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REVIEW

The interplay of direct and mycorrhizal pathways for plants to efficiently acquire phosphorus from soil

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KEYWORDS

Arbuscular mycorrhizal fungi, direct pathway, mycorrhizal pathway, trade-offs, organic phosphorus-mineralizing bacteria

HIGHLIGHTS

- Plants make potential trade-off between direct and mycorrhizal pathways based on C input and P gain.
- AM fungi sense soil P heterogeneity and release exudates that select for organic P-mineralizing bacteria.
- AM fungi and soil bacteria develop a C–P mutualistic exchange in organic P patches.

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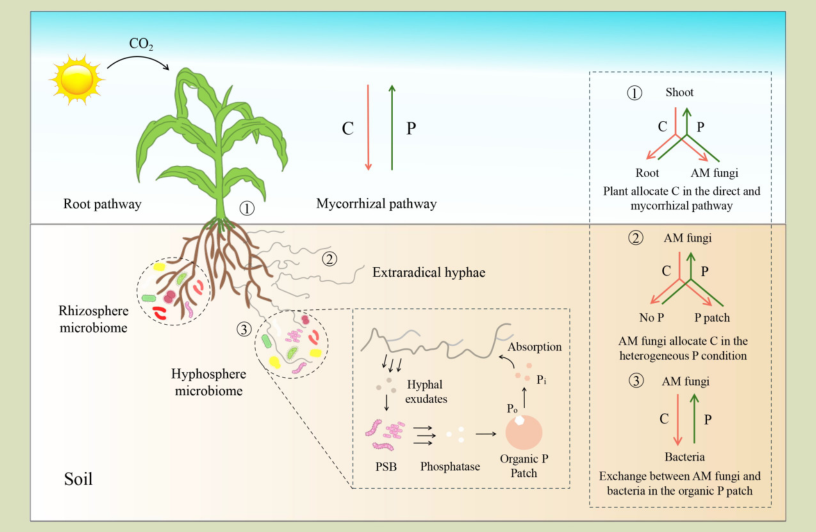
GRAPHICAL ABSTRACT



ABSTRACT

To efficiently obtain P from soil, most terrestrial plants form symbiosis with arbuscular mycorrhizal (AM) fungi and thus have two P uptake pathways, i.e., the direct pathway (DP) via roots, particularly root hairs, and the mycorrhizal pathway (MP) via AM fungal hyphae. AM fungi form an extraradical hyphal network to expand their contact area with soil and release carbon-rich compounds, which provide a high-energy habitat for soil bacteria. The bacteria affected by AM fungi support P nutrition of AM fungi by secreting extracellular phosphatases. During the P acquisition process, both DP and MP function and require C fixed by plant photosynthesis to maintain P transport. Plants make trade-offs between DP and MP based on C inputs and P benefits. This review first systematically explores the potential trade-offs between plant C inputs and P gains of DP and MP as well as the factors that influence such trade-offs. Then the response of AM fungi to soil nutrient heterogeneity and the mechanisms by which AM fungi select bacteria to mineralize organic P and increase the P contribution of MP were analyzed. Future studies need to apply emerging methods and technologies to accurately quantify the contribution of DP and MP to plant P absorption under different conditions and provide the theoretical basis for optimizing sustainable agricultural production systems.

1 Introduction

Phosphorus is one of the essential nutrients for plants. To meet the growth and development requirement of plants and maintain high yield of crops, large amounts of P fertilizers are applied to the soil annually[1]. However, most of the applied P becomes unavailable to plants by being converted into non-soluble complexes by soil minerals such as calcium, magnesium, iron and aluminum and through immobilization into organic P forms strongly limiting seasonal P fertilizer use efficiency[2]. It is estimated that the P surplus of global farmland in 2021 was about 8.27 Mt, accumulating mainly as organic P and non-soluble P, which cannot be directly absorbed and used by plants, posing a potential threat to sustainable crop production. This accumulation of P in soils has been termed legacy P and tends to be the norm in systems where P fertilizer is applied. Therefore, there is a conundrum around how to produce more food with less P fertilizer inputs, utilizing some of the legacy P, while protecting the environment and improving livelihoods of farmers.

To efficiently acquire P from soil, most plants have evolved different strategies. They can absorb P directly from soil via root epidermal cells and root hairs, named the direct pathway (DP). In addition, more than two thirds of terrestrial plants form symbiosis with arbuscular mycorrhizal (AM) fungi, which acquire P beyond the rhizosphere by producing an extensive network of extraradical hyphae and accessing soil pores that are inaccessible to roots. This pathway is called the mycorrhizal pathway (MP) (Fig. 1)[3]. In addition, the extraradical hyphae of AM fungi have strong growth and unlimited branching capabilities that can extend quickly in soil. They release carbon-rich compounds (e.g., carbohydrates, amino acids and carboxylates) into soil, changing the physical, chemical and biological properties of the thin layer of soil adjacent to extraradical hyphae and forming a unique hyphosphere[4]. A large number of bacteria colonize in the hyphosphere, and they generally have the functions of mineralizing organic P. These bacteria functionally complement AM fungi to compensate for their limited saprophytic capabilities, which has the potential to make a great contribution to the availability of soil P[5].

