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RELATIONSHIPS BETWEEN MYCORRHIZAE AND ROOT HAIRS

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Abstract

Mycorrhizal extraradical hyphae and root hairs coexist on the root surface and are responsible for water and nutrient absorption from the soil. Root hairs generally are a preferential adhesion point colonized by ectomycorrhizal hyphae, and eventually are suppressed or incorporated in the fungal mantle. However, arbuscular mycorrhizal (AM) fungi occasionally penetrate root hairs of host plants. A root hair feature is not a reliable indicator of mycorrhizal dependency in plants, as well a mycorrhizal growth response. AM fungal inoculation has increased and reduced effects on root-hair growth (including length, density, and diameter), which is related mainly with auxin and some potential factors (i.e. P and glucose). Such AM effects on root hair can be regulated by substrate P and soil water levels. Root hairs have the preponderant role in soil adhesion under sand or semi-arid conditions, in comparison with extraradical hyphae. In addition, root hairs have higher effectiveness in P acquisition and utilization in biomass production than extraradical hyphae under P-deficient conditions. Under drought stress, AM fungi almost replace the absence of root hairs to enhance plant tolerance through alternative pathways.

Key words: Arbuscular mycorrhiza, Auxin, Extraradical hyphae, Root hair, P acquisition.

Introduction

Root hairs are tubular and cellular outgrowths of epidermal cells in plant roots that extend from the root surface into the soil to absorb water and inorganic nutrients mainly including immobile phosphorus (P), and to interact with soil microflora (Tominaga-Wada & Wada, 2014; Dolan, 2017). In general, long and dense root hairs are the important trait in ensuring efficient acquisition of both macro- and micro-nutrients in the early establishment of crop plants in nutrient-limited soils and low nutrient input cropping systems (Wang *et al*., 2016). Furthermore, root hairs are considered as the preferred site of infection by nitrogen-fixing rhizobium (Hossain *et al*., 2015). Therefore, root hairs have an important role in resource exchanges between the rhizosphere and plants. Root hairs are regarded as a determinant factor of the microbiota thriving at the root-soil interface (Robertson-Albertyn *et al*., 2017). For example, the beneficial bacterium *Pseudomonas* sp. could efficiently colonize root hairs of barley, and *Enterobacter* sp. infected into root hairs of finger millet (*Eleusine coracana*) (Kellogg, 1998; Buddrus-Schiemann *et al*., 2010). As stated by Zhu *et al*., (2009), the acquisitions of mobile nutrients such as NO_3^- are less important by means of root hairs.

Besides root hair, mycorrhizas that are the symbiotic associations formed between soil mycorrhizal fungi and roots of terrestrial plants, can extend their well-developed extraradical hyphae from the roots into growth substrates for nutrient acquisition (Hashem *et al*., 2018). Both root hairs and mycorrhizal extraradical hyphae collectively exist in the root surface (Fig. 1) to increase surface areas of root systems for nutrient acquisition. In general, root hairs (Φ 30 µm) are less extensive and wider than mycorrhizal fungal hyphae (Φ 10 µm, whilst tip hyphae Φ 2 µm) (Novero *et al*., 2008; Allen, 2009), which can entry into smaller soil pores and ultimately take up more soil nutrients (Peterson & Farquhar, 1996). As a general rule, a plant with abundant root hairs is less dependent on mycorrhizal symbiosis for nutrient uptake (Baylis, 1975). This suggests a strong negative relationship between mycorrhizas and root hairs. Thus, it seems that root-hair length and abundance may indicate the degree of mycorrhizal dependence (Baylis, 1975). For example, plants that have large-diameter roots and few root hairs, such as *Citrus* sp., are strongly mycorrhiza-dependent, while these having thinner roots and a huge number of root hairs, such as *Echinops exaltatus* are less dependent on mycorrhizal symbioses (Novero *et al*., 2008). Other typically non-mycorrhizal plants, including rushes, sedges, and grasses have highly developed root hairs (Hetrick, 1988). Plants under the absence of root hairs condition may recruit arbuscular mycorrhizal (AM) fungi in an attempt to improve both P acquisition and plant growth (Brown *et al*., 2013). As a result, root hairs possess more effective capacity in P-acquisition than AM fungi under P-deficient condition (Brown *et al*., 2013). As reported by Li *et al*., (2014) under drought stress, AM fungi mainly improved plant P and water uptake, and root hairs presumably increased shoot P levels, suggesting the different role between AMs and root hairs. Such strategies strongly imply the complex relationship between root hairs and mycorrhizas.

