Mycorrhiza-improved P acquisition of host plants: A mini-review

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Abstract

As a beneficial endophytic fungus, arbuscular mycorrhizal fungi (AMF) are widely distributed in nature and can symbiotically grow with approx. 80% of terrestrial plants, helping host plants to grow and develop with increased tolerance to various stresses. One of the most important functions of AMF is to promote the uptake of P from the soil by the host plant. The available findings explain the role of mycorrhizal fungi. For example, AMF increase the phosphorus uptake area of plant roots by improving the root architecture, and the extraradical mycelium can extend beyond the phosphorus-deprived areas that are inaccessible to the root, helping to expand new phosphorus sources. AMF also increase the secretion of phosphatases and organic acids in plant roots to improve the soil environment for accelerating the conversion of insoluble phosphorus. The phosphorus transporter protein genes expression is induced by AMF to enhance host P acquisition. The review briefly outlines these potential mechanisms and suggests outlooks for future research.

Keywords: Acid phosphatase; Mycorrhizal fungi; Low phosphorus; Phosphate transporter

1. Introduction

Arbuscular mycorrhizal fungi (AMF) are beneficial fungi in soil that are widely distributed in various ecosystems. After colonizing plant roots, AMF can form a mutual symbiosis with the host root, namely, arbuscular mycorrhiza. In roots, AMF establishes special structures inside and outside the root, such as arbuscules, spores, intraradical mycelium, and extraradical mycelium. These mycorrhizal structures help the root to expand the absorption area of water and mineral nutrients, as well as extend into the soil where the root hairs cannot reach the region to absorb mineral elements. In addition, AMF can colonize neighboring plant roots to form underground common mycelial network. Hence, AMF can promote plant growth, improve root architecture, increase photosynthetic rate and uptake of mineral nutrients, and enhance stress tolerance [1-5].

Low phosphorus stress is one of the major factors limiting agricultural production. In practice, people mainly supplement the phosphorus (P) required by crops by applying P fertilizers, but plants without low P stress adaptations difficulty absorb enough P for normal growth because 80-90% of P in arable land is adsorbed by soil particles [6]. In addition, the diffusion coefficient of P in the soil is small and the uptake of effective soil P by plants depends largely on the root morphology, such as root surface area, root volume, total root length, and lateral root development at all levels.

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[7]. Under low P stress, the P content of plant cells decreases, which is detrimental to photosynthetic phosphorylation and hinders the cycling of NADP+ and NADPH in the Calvin cycle. As a result, low P in plants affects the efficiency of the photosynthetic electron transport chain, which in turn reduces the intensity of various physiological activities of plants [8]. Therefore, it is very urgent to improve the efficiency of plant P uptake.

It has been shown that AMF promote soil P uptake by host plants, and the positive effect has been widely demonstrated under different crop and environmental conditions [9]. The review simply summarizes the advance in mycorrhiza-improved P acquisition of host plants by means of three potential paths (improved root architecture, released soil phosphatase, and induction of phosphorus transporter protein gene expression).

2. Improved root architecture by mycorrhization

P is easily fixed by the colloids in the soil and difficult to diffuse. Plants rely mainly on the root in the uptake and utilization of P in the soil, and their root architecture determines the spatial structure of the root system in the soil and the size of the soil contacted area, which is proportional to the efficiency of plant P uptake [10]. When low P stress occurs, plants often need to change their root architecture by increasing root length, root : shoot ratio, number of lateral roots, root hair length and density, to increase the area of P uptake by the root system [11-12].

It is assumed that the effect of AMF on plant physiological and biochemical processes is closely related to changes in root architecture, as AMF forms an unique arbuscule structure. The effect of AMF on root architecture is associated with two paths: (1) the root biomass, root surface area, and total root length are increased significantly after AMF inoculation, e.g. Stylonisantes guianenisias and Ceratonia siliqua [13-14]; (2) AMF significantly promoted the occurrence of lateral roots and the spatial distribution of roots in the soil. For example, AMF inoculation dramatically elevated the number of lateral roots in grape [15], litchi [16], and rice [17]. In tea, Claroidelglomus etunicatum inoculation significantly increased root-hair length, but not root-hair diameter and density under low soil P levels conditions, indicating the synergistic benefit of AMF and root hairs [18].

