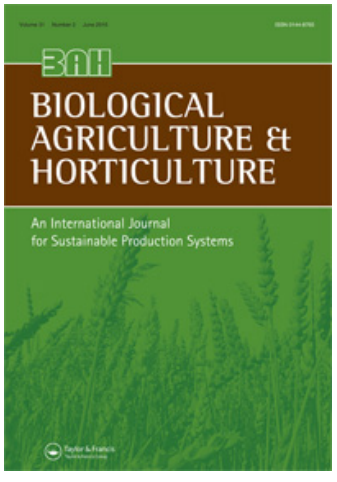

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Phosphorus supply to vegetable crops from arbuscular mycorrhizal fungi: a review

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Increasing cost of inorganic P fertilizers manufactured from non-renewable phosphate rock and agro-environmental guidelines compel vegetable producers to re-evaluate and possibly reduce P fertilizer use in their operations. Greater reliance on arbuscular mycorrhizal (AM) fungi could compensate for lower P fertilizer inputs to vegetable crops. The objective of this review was to examine how AM fungi dependency and AM fungi-mediated P uptake in the Alliaceae, Fabaceae and Solanaceae families are affected by agronomic practices, soil biogeochemistry, and characteristics of the host plant and the AM fungal symbiont. Fertilization and geochemical reactions affecting the plant-available P concentration in the soil solution determine the degree of AM fungus colonization of roots, as well as the quantity of phosphate transferred to the plant via the hyphal network of AM fungi. The hyphae of AM fungi physically extend the rhizosphere into a larger soil volume and access more plant-available P; as well, AM fungi secrete organic acids and phosphatase enzymes than increase the plant-available P concentration. Feedback in the host-AM fungi system (mycorrhiza) due to plant morphology and physiology as well as mycorrhizal phenotype and high-affinity P transporters control the AM fungi-induced P uptake. Although inoculation with *Glomus* species is often beneficial for Alliaceae seedlings and transplants, gains in yield and better P nutrition of mycorrhizal vegetable crops can be achieved by boosting the indigenous AM fungus populations in agricultural fields with the following techniques: including mycorrhizal hosts in crop rotations or as intercrops and cover crops, reducing cultivation intensity and decreasing P fertilizer inputs.

Keywords: horticultural crop; integrated nutrient management; mycorrhizal fungi; phosphorus; sustainable agriculture; symbiosis

Introduction

Global reserves of high-grade phosphate rock, the base material for inorganic phosphorus (P) fertilizers, are diminishing, and "peak P" projections estimate that maximum production of P fertilizer will occur by 2030 (Cordell et al. 2009). Agricultural producers have already seen the effects of a global P shortage; for instance, from 2007 to 2008, the price of phosphate rock increased by 700% (Elser & Bennett 2011) and the cost of P fertilizer soared, such that agricultural producers in the United States paid two to three times more for triple superphosphate and diammonium phosphate during the period 2007–2013 than they did in the previous decade (USDA Economic Research Service 2013). Consequently, agricultural producers would like to cut back on inorganic P fertilizer use and rely on soil P reserves that were built up from past fertilizer applications.

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Reducing inorganic P fertilizer use is an appropriate strategy when growing crops in regions where soil test P levels are high to very high from historical inputs of inorganic P fertilizer and P-rich organic fertilizer such as animal manure (Sharpley & Tunney 2000). Yan et al. (2013) reported that intensive vegetable crop production systems in China (greenhouse and field) were grossly overfertilized with P due to excessive use of inorganic fertilizer and animal manure, such that P inputs were approximately 10-fold greater than P removal in harvested vegetables. In agricultural fields, Olsen-P levels in surface soil (0–20 cm depth) were, on average, double the critical level (46–58 mg P kg^{-1}) for optimal vegetable production and high soil test P levels in the subsoil (40–60 cm depth) were evidence that P fertilizer leached below the crop root zone (Yan et al. 2013). Similarly, Evanylo et al. (2008) found a 3.3-fold increase in Mehlich-1 extractable P concentration of soil that was amended with composted poultry litter/yard waste at the agronomic N rate for vegetables in a 3-year rotation [pumpkin (*Cucurbita pepo*) – sweet corn (*Zea mays*) – bell pepper (*Capsicum annuum*)], and there was 1.6 times more Mehlich-1 extractable P in plots that received agronomic rates of triple superphosphate during the same period. Currently, fertilization guidelines for vegetable crop production emphasize attention to P inputs (i.e. source, amount, placement, timing) to avoid overfertilization, to reduce fertilizer costs and to prevent P leaching and runoff from agricultural fields to waterways (Hartz 2010; Obreza & Sartain 2010).

At the farm scale, decisions about inorganic P fertilizer use are affected by fertilizer cost and agro-environmental legislation/guidelines to protect water quality from non-point source P pollution. Integrated nutrient management strategies stress judicious use of inorganic P fertilizers and appropriate application rates of organic P fertilizers, in combination with beneficial management practices for irrigation and drainage control structures to minimize P losses through leaching and surface runoff. Selection of cultivars with characteristics that favour P acquisition, such as extensive fibrous root systems and the ability to solubilize insoluble P compounds through organic acid production in the rhizosphere, should improve P use efficiency from fertilizers. Crops also benefit from symbiotic association with arbuscular mycorrhizal (AM) fungi, which are known for their ability to take up and transfer P and other growth limiting nutrients from soils to plants.