For mycorrhizal plants, both DP and MP are effective pathways to obtain P from soil. These two pathways interact with each other and both require the consumption of photosynthetically fixed C to maintain nutrient transport. For DP, plants allocate C into their own roots for metabolism and thereby change root morphology to facilitate P absorption[6]. Roots also produce phosphatases and carboxylates that are released into the rhizosphere, accelerating the mineralization of organic P and the solubilization of non-soluble P, resulting in nutrient depletion in the rhizosphere[7,8]. In contrast, for MP, plants allocate C to their symbiotic partner AM fungi in the form of fatty acids and sugars and obtain P via extraradical hyphae far away from the roots[9,10]. Both roots and hyphae can release exudates to recruit soil bacteria to colonize in the rhizosphere and hyphosphere, which increase the availability of soil P and accelerate the turnover of nutrients[4]. Plants need to efficiently allocate limited C sources in different pathways based on C input costs (investment) and P resource benefits (return on investment)[11]. In this review, we first explore the potential trade-offs between plant C allocation and P acquisition in DP and MP as well as the effects of biotic and abiotic factors on such potential trade-offs. Secondly, we analyze the mechanisms of AM fungi selecting bacteria that mineralize soil P and improve plant P use efficiency via MP. Finally, we discuss emerging methods and technologies for studying the DP and MP to improve the availability of soil P and provide possible directions for future research efforts.

2 Plant carbon input and phosphorus gain between the direct pathway and mycorrhizal pathway

The allocation of C by plants to roots and AM fungi drives biogeochemical cycling of soil nutrients, while also satisfying their P needs. The contribution of roots and AM fungi to plant P uptake is often positively correlated with the allocation of C in these two pathways. If AM fungi contribute more P to plants, the more C they tend to obtain. However, this process is controlled by multiple factors and is difficult to accurately estimate quantitatively.

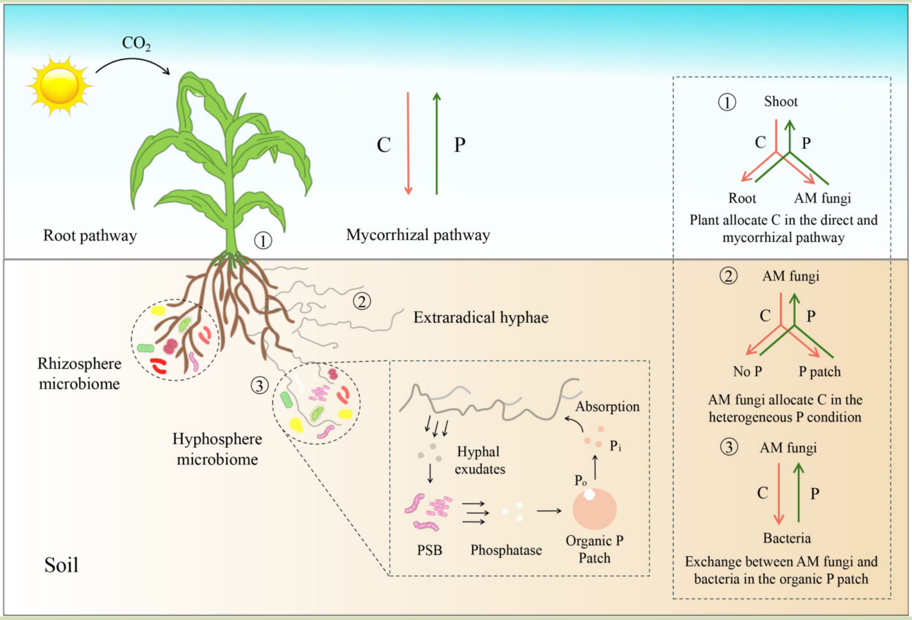


Fig. 1 Schematic of the direct and mycorrhizal pathways for plant to efficiently obtain P. Plants fix atmospheric CO_2 and transfer photosynthetic products underground for roots and arbuscular mycorrhizal (AM) fungal metabolism. The extraradical hyphae of AM fungi grow into soil micropores far away from the rhizosphere and sense soil nutrient heterogeneity. Both roots and AM fungi can release carbon-containing compounds to recruit bacteria to colonize the rhizosphere and hyphosphere to form a microbiome. The bacteria affected by hyphal exudates secrete phosphatase to mineralize soil organic into inorganic P (Po into Pi) for absorption and use by AM fungi. During nutrient acquisition, multiple strategies may be involved. First, plants make trade-offs between direct pathway and mycorrhizal pathway based on C input and P gain. Second, AM fungi allocate C in the heterogeneous P soil. Third, AM fungi and bacteria exchange C and P in organic P patches.

2.1 Methods to evaluate the contribution of direct pathway and mycorrhizal pathway for plants to acquire phosphorus

Mycorrhizal symbiosis has been considered a model system for comparing P acquisition by plants via different pathways. Previous studies have evaluated the contribution of DP and MP to plant growth and P uptake by calculating the mycorrhizal growth responsiveness and mycorrhizal P responsiveness, which use shoot dry weight and shoot P content of mycorrhizal and non-mycorrhizal plants to infer the difference[12]. This method can intuitively reflect the relative contributions of different AM fungi to host plant growth and P absorption, but cannot be used in the absence of positive responses and requires DP and MP to be mutually independent and not interfere with each other. Subsequently, the preference for plant P acquisition in the DP and MP has been further revealed by the development of integrated compartments and ^{33}P stable isotope labeling systems[13]. Using this method, the MP was found to contribute 70% of P for plants in the symbiosis between *Funneliformis caledonius* and *Solanum lycopersicum*, and in the symbiosis between *F. caledonius* and *Medicago truncatula*, the plants predominantly rely on the MP to obtain P from soil[13,14], indicating that MP can replace DP to meet plant demand for P to a certain extent. Recently, the expression of genes encoding P transporters in DP and MP were used to characterize the relative contribution of different pathways to plant P uptake[15,16]. The gene *ZmPHT1;6* was expressed a thousand-fold after colonized by AM fungi, which are responsible for the transport of P released by AM fungi. However, the genes *ZmPHT1;1*, *ZmPHT1;3*, and *ZmPHT1;4*, which are used by roots to absorb P from soil, were barely expressed[15]. However, gene expression and function are not always in direct correspondence due to the occurrence of post-transcriptional and post-translational events. In the future, it will be necessary to comprehensively consider the expression of P transporter genes and the morphological and physiologic characteristics of these two pathways and calculate multiple indices such as the preference index of P uptake, P-transporter-based and P-efficiency-based preferential index, C investment index in different contexts to maximize the quantification of the contributions of DP and MP to plant P absorption.

