1986) Root-induced changes in the rhizosphere – importance for the mineral-nutrition of plants. *Zeitschrift Fur Pflanzenernahrung Und Bodenkunde* 149:441–456
- Mohammad MJ, Malkawi HI (2004) Root, shoot and nutrient acquisition responses of mycorrhizal and nonmycorrhizal wheat to phosphorus application to highly calcareous soils. *Asian J Plant Sci* 3:363–369
- Nacry P, Canivenc G, Muller B, Azmi A, Van Onckelen H, Rossignol M, Doumas P (2005) A role for auxin redistribution in the responses of the root system architecture to phosphate starvation in *Arabidopsis*. *Plant Physiol* 138:2061–2074
- Neumann E, George E (2010) Nutrient uptake: the arbuscular mycorrhiza fungal symbiosis as a plant nutrient acquisition strategy. In: *Arbuscular mycorrhizas: physiology and function*. Springer, Amsterdam
- Neumann G, Martinoia E (2002) Cluster roots—an underground adaptation for survival in extreme environments. *Trends Plant Sci* 7:162–167
- Neumann G, Massonneau A, Martinoia E, Römheld V (1999) Physiological adaptations to phosphorus deficiency during proteoid root development in white lupin. *Planta* 208:373–382
- Norman J, Atkinson D, Hooker J (1996) Arbuscular mycorrhizal fungal-induced alteration to root architecture in strawberry and induced resistance to the root pathogen *Phytophthora fragariae*. *Plant Soil* 185:191–198
- Ortas I (1997) Determination of the extent of rhizosphere soil. *Commun Soil Sci Plant Anal* 28:1767–1776. <https://doi.org/10.1080/00103629709369914>
- Ortas I (2003) Effect of selected mycorrhizal inoculation on phosphorus sustainability in sterile and non-sterile soils in the Harran Plain in South Anatolia. *J Plant Nutr* 26:1–17. <https://doi.org/10.1081/pln-120016494>
- Ortas I (2012) The effect of mycorrhizal fungal inoculation on plant yield, nutrient uptake and inoculation effectiveness under long-term field conditions. *Field Crop Res* 125:35–48. <https://doi.org/10.1016/j.fcr.2011.08.005>
- Ortas I (2015) Comparative analyses of Turkey agricultural soils: potential communities of indigenous and exotic mycorrhiza species' effect on maize (*Zea mays* L.) growth and nutrient uptakes. *Eur J Soil Biol* 69:79–87. <https://doi.org/10.1016/j.ejsobi.2015.05.006>
- Ortas I, Akpinar C (2011) Response of maize genotypes to several mycorrhizal inoculums in terms of plant growth, nutrient uptake and spore production. *J Plant Nutr* 34:970–987. <https://doi.org/10.1080/01904167.2011.555580>
- Ortas I, Rafique M, Akpinar C, Aka Kacar Y (2017) Growth media and mycorrhizal species effect on acclimatization and nutrient uptake of banana plantlets. *Sci Hortic* 217:55–60
- Pearson J, Jakobsen I (1993) Symbiotic exchange of carbon and phosphorus between cucumber and three arbuscular mycorrhizal fungi. *New Phytol* 124:481–488

- Pinior A, Grunewaldt-Stöcker G, von Alten H, Strasser RJ (2005) Mycorrhizal impact on drought stress tolerance of rose plants probed by chlorophyll a fluorescence, proline content and visual scoring. *Mycorrhiza* 15:596
- Ponton F, Piche Y, Parent S, Caron M (1990) The use of vesicular-arbuscular mycorrhizae in Boston fern production: I. Effects of peat-based mixes. *Hortscience* 25:183–189
- Prasad R, Bhola D, Akdi K, Cruz C, Sairam K, Tuteja N, Varma A (2017) Introduction to mycorrhiza: historical development. In: *Mycorrhiza-function, diversity, state of the art*. Springer, Cham
- Pritchard SG, Rogers HH (2000) Spatial and temporal deployment of crop roots in CO₂-enriched environments. *New Phytol* 147:55–71
