Chapter 8
Role of Arbuscular Mycorrhizal Fungi in Plant Phosphorus Acquisition for Sustainable Agriculture

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Abstract Mycorrhizae are essential for the acquisition of phosphorus (P) and are critical in the acquisition of nutrients that are not readily available to plants. Soil P can be classified into organic and inorganic P. Plant nutrient uptake occurs in two ways: the acquisition by root epidermis and root hairs, which is the direct root absorption method; and mycorrhizal association. Arbuscular mycorrhizal fungi are rhizosphere microorganism that are widely distributed in nature and have important ecological functions. Arbuscular mycorrhizal fungi form a symbiosis with vascular plant roots. Arbuscular mycorrhizal fungi provides plants with essential nutrients including P and nitrogen, and at the same time obtains the required carbon from the plant root system. This chapter presents the mechanisms of arbuscular mycorrhizal fungi for the acquisition of P and promoting plant growth.

Keywords Arbuscular mycorrhizal fungus · Phosphorus · Microorganisms · Mycorrhizal association · Phosphorus absorption · Symbiotic relationship · Mycelium

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Abbreviations

AMF	Arbuscular mycorrhizal fungi
Ca	Calcium
K	Potassium
N	Nitrogen
P	Phosphorus
Pi	Inorganic phosphate
Zn	Zinc

8.1 Introduction

Phosphorus (P) is a crucial macronutrient in the ecosystem, and essential for plants (Khan et al. 2017; Iqbal et al. 2019a). The P in the soil that can be absorbed and utilized by plants is called soil available P (Amanullah et al. 2019; Iqbal et al. 2019b). Many soils are deficient in P in a form usable by plants. As a result, P-based fertilizers are often used for increasing agricultural output and to feed the world's rising population (Richardson 2001; Richardson et al. 2009). Since the soil has a strong adsorption and fixation effect on P, the applied phosphate fertilizer can soon be fixed by the soil, resulting in lower soil available P content, and soil P stress greatly limits productivity (Richardson et al. 2009; Anwar et al. 2017). As a result, this deposit of P in the soil, commonly known as "fixation," increases the input cost of phosphate fertilizer for producers, but it also brings environmental threats.

The use of manure-based fertilizers or organic fertilizers is not usually encouraged due to their cost, insufficient supply, and limited effectiveness in broad-scale agricultural production. It is important to replace the P extracted by crops with a sufficient P supply available to plants to make the farming system sustainable. As a consequence, there is a buildup of net P in the soil, (Burkitt et al. 2007; Richardson et al. 2009; Riaz et al. 2020), and a large portion of it remains in the soil. Therefore, more in-depth knowledge of the methods by which plants may access soil P and/or alter the quantity of P in the soil is also desired. The arbuscular mycorrhizal fungi are considered an efficient strategy to supply P to plants in order to sustain agricultural production under P deficient/stress conditions (Riaz et al. 2020).

8.2 Soil Phosphorus and Acquisition by Plant Roots

Phosphorus is acquired by plants as inorganic phosphate (Pi, $H_2PO_4{}^-$, $HPO_4{}^{2-}$, or $PO_4{}^{3-}$) via the roots (Fig. 8.1) (Plassard and Dell 2010). Unfortunately, P supply is limited due to the poor diffusion rates of Pi (Shen et al. 2011), and aluminum hydroxides and iron adsorb this P to calcium (Ca) in alkaline soil with different