The AM fungi association is most beneficial to crops grown in fields with low soil test P levels because the fungus increases P availability and uptake by plants through several mechanisms, illustrated in Figure 1. The vast hyphal network of AM fungi effectively extends the rooting zone of the plant, allowing it to access plant-available P (phosphate ions, $H_2PO_4^-$ and HPO_4^{2-}) that would otherwise be out of reach. Phosphate ions diffuse faster into hyphae than into root hairs, due to the higher affinity of P uptake and the lower threshold concentration for absorption into the hyphae (Bolan 1991). AM fungi alter soil pH in the rhizosphere and secrete organic acids (Tawaraya et al. 2006), which can solubilize P complexes and cause desorption of phosphate ions that are chemically bound to soil mineral surfaces (Kirk 1999). In addition, some hyphae of AM fungi exude phosphatase enzymes that mineralize organic P and release phosphate ions into the soil solution (Koide & Kabir 2000). Crops can be inoculated with AM fungus spores or naturally partner with symbionts from the pool of indigenous AM fungi in the soil (Plenchette et al. 2005).

Given that most vegetable and horticultural crops associate with AM fungi and there are multiple ways that AM fungi can contribute to crop P nutrition, the plant-AM fungi relationship, hereafter referred to as mycorrhiza, should be part of the integrated nutrient management strategy for vegetable crops. There has been relatively little discussion of AM fungi in this context because it is not considered an economic substitute for P fertilizer. A field trial in 1994–1995 that compared fumigated (AM fungi −) and non-

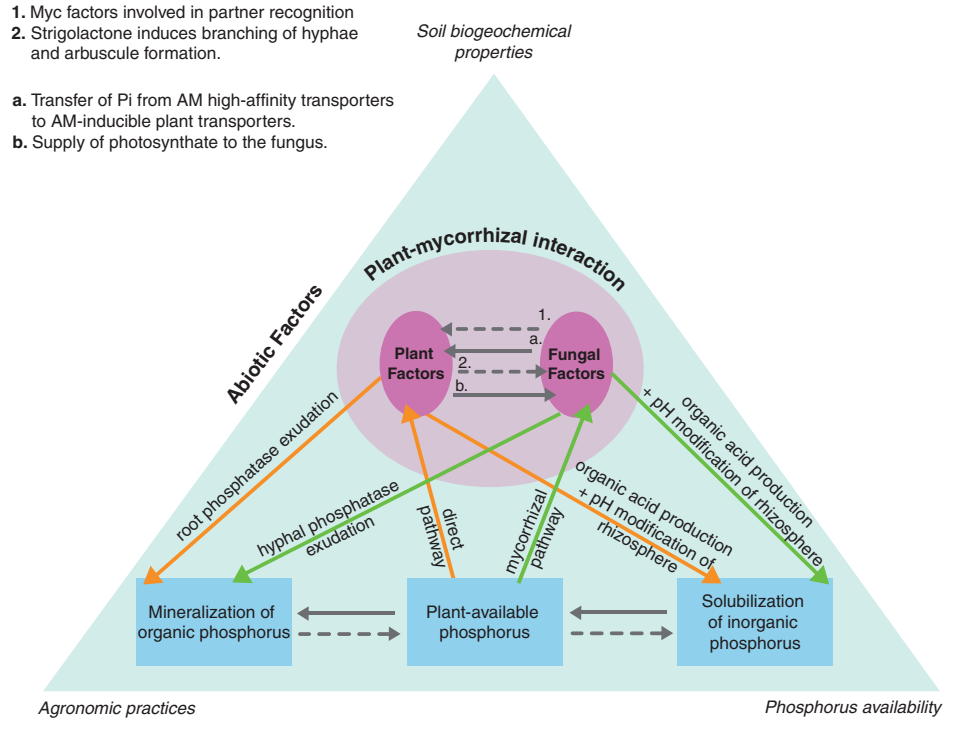

Figure 1. Factors affecting the plant–mycorrhizal interaction and mechanisms for phosphorus (P) uptake in arbuscular mycorrhizal (AM) fungi symbioses. Abbreviations: Myc, mycorrhizal; Pi, inorganic phosphate; AM, arbuscular mycorrhizae.

fumigated (AM fungi +) plots with five rates of single superphosphate fertilizer for bell pepper production concluded that AM fungi − plants required 87 kg P ha^{-1} to reach the same marketable yield as AM fungi + plants; however, because the cost of P fertilizer was less than 10% of the total production cost, Olsen et al. (1999) concluded that any decision to include AM fungi into the cropping system should not be based solely on the saving in inorganic P fertilizer costs. Much has changed in our view of P fertilization in the past 20 years, considering the decline in accessible reserves of rock phosphate, the rising price of inorganic P fertilizers and the eutrophication of surface water bodies due to non-point source P pollution from the agricultural sector. The authors believe that it is time to re-examine the contribution that AM fungi can make in supplying P to vegetable crops, in the context of sustainable and ecological agriculture.