Mycorrhizal colonization in root hairs: Root hairs are highly sensitive to the diffusible factors released by soil mycorrhizal fungi, such as hypathorine and indole-3-acetic acid (IAA) (Novero *et al*., 2008). During the first stage of ectomycorrhizal development, root hairs are generally a preferential adhesion point colonized by ectomycorrhizal hyphae which are detected as one of abundant extra-cellular fibrillar polysaccharidic nature (Sisti *et al*., 2003; Novero *et al*., 2008) and developed between root epidermal cells and in the first layers of the root cortex, eventually, formed the Hartig net and further the mantle. As a result, root hairs are incorporated in the mantle of ectomycorrhizas.

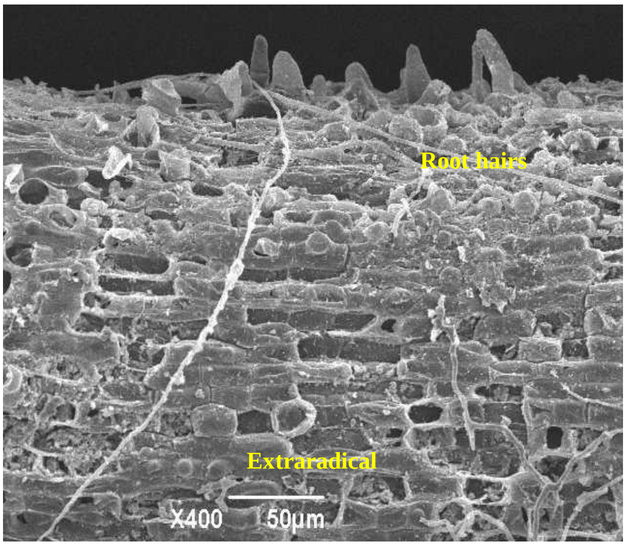

Fig. 1. Collective presence of both root hairs and extraradical hyphae of an AM fungus, *Funneliformis mosseae*, on the root surface of *Poncirus trifoliata* plants.

During the AM development of plants, mycorrhizal hyphae can colonize root hairs, without the appressorium-like structure (Novero *et al*., 2008). Root hairs of *Avena* sp., *Clintonia borealis*, *Festuca rubra*, *Lilium formologo*, *Panax quinquefolius*, *Pisum sativum*, *Taxus baccata*, and *Taxus canadensis* plants were colonized mainly by AM fungi, while *Hordeum* sp., *Melilotus alba*, *Secale* sp., *Narcissus* sp. and *Triticum* sp., occasionally represented root hair entry of mycorrhizas (Guinel & Hirsch, 2000). In fact, mycorrhizal hyphae can produce either some hydrolases or small molecules to relax plant cell walls, which is subsequently colonized by mycorrhizal hyphae (Peretto *et al*., 1995; Mousa *et al*., 2016). In *Lotus japonicus* plants, root mycorrhizal colonization with *Glomus intraradices* was absolutely independent on the presence or absence of root hairs (Novero *et al*., 2008). Up to 92 % of root hairs in *Festuca rubra* plants were colonized by AM fungi (Nicolson, 1959). The wood plants in Ontario, Canada had the hyphal colonization in root hairs by native mycorrhizal fungi (Guinel & Hirsch, 2000). And, inoculation with *G. aggregatum* frequently penetrated root hairs in pea plants (Guinel & Hirsch, 2000). In addition, the AM fungal hyphae in pea often wrapped the root hair in a twisted coil, and grew along its surface for a while to reach the base of the root hair, finally, penetrating the cortical cells. In short, root hairs can be colonized by mycorrhizal hyphae, especially by ectomycorrhizal hyphae, although AM fungi occasionally penetrate root hairs.