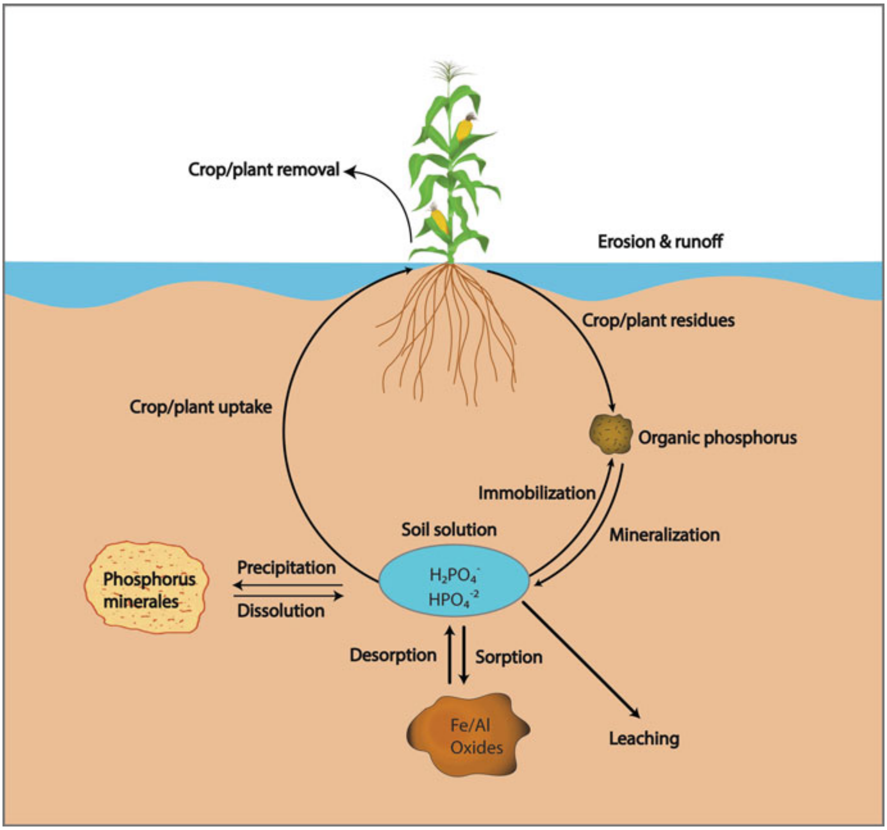

Fig. 8.1 Phosphorus cycle illustration, sources, and plant uptake

solubility (Prietzel et al. 2016), and some of them are bonded to organic matter present in the soil in a different environment (Lambers et al. 2015). Furthermore, the amount of P that enters the soil by deposition is quite low. Thus, changes in P availability are caused by weathering and P utilization in soils throughout the geological aging process (Turner and Condron 2013). As a consequence, the quantity of P available differs dramatically in various soils (Lang et al. 2016).

Most of the soil has a large amount of accumulated P (Amanullah et al. 2016a). The total amount of P in the soil is made up of both organic and inorganic sources. However, only a few plants can access this P (usually 1%). Most of the inorganic P is absorbed by soil components, including clay, sesquioxide, and organic matter, or appears in the form of precipitation of the mineral P (Amanullah et al. 2016b). Organic P accounts for at least 30% to as much as 80% of the total P in the soil. It is mainly composed of monoesters (up to 90%), of which the concentration of diesters, teichoic acid, and phosphonates are small (Condron et al. 1990). It was found that monoester P is mainly a cationic derivative of phytate (mainly oxalate), and a small part (5%) exists as sugar phosphate and diester P (phospholipids and nucleic acids).

The factors that affect the accumulation and transformation of several kinds of organic and inorganic P in the soil are intricate and are exaggerated by numerous challenging courses. The desorption or dissolution of inorganic P from the reservoir of total soil P is required, as is the mineralization of organic P, in order to release ortho-P into the soil solution and make inorganic P more readily available for plant uptake (Amanullah et al. 2021). However, the proportional role of organic P in supplying ortho-P for plant uptake and mobilizing P directly from soil mineral components remains unidentified (Frossard et al. 2000).

Plant roots uptake P in orthophosphate anions from the soil solution, and are absorbed by P transporters in the roots. The concentration of ortho-P (usually 5 μ M) in the soil solution is very low in the majority of soils, and the soil solution P must be quickly replenished from other soil P pools. Therefore, the shortage of P in plants is caused by a low concentration of ortho-P in the soil solution, a slow rate of P diffusion in the soil, and a limited potential for P replenishment in the soil solution (Conyers and Moody 2009). The concentration of ortho-P in the soil solution is influenced by a variety of physical and chemical parameters (Conyers and Moody 2009). P absorbed by plants from soil is dependent not only on the diffusion rate of orthophosphate into the roots (Barber 1995) but also on the growth of the root system, which will allow it to intercept additional sources of P. The low P diffusion from soil to root fundamentally reduces P absorption and inhibits plant growth (Silberbush and Barber 1983; Tinker and Nye 2000). As a result, the application of phosphate fertilizer is beneficial to plant growth by increasing the diffusion rate of P to roots and promoting the development of roots in unexploited soil (Wissuwa 2003).

The maximum concentration of plant-available P is typically present in the 0–0.10 m surface layer of the soil profile. In a study on traits related to the absorption of more P by wheat, it was found that the density of root length in the topsoil was the most significant P absorption attribute. Furthermore, since the majority of the P is found in the topsoil, drying this layer will impair the absorption of P, resulting in “nutrient deficiency”. However, when it comes to relatively fixed nutrients in the soil (such as P) and plants competing for the same nutrient, the situation is different, and root proliferation may be the most effective way to develop nutrient-rich patches.

8.2.1 Microorganism in the Acquisition of Phosphorus

Microorganisms mediate the supply of P to plants by a number of methods, including direct root expansion (Mycorrhizal association), and increased mobilization of orthophosphate by soil organic and inorganic P (Riaz et al. 2020). A significant quantity of fixed P assets is also present in the microbial biomass, which, according to estimates, contributes to about 5% of the total P in the soil. Microorganisms can easily immobilize P from soil solutions and fertilizers, but they often release large amounts of P back into the soil in the form of orthophosphate or organic forms that are readily mineralized are examples of such substances, which may be utilized by the plant (Oberson and Joner 2005). The P turnover rate in biomass of microbes is very fast, and P turnover may occur regardless of the size of the microbial pool. Higher turnover rates were reported in unfertilized soils containing organic inputs, particularly soils that have received readily accessible carbon e.g., glucose. This means that the ability of microorganisms that supply P to plants in the root zone has been significantly improved.