The objectives of this review article are to (1) discuss the key factors that influence crop responsiveness to AM fungi for three plant families (Alliaceae, Fabaceae and Solanaceae), (2) highlight the major mechanisms by which AM fungi improve P uptake efficiency and yield in those families, (3) determine ways of selecting compatible plant/fungus pairs, and (4) make recommendations for how to include AM fungi associations in the integrated nutrient management strategies for vegetable crops. Nearly all AM fungi species described in this paper were identified by classical characterization based on spore structures, which has limitations in positively identifying cryptic taxa and species that form multiple spore morphs, compared to molecular taxonomic analysis. The revised nomenclature of Schüßler and Walker (2010) and Krüger et al. (2012) should be consulted for accurate identification of AM fungi discussed in this review.

Factors affecting crop dependency on mycorrhiza

Mycorrhizal dependency (MD) is the standard indicator of host plant responsiveness to AM fungi, defined as the percent change in growth of a given crop due to mycorrhiza (Plenchette et al. 1983). The MD of selected crops in the Alliaceae, Fabaceae and Solanaceae families are summarized in Table 1. Variability in MD among crops is attributed partially to agronomic practices and soil biogeochemical factors that alter the plant-available P concentration in soil solution (F.A. Smith & S.E. Smith 2011). Genomic traits of the host plant, e.g. root morphology, and the mycorrhizal symbiont, e.g. distribution and abundance of hyphae, are equally important in determining MD and the P uptake that is induced by AM fungi, as reviewed by several authors (Plenchette et al. 1983; Krishna et al. 1985; Burleigh et al. 2002). If productivity of crops in the Alliaceae, Fabaceae and Solanaceae families can be improved through greater reliance on AM fungi, factors illustrated in Figure 1 that control the acquisition and transfer of P through mycorrhiza need to be understood.

AM fungi-induced P uptake: influence of agronomic practices and soil biogeochemistry

Agronomic practices affecting AM fungus spore populations and AM fungus colonization of roots include tillage, crop rotations, winter cover crops, agrochemical use, organic matter addition and P fertilizer inputs (Miller & Jackson 1998; F.A. Smith & S.E. Smith

Table 1. MD and primary mechanisms for P acquisition by selected crop species in the Solanaceae, Fabaceae and Allium families.

Crop family	Species	Inoculated (Y/N)	Prevalent fungi species	Primary mechanisms for P acquisition	Mycorrhizal dependency (%)	Ref.
Solanaceae	*Capsicum annuum*	N	Indigenous	P solubilization	90	Krikun et al. (1990)
	Solanum lycopersicum	N	Indigenous	ND	59	Plenchette et al. (1983)
	Solanum tuberosum	N	Indigenous	ND	42	Plenchette et al. (1983)
Fabaceae	*Glycine max*	Y	*Gigaspora margarita, Glomus intraradices*	Greater phosphatase activity	40–94	Khalil et al. (1994)
	Pisum sativum	N	Indigenous	ND	96	Plenchette et al. (1983)
	Phaseolus vulgaris	N	Indigenous	ND	94	Plenchette et al. (1983)
	Vicia faba	N	Indigenous	ND	93	Plenchette et al. (1983)
Alliaceae	*Allium cepa*	N	Indigenous	P solubilization, extend root system	46–70	Krikun et al. (1990)
	Allium porrum	N	Indigenous	ND	96	Plenchette et al. (1983)
	Allium fistulosum	Y	*Glomus fasciculatum*	Extend root system	73–95	Tawaraya et al. (2001)

Notes: When different cultivars were assayed, the variation in MD was reported. ND, not determined.

2011). Soil disturbance associated with increasing tillage intensity may damage the fungal hyphal network and reduce colonization of roots by AM fungi (Evans & Miller 1988; McGonigle & Miller 1993; Jansa et al. 2006). Corn had greater AM fungus colonization of roots when grown in no-till than tilled (e.g. moldboard plow, chisel-disk) soils, but higher P use efficiencies were measured in the cultivated soils than those under no-till (Galvez et al. 2001). Inclusion of mycorrhizal crops in the crop rotation, as intercrops and winter cover crops, can increase the soil inocula and favour early infection of subsequent short-season crops, whereas cropping with non-mycorrhizal plants (e.g. Brassicaceae) and fallow periods reduce AM fungus spore numbers (Black & Tinker 1979; Miller & Jackson 1998). Use of insecticides, fungicides and herbicides was negatively correlated with AM fungus colonization of lettuce (*Lactuca sativa*) roots, either due to direct effects, e.g. inhibition of AM fungi by fungicides, or indirect effects, e.g. larger weed populations, were correlated with higher AM fungus spore counts in soil, implying that some weeds were mycorrhizal hosts; Miller & Jackson 1998). Field soils receiving organic amendments exhibited greater AM fungus colonization of roots in lettuce, cowpeas (*Vigna unguiculata*) and common bean (*Phaseolus vulgaris*; Miller & Jackson 1998; Muthukumar & Udaiyan 2002; Aryal et al. 2003). Organic amendments need to be selected carefully, as olive mill residues reduced tomato (*Solanum* lycopersicum) root colonization by *Glomus deserticola* (Aranda et al. 2009) and AM fungi colonization of onion (*Allium cepa*) roots by *G. mosseae* was inhibited in sphagnum peat and composted olive pumice substrates (Calvet et al. 1993).