The effect of AMF on improving root architecture is more pronounced under stressful environments. For example, Berta et al. [19] found that inoculation of Glomus mosseae BEG12 to tomato infected with Rhizoctonia solani 1556 increased the number of root hairs, which resulted in enhanced P acquisition of the plants. Vallino et al. [20] showed that AMF significantly promoted the increase of root branching in rice under either drought or flooding. Other studies also found that AMF improved plant root architecture under stress conditions such as low temperature, salt stress, and crude oil pollution. [21-23].

3. Secretion of phosphatase in the soil by mycorrhization

Most of the P in the soil are organic, and plants lacking P secrete phosphatases that act on chelates of insoluble P in the soil, activating the conversion of organic P into inorganic P, which can then be absorbed and used. Phosphatase dephosphorylates the corresponding substrates such as phosphates chelated by heavy metal ions (iron and aluminum), completely removing the phosphate group from the substrate molecule by hydrolyzing the phosphate monoester, while generating phosphate ions and free hydroxyl groups [24]. Phosphatases can be classified as acidic, alkaline and neutral phosphatases based on the pH value. Among them, acid phosphatase is commonly responsive to increased secretion in plants undergoing low P stress. Purple acid phosphate (PAP) is one of the more specific phosphatases. Plants are induced to express PAPs in large amounts under low P stress and can secrete them into the soil to release soil Pi for plant use [25]. The detection of Arabidopsis revealed that the genes encoding PAPs are AtPAP10, AtPAP12 and AtPAP26, of which AtPAP10 has the strongest ability to hydrolyze insoluble P and the utilization of insoluble P by transgenic Arabidopsis was significantly increased when it was overexpressed [26]. Double mutants of AtPAP12 and AtPAP26 represented lower capacity of the hydrolysis of DNA, glucose-6 phosphate, and glycerol triphosphate [27], indicating that the activation and utilization of exogenous organophosphorus involved in different species of PAP may be different. Rubio et al. [28] showed that AMF increased soil acid phosphatase activity under soil contamination. The study by Javot et al. [29] found that AMF-colonized plants promoted an increase in plant phosphatase secretion and thus improved plant P uptake. Our study also revealed that under 0.1 mM and 1 mM P levels, Funneliformis mosseae dramatically reduced leaf PtPAP1 and PtPAP3 and root PtPAP3, but induced the expression of root PtPAP1 in trifoliate orange under 1 mM P levels [30]. This seems to infer that the release of mycorrhizal-induced phosphatase may originate from the mycorrhizal fungus itself rather than from the plant, but more experiments are needed to be done. At the same time, Funneliformis mosseae further stimulated soil acid phosphatase activity of trifoliate orange grown in 0 mM, 3 mM, and 30 mM P levels [31]. However, in tea, Claroidelglomus etunicatum significantly reduced root acid phosphatase activity
under low P levels conditions, but increased it under optimal P levels [18]. This implies that mycorrhiza-effect changes in plant phosphatase are dependent on soil P levels.

4. Induction of phosphorus transporter protein gene expression by mycorrhization

When soil P deficiency occurs, plants increase the synthesis of P transport (PT) proteins. PTs can be classified into low and high affinity systems [32]. Among the PTs, all genes of the Ph1 family belong to the high-affinity system, and this part of genes is mainly responsible for the basic processes of P uptake and transport in plants [33]. Earlier studies revealed that the genome of rice contained 11 Ph1 family genes based on transcriptional analysis, 10 of which are expressed in the roots [34]. In addition, Mudge et al. [35] analyzed the expression of Ph1;3 and Ph1;4 in Arabidopsis thaliana and found that this class of genes has two functions, namely, promotion of soil P uptake by plants and the translocation of P from the plant to the vascular bundle. Studies on Ph1 genes in tomato and potato showed that among StPT1, StPT2, LePT1 and LePT2, only StPT1 and LePT1 were expressed in large amounts in both P-deficient and non-P-deficient environments, whereas StPT2 and LePT2 were expressed only in P-deficient environments [36-38].