In the rhizosphere, a significant quantity of metabolizable carbon originates from plant roots (Kouno et al. 2002). A variety of bacteria and fungi has been discovered that soil microbes can mineralize organic P and dissolve precipitated inorganic P. These bacteria and fungi have the potential to offer significant pathways for the release of P from different soil P pools. Related microbes have been isolated and utilized as inoculants in the industrial setting in a few instances. Further understanding of rhizosphere microorganisms and their contribution to plant P nutrition is essential (Chen et al. 2002). Although the content of organic and inorganic P in the root zone is significantly reduced, when compared to plant systems, the proportional involvement of microbes in these activities is still unclear (George et al. 2002). In contrast, the unique relationship between roots and mycorrhizal fungi and their role in plant P uptake has been widely known. Mycorrhizal fungi form an interrelationship with most plant species.

Arbuscular mycorrhizal fungi (AMF) are very beneficial to several plant species. The main advantage of mycorrhizal interaction for the absorption of P and a number of other nutrients is that it has the potential to enhance the surface area of plant roots, which can extract a larger volume of soil (Fig. 8.2). Mycorrhizae have the potential to improve the use of organic P and use of nutrient-rich regions (Riaz et al. 2020). Because P is a macronutrient, it involves a significant effect on productivity (Becquer et al. 2014). Even if inorganic P concentrations are low in the soil, plants have limited ability to use it. Plants have evolved a number of strategies for dealing with the P shortages in their environment, including strengthening the soil-root interaction to boost P transport and establish a symbiotic partnership with AMF are just a few of the initiatives (López-Arredondo et al. 2014). AMF inoculation seems to boost nitrogen (N) and P absorption, which results in greater plant development and growth (Balliu et al. 2015). According to Garcés-Ruiz et al. (2017) and Begum et al. (2019), P absorption in the AMF inoculation maize was much improved than in control treatments. AMF has been revealed to improve seedling weight in *Leymuschinensis* by increasing, intercellular CO_2, contents of water and N, and P (Lin et al. 2018). It is believed that AMF inoculation speeds up the uptake and transfer of nutrients specifically P (Zarei et al. 2006; Clausing and Polle 2020). The present data support the notion that the management of P uptake by mycorrhizal interaction is critical for the provision of root P. Dalla Costa et al. (2021) confirmed that AMF significantly increased the nutrient use efficiency of apples. The inoculation of *G. albida* with acerola cherry enhanced the nutrient use efficiency of P (Balota et al. 2011), while nutrient use efficiency of N, P, and potassium (K) was reduced in olive trees after *Funneliformis mosseae* was introduced (Porras-Soriano et al. 2009). So, the AMF affects the nutrient use efficiency of woody plant species as well. A significant increase in nutrient use efficiency in mycorrhizal plants was seen