Changes in the plant-available P concentration in soil solution resulting from P fertilizer inputs strongly affect AM fungus colonization of roots. Mycorrhizal benefits to plant growth and P uptake are highest in soils with low to moderate soil test P levels (Tawaraya 2003; Plenchette et al. 2005). MD declines with repeated P fertilizer applications due to the fact that higher plant P concentrations reduce AM fungus colonization of roots and consequently can reduce the mycorrhizal fungus population (Hayman et al. 1975; Habte and Manjunath 1987). The inhibition of AM fungus colonization of roots in soils with high plant-available P concentrations is controlled by the host, which down-regulates the genetic and biochemical signalling pathways that facilitate AM fungi symbiosis and opts to transfer P directly from the soil solution into roots (Javot et al. 2007; Balzergue et al. 2011). The soil test P level must therefore be considered when assessing the potential for mycorrhizal benefits in vegetable production systems.

Plant-available P moves through the soil solution by diffusion, primarily, and the ability of P diffusion to meet plant P requirements depends on soil biogeochemical reactions. In mineral soils, geochemical reactions control the phosphate transfer between soil solution and the soil solid phase, which can be described with process-based models of the sorption–desorption reaction (Ziadi et al. 2013). Soil pH is a key factor regulating P sorption with soil minerals because it controls their surface charge. In acidic soils, such as the highly weathered Oxisols and Ferralsols of the tropics, phosphates in the soil solution are readily bound to charged Al and Fe oxides and hydroxyls on clay surfaces, or precipitate with Al^{3+} and Fe^{3+}/Fe^{2+} ions present in the soil solution (Bolan 1991). Calcareous soils with alkaline pH also have high capacity for P sorption, either with Ca minerals on clay colloids or precipitation with Ca^{2+} in soil solution (Bolan 1991). Phosphates thus bound or precipitated with soil minerals are considered to be "fixed" because the rates of desorption and solubilization are typically an order of magnitude lower than the rates of P sorption and precipitation. Soils with high P fixation capacity have a limited amount of phosphate diffusing between the bulk soil and the root surface, such that P uptake by plants comes from phosphates located within a few millimeters of

the root surface. However, AM fungi-mediated transfer of P to plant roots is more efficient than P diffusion to the roots and is accomplished by physically extending the rooting zone through the hyphal network of AM fungi, thereby decreasing the distance for phosphate diffusion to the plant root (Olsson et al. 2002; F.A. Smith & S.E. Smith 2011). Greater P uptake achieved with mycorrhiza makes AM fungi a promising solution for improving plant P nutrition in soils with a high P-fixation capacity.

Greater yields are expected for mycorrhizal than non-mycorrhizal crops in soils with low plant-available P concentration, although the yield gain depends on the level of MD (Plenchette et al. 2005; F.A. Smith & S.E. Smith 2011). Onion yield was two to three times greater in mycorrhizal than non-mycorrhizal plants (Figure 2(a)), whereas bell peppers that received single superphosphate fertilizer had a 10–12-fold increase in yield when mycorrhizal, and mycorrhiza yielded 34 times greater than non-mycorrhiza in the absence of P fertilizer (Figure 2(b); Krikun et al. 1990). Soyabean yield was four times greater in mycorrhizal than non-mycorrhizal plants when no fertilizer was added, but increasing the P fertilizer input reduced the yield gap (Figure 2(c)). These findings are consistent with the general observation that increasing plant-available P concentration by applying P fertilizer reduces the marginal gain in yield of plants associated with AM fungi, until gradually AM fungi no longer provide a growth advantage (Smith & Read 2008). It is notable that mycorrhiza produced similar or greater yields as non-mycorrhizal crops receiving P fertilizer (Figure 2). Similarly, Tawaraya et al. (2012) observed that Welsh onion (*Allium fistulosum*) with AM fungi that received 300 mg P_2O_5 kg^{-1} soil produced yields that were comparable to non-mycorrhizal Welsh onion fertilized with 1000 mg P_2O_5 kg^{-1} soil. These results demonstrate the potential for vegetable producers to reduce their P fertilizer inputs and obtain comparable or superior yields with the help of AM fungi.