Root hairs and mycorrhizal dependency of plants: In arbuscular mycorrhizas (AMs), many studies have confirmed the Baylis (1975) hypotheses, namely, root hair number is negatively correlated with mycorrhizal dependent degree. For example, citrus plants possess few root hairs, with highly mycorrhizal dependence (Wu *et al*., 2016). Possibly, plants with a coarse root possess a limited intrinsic ability to absorb nutrients, and in return, thereby, benefit from the mycorrhizas to increase their absorbed surface area for nutrients (Maherali, 2014). Plants under rich soils have generally abundant root hairs and poor mycorrhizal colonization (Muthukumar *et al*., 2004). Manjunath & Habte (1991) concluded that root hair-length and root-hair incidence were important determinants of mycorrhizal dependency. However, in some pasture species inoculated with a *Glomus sp*., mycorrhizal effectiveness of P was negatively related to root-hair length (Schweiger *et al*., 1995). Similarly, high mycorrhizal dependent represented fine roots (Φ 4 mm) in warm-season than in cool-season grasses (Hetrick *et al*., 1988). In *Leucaena* species, *L. retusa* possesses less mycorrhizal dependent than other *Leucaean* species, despite all *Leucaena* species have coarse roots with few root hairs (Manjunath & Habte, 1991). The families of *Medicago sativa* with shorter root hairs had less mycorrhizal colonization with *G. versiforme* than these with longer root hairs (Lackie *et al*., 1988). The hairy roots of tomato and carrot having numerous and long root hairs were still easily colonized by AM fungi (Novero *et al*., 2008). Novero *et al*., (2008) used the root-hair-mutants of *Lotus japonicus* that was inoculated with *G. intraradices* to address the relation between mycorrhizal colonization and root hairs, and found that the frequency and intensity of root mycorrhizal colonization and the percentage of arbuscles were independent on root hair status. It seems that root hair feature is not a reliable indicator of mycorrhizal dependency, as well mycorrhizal growth responses (Maherali, 2014).

Relative importance of mycorrhizas versus root hairs: AM hyphae represent an absorbing role at a lower metabolic cost than root hairs (Price *et al*., 1989). Moreno-Espíndola *et al*., (2007) found that Bermuda grass and maize plants possessed greater root-hair density and three times more sand particles but less extraradical hyphae than those of amaranth and sunflower. They, thus, concluded that root hairs may have a preponderant role in soil adhesion under sand or semi-arid conditions, in comparison with extraradical mycorrhizal hyphae. In addition, in litchi plants, the application of girding greatly reduced root-hair length, which is closely associated with decreasing the C pools in host plants (Shu *et al*., 2016).

Mycorrhizal hyphae and root hairs collectively absorb soil P at the root surface. To compare the relative importance of them in P acquisition ability, a root hairless barley mutant and its wild type were colonized by seven AMF species (Jakobsen *et al*., 2005). The results showed that mycorrhizal hairless mutant roots exhibited a 50–130% higher P level than non-mycorrhizal roots of wild type, indicating a relatively greater contribution of mycorrhizal hyphae (10–15 cm) through longer extension than root hairs (< 1–2 cm) in non-P-depleted soils. In addition, mycorrhizas generally increase below-ground respiration than non-mycorrhizal controls, resulting in more C expenditure. If plants grown in P-deficient conditions are absent of root hairs, plants might recruit AMF to improve P acquisition, in order to compensate the absence of root hairs, only partly, but not fully (Brown *et al*., 2013). Hence, root hairs may possess a greater capacity in P acquisition than AMF under soil P deficient condition. Moreover, mycorrhizal plants possibly contribute low efficiency in P utilization for biomass production under soil P deficient condition (Jakobsen *et al*., 2005).

As a result, P utilization of root hair pathway is used more effectively in plant growth than those of mycorrhizal pathway.

The bald root hair mutant of barley inoculated with *R. intraradices* represented relatively lower root U uptake efficiency than the wild type barley, irrespective of substrate P levels (Chen *et al*., 2005). This indicated that mycorrhiza represented higher effectiveness in remediation of heavy metal contaminated soils than root hairs.

The presence of root hairs is critical for drought tolerance (Brown *et al*., 2012). Under soil drought stress, mycorrhizas almost replace root hairs to function the nutrient and water absorption (Li *et al*., 2014), while they have different mechanisms to respond drought stress: improving uptake of water and P by mycorrhizas, and the improvement of shoot P by root hairs (Li *et al*., 2014).

Mycorrhizal effects on root-hair growth: In general, root exudates (e.g., rutin) substantially stimulate mycorrhizal fungal growth (Lagrange *et al*., 2001). In contrast, a fungal exudate, such as hypathorine, inhibits root-hair growth, and another fungal exudate, IAA, can counteract the negative effect (Béguiristain & Lapeyrie, 1997; Ditengou *et al*., 2000). These exudates of roots and mycorrhizal fungi possibly could modulate the growth and development of one or another.