- Puthur JT, Prasad K, Sharmila P, Saradhi PP (1998) Vesicular arbuscular mycorrhizal fungi improves establishment of micropropagated *Leucaena leucocephala* plantlets. *Plant Cell Tissue Organ Cult* 53:41
- Quatrini P, Gentile M, Carimi F, Pasquale FD, Puglia AM (2003) Effect of native arbuscular mycorrhizal fungi and *Glomus mosseae* on acclimatization and development of micropropagated *Citrus limon* (L.) Burm. *J Hortic Sci Biotechnol* 78:39–45
- Rancillac M, Cadoux F, Leduc D, Kahane R (1996) Improvement of a protocol to establish in vitro arbuscular mycorrhizal strains with vitro bulbs of onion, *Allium cepa* L. Novel biotechnological approaches to plant production: from sterile root to mycorrhizosphere Joint COST meeting
- Rapparini F, Baraldi R, Bertazza G (1996) Growth and carbohydrate status of *Pyrus communis* L plantlets inoculated with *Glomus* sp. *Agronomie* 16:653–661
- Rodríguez-Romero AS, Guerra MSP, Jaizme-Vega MDC (2005) Effect of arbuscular mycorrhizal fungi and rhizobacteria on banana growth and nutrition. *Agron Sustain Dev* 25:395–399
- Rogers HH, Runion GB, Prior A (1999) Response of plants to elevated atmospheric CO₂: root growth, mineral. Carbon dioxide and environmental stress, p 215
- Rouphael Y, Franken P, Schneider C, Schwarz D, Giovannetti M, Agnolucci M, Pascale SD, Bonini P, Colla G (2015) Arbuscular mycorrhizal fungi act as biostimulants in horticultural crops. *Sci Hortic* 196:91–108. <https://doi.org/10.1016/j.scienta.2015.09.002>
- Sbrana C, Vitagliano C, Avio L, Giovannetti M (1992) Influence of vesicular-arbuscular mycorrhizae on transplant stress of micropropagated apple and peach rootstocks. Micropropagation, root regeneration, and mycorrhizas Joint meeting between COST
- Schachtman DP, Reid RJ, Ayling SM (1998) Phosphorus uptake by plants: from soil to cell. *Plant Physiol* 116:447–453
- Schubert A, Bodrino C, Gribaudo I (1992) Vesicular-arbuscular mycorrhizal inoculation of kiwifruit (*Actinidia deliciosa*) micropropagated plants. *Agronomie* 12:847–850
- Sharma S, Sharma AK, Prasad R, Varma A (2017) Arbuscular mycorrhiza: a tool for enhancing crop production. In: *Mycorrhiza-nutrient uptake, biocontrol, ecorestoration*. Springer, New York
- Shrivastava S, Prasad R, Varma A (2014) Anatomy of root from eyes of a microbiologist. In: *Root engineering*. Springer, Berlin
- Singh S, Minakshi G, Khawale R, Patel V, Krishna H, Saxena A (2003) Mycorrhization as an aid for biohardening of in vitro raised Grape (*Vitis vinifera* L.) plantlets. VII International symposium on temperate zone fruits in the tropics and subtropics, p 662
- Smith S, De Smet I (2012) Root system architecture: insights from Arabidopsis and cereal crops. *Philos Trans R Soc B Biol Sci* 367(1595):1441–1452
- Smith SE, Read DJ (2010) *Mycorrhizal symbiosis*. Academic, San Diego, CA
- Smith SE, Smith FA (2011) Roles of arbuscular mycorrhizas in plant nutrition and growth: new paradigms from cellular to ecosystem scales. *Annu Rev Plant Biol* 62:227–250
- Smith SE, Facelli E, Pope S, Smith FA (2010) Plant performance in stressful environments: interpreting new and established knowledge of the roles of arbuscular mycorrhizas. *Plant Soil* 326:3–20
- Smith SE, Jakobsen I, Grønlund M, Smith FA (2011) Roles of arbuscular mycorrhizas in plant phosphorus nutrition: interactions between pathways of phosphorus uptake in arbuscular

- mycorrhizal roots have important implications for understanding and manipulating plant phosphorus acquisition. *Plant Physiol* 156:1050–1057