2.2 The effects of biotic and abiotic factors on plant carbon allocation and phosphorus acquisition in the mycorrhizal pathway

The contribution of DP and MP to plant P absorption can affect the allocation of plant C to roots and AM fungi, which is regulated by multiple factors. The availability of nutrient (especially P) in soils can directly regulate the allocation of plant C to AM fungi[17]. The photosynthesis of plants is inhibited in P-deficient soil and plants actively allocate C to roots to meet their own survival and growth requirements. When the P needs of plants are met by roots in P-rich soil, C allocation to AM fungi is reduced[18]. When the availability of soil P supply is maintained within a certain range (e.g., 8–15 mg·kg^{-1} for maize), plants will allocate more C to AM fungi and MP contribution to plant P uptake reaches a maximum of about 60%[15,16]. In addition, the application of different P forms (e.g., dicalcium phosphate and ammonium polyphosphate) can directly affect P availability in soil, thereby regulating the allocation of plant C to AM fungi and reducing the colonization of AM fungi in roots and the hyphal length density in soil[19]. In fact, the colonization by AM fungi is not invariably beneficial to plant growth, and some studies show that AM fungi colonization cause a negative impact on host plant growth[20,21]. If plant photosynthetic C consumption exceeds the growth benefit gained from the increased P uptake, the growth inhibition occurs because P uptake by mycorrhizal plants via DP and MP is not entirely additive[22]. For many plants, the mycorrhizal colonization causes a reduction in the contribution of DP to P uptake, which requires MP to maximize its effect[3]. However, plant growth inhibition is generally attributed to *cheating behavior* by AM fungi. For example, the symbiosis of AM fungi with different plants can obtain larger C gains with smaller P contributions[23], which may be due to the different characteristics of the mycorrhizal symbiosis (e.g., plant sink intensity, resource exchange surplus and environmental conditions)[24]. The above evidence suggests the potential trade-offs between DP and MP.

In both natural and agricultural systems, AM fungal species simultaneously colonize several different plants, and a plant species is also simultaneously colonized by several different species of AM fungi[25,26]. These AM fungi vary in their ability to provide P to their host plants, and plants can regulate C allocation to more beneficial AM fungi than non-beneficial AM fungi[11,27]. This prioritization can overcome the costs of reciprocity and maximize C utilization while stabilizing mutually beneficial interactions. Using $^{14}CO_2$ stable isotope labeling[11] explored the distribution of plant C when two different AM fungi (*Entrophospora claroidea* and *Dentiscutata erythropus*) simultaneously colonize onion *Allium vineale*. *D. erythropus* contributed more to *A. vineale* growth and development, and *A. vineale* allocated more C to *D. erythropus* to obtain more resources. Recently, two insightful studies demonstrated that host plants and its P status can influence the establishment of mycorrhizal symbiosis and P transfer, which is mainly regulated by the conserved P-sensing pathway, centered on phosphate starvation response (PHR) transcription factors[28,29]. In rice, the transcriptional regulatory network map of mycorrhizal symbiosis consists of 266 transcription factors and promoters of 47 mycorrhiza-related genes that control P uptake by the DP and MP at different P levels[29]. Low P levels induced PHR to activate genes that are involved in several steps of AM fungi development from initiation of root colonization to its functioning in nutrient exchange. High P levels strongly inhibit the movement of PHR to the nucleus and/or its binding to promoters, impairing root colonization and the contribution of MP to plant P uptake and reducing C allocation[28].

The C and P exchange is not just dominated by the plant, AM fungi can also determine the P supply to the plant[27]. Recently this understanding has deepened as a consequence of the development of a method using labeling with fluorescent quantum-dot nanoparticles of different colors, which allows visualization of the P redistribution process within the hyphal network. Using this method, AM fungi were exposed to the environments with high resource heterogeneity (i.e., P availability) resulting in increased P transfer. This is due to the ability of AM fungi to translocate P from the P-rich to P-poor patches to exchange resource with plants for larger C returns[30]. AM fungi can control P transfer in the trade with plants when P availability in the hyphal network is rapidly increased or decreased. If a mycorrhizal network was exposed to a P surge, AM fungi would store the surplus P, rather than immediately trading it, until plant demand for P increases again, thereby increasing the value of P. If P availability then declines, AM fungi can reallocate P in the mycorrhizal network, transferring P that was closer to roots for the stable trade returns with the P-starved plants[31]. Since the mycorrhizal network can connect to different plants within its growing area, it is critical that this trade preferably occurred with the host plants which shows the higher P demand[32]. At the genetic level, the SPX domain-containing proteins constitute a regulatory network for AM fungi to deliver P to plants, mainly composed of P signaling and transport proteins, polyphosphate (poly-P) synthesis-associated proteins and scavenging P protein[33]. The transcription factor Pho4 and its cofactor Pho2 jointly regulate P uptake and homeostasis of AM fungi during P starvation to maintain arbuscule development by activating downstream genes of conserved phosphate (PHO) signaling pathway[34]. The market economic theory has been raised to explain the mechanisms of C and P exchange between plants and AM fungi[27]. Resource heterogeneity is a common feature of ecosystems, and trading partnerships (e.g., mutualistic symbiosis) between different species can help individuals of a species cope with the resource inequality and improve their adaptability in the ecosystem.