Is there a link between the ability of mycorrhiza to aid P uptake by host plants and PT proteins? Harrison et al. [39] originally isolated the cellular transmembrane P-running protein gene Gvpt, which has a very similar machinery to the Ph1 family of genes, from Glomus versiforme. Maldonado et al. [40] identified the GipT in Glomus intraradices, which is functionally similar to Gvpt. Hence, it is hypothesized that mycorrhizal roots can improve P nutrition in host plants through two pathways, viz., a high-affinity PTs from the host and AMF [41].

In addition to the P acquisition by mycorrhizal fungi themselves, the P transport system of plants is also influenced by AMF. Mycorrhizal roots were found to induce massive expression of StPT3, indicating the specificity of StPT3 induced by mycorrhization [42]. Harrison et al. [43] also isolated a high-affinity PT gene, OsPT11, from alfalfa that was specifically induced by mycorrhizal colonization. Paszkowski et al. [44] obtained the mycorrhiza-induced high-affinity PT protein gene OsOT11 from rice. Grace et al. [45] showed that AMF significantly up-regulated the expression of HvPT8 in the root system. AMF also contain three PT proteins, GvPT, GipT and GmosPT, and low P promotes the expression of these three PTs in mycelium, enhancing the uptake of P from soil by AMF and transporting P to the plant, indirectly improving the P uptake efficiency of the plant [40]. In addition, Clarideoglomus etunicatum dramatically induced CsPT1 expression but reduced CsPT4 expression in tea plants, irrespective of soil P status, suggesting that CsPT1 is specific for mycorrhization [18]. In trifoliate orange, Funelliformis mosseae inoculation up-regulated the expression of PtaPT3, PtaPT5, and PtaPT6 in roots, regardless of 0.1 mM and 1 mM P levels [30]. AMF up-regulates the expression level of PTs and promotes P transport in plants [43, 46].

The fact that both mycorrhizal-specific PT genes and other high-affinity PT genes are enhanced in expression in response to low P stress is well established. StPT3 expression in potato colonized by AMF decreased with increasing soil P levels [41]. Using isotope labeling, mycorrhiza-colonized plants take up P mainly through mycelium, while P uptake through root hairs and root surface is almost negligible [47-48]. It is clear that mycorrhizae are essential for up-regulating the expression of certain high-affinity PT genes in plants.

5. Conclusion

In summary, AMF promote P uptake in host plants mainly through three paths: (i) improving root architecture to increase soil P uptake area; (ii) promoting the decomposition of organic P in soil into inorganic P available for plant uptake by increasing the secretion and activity of phosphatase; (iii) up-regulating the expression level of mycorrhizal-specific PT genes to increase the efficiency of P transport in hosts. The three mechanisms described above may occur together on some plants, or one or more may occur on some plants. However, this study also has many urgent prospects, mainly in the following areas:

- How do mycorrhizal fungi regulate root architecture and stimulate lateral root formation? The occurrence of lateral roots depends on various factors, such as nutrient levels, specific genes, etc. The role of mycorrhiza is to be analyzed.
- Numerous studies have shown that mycorrhizal fungi are able to secrete phosphatases into the root zone, but how do mycorrhizal fungi promote phosphatases? Does this phosphatase originate from the plant or AMF?
- Both plants and AMF have a PT system to promote P uptake. Do the two act synergistically or do they compete? Will they be dependent on soil P levels?
Compliance with ethical standards

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Disclosure of conflict of interest

All authors declare that they have no conflict of interest.

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