Earlier studies revealed that ectomycorrhizal formation frequently collapsed and degraded root hairs in the mantle develops (Brown & Sinclair, 1981; Novero *et al*., 2008)., The root-hair inhibition may be due to the accumulation of the trypotophan betaine hypaphorine released by ectomycorrhizal fungi (Béguiristain & Lapeyrie, 1997; Ditengou *et al*., 2000). Such suppressions often give rise to the vacuolation of root hairs, resulting in the accumulation in root hairs (Thomson *et al*., 1989). Additionally, root hairs do present recognizable or binding conduits for fungal hyphae to establish ectomycorrhizal associations.

In an evergreen tropical forest, root hairs and AM symbiosis showed a negative relation in herb plants (Herrera-Peraza *et al*., 2004). In contrast, trees, shrubs and vines did not show such a characteristic, or even exhibited positive correlations between AM and root hairs. In potted environments, AM fungal inoculation showed different changes in root-hair growth (Table 1). For example, in *Alnus glutinosa* seedlings, inoculation with *Gigaspora rosea* significantly increased the total number of root hairs but reduced the density of root hairs (Orfanoudakis *et al*., 2010). They assumed that such reduction in root-hair density did not result from the nutrient (especially P) mechanism but from some carbon expenditure caused by mycorrhizal symbioses. Similarly, maize plants colonized by *G. mosseae* represented lower root-hair density and length, respectively, as compared with non-AMF-colonized controls (Kothari *et al*., 1990). The *G. mosseae*- and *G. intraradices*-colonized sorghum plants had substantially lower length and incidence of root hairs, as compared with their non-AM counterparts (Sun & Tang, 2013). In tea plants, inoculation with *Claroideglomus etunicatum*, *Diversispora spurca*, *D. versiformis* and a mixture of the three AMF species significantly reduced root-hair number and root-hair length, relative to non-AMF inoculation (Shao *et al*., 2018). A significantly negative correlation was found between root hair number and mycorrhizal colonization in tea plants. In fact, AMF-inoculated plants have greater tissue P concentrations (Smith & Smith, 2011; Smith *et al*., 2011), which generally are negatively correlated with density and length of root hairs.

Recently, Wu *et al*., (2016) evaluated the effects of four AM fungal species on root-hair growth in a root-hair-deficient trifoliate orange. They found that AM trifoliate orange plants recorded greater root-hair density than non-mycorrhizal plants, irrespective of AM fungal species and lateral root orders, implying that mycorrhizal colonization might take part in the event of root-hair origination. In addition, AM-modulated changes in root-hair length were possibly dependent on the diameter and age of lateral roots. Liu *et al*., (2018a) reported a significantly higher root hair density in trifoliate orange under 0.1 mM P levels of substrates, while a significantly lower root-hair density under 1 mM P levels of substrates. Furthermore, exogenous abscisic acid (ABA), indole butyric acid (IBA), or jasmonic acid (JA) application to hyphae could strengthen the *D. versiformis*-induced change in root hair density, while weaken the root hair length in trifoliate orange (Liu *et al*., 2016). It seems that mycorrhizal fungi could positively regulate root-hair growth of plants with root-hair deficiency, which might be further affected by soil water status and exogenous phytohormones.

Substrate P and water levels alter mycorrhizal roles in root hairs: Mycorrhizal roles in regulating root-hair growth can be affected by substrate P and water levels. Zou *et al*., (2017) reported that AMF effects on root-hair length were absolutely dependent on soil water status. Inoculation with *D. versiformis* conferred a significantly lower root-hair length under well-watered and a markedly higher root-hair length under drought stress (Zou *et al*., 2017). Effects of AMF on root-hair length under well-watering could be also reversed by soil drought stress. Obviously, soil nutrients move slowly under drought stress, and a collective cooperation of both mycorrhizas and root hairs is needed to help plants to absorb water and nutrients.

In addition to soil water status, substrate P levels heavily alter AMF-effects on root-hair growth. In root-hair-deficient trifoliate orange seedlings, inoculation with *F. mosseae* significantly increased root-hair density under 0.1 mM P levels of sands, while dramatically decreased root-hair density under 1 mM P levels of sands (Liu *et al*., 2018a). Possibly, P deprivation can induce the initiation and elongation of root hairs (Cao *et al*., 2013). It seems that AMF effects on root-hair density are dependent on substrate P levels, at least in root-hair-deficient plants.