3 Bacteria in the hyphosphere facilitate phosphorus acquisition by arbuscular mycorrhizal fungi

The intraradical hyphae of AM fungi penetrate the plant cortical cells forming dendriform arbuscule structures and delimit a narrow space called the periarbuscular space between the two membranes at the symbiotic interface for nutrient exchange with plants; the extraradical hyphae of AM fungi grow into soil micropores away from the roots, interacting closely with hyphosphere bacteria and exchanging nutrients[4,35]. The contribution of MP to plant P uptake is closely related to the nuanced communication of these two distant interfaces via the hyphae of AM fungi and bacteria dwelling in the hyphosphere can reinforce C and P exchange between plants and AM fungi in the periarbuscular space.

3.1 Arbuscular mycorrhizal fungi respond to soil nutrient heterogeneity

Spatial heterogeneity in nutrient availability is a common phenomenon in terrestrial ecosystems, and mycorrhizal plants have explored growth strategies to adapt to such heterogeneity. They can alter C allocation in heterogeneous soil, with more C used for root proliferation in patches of high nutrient availability[36]. Similarly, extraradical hyphae of AM fungi are also able to respond to soil nutrient heterogeneity. As early as half a century ago, it was found that “endophytic mycorrhizal” hyphae can grow into leaf litter and it was speculated that the fungi absorbed and transferred litter-bound mineral nutrients to host plants[37]. Decades later, stable isotope labeling experiments have provided definitive evidence that AM fungi can promote the decomposition of complex organic matter (grass leaves) and N acquisition in soil, and up to a third of N is captured by AM fungi and transferred to host plants[36,38].

Recently, with the rapid development of omics technology, only a small number of genes encoding carbohydrate-degrading enzymes were found in the published genomes of AM fungi[39,40], meaning they appear incapable of producing the lytic enzymes necessary to cleave organic molecules. Therefore, AM fungi alone are unlikely to acquire organically combined nutrients. Evidence suggests that AM fungi cannot mobilize and acquire organically bound nutrients in the absence of other soil microbes. However, in the presence of other soil microbes, AM fungi can accelerate the degradation of complex organic materials[41,42]. In other words, AM fungi do not function in isolation and the degradation of organic materials by AM fungi is mediated by other organisms.

3.2 Arbuscular mycorrhizal fungi recruit bacteria to mineralize soil organic phosphorus in the heterogeneous soil

Soil bacteria, as decomposers in the ecosystem, significantly influence global C and nutrient cycling as well as overall ecosystem function. A single gram of surface soil contains more than 10^9 bacterial cells[43]. These bacteria typically remain a viable but non-active/dormant state thus slowing metabolism without easily available C inputs[44], which weakens their ability to participate in the biogeochemical processes of many elements. AM fungi use plant-derived C for metabolism and release C sources into soil in the form of hyphal exudates, which can promote the growth of bacteria and stimulate the metabolic activity of those bacteria. The determination of hyphal exudates is usually done in the sterile bi-compartmented Petri dishes, which is the most reliable system to produce large quantities of hyphae on a gel medium free of any undesired contaminant[45]. One compartment (both roots and AM fungal hyphae, solid) is used for culture of hairy roots that are symbiotic with AM fungi, and hyphal exudates are collected on the other compartment (only AM fungal hyphae, liquid) followed by composition analysis[46]. Hyphal exudates are mainly found to include five categories of compounds, namely sugars, amino acids, carboxylates and nucleic acids as well as proteins and peptides[4], all of which can be used as easily available C and energy sources for bacteria. By co-culturing collected hyphal exudates with extracted soil bacterial communities, Toljander et al.[47] obtained the first evidence that hyphal exudates of AM fungi can directly influence soil bacterial community composition. Several Gammaproteobacteria, including a taxon within the Enterobacteriaceae, increased in frequency in the presence of hyphal exudates. However, AM fungi do not benefit all bacteria. AM fungus *Glomus hoi* was found to actively recruit taxa from Firmicutes, while taxa from the Actinobacteria and Comamonadaceae were repelled[48], which may be due to the bacterial preference for specific components of hyphal exudates.

Hyphal exudates of AM fungi actively facilitate soil bacteria to colonize in the hyphosphere, largely compensating for their limited saprophytic ability. Many studies have shown that the bacteria (i.e., P-releasing bacteria) positively influenced by AM fungi typically have *phoD* and/or *gcd* genes encoding alkaline phosphatase and gluconic acid in their genome, which can accelerate the mineralization and solubilization of soil organic P and non-soluble inorganic P[49,50]. A typical example is the exchange of C and P between AM fungus *Rhizophagus irregularis* and organic P-mineralizing bacterium *Rahnella aquatilis* to improve the availability of P for AM fungi. Each gram of *R. irregularis* hyphae (dry weight) released about 30 mg C in 4 weeks, which can be taken up by *R. aquatilis*[51]. At the transcriptional level, hyphal exudates significantly induced the expression of key genes involved in the tricarboxylic acid cycle as well as phosphatase genes, greatly stimulating *R. aquatilis* growth and enhancing the ability of *R. aquatilis* to mineralize organic P[52,53]. In addition, *R. aquatilis* has been shown to swim along *R. irregularis* hyphae in a water film, nourished by the hyphal exudates on its way toward an organic P patch, where it extends the capability of *R. irregularis* to efficiently utilize this otherwise inaccessible P resource[54]. Recently, two pioneering studies have shown the existence of a taxonomically conserved core microbiome in the hyphosphere, which does not change dramatically with the species of AM fungi and some external environmental factors[55,56]. The study results consistently showed that the core members were co-enriched in the hyphosphere, which dominated by Alphaproteobacteria and Gammaproteobacteria and highlighted the dominance of Myxococcales, Betaproteobacteriales, Fibrobacterales, Cytophagales and Chloroflexales[5,56]. Importantly, the relative abundance of hyphosphere core microbiome members was significantly positively correlated with soil phosphatase activity, contributing to soil P turnover and nutrient availability.