Because the mycorrhizal contribution to P uptake ranges from negligible to more than 90% of the crop P requirements, depending on the soil test P level (Reinhard et al. 1994; Table 1), it is important to understand how plants control the MD to avoid parasitism by AM fungi. Plant-derived chemical signals mediate the symbiosis with AM fungi and can halt delivery of carbon to the fungus when the plant has sufficient P (Olsson et al. 2002), thereby reducing fungal hyphae development and suppressing future AM fungus colonization of roots (Balzergue et al. 2011; Smith et al. 2011). Mycorrhizal development is controlled partially by strigolactone, a plant-derived root exudate that is responsible for early signalling events leading to hyphal branching and AM fungus spore germination (Akiyama et al. 2005; Balzergue et al. 2011). Strigolactone production declines when there is high plant-available P concentration in the soil solution (Yoneyama, Xie, et al. 2007; Yoneyama, Yoneyama, et al. 2007; Lopez-Raez et al. 2008), leading Balzergue et al. (2011) to hypothesize that the down-regulation of mycorrhiza in soils with high soil test P levels is due in part to the decrease in strigolactone production by the plant. Root exudates also contain a number of other compounds potentially active on AM fungi, including various flavonoids (Scervino et al. 2007) and hydroxy fatty acids (Nagahashi & Douds 2011). Balzergue et al. (2013) reported that high phosphate supply did not interfere with the exchange of molecular signals between plants and AM fungi, but impacted the ability of plant roots to host AM fungi by reducing fungal attachment to the roots, although roots still perceived that AM fungi were present. Because exogenous strigolactone did not improve AM fungus colonization of *Pisum* roots (Balzergue et al. 2011) and only plants grown under in soils with low P concentration can be colonized efficiently by AM fungi (Balzergue et al. 2013), future research efforts should focus on how the plant controls AM fungus colonization of its roots.

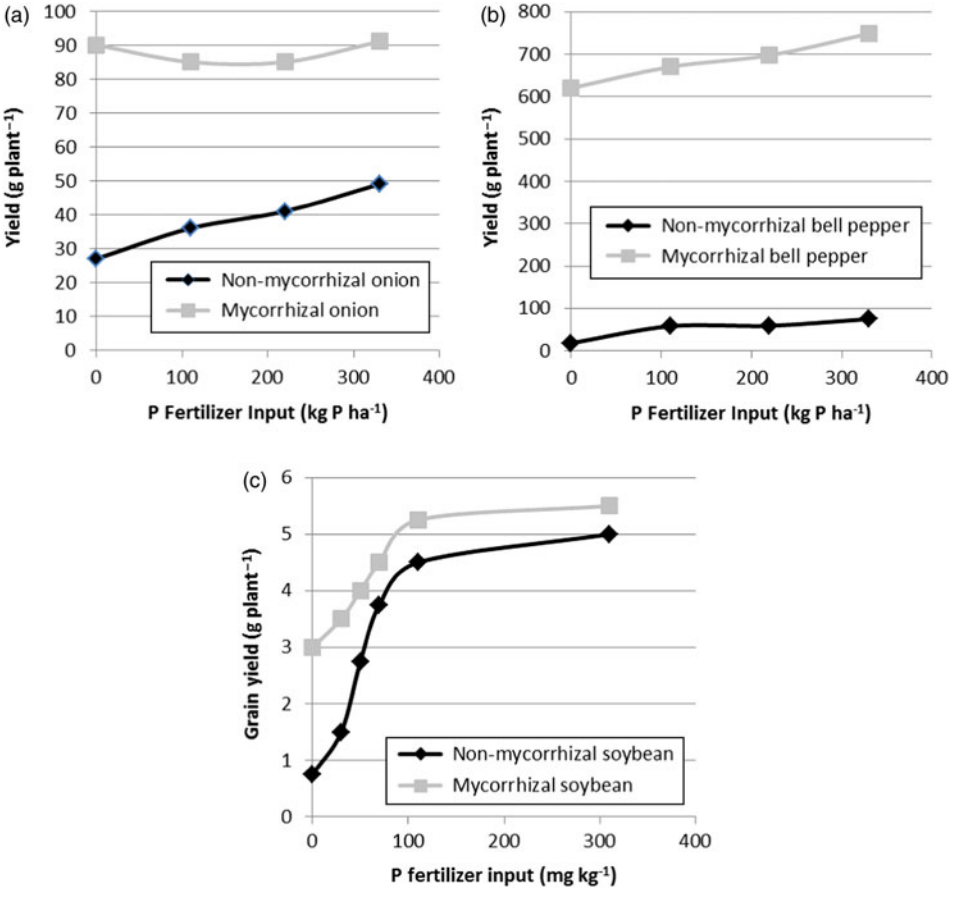

Figure 2. Variation in yield (g plant$^{-1)}$ with increased phosphorus (P) fertilizer of representative species in the Alliaceae, Fabaceae and Solanaceae families, showing (a) yield of mycorrhizal and non-mycorrhizal onion at four P fertilizer rates (0, 110, 220 and 330 kg P ha^{-1}) applied as single superphosphate [data from Krikun et al. (1990)], (b) yield of mycorrhizal and non-mycorrhizal bell peppers at four P fertilizer rates (0, 110, 220 and 330 kg P ha^{-1}) applied as single superphosphate [data from Krikun et al. (1990)], and (c) yield of mycorrhizal and non-mycorrhizal soybean at six P fertilizer rates (0, 30, 50,70,110 and 310 mg P kg^{-1}) applied as sodium phosphate dihydrate [data from Plenchette and Morel (1996)].