Table 1. Responses of root-hair variables to arbuscular mycorrhizal (AM) fungal inoculations.

Host plants	AM fungus	Root-hair variables	Reference
Alnus glutinosa	*Gigaspora rosea*	Root-hair density↓	Orfanoudakis *et al*., 2010
Camellia sinensis	*Claroideoglomus etunicatum*	Root-hair length↓ Root-hair diameter↑ Root-hair number↓	Shao *et al*., 2018
	Diversispora versiformis	Root-hair length↓ Root-hair diameter↑ Root-hair number↓	
	D. versiformis	Root-hair length^{ns} Root-hair diameter↑ Root-hair number↓	
	AMF mixture	Root-hair length^{ns} Root-hair diameter^{ns} Root-hair number↓	
Poncirus trifoliata	*Claroideoglomus etunicatum*	Average root-hair density↑ Average root-hair length↓ Average root-hair diameter^{ns}	Wu *et al*., 2016
	Diversispora versiformis	Average root-hair density↑ (exogenous ABA, IBA and JA strengthen the effect) Average root-hair length↓ (exogenous ABA, IBA and JA weaken the effect, whereas soil drought reverses the AM effect) Average root-hair diameter↑ (exogenous ABA, IBA and JA and soil drought stress had no significant effect)	Liu *et al*., 2016; Wu *et al*., 2016; Zou *et al*., 2017
	Funneliformis mosseae	Root-hair density↑, root-hair density↓ in 1 mM P Root-hair length↓, root-hair density↑ in 1 mM P and drought stress Root-hair diameter^{ns}, root-hair diameter↑ in 1 mM P and drought stress	Wu *et al*., 2016; Liu *et al*., 2018a, 2018b
	Rhizoglomus intraradices	Root-hair density↑ Root-hair length↓ Root-hair diameter^{ns}	Wu *et al*., 2016
Sorghum bicolor	*Glomus mosseae*	Root-hair length↓ Root-hair incidence↓	Sun and Tang, 2013
	G. intraradices	Root-hair length↓ Root-hair incidence↓	
Zea mays	*Glomus mosseae*	Root-hair density↓ Root-hair length↓	Kothari *et al*., 1990

↑, ↓, and ^{ns} indicate that the variable is significantly increased, decreased, and no responses to mycorrhizal colonization