3.3 Hyphosphere interactions promote carbon and phosphorus exchange between plants and arbuscular mycorrhizal fungi

In plants, β-monoacylglycerols (β-MAGs) is synthesized from acetyl-CoA via the catalysis of multiple fatty acid synthases (e.g., FatM and RAM2), which is regulated by the master transcriptional regulatory factors WRI5a and RAM1[57,58]. β-MAGs can enter the periarbuscular space via the fatty acid transporters STR/STR2 located on the periarbuscular membrane and then are absorbed and metabolized by AM fungi[59]. Phosphate is first taken up by the extraradical hyphae of AM fungi via high-affinity P transporters belonging to the Phosphate Transporter 1 family and moves to the intraradical hyphae via poly-P polymerized by the vacuolar transporter chaperone complex[60]. In the intraradical hyphae, poly-P is hydrolyzed to P and enters the periarbuscular space via two different P transporters (PHO91 on the vacuole membrane and PT7 on the perifungal membrane)[61]. Finally, P is acquired by plants via another P transporter (e.g., MtPT4 from *M. truncatula*) located on the periarbuscular membrane[62]. A study focusing on the transcriptional level found that *R. aquatilis* dwelling in the hyphosphere facilitated C and P exchange between *M. truncatula* and *R. irregularis* as well as supported the formation and development of mycorrhizal symbiosis. The expression of genes involved in fatty acid synthesis (*FatM* and *RAM2*), transport (*STR*) and regulation (*RAM1* and *WRI5a*) in *M. truncatula* and genes involved in P transporters (*RiPHO84*, *RiPHO91*, and *RiVTC4*) in *R. irregularis* are significantly increased in the presence of *R. aquatilis*, which ultimately promoted *M. truncatula* and *R. irregularis* growth as well as *M. truncatula* P absorption efficiency[63]. The evidence clearly shows that mycorrhizae and mycorrhizae-associated bacteria increase plant P use efficiency. This fundamental interaction may provide promise for sustainable agriculture and their successful application may improve soil P status and reduce the dependence of crop on P fertilizers. Together plant and AM fungi as a holobiont have an evolutionary history of nearly 450 million years and this holobiont must also include the bacteria tightly related to AM fungal hyphae in the future.

4 Conclusions and future prospects

Plants absorb P from soil via DP and MP, and regulate both pathways through the distribution of carbohydrates. AM fungi serve as reliable symbiotic partners of plants, profoundly affecting soil P turnover and plant P absorption in terrestrial ecosystems, while bacteria colonizing in the hyphosphere can accelerate this process. The mechanism of MP for plants to effectively acquire soil P can provide the theoretical basis for the application of P fertilizers and the development of new fertilizers. However, the contribution of DP and MP for plant P absorption needs to be accurately quantified under different conditions such as soil P availability and P resource heterogeneity and the critical and active hyphosphere interactions still requires further research. The following are some research questions that we consider to be the most pressing, but also recognize additional lines of inquiry could validly be formulated.

(1) What is the mechanism of mycorrhizal plants allocating C within their roots and mycorrhizae? How to accurately distinguish the contribution of DP and MP to plant nutrient acquisition?

(2) How to maximize the effect of mycorrhizae on plant P

absorption while reducing P fertilizer application in the field?

(3) How do plants precisely control C input and P gain between DP and MP? Is there a priority between the two pathways?

(4) How soil bacteria accurately sense AM fungal signals? Are there other regulatory mechanisms regulating the delicate communication between AM fungi and bacteria that promote soil P availability?

It should be possible to comprehensively answer these questions with a wide range of interdisciplinary collaboration and the application of emerging technologies. For example, botanists, ecologists and statisticians can quantitatively estimate the C flow from plants to AM fungi as well as the C flow from AM fungi to bacteria using data set analysis. Quantum-dot technology visualizes the movement of P through hyphae and even soil to analyze the strategies of interaction between plants and AM fungi focusing on C and P exchange. High throughput stable isotope probing (HT-SIP) and nanoscale secondary ion mass spectrometry (NanoSIMS) imaging are helpful to improve the understanding of plant C allocation within hyphae and even elucidating the mechanisms of how the hyphosphere bacteria assist AM fungi in mineralizing organic P. Combining multi-omics (e.g., genome, transcriptome and metabolome) approaches can further elucidate potential signaling substances in hyphal exudates in regulating the hyphosphere microbiome and help explore the functions of the hyphosphere microbiome. All of these provide both research opportunities and a theoretical basis for efficient soil P utilization.