- Solaiman M, Hirata H (1998) Glomus-wetland rice mycorrhizas influenced by nursery inoculation techniques under high fertility soil conditions. *Biol Fertil Soils* 27:92–96
- Taylor J, Harrier LA (2001) A comparison of development and mineral nutrition of micropropagated *Fragaria* × *ananassa* cv. Elvira (strawberry) when colonised by nine species of arbuscular mycorrhizal fungi. *Appl Soil Ecol* 18:205–215
- Teotia P, Kumar M, Prasad R, Kumar V, Tuteja N, Varma A (2017) Mobilization of micronutrients by mycorrhizal fungi. *Mycorrhiza-function, diversity, state of the art*. Springer, Cham
- Tingey DT, Phillips DL, Johnson MG (2000) Elevated CO₂ and conifer roots: effects on growth, life span and turnover. *New Phytol* 147:87–103
- Uosukainen M, Vestberg M (1997) Timing of AMF inoculation to microcuttings of crab apple cv. Marjatta. COST Action 821: arbuscular mycorrhizas in sustainable soil-plant systems: report of 1996 activities
- Upadhyaya CP, Gururani MA, Prasad R, Varma A (2013) A cell wall extract from *Piriformospora indica* promotes tuberization in potato (*Solanum tuberosum* L.) via enhanced expression of Ca²⁺ signaling pathway and lipoxygenase gene. *Appl Biochem Biotechnol* 170(4):743–755
- Vallino M, Fiorilli V, Bonfante P (2014) Rice flooding negatively impacts root branching and arbuscular mycorrhizal colonization, but not fungal viability. *Plant Cell Environ* 37:557–572
- Vance CP (2010) Quantitative trait loci, epigenetics, sugars, and microRNAs: quaternaries in phosphate acquisition and use. *Plant Physiol* 154:582–588
- Varma A, Prasad R, Tuteja N (2017) *Mycorrhiza: nutrient uptake, biocontrol, ecorestoration*. Springer International Publishing (ISBN: 978-3-319-68867-1) <http://www.springer.com/us/book/9783319688664>
- Vidal M, Azcón-Aguilar C, Barea J, Pliego-Alfaro F (1992) Mycorrhizal inoculation enhances growth and development of micropropagated plants of avocado. *Hortscience* 27:785–787
- Volkmar K (1997) Water stressed nodal roots of wheat: effects on leaf growth. *Funct Plant Biol* 24:49–56
- Wang B, Tang X, Cheng L, Zhang A, Zhang W, Zhang F, Liu J, Cao Y, Allan D, Vance C (2010) Nitric oxide is involved in phosphorus deficiency-induced cluster-root development and citrate exudation in white lupin. *New Phytol* 187:1112–1123
- Wirsel SG (2004) Homogenous stands of a wetland grass harbour diverse consortia of arbuscular mycorrhizal fungi. *FEMS Microbiol Ecol* 48:129–138
- Wu Q-S, Zou Y-N, He X-H (2010) Contributions of arbuscular mycorrhizal fungi to growth, photosynthesis, root morphology and ionic balance of citrus seedlings under salt stress. *Acta Physiol Plant* 32:297–304
- Wu F, Wang W, Ma Y, Liu Y, Ma X, An L, Feng H (2013) Prospect of beneficial microorganisms applied in potato cultivation for sustainable agriculture. *Afr J Microbiol Res* 7:2150–2158
- Wu Q-S, Srivastava A, Zou Y-N, Malhotra S (2017a) Mycorrhizas in citrus: beyond soil fertility and plant nutrition. *Indian J Agric Sci* 87:427–443
- Wu QS, Sun P, Srivastava AK (2017b) AMF diversity in citrus rhizosphere. *Indian J Agric Sci* 87:653–656
- Yao M, Tweddell R, Desilets H (2002) Effect of two vesicular-arbuscular mycorrhizal fungi on the growth of micropropagated potato plantlets and on the extent of disease caused by *Rhizoctonia solani*. *Mycorrhiza* 12:235–242
- Zhu X, Song F, Liu S, Liu F (2016) Role of arbuscular mycorrhiza in alleviating salinity stress in wheat (*Triticum aestivum* L.) grown under ambient and elevated CO₂. *J Agron Crop Sci* 202:486–496