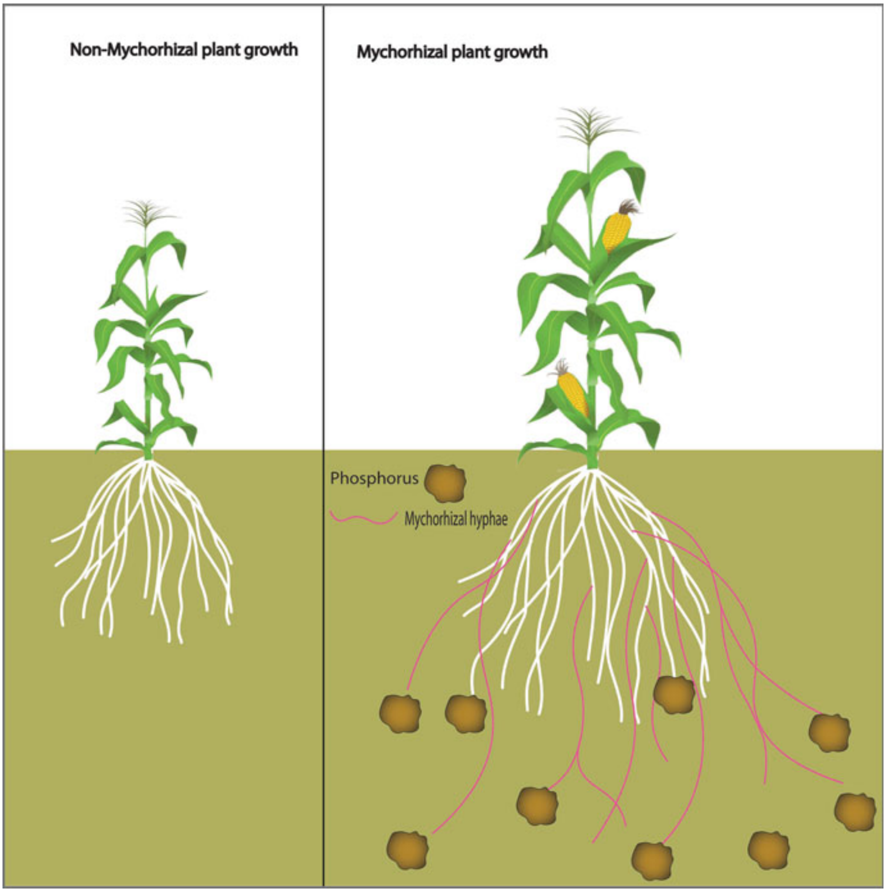

Fig. 8.2 Plant growth difference between mycorrhizal and nonmycorrhizal plants

in plants growing in the presence of *Acaulospora morrowiae* and *Gigaspora albida* in the absence of 50% P. When growing under carbon-limiting circumstances, the buildup of P on AMF hyphae might be ninefold more than on the roots (Hammer et al. 2011). P was improved if shoot of non-mycorrhizal plants by threefold in relation to mycorrhizal plants, demonstrating that AMF enhances nutrient acquisition underneath restrictive P soil conditions and control the delivery of P to plant metabolism within narrow boundaries (Nazeri et al. 2014). As a result of the increased nutrient use efficiency due to AMF inoculation, the requirement for fertilization is reduced, which has an influence on both production costs and environmental pollution.

Due to low soil nutrient levels, AMF is also believed to have a significant role in plant P nutrients in other low-P input systems (Ryan et al. 2000). Different plants depend on mycorrhizal infection to varying degrees, and the P status of the plant as well as the availability of P in the soil influence the degree of infection of the host. In agricultural systems with large amounts of accessible soil P for plants, the plants' need for mycorrhizal infections is also substantially decreased. When the mycorrhizal plant has almost no nutritional benefit in the absorption of P, AMF (although it is widely referred to as a beneficial symbiont) can harm the growth of the plant by consuming host carbon (Ryan et al. 2000). In the colder subtropical crop growing areas of northeastern Australia, where the input of phosphate fertilizer is low, to obtain sufficient nutrients for various crops, high levels of AMF colonization are often required.

8.2.2 Role of Arbuscular Mycorrhizal Fungi in the Acquisition of Phosphorus

The improvement of P efficiency is essential to encourage plant development, crop yields, and decrease the environmental pollution. The soil microbial resources can efficiently relieve P stress in the soil environment (Cibichakravarthy et al. 2015), among which AMF can improve the absorption of P, by the mycorrhizal plant via infecting plant roots which then increase the nutritional status of plants, promote their growth and development, and increase stress resistance (Table 8.1) (Xie et al. 2014). AMF forms a mutually beneficial symbiotic partnership with most plants in more than 80% of terrestrial plant roots (Hooker et al. 1992; Sharif and Claassen 2011; Manaut et al. 2015). In the soil, AMF combines with plant roots to form mycorrhiza, which can form a dense mycelial network system, which has an impact on the morphological structure, physiology, and cell level of mycorrhizal plants, which improve plant water metabolism and nutritional status and increase plant stress resistance (Liu et al. 2014), among which AMF improves the absorption and utilization of P by plants, which has attracted the attention of many researchers (Chen et al. 2017).

AMF help mycorrhizal plants in absorbing P in the soil, and plants provide some products of photosynthesis to help the growth and development of AMF, that is, AMF and plants form arbuscular branches in the mycorrhizal symbiosis (Fig. 8.3) (Smith et al. 2011; Smith and Smith 2011). Rice, in a symbiotic relationship with AMF, absorbs more than 70% of the P available (Yang et al. 2012). As the amount of P present in the soil rises, the efficacy of the AMF symbiosis and P translocation diminishes as well (Miao et al. 2009). Compared with plant roots, AM fungi increase the root surface area of plants and increase the absorption area of nutrients, which ultimately promotes plant growth (Sharif and Claassen 2011). The capacity of mycorrhizal plants to absorb and use P is considerably greater than that of non-mycorrhizal plants, and this difference is substantial (Cui et al. 2019). AMF stimulates the roots of the mycorrhizal plant to produce acid phosphatase and organic acids, activates some insoluble P, and improves plant P acquisition. For example, polyphosphate can be utilized by florae through the transformation of polyphosphatase, which can alleviate the deprivation of P in the rhizosphere of plants.

Table 8.1 Arbuscular mycorrhizal fungi in the uptake of phosphorus under different stress conditions

Serial number	Arbuscular mycorrhizal fungi	Plant type	Stress condition	Effect	References
1	*Rhizophagus irregularis*	*Zea mays*	Low phosphorus	Larger root hair and AMF inoculation increased P uptake	Ma et al. (2021)
2	*Rhizolive consortium*	*Picholine Marocaine*	Nutrient deficiency and Verticillium wilt	AMF increased Ca, K, Na, and P uptake	Boutaja et al. (2020)
3	*Claroideoglomus etunicatum, Rhizophagus intraradices, Funneliformis mossea*	*Glycine max*	P- deprivation under field conditions	AMF enhanced the soybean growth under P deficient condition	Adeyemi et al. (2021)
4	*Glomus* species	*Zea mays*	Regulation of P and Zn	AMF increased plant growth parameters	Saboor et al. (2021)
5	*Glomus intraradices*	(Fenugreek)	Drought stress	AMF showed good effect on diosgenin content and has significant effect on P uptake	Irankhah et al. (2021)
6	*Arbuscular mycorrhizal fungi*	*Zea mays*	Zn deficient and toxic condition	AMF increased Zn contents under bother Zn deficient and toxic conditions	Saboor and Ali (2021)
7	*Funneliformis mosseae*	*Zea mays*	Red soil, rainfall	*R*educes p losses	He et al. (2021)
8	*Glomus intraradices*	*Zea mays*	Field condition	Increased P concentrations	Cozzolino et al. (2013)
9	*Glomus intraradices*	*Hordeum vulgare*	Uranium stress	AMF enhanced the P uptake while decreased uranium uptake	Chen et al. (2005)
10	*Funneliformis mosseae*	*Zea mays*	N/A	AMF enhanced the P uptake	Sawers et al. (2017)
11	*Mixture of AMF strains*	*Glycine max*	Natural field conditions	Increased plant growth parameters and enhanced nutrient uptake	Adeyemi et al. (2020)
12	*Glomus intraradices Scutellospora calospora, Glomus mosseae*	*Vitis vinifera*	Two soils with contrasting P levels	AMF enhanced P, Ca and S uptake,	Schreiner (2007)
13	*Arbuscular mycorrhizae*	*Triticum aestivum*	Calcareous soil, Zn uptake	AMF and P application affected Zn uptake in plant parts	Zhang et al. (2016)