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Compliance with ethics guidelines

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REFERENCES

1. Bindraban P S, Dimkpa C O, Pandey R. Exploring phosphorus fertilizers and fertilization strategies for improved human and environmental health. *Biology and Fertility of Soils*, 2020, **56**(3): 299–317
2. Balemi T, Negisho K. Management of soil phosphorus and plant adaptation mechanisms to phosphorus stress for sustainable crop production: a review. *Journal of Soil Science and Plant Nutrition*, 2012, **12**(3): 547–562
3. Smith S E, Jakobsen I, Grønlund M, Smith F A. 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 Physiology*, 2011, **156**(3): 1050–1057
4. Zhang L, Zhou J, George T S, Limpens E, Feng G. Arbuscular mycorrhizal fungi conducting the hyphosphere bacterial orchestra. *Trends in Plant Science*, 2022, **27**(4): 402–411
5. Wang G, Jin Z, George T S, Feng G, Zhang L. Arbuscular mycorrhizal fungi enhance plant phosphorus uptake through stimulating hyphosphere soil microbiome functional profiles for phosphorus turnover. *New Phytologist*, 2023, **238**(6): 2578–2593
6. Prescott C E, Grayston S J, Helmisaari H S, Kaštovská E, Körner C, Lambers H, Meier I C, Millard P, Ostonen I. Surplus carbon drives allocation and plant–soil interactions. *Trends in Ecology & Evolution*, 2020, **35**(12): 1110–1118
7. Badri D V, Vivanco J M. Regulation and function of root exudates. *Plant, Cell & Environment*, 2009, **32**(6): 666–681
8. Richardson A E, George T, Hens M, Delhaize E, Ryan P, Simpson R, Hocking P. Organic anions facilitate the mobilization of soil organic phosphorus and enhances its subsequent lability to phosphatases. *Plant and Soil*, 2002, **476**(1): 161–180
9. Jiang Y, Wang W, Xie Q, Liu N, Liu L, Wang D, Zhang X, Yang C, Chen X, Tang D, Wang E. Plants transfer lipids to sustain colonization by mutualistic mycorrhizal and parasitic fungi. *Science*, 2017, **356**(6343): 1172–1175
10. An J, Zeng T, Ji C, De Graaf S, Zheng Z, Xiao T T, Deng X, Xiao S, Bisseling T, Limpens E, Pan Z. A *Medicago truncatula* SWEET transporter implicated in arbuscule maintenance

during arbuscular mycorrhizal symbiosis. *New Phytologist*, 2019, **224**(1): 396–408

11. Bever J D, Richardson S C, Lawrence B M, Holmes J, Watson M. Preferential allocation to beneficial symbiont with spatial structure maintains mycorrhizal mutualism. *Ecology Letters*, 2009, **12**(1): 13–21
12. Zhu Y G, Smith S E, Barritt A R, Smith F A. Phosphorus (P) efficiencies and mycorrhizal responsiveness of old and modern wheat cultivars. *Plant and Soil*, 2001, **237**(2): 249–255
13. Smith S E, Smith F A, Jakobsen I. Mycorrhizal fungi can dominate phosphate supply to plants irrespective of growth responses. *Plant Physiology*, 2003, **133**(1): 16–20
14. Smith S E, Smith F A, Jakobsen I. Functional diversity in arbuscular mycorrhizal (AM) symbioses: the contribution of the mycorrhizal P uptake pathway is not correlated with mycorrhizal responses in growth or total P uptake. *New Phytologist*, 2004, **162**(2): 511–524
15. Chu Q, Zhang L, Zhou J, Yuan L, Chen F, Zhang F, Feng G, Rengel Z. Soil plant-available phosphorus levels and maize genotypes determine the phosphorus acquisition efficiency and contribution of mycorrhizal pathway. *Plant and Soil*, 2020, **449**(1-2): 357–371
16. Zhang L, Chu Q, Zhou J, Rengel Z, Feng G. Soil phosphorus availability determines the preference for direct or mycorrhizal phosphorus uptake pathway in maize. *Geoderma*, 2021, **403**: 115261
17. Sheldrake M, Rosenstock N P, Mangan S, Revillini D, Sayer E J, Olsson P A, Verbruggen E, Tanner E V J, Turner B L, Wright S J. Responses of arbuscular mycorrhizal fungi to long-term inorganic and organic nutrient addition in a lowland tropical forest. *ISME Journal*, 2018, **12**(10): 2433–2445
18. Nagy R, Drissner D, Amrhein N, Jakobsen I, Bucher M. Mycorrhizal phosphate uptake pathway in tomato is phosphorus-repressible and transcriptionally regulated. *New Phytologist*, 2009, **181**(4): 950–959
19. Li H, Smith S E, Holloway R E, Zhu Y, Smith F A. Arbuscular mycorrhizal fungi contribute to phosphorus uptake by wheat grown in a phosphorus-fixing soil even in the absence of positive growth responses. *New Phytologist*, 2006, **172**(3): 536–543
20. Graham J H, Abbott L K. Wheat responses to aggressive and non-aggressive arbuscular mycorrhizal fungi. *Plant and Soil*, 2000, **220**(1–2): 207–218
21. Grace E J, Cotsaftis O, Tester M, Smith E A, Smith S E. Arbuscular mycorrhizal inhibition of growth in barley cannot be attributed to extent of colonization, fungal phosphorus uptake or effects on expression of plant phosphate transporter genes. *New Phytologist*, 2009, **181**(4): 938–949
22. Jacott C, Murray J, Ridout C. Trade-offs in arbuscular mycorrhizal symbiosis: disease resistance, growth responses and perspectives for crop breeding. *Agronomy (Basel)*, 2017, **7**(4): 75
23. Walder F, Niemann H, Natarajan M, Lehmann M F, Boller T, Wiemken A. Mycorrhizal networks: common goods of plants shared under unequal terms of trade. *Plant Physiology*, 2012, **159**(2): 789–797
24. van der Heijden M G A, Walder F. Reply to 'Misconceptions on the application of biological market theory to the mycorrhizal symbiosis'. *Nature Plants*, 2016, **2**(5): 16062
25. Daniell T J, Husband R, Fitter A H, Young J P W. Molecular diversity of arbuscular mycorrhizal fungi colonising arable crops. *FEMS Microbiology Ecology*, 2001, **36**(2–3): 203–209
26. Wang Y, Li T, Li Y, Björn L O, Rosendahl S, Olsson P A, Li S, Fu X. Community dynamics of arbuscular mycorrhizal fungi in high-input and intensively irrigated rice cultivation systems. *Applied and Environmental Microbiology*, 2015, **81**(8): 2958–2965
27. Kiers E T, Duhamel M, Beesetty Y, Mensah J A, Franken O, Verbruggen E, Fellbaum C R, Kowalchuk G A, Hart M M, Bago A, Palmer T M, West S A, Vandenkoornhuyse P, Jansa J, Bücking H. Reciprocal rewards stabilize cooperation in the mycorrhizal symbiosis. *Science*, 2011, **333**(6044): 880–882
28. Das D, Paries M, Hobecker K, Gigl M, Dawid C, Lam H M, Zhang J, Chen M, Gutjahr C. PHOSPHATE STARVATION RESPONSE transcription factors enable arbuscular mycorrhiza symbiosis. *Nature Communications*, 2022, **13**(1): 477
29. Shi J, Zhao B, Zheng S, Zhang X, Wang X, Dong W, Xie Q, Wang G, Xiao Y, Chen F, Yu N, Wang E. A phosphate starvation response-centered network regulates mycorrhizal symbiosis. *Cell*, 2021, **184**(22): 5527–5540
30. Whiteside M D, Werner G D A, Caldas V E A, Van't Padje A, Dupin S E, Elbers B, Bakker M, Wyatt G A K, Klein M, Hink M A, Postma M, Vaitla B, Noë R, Shimizu T S, West S A, Kiers E T. Mycorrhizal fungi respond to resource inequality by moving phosphorus from rich to poor patches across networks. *Current Biology*, 2019, **29**(12): 2043–2050
31. van't Padje A, Werner G D A, Kiers E T. Mycorrhizal fungi control phosphorus value in trade symbiosis with host roots when exposed to abrupt 'crashes' and 'booms' of resource availability. *New Phytologist*, 2021, **229**(5): 2933–2944
32. van't Padje A, Oyarte Galvez L, Klein M, Hink M A, Postma M, Shimizu T, Kiers E T. Temporal tracking of quantum-dot apatite across *in vitro* mycorrhizal networks shows how host demand can influence fungal nutrient transfer strategies. *ISME Journal*, 2021, **15**(2): 435–449
33. Duan S, Feng G, Limpens E, Bonfante P, Xie X, Zhang L. Cross-kingdom nutrient exchange in the plant–arbuscular mycorrhizal fungus–bacterium continuum. *Nature Reviews. Microbiology*, 2024 [Published Online] doi:10.1038/s41579-024-01073-7
34. Zhang S, Nie Y, Fan X, Wei W, Chen H, Xie X, Tang M. A transcriptional activator from *Rhizophagus irregularis* regulates phosphate uptake and homeostasis in AM symbiosis during phosphorous starvation. *Frontiers in Microbiology*, 2023, **13**: 1114089
35. Genre A, Lanfranco L, Perotto S, Bonfante P. Unique and common traits in mycorrhizal symbioses. *Nature Reviews. Microbiology*, 2020, **18**(11): 649–660