AM fungi-induced P uptake: influence of crop species

Three general mechanisms are responsible for enhanced P uptake in mycorrhizal crops, namely (1) the hyphal network of AM fungi that extends the plant root system, (2) release of organic acids that solubilize phosphate from insoluble Al-P, Fe-P and Ca-P complexes, and (3) greater phosphatase enzyme production that accelerates organic P mineralization to inorganic phosphate. As noted in Table 1, extension of the root system was cited as the mechanism responsible for AM fungi-induced P uptake in two Alliaceae species, while P solubilization was reported for Alliaceae and Solanaceae crops, and enhanced phosphatase activity was found for a Fabaceae crop.

Phosphate acquisition by plants is largely based on the physiological characteristics and architecture of the root system. Baylis (1970) was the first to suggest that

graminoid root systems, characterized by fine, dense root clusters, are most effective at acquiring soil P because they have more contact with soil solution and mineral surfaces, thereby reducing the distance that phosphate must diffuse to reach the root surface. This characteristic is enhanced in mycorrhizal crops because the hyphal network consists of diffuse hyphae (1–5 μm diameter at the growing tips) that absorb nutrients from the soil solution and transport nutrients through large diameter hypha (up to 30 μm diameter) to the root surface (Smith & Read 2008). The area of a 2-μm-diameter mycorrhizal hypha (per unit of biomass volume) is 100 times greater and that of a 20-μm-diameter root hair (per unit of biomass volume) is 10 times greater, than a 200-μm-diameter root (Raven & Edwards 2001). Root morphology is linked to MD, such that onions and other alliums having a short root system typically exhibit high MD, with values of up to 96% reported (Plenchette et al. 1983; Krikun et al. 1990; Tawaraya et al. 2012) and crop species with extensive root systems rely less on AM fungi to exploit soil P. A study of 27 cultivars of Welsh onion, which has a shallow adventitious root system, demonstrated that MD of shoot P uptake was negatively correlated with the specific P uptake of non-mycorrhizal plants ($\mu g\,P\,cm^{-1}$ root), meaning that cultivars with the lowest capacity to acquire P through their root system get the greatest gain in P uptake from AM fungus, in this case *G. fasciculatum* (Tawaraya et al. 2001). Because MD is linked to root morphology and the effectiveness of the AM fungus association, it needs to be considered when determining which vegetable crop species and cultivars will benefit from mycorrhiza.

Exudation of organic acids is a strategy used by both mycorrhizal and non-mycorrhizal crops to acquire P from insoluble P compounds (Hoffland et al. 1989; Otani et al. 1996). This is achieved by organic acid excretion through the roots, which leads to phosphate solubilization in three ways: (1) by acidifying the rhizosphere, which solubilizes calcium phosphates such as dicalcium phosphate, octocalcium phosphate and hydroxyapatite in calcareous soils, (2) by displacing phosphate from sorption sites on soil mineral surfaces and (3) by chelating metal ions (Al^{3+}, Fe^{3+}/Fe^{2+} and Ca^{2+}) present in the soil solution (Bolan 1991). Tawaraya et al. (2006) reported that AM fungi released P-solubilizing organic acids in the rooting zone of onions, such that AM fungi + onions had a 7–10-fold increase in shoot P uptake and 3–5 times greater dry weight compared with the non-mycorrhizal onions. Organic acid exudation was not detected in non-mycorrhizal onions. Furthermore, Tawaraya et al. (2006) partitioned onion roots and AM fungi hyphae (of *G. margarita* and *G. etunicatum*), noting that both roots and hyphae were able to solubilize $FePO_4$, in part due to the secretion of citric acid.

Some crops stimulate organic P mineralization by secreting phosphatase enzymes from their roots when soil solution contains low phosphate concentrations (Duff et al. 1994). AM fungus colonization of roots enhances organic P mineralization by inducing the expression of the genes responsible for root-derived phosphatase secretion (Ezawa et al. 2005) and possibly through secretion of phosphatase through their hyphae (Khalil et al. 1994; Koide & Kabir 2000). The latter hypothesis was the subject of debate, as the origin of phosphatase enzymes in the hyphal zone of mycorrhizal crops could not be determined. According to Tarafdar and Marschner (1994), hyphae of AM fungi exhibited phosphatase activity in experimental compartment systems, but it was not known if AM fungi were exclusively responsible because rhizobacteria also produce phosphatases. Still, Koide and Kabir (2000) observed production of extracellular phosphatases *in vitro* by AM fungi in a species of *G. intraradices* associated with carrot (*Daucus carota*); not only did *G. intraradices* have significant phosphatase activity, but it also delivered P from mineralized organic P compounds to the plant via the mycorrhizal uptake pathway. The

ability of mycorrhiza to mineralize organic P compounds varies among fungal species and among plant/fungus pairs (Ezawa et al. 2005). The dependency of crops on fungal P mineralization may also vary, based on the crop's ability to mineralize organic P sources itself. For instance, Khalil et al. (1994) found a negative correlation between MD values of *Glycine max* and the plant-derived phosphatase activity of the host, which varied among cultivars (Table 1). More research is needed to understand the fundamental interactions in mycorrhiza that control phosphatase activity, the specificity of the enzyme for organic P compounds present in soil and the subsequent efficiency of phosphate uptake through the hyphal network. This will help vegetable producers identify the crop species and cultivars that will benefit most from AM fungi in this context.