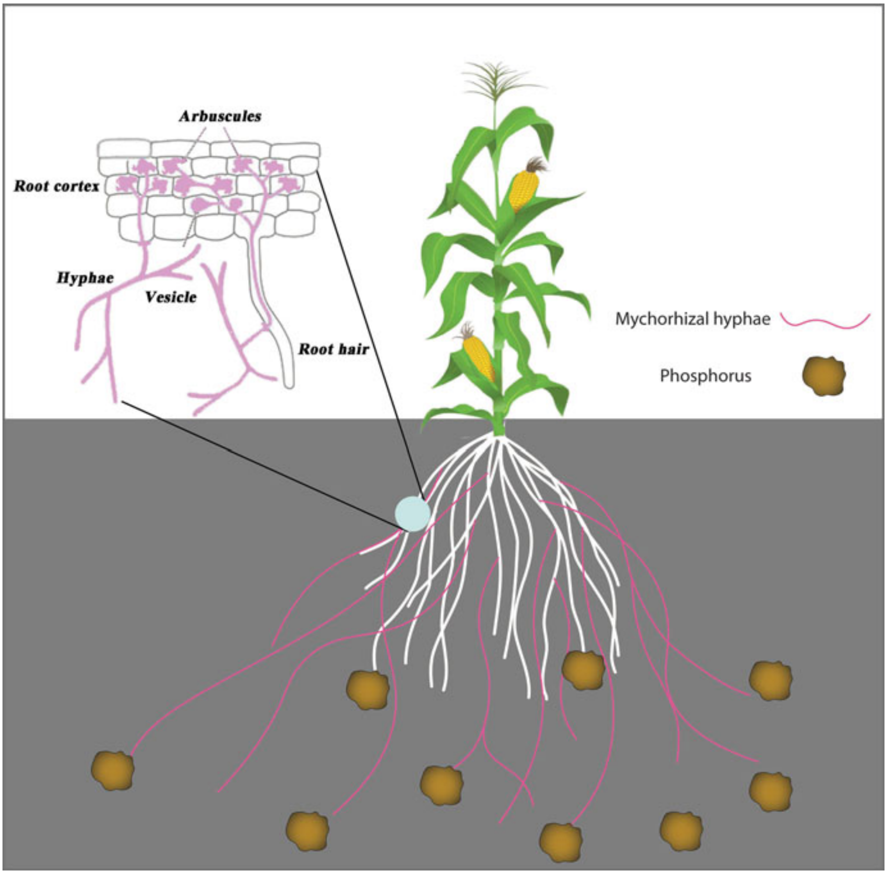

Fig. 8.3 Mechanisms of phosphorus uptake by arbuscular mycorrhizal fungi

The formation of mycorrhiza is affected by soil P levels. When the soil suffers from low P stress, the P supply can be increased by applying P fertilizers to promote plant growth and development; but when the P level exceeds a certain limit, it will inhibit the growth of AMF (Liu et al. 2014). In soils having high fixing ability and low P, AMF can mineralize organic P or help plants effectively use insoluble inorganic P, improving the availability of P in the rhizosphere soil. Therefore, inoculation with AMF can effectively promote changes in soil P form and the uptake of nutrients by the host, and colonization with appropriate AMF can better promote the conversion of soil P in the direction that is beneficial to the mycorrhizal plant absorption. AMF promotes the uptake of P by plants. AMF and P facilitated improvements of *N. tabacum* traits during drought circumstances were shown to be connected with higher absorption of important mineral ions, including N, K, and P, according to the research of (Begum et al. 2020).

AM fungi and plants have a certain level of sensitivity when they establish a symbiotic relationship. Based on results from a bait-plant method (Delavaux et al. 2017) discovered there were statistically noteworthy correlations between AMF and soil P (negative), N (positive), and rarefied tree diversity (Positive), indicating that soil P and N nutrient have had an impact on AMF levels. Fall et al. (2015) found that after 4 months of experiment in sterilized soil and under greenhouse conditions, grass seedlings colonized by AMF produced considerably more total biomass as compared to non-inoculated plants. Franco et al. (2019) demonstrated for the first time that AMF influences the mobilization of P, Fe, Ca, B, Zn, Mn, K, Cu, Mg, and N, in gymnosperms. A significant decrease in nutrient absorption (NPK) was seen in non-inoculated plants due to drought.