36. Hodge A. The plastic plant: root responses to heterogeneous supplies of nutrients. *New Phytologist*, 2004, **162**(1): 9–24

37. Went F W, Stark N. The biological and mechanical role of soil fungi. *Proceedings of the National Academy of Sciences of the United States of America*, 1968, **60**(2): 497–504

38. Leigh J, Hodge A, Fitter A H. Arbuscular mycorrhizal fungi can transfer substantial amounts of nitrogen to their host plant from organic material. *New Phytologist*, 2009, **181**(1): 199–207

39. Tisserant E, Malbreil M, Kuo A, Kohler A, Symeonidi A, Balestrini R, Charron P, Duensing N, Frei Dit Frey N, Gianinazzi-Pearson V, Gilbert L B, Handa Y, Herr J R, Hijri M, Koul R, Kawaguchi M, Krajinski F, Lammers P J, Masclaux F G, Murat C, Morin E, Ndikumana S, Pagni M, Petitpierre D, Requena N, Rosikiewicz P, Riley R, Saito K, San Clemente H, Shapiro H, Van Tuinen D, Bécard G, Bonfante P, Paszkowski U, Shachar-Hill Y Y, Tuskan G A, Young J P W, Sanders I R, Henrissat B, Rensing S A, Grigoriev I V, Corradi N, Roux C, Martin F. Genome of an arbuscular mycorrhizal fungus provides insight into the oldest plant symbiosis. *Proceedings of the National Academy of Sciences of the United States of America*, 2013, **110**(50): 20117–20122

40. Venice F, Ghignone S, Salvioli Di Fossalunga A, Amselem J, Novero M, Xianan X, Sędzielewska Toro K, Morin E, Lipzen A, Grigoriev I V, Henrissat B, Martin F M, Bonfante P. At the nexus of three kingdoms: the genome of the mycorrhizal fungus *Gigaspora margarita* provides insights into plant, endobacterial and fungal interactions. *Environmental Microbiology*, 2020, **22**(1): 122–141

41. Leigh J, Fitter A H, Hodge A. Growth and symbiotic effectiveness of an arbuscular mycorrhizal fungus in organic matter in competition with soil bacteria. *FEMS Microbiology Ecology*, 2011, **76**(3): 428–438

42. Cheng L, Booker F L, Tu C, Burkey K O, Zhou L, Shew H D, Rufty T W, Hu S. Arbuscular mycorrhizal fungi increase organic carbon decomposition under elevated CO_2. *Science*, 2012, **337**(6098): 1084–1087

43. Tecon R, Or D. Biophysical processes supporting the diversity of microbial life in soil. *FEMS Microbiology Reviews*, 2017, **41**(5): 599–623