AM fungi-induced P uptake: effect of symbiotic fungus

Functional traits of AM fungi species and isolates that control their ability to acquire soil P and transmit it to crops are (1) morphological, according to the physical development and growth of the hyphal network of AM fungi, or (2) physiological, based on the efficiency of P uptake and transport via the mycorrhizal pathway (Thonar et al. 2011). These traits are influenced by the host plant and the soil environment, and depend on the crop species or cultivar that is associated with a particular AM fungi. This makes it challenging to link functional traits to each AM fungi species (Munkvold et al. 2004; van der Heijden & Scheublin 2007). Factors that are determinants of mycorrhiza-mediated P uptake include AM fungus morphology, the abundance and distribution of hyphae, and the efficiency of high-affinity P transporters at the soil/fungal interface (Johnson et al. 1997; Burleigh et al. 2002; Smith et al. 2011; Thonar et al. 2011).

Two morphological types are described for AM fungi: (1) the "Arum-type," which is characterized by the presence of individual arbuscules in the cortical cells of the root tissue, and the establishment of hyphae within the intercellular spaces, and (2) the "Paris-type," which does not form individual arbuscules, but rather arbusculate coils, within the root cortex (Smith & Smith 1997). Morphology is strongly influenced by the host plant species and the fungal species involved (Smith & Smith 1997; Cavagnaro et al. 2001), and some examples of the plant host and corresponding fungal symbionts that develop these morphotypes are summarized in Table 2. Crops in the Alliaceae family are the "robust" Arum-type, with consistent morphology across plant species (Table 2). The AM fungi that are associated with Solanaceae crops exhibit a range of Arum-type and Paris-type morphologies, depending on the fungal symbiont (Table 2). The vast majority of legumes exhibit Arum-type morphology, but there are a few cases of legumes forming Paris-type, or intermediate morphologies (Smith & Smith 1997). A plant can be colonized simultaneously by multiple fungal species, which leads to confusion in determining the morphotype of a specific individual (Ahulu et al. 2006). According to Smith and Smith (1997), the majority of plant families express "robust" morphotypes, which are more common than mixed morphotypes. The AM fungi-induced P uptake varies among morphotypes (Table 2), probably due to differences in carbon demands by the fungus (Smith et al. 2004, 2011). Both Arum- and Paris-type structures include AM fungi-inducible plant P transporters, which are involved in P transfer in the mycorrhiza, and both types have demonstrated phosphatase activity (S.E. Smith & F.A. Smith 2011). The relationship between morphotype and P uptake efficiency is not fully understood, and additional research is needed to establish the functional significance of AM fungus morphotypes for vegetable crops, including more information on the mode of P acquisition and P uptake for each morphotype.

Table 2. Morphology of AM fungus colonization of roots and mycorrhizal P uptake efficiency.

Fungal species	Crop host	Morphotype	Mycorrhizal P contribution	Plant growth benefit	Ref.
Gigaspora rosea	*S. lycopersicum*	Paris	ND	−33%	Smith et al. (2004)
Gigaspora margarita	*S. lycopersicum*	Paris	ND	ND	Cavagnaro et al. (2001)
	M. trunculata	NR	105%	52%	Thonar et al. (2011)
Glomus caledonium	*S. lycopersicum*	Paris + Arum	30%	−13%	Smith et al. (2004)
Glomus claroideum	*M. trunculata*	NR	390%	144%	Thonar et al. (2011)
Glomus intraradices	*A. porrum*	Arum	ND	ND	Cavagnaro et al. (2001)
	S. lycopersicum	Arum	90%	−20%	Smith et al. (2004)
	M. trunculata	NR	745%	145%	Thonar et al. (2011)
S. calospora	*A. porrum*	NR	135–324%	46%	Dickson et al. (1999)
	S. lycopersicum	NR	ND	ND	Thonar et al. (2011)

Notes: Plant growth benefit refers to the gain in plant biomass (dry matter basis) as a result of AM fungus colonization of roots. NR, not reported. ND, no data available.