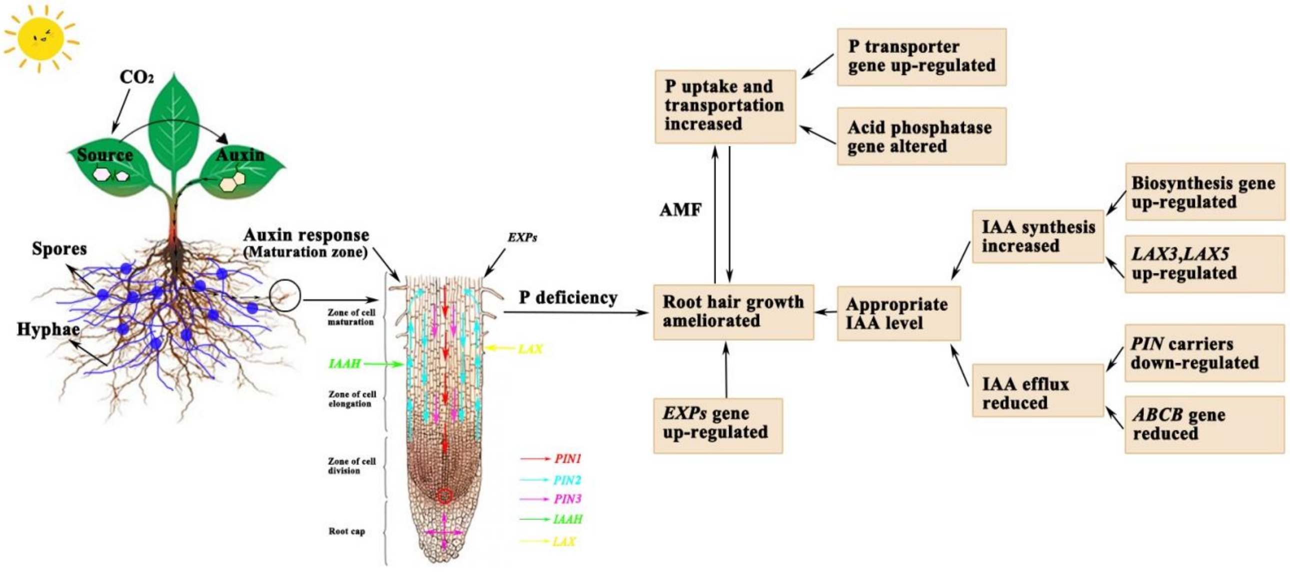

Fig. 2. AM plants showing better root hair growth under P deficient conditions. Under P adequate conditions, mycorrhizas reduce root hair growth, while under P deficient conditions, mycorrhizas increase root hair growth, which is originated from the up-regulation of *EXPs* and the appropriate IAA levels from the increase of IAA synthesis and the decrease of IAA effluxes (Liu, 2018).

Underlying mechanisms regarding mycorrhiza-modifying root-hair growth: During root-hair morphogenesis, some phytohormones, including abscisic acid (ABA), auxin, brassinosteroid (BR), ethylene, JA, and strigolactone (SL), potentially modulate the development and both root hairs and mycorrhizas, whilst auxins play an organizing node for environmental/ hormonal pathways (Lee & Cho, 2013; Li & Lan, 2015; Wang *et al.*, 2017). For instance, ABA accelerates auxin biosynthesis and polar transport in the root tip, resulting in the accumulation of auxin in root-hair zone to affect root hair growth (Wang *et al.*, 2017). Most microorganisms are known to produce auxin and auxin precursors to alter root (including root hairs) development of host plants (Sukumar *et al.*, 2013). Mycorrhizal inoculation considerably increased root IAA concentration of trifoliate orange seedlings to induce greater root-hair density (Wu *et al.*, 2016). As stated by Liu (2018), under P deficient conditions, mycorrhizal presence stimulated root-hair growth, which is associated with up-regulation of *PtEXPs* and IAA levels (Fig. 2). Meanwhile, IAA accumulation was derived from the increase of IAA synthesis and the reduction of IAA effluxes in roots. Nitric oxide (NO), a downstream molecule in auxin signal pathway, was strongly increased by AMF inoculation (Wu *et al.*, 2016). These results suggest that AMF-modulated root-hair growth is related to auxin signaling and homeostasis. The IAA increase in AM plants is possibly due to two factors: (i) spores of AMF (i.e. *Rhizoglomus intraradices*) could produce a small quantity of auxins (Ludwig-Müller, 2010); and (ii) both root auxin synthesizing genes and root auxin-species influx carrier genes are up-regulated, and root auxin efflux carrier genes are down-regulated by mycorrhization (Liu *et al.*, 2018a, 2018b; Zhang *et al.*, 2016, 2018).

Besides auxin, P, glucose, and methyl jasmonate (MeJA) are also involved in regulating root-hair growth under mycorrhization (Wu *et al.*, 2016). A contribution of AMF to plants is the P acquisition from soils (Smith *et al.*, 2011), which is due to the up-regulation of P transporter genes and the changes in acid phosphatase genes (Fig. 2) (Liu, 2018; Liu *et al.*, 2017). Greater P levels in AM roots will regulate root-hair development through modifying epidermal cell specification and root-hair initiation (Zhang *et al.*, 2003). Mycorrhizal C pools in roots acquire more glucose for AM development, which also shift the expression of Aux/IAAs to induce root-hair initiation (Mishra *et al.*, 2009). A considerably higher MeJA levels in AM plants (Wu *et al.*, 2016) could possibly promote the formation of root hairs by means of an interaction with ethylene (Zhu *et al.*, 2006).

Future perspectives

This review states the relationship between mycorrhizas and root hairs, especially when the host plants were inoculated with AM fungi. The relative importance of both root hairs and mycorrhizas in P absorption, soil adhesion, and drought tolerance will be helpful for crop breeding. Here, some researches in this field need to focus on the following:

(1) Studies are needed to provide more evidence in the colonization of root hairs by AM fungi, especially electron microscope images.

(2) Transcriptome assay can provide the detailed characterizations of transcriptional levels associated with root-hair growth and mycorrhizas development.

(3) The regulatory networks in molecule levels regarding AM-modified root-hair growth are also needed to be further studied.

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