44. McDonald M D, Owusu-Ansah C, Ellenbogen J B, Malone Z D, Ricketts M P, Frolking S E, Ernakovich J G, Ibba M, Bagby S C, Weissman J L. What is microbial dormancy. *Trends in Microbiology*, 2024, **32**(2): 142–150

45. Duan S, Declerck S, Zhang L, Feng G. Two-component system in *Rahnella aquatilis* is impacted by the hyphosphere of the arbuscular mycorrhizal fungus *Rhizophagus irregularis*. *Environmental Microbiology Reports*, 2022, **14**(1): 119–129

46. Luthfiana N, Inamura N, Tantriani, Sato T, Saito K, Oikawa A, Chen W, Tawaraya K. Metabolite profiling of the hyphal exudates of *Rhizophagus clarus* and *Rhizophagus irregularis* under phosphorus deficiency. *Mycorrhiza*, 2021, **31**(3): 403–412

47. Toljander J F, Lindahl B D, Paul L R, Elfstrand M, Finlay R D. Influence of arbuscular mycorrhizal mycelial exudates on soil bacterial growth and community structure. *FEMS Microbiology Ecology*, 2007, **61**(2): 295–304

48. Nuccio E E, Hodge A, Pett-Ridge J, Herman D J, Weber P K, Firestone M K. An arbuscular mycorrhizal fungus significantly modifies the soil bacterial community and nitrogen cycling during litter decomposition. *Environmental Microbiology*, 2013, **15**(6): 1870–1881

49. Zhang L, Shi N, Fan J, Wang F, George T S, Feng G. Arbuscular mycorrhizal fungi stimulate organic phosphate mobilization associated with changing bacterial community structure under field conditions. *Environmental Microbiology*, 2018, **20**(7): 2639–2651

50. Qin Y, Zhang W, Feng Z, Feng G, Zhu H, Yao Q. Arbuscular mycorrhizal fungus differentially regulates P mobilizing bacterial community and abundance in rhizosphere and hyphosphere. *Applied Soil Ecology*, 2022, **170**: 104294

51. Zhang L, Xu M, Liu Y, Zhang F, Hodge A, Feng G. Carbon and phosphorus exchange may enable cooperation between an arbuscular mycorrhizal fungus and a phosphate-solubilizing bacterium. *New Phytologist*, 2016, **210**(3): 1022–1032

52. Zhang L, Fan J, Feng G, Declerck S. The arbuscular mycorrhizal fungus *Rhizophagus irregularis* MUCL 43194 induces the gene expression of citrate synthase in the tricarboxylic acid cycle of the phosphate-solubilizing bacterium *Rahnella aquatilis* HX2. *Mycorrhiza*, 2019, **29**(1): 69–75

53. Zhang L, Feng G, Declerck S. Signal beyond nutrient, fructose, exuded by an arbuscular mycorrhizal fungus triggers phytate mineralization by a phosphate solubilizing bacterium. *ISME Journal*, 2018, **12**(10): 2339–2351

54. Jiang F, Zhang L, Zhou J, George T S, Feng G. Arbuscular mycorrhizal fungi enhance mineralisation of organic phosphorus by carrying bacteria along their extraradical hyphae. *New Phytologist*, 2021, **230**(1): 304–315

55. Wang L, Zhang L, George T S, Feng G. A core microbiome in the hyphosphere of arbuscular mycorrhizal fungi has functional significance in organic phosphorus mineralization. *New Phytologist*, 2023, **238**(2): 859–873

56. Emmett B D, Lévesque-Tremblay V, Harrison M J. Conserved and reproducible bacterial communities associate with extraradical hyphae of arbuscular mycorrhizal fungi. *ISME Journal*, 2021, **15**(8): 2276–2288

57. Bravo A, Brands M, Wewer V, Dörmann P, Harrison M J. Arbuscular mycorrhiza-specific enzymes FatM and RAM2 fine-tune lipid biosynthesis to promote development of arbuscular mycorrhiza. *New Phytologist*, 2017, **214**(4): 1631–1645

58. Jiang Y, Xie Q, Wang W, Yang J, Zhang X, Yu N, Zhou Y, Wang E. Medicago AP2-domain transcription factor WRI5a is a master regulator of lipid biosynthesis and transfer during mycorrhizal symbiosis. *Molecular Plant*, 2018, **11**(11): 1344–1359

59. Zhang Q, Blaylock L A, Harrison M J. Two *medicago truncatula* half-ABC transporters are essential for arbuscule development in arbuscular mycorrhizal symbiosis. *Plant Cell*,

2010, **22**(5): 1483–1497

60. Ezawa T, Saito K. How do arbuscular mycorrhizal fungi handle phosphate? New insight into fine-tuning of phosphate metabolism. *New Phytologist*, 2018, **220**(4): 1116–1121
61. Xie X, Lai W, Che X, Wang S, Ren Y, Hu W, Chen H, Tang M. A SPX domain-containing phosphate transporter from *Rhizophagus irregularis* handles phosphate homeostasis at symbiotic interface of arbuscular mycorrhizas. *New Phytologist*, 2022, **234**(2): 650–671
62. Volpe V, Giovannetti M, Sun X, Fiorilli V, Bonfante P. The phosphate transporters LjPT4 and MtPT4 mediate early root responses to phosphate status in non mycorrhizal roots. *Plant, Cell & Environment*, 2016, **39**(3): 660–671
63. Duan S, Declerck S, Feng G, Zhang L. Hyphosphere interactions between *Rhizophagus irregularis* and *Rahnella aquatilis* promote carbon–phosphorus exchange at the peri-arbuscular space in *Medicago truncatula*. *Environmental Microbiology*, 2023, **25**(4): 867–879