Plants infected with AMF had elevated levels of NPK, which was similar to earlier studies on the subject (Calvo-Polanco et al. 2014). The studies showed a considerable upsurge in the absorption of important nutrients such as NPK, magnesium, and Ca under normal and shortage irrigation circumstances due to AMF addition (Abbaspour et al. 2012; Armada et al. 2015). Sitko et al. (2019) have proven that increasing the accessibility of P increases the growth of maize by increasing the intake of other important minerals such as K, magnesium, and Ca. This increase in mineral uptake may be attributed to the effects of minerals on the morphology and hydraulics of roots, respectively (Armada et al. 2015). AM fungal isolate produced favorable results in apple micro when colonized by 4 different isolates of AMF with varying amounts of P (Dalla Costa et al. 2021). Indigenous AMF in the soil has the most significant promotion effect on plants. At present, research on the improvement of P uptake by the mycorrhizal plant by AMF has been extensively carried out, and the research on improving crop yield and the plant survival rate has made great progress, but the research on the mechanism is still in its infancy.

8.2.3 Arbuscular Mycorrhizal Fungi Effect on the Roots of Mycorrhizal Plants

AMF are abundant in the environments. They can form a symbiosis with plants-arbuscular mycorrhizas, thereby changing the plant's root morphology and expanding the range of nutrient absorption by the root system, in that way enhancing the mycorrhizal plant absorption and utilization of nutrients such as P and N. After the plant is infected by AMF, its biomass increases, and the root morphology of the plant changes (Liu et al. 2014).

AM-plants have two mechanisms for extracting P from soil solution at a fast rate and with great efficiency. The root epidermis and root hairs are responsible for direct P uptake in the plant body and in the 2nd pathway which is facilitated by AM, P is absorbed by exterior AM hyphae and delivered to colonized root cortical cells through the AM route (Smith and Smith 2011). Furthermore, mycorrhizal hyphae can collect soil P, which is inaccessible to the majority of nonmycorrhizal plants (Aparna et al. 2011; Sharif and Claassen 2011). As a result, the formation of mycorrhizal symbiosis with suitable fungus species may be used as an alternative technique for reducing plant P deficit. AMF regulates plant auxin signaling pathways by secreting sesquiterpenes to encourage mycorrhizal plants' lateral root growth (Sugiyama and Yazaki 2014). The mycorrhization of clover plants significantly increased primary and secondary lateral roots in the root system (Chen et al. 2017). When subjected to environmental stress, the roots of plants inoculated with AMF will be adjusted accordingly to enhance plant resistance. For example, under drought stress, citrus inoculated with *Funneliformis mosseae* significantly improved root growth parameters including root volume, root area, and root diameter (Liu et al. 2016).

Different types of AMF have differences in the colonization time and colonization effect of the mycorrhizal plant. The higher the adaptability of the two, the greater the contribution of AMF to the mycorrhizal plant. Because there are often multiple strains in the natural environment, molecular biology methods must be used to determine whether the infection impact of AMF on the mycorrhizal plant is better than that of a single strain when used in a mixed application of different strains, in order to be more in line with ecology. The extra-root hyphae, arbuscular branches, and vesicles produced by inoculation with AMF can expand the absorption range and promote the acquisition of P. A five-year field study was conducted on *Lonicera confusa* colonized by AMF, *G. intraradices,* and *G. etunicatum.* AM inoculation resulted in substantial increases in the number of new branches, crown diameter, and plant height. The concentrations of P in leaves and flowers rose, and the absorption of nutrients by plants increased after the administration of AM (An-Dong et al. 2013). The majority of dicotyledons often respond positively to AM inoculation, with improvements in growth and enhanced P absorption, as opposed to cereal crops, which are often believed to be nonresponsive (Grace et al. 2009). Gao et al. (2020) reported that AMF species have a strong symbiotic relationship i.e., *Rhizophagus irregularis* with the cotton.

The expression of specific phosphate transporter family genes and phosphate in cotton biomass were both dramatically increased during the symbiotic relationship between AMF and cotton. These data indicate the advantages of AMF-based inoculation on the uptake of P in cotton. It is important to note that trait flexibility, or the capacity of a species to modify the values of its traits in response to changing environmental circumstances, is an important component influencing a plant's capacity to endure environmental stress (Callaway et al. 2003). Fort et al. (2015) discovered that *Fabaceae* family increased their root/shoot ratio and root surface phosphatase activity when there was a lack of P available. AMF also affect the flexibility of root characteristics. According to a meta-analysis, AMF often increase biomass and length of the root while decreasing the ratio of root/shoot in most cases (Veresoglou et al. 2012), however, the mycorrhizal impact on root/shoot ratio remained non-significant. Additionally, Ryan et al. (2016) discovered that AMF dramatically reduced the root mass ratio of *Trifolium subterraneum.*

A large number of experiments (Guo et al. 2011) have proved that the supply of different concentrations and forms of P can cause significant changes in plant root morphology, including total root length, main root length, lateral root length, root projection area, specific surface area, and volume. When plants are subjected to low-P stress, the root system will undergo morphological changes under the influence of genetic factors, and the root system changes involved in different plants and different genotypes are complex.

8.2.4 Uptake Mechanism of Soil Phosphorus by Mycelium

Arbuscules are considered to be the most critical part of the symbiosis system. It is the place where AMF and the mycorrhizal plant exchange substances, and is regarded as the core of the functional structure of AMF (Gutjahr and Parniske 2017). The arbuscule double-membrane structure separates and combines the AMF and the mycorrhizal plant. From the aspect of form, AMF is located on the side of the arbuscule membrane, and the mycorrhizal plant is located on the side of the arbuscule precursor plasma membrane; from the functional aspect, the double membrane structure is the ion channel and the transporter attached to it are the places for material exchange between symbionts. After the arbuscule branches mature into the plant cells, the survival time is only 1–3 days before they begin to senesce and die. At the same time, the host cells return to the most primitive state and can be colonized by new arbuscule branches which export mineral nutrients while acquiring carbon sources to maintain symbiotic efficiency (Gutjahr and Parniske 2017). Compared with the direct acquisition of plant roots, mycelium has more advantages. Due to its huge biomass and surface area, it enhances the interaction with the soil and expands the absorption range of the mycorrhizal plant roots.

The average diameter of the mycelium is smaller than that of the root system. Therefore, it can enter the soil pores that the root system cannot penetrate (Qiang-Sheng et al. 2011). The extra-root hyphae (often called extra hyphae, extraradical hyphae, or mycelium.) can replace the root hair to uptake P. However, because the specific surface area of hyphae in roots is far less than that of arbuscule branches, although intracellular hyphae and intercellular hyphae are also involved in the transfer of P, their transport efficiency is not as good as that of arbuscule branches. Since AMF and plants do not have firm specificity when forming symbiosis, when the extra-root hyphae encounter other plants during the outward extension process, the root system will be infected again to form a hyphae network (Kytöviita et al. 2003). These mycelial networks can transfer nutrients between the same species and different plants and play an important role in the process of nutrient transfer between plants and natural nutrient cycling (Yao et al. 2003). The mycelial network infects different plants and connects plants with different nutritional statuses to transmit nutrients so that the distribution of nutrient resources forms a dynamic balance (Simard et al. 2003).

Under the premise of the difference in P nutrition between donor and recipient plants, the uptake of P can also be completed through the migration of the hyphae network. In an environment where soil nutrients are relatively scarce, the transfer effect of mycelium on P is more significant. Increased P fertilization, protracted fallow periods, and the growth of non-host crops may result in a reduction in mycorrhizal inoculum levels. The use of appropriate AMF in agricultural systems is essential because it not only makes use of the biopotential for effective P mining and uptake, but also minimizes P fertilizer usage and contamination in the environment. Regardless of the P levels in the soil, inoculating maize plants with AMF lead to a significant enhancement in P absorption as well as grain output (Zhang et al. 2012). AMF and strains that infect effectively, use less carbon, and deliver more P to the host are other key considerations for selecting crop species-preferred AMF and strains.

8.2.5 Arbuscular Mycorrhizal Fungi Modulate the Expression of Phosphorus Related Genes

P deficiency in the mycorrhizal plant encourages infection and AMF symbiosis. AMF induces high-affinity P transporter expression in itself and plants roots to enhance the uptake of available P in the soil and transport it to the desired part of the plant (Table 8.2) (Karandashov and Bucher 2005). At present, there are three kinds of P transporters detected in AMF: *GvPT*, *GiPT,* and *GmosPT*. When subjected to low P stress, the extra-root hyphae will increase the expression of the P transporter gene and promote P absorption in the soil. When P is transported from hyphae to arbuscule branches, AMF induces the expression of some members of the mycorrhizal plant's *Pht 1* family on the plasma membrane of the arbuscule precursor to enhance the plant's uptake of P in mycorrhiza, such as inoculation on *Medicago truncatula, G. radiata* significantly enhanced the expression of certain P transporters in arbuscule branches (Fiorilli et al. 2013).

OsPHT1.11 is the first AM-specific P transporter identified in rice, and a homologous (*MEDtr; PHT1.4*) in *Medicago truncatula* (Paszkowski et al. 2002). *OsPHT1.11* is also required for the establishment of AMF symbiosis in rice. Both *OsPHT1.11* and *OsPHT1.13* are essential for the establishment of an AMF symbiosis, indicating that grasses have developed a particular strategy for P acquisition via symbiosis with the AMF (Sun et al. 2012). In a symbiotic system, the P transporters of AMF influence P absorption and the expression levels of the transporter genes in the mycorrhizal plant. In the root periphery, mycorrhiza-inducible *PHT1* is involved in P absorption, and its loss causes P deficit in the plant (Rausch and Bucher 2002; Tian et al. 2013). In relation to non-infected control, AMF infection increases *ZmPHT1.3* expression 44-fold and reduces *ZmPHT1.6* expression 135-fold in maize (Tian et al. 2013). AMF colonization also has an effect on auxin and ethylene levels in the mycorrhizal plant, which are important regulators of lateral root and root hair formation (Rubio et al. 2009).

Table 8.2 Transporters in plants and arbuscular mycorrhizal fungi involved in nutrient uptake

Sr. No	Name	Transporter	Fungal/plant	References
1	*Glomus mosseae*	GmosPT	Fungal phosphorus transporter	Balestrini et al. (2007)
2	*Lotus japonicus*	LjAMT2;2	Plant N transporters	Guether et al. (2009)
3	*Glomus intraradices*	GiPT	Fungal phosphorus transporter	Maldonado-Mendoza et al. (2001)
4	*Lotus japonicus*	LjPT4	Plant phosphorus transporter	Volpe et al. (2016)
5	*Solanum lycopersicum*	StPT3	Plant phosphorus transporter	Rausch et al. (2001)
6	*Glycine max*	GmAMT4.1	Plant N transporters	Kobae et al. (2010)
7	*Petunia hybrida*	PhPT5	Plant phosphorus transporter	Breuillin et al. (2010)
8	*Oryza sativa*	OsPT2, 6, 11	Plant phosphorus transporter	Paszkowski et al. (2002)
9	*Gigaspora margarita*	GigmPT	Fungal phosphorus transporter	Xie et al. (2016)
10	*Medicago truncatula*	AMT2;3	Plant N transporters	Breuillin-Sessoms et al. (2015)
11	*Medicago truncatula*	MtPT4	Plant phosphorus transporter	Breuillin Sessoms et al. (2015)
12	*Glomus intraradices*	GintAMT 2,	Fungal N transporter	Perez Tienda et al. (2011)
13	*Glomus versiforme*	GvPT	Fungal phosphorus transporter	Harrison and Vanbuuren (1995)

The mycorrhizal plant can absorb substantial amounts of P nutrients via symbiosis with fungus. Both symbiosis and mycorrhizal P absorption are unaffected by tomato *PHT1.4* (a tomato homolog of the *PHT1.11*) (Bari et al. 2006). In dicots, direct P absorption is the dominant mode of absorption. The isolation of StPT3 protein from potato mycorrhiza enhanced P absorption (Rausch et al. 2001). The expression of *MtPT4* P transporter gene was significantly enhanced after the mycorrhization of *Medicago truncatula* (Pumplin and Harrison 2009). Through gene sequence and transcription analysis of multiple plants, it is found that there are differences in the number of Pht 1 family members in different plants, and the regulation mechanism of Pht1 family genes by AMF is also different, such as *A. thaliana* and rice genome determination. It was shown that there were 9 and 11 Pht 1 transporter family members for soil available P uptake and plant P transport (Goff et al. 2002), among the 11 Pht 1 transporter family members of rice, *OsPT11* was only used when AMF invaded.

Through the study of the P transporter promoter in *Arabidopsis thaliana* (Mudge et al. 2002), it was found that the *Pht1; 3* and *Pht1; 4* promoters in this family are responsible for the uptake of P from the soil by the roots of the plant. Chiou et al. (2001) studied specific binding alfalfa and found that when P is deficient, it stimulates the roots to increase the abundance of *MtPT1* P transporter, and this protein is significantly related to the P concentration in rhizosphere soil. These genes will respond when P is deficient, but there is no obvious positive correlation with AMF infection, and they may even be inhibited due to the establishment of a symbiotic relationship. For example, the *MtPT2* gene in *Medicago truncatula* inoculated with fungi (Harrison et al. 2002) and the *ZEAma: Pht1; 3* genes after maize mycorrhization (Benedetto et al. 2005).

8.3 Conclusion

Phosphate rock deposits are expected to be depleted in the next 80–100 years, and the inherent inadequacy of phosphate fertilizers is low. It is important to improve the P absorption efficiency of agricultural plants and agricultural systems. Agricultural practices, such as using soluble P fertilizers instead of poorly soluble fertilizers, designing fertilizer granules, and using liquid P fertilizers instead of granular fertilizers (highly Ca) should all be improved and all these are examples of methods for improving phosphate fertilizer absorption efficiency. Research has worked on the relationship between annual crops and AMF inoculation in the greenhouse. A deeper knowledge of the interplay between AMF and perennial plants, particularly under natural field conditions, is necessary to investigate its potential. AMF and plants have a certain degree of selectivity when they establish a symbiotic relationship. Different types of AMF may have completely different effects on the same plant. Indigenous AMF in the soil has the most significant promotion effect on plants. Different types of AMF have differences in the colonization time and colonization effect of the mycorrhizal plant. The higher the adaptability of the two, the greater the contribution of AMF to the mycorrhizal plant. Because there are often multiple strains in the natural environment, molecular biology methods must be used to determine whether the infection impact of AMF on the mycorrhizal plant is better than that of a single strain when used in a mixed application of different strains, to be more in line with ecology.

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