Physiological traits of the AM fungi that influence the P uptake of mycorrhizae include the distribution and extent of the external hyphal network, since this permits the fungus to colonize roots and scavenge plant-available P from the soil. Hyphal distribution varies among fungal species; for instance, *G. intraradices* is an extensive and rapid colonizer, able to access and transport soil P from distances of up to 15 cm away from corn roots, much further than the few mm that can be exploited by fine root hairs (Jansa et al. 2003). Commercial inoculants are often developed from *G. intraradices* strains because they are easily reproduced and aggressively colonize a number of crop species. However, there are other AM fungus species that could be equally effective. The P acquired by the model legume *Medicago trunculata* in association with *G. intraradices* was 745% higher than the P uptake by non-mycorrhizal *M. trunculata*, but similar growth benefits were achieved with *G. claroideum*, although this AM fungus delivered half as much P to the host plant and its hyphal network was far less extensive in the soil (Thonar et al. 2011). Differences in P transport efficiency were attributed to differences in the carbon supplied to the AM fungi, as *G. intraradices* is expected to have a higher carbon demand than *G. claroideum* to support the biomass generated in its extensive hyphal network. The hyphal network of *Scutellospora calospora* is equally large and provides significant growth benefits for onion and leek (*A. porrum*) (Dickson et al. 1999); however, its colonization of subterranean clover (*Trifolium subterraneum*) roots declined with time as it developed more non-infective hyphae for AM fungus spore production rather than soil exploration (Pearson & Schweiger 1994). Together, the distribution, extent and functions of the hyphal network, the corresponding carbon demands of the AM fungus and the specific P nutritional needs of the host crop influence efficient P acquisition. Finding the appropriate balance is necessary to deliver maximum growth benefits to the host when P is limiting. As discussed by Smith et al. (2011), poor growth of mycorrhizal plants may occur when direct P uptake by the roots is inhibited and there is no compensatory response of the mycorrhizal P uptake pathway, which suggests a crucial interplay between carbon and P transfers in mycorrhiza.

As mentioned, AM fungi possess high-affinity P transporters at the soil/fungal interface that are responsible for transporting soil P to the hyphae. Transporters were

identified from three species: *G. versiforme* (GvPT), *G. intraradices* (GiPT) and *G. mosseae* (GmosPT) (Javot et al. 2007). Uptake and growth promotion in a host plant varies between AM fungal species and isolates based on the expression of these high-affinity P transporters (Johnson et al. 1997; Munkvold et al. 2004). For example, tomato colonized by *G. mosseae* had an average shoot P content of 2.25 mg and shoot dry weight of about 1.8 g at harvest, whereas the same host colonized by isolates of *G. caledonium* and *G. intraradices* in an identical growing environment had shoot P contents of about 0.75–1.5 mg, and shoot dry weights between 0.6 and 1.1 g (Burleigh et al. 2002). This was attributed to higher efficiency of P transfer from soil to the hyphae of *G. mosseae* due to expression of the P transporter gene GmosPT by *G. mosseae*, since the other isolates did not express high-affinity P transporters (Burleigh et al. 2002). Molecular tools will be helpful in identifying other AM fungus that possess high-affinity P transporter genes and selecting the most desirable species for inoculation of vegetable crops based on their gene expression in greenhouse and field environments.

Integrating AM fungi associations into nutrient management strategies

Integrated nutrient management strategies aim to match P fertilizer inputs with crop P requirements, such that under- and over-fertilization is avoided. The previous sections explained how AM fungi contribute to crop P nutrition, with emphasis on crops in the Alliaceae, Fabaceae and Solanaceae families. There is considerable variation in AM fungi-induced P uptake among plant/fungus pairs, due in part to the differences in MD and multiple mechanisms responsible for P acquisition by both plant and fungi, which is further confounded by environmental feedback, e.g. agronomic practices and soil biogeochemistry. Vegetable producers relying on commercial inoculants such as *Glomus* species during the greenhouse growth phase of vegetable production know that these AM fungi form mycorrhiza with many crops, they are easily reproduced and, after colonizing the root, rapidly develop an extensive hyphal network. However, these characteristics do not necessarily guarantee that the crop is receiving the greatest benefit in terms of P uptake. To select the most effective strains for AM fungi-induced P uptake requires in-depth knowledge of the functional traits of the AM fungus, including the magnitude of intra- and inter-specific variation in morphological and physiological attributes of the fungus across a range of hosts (Munkvold et al. 2004). Finally, the efficiency of P acquisition through the hyphal network as influenced by high-affinity P transporters is virtually unknown for most mycorrhiza.

Given that commercial AM fungi strains are not well characterized with respect to their role in P uptake, the best alternative is for vegetable producers to implement agronomic practices that maintain or enhance the indigenous AM fungi population on their farms. The indigenous AM fungi "inoculum" in the soil is composed of AM fungus spores, hyphal strands and sections of plant roots bearing fungal vesicles, which under appropriate conditions will germinate and lead to mycorrhizal development (Plenchette et al. 2005). Agronomic practices that lower the population of AM fungi inoculum should be avoided, including P fertilization that increases the soil test P to a high or very high level, excessive tillage and frequent cultivation of non-mycorrhizal host crops (Jansa et al. 2006). Increasing the AM fungus spore population of inoculum and encouraging AM fungus colonization of roots is achieved by growing more mycorrhizal plants, including cover crops and intercrops, which is already done by many vegetable producers to maintain soil health and fertility. Implementing crop rotations that exclude or lengthen the time between plantings of non-mycorrhizal crop species is also beneficial for the indigenous AM fungal

pool (Koide et al. 1999). If vegetables seedlings are transplanted rather than directly seeded, the transplants can be grown in media containing AM fungi, e.g. field soil with indigenous AM fungus or peat-based growth media that is inoculated with a commercial AM fungus strain, to boost AM fungus colonization of roots at the earliest growth stages.

Crop rotations are already common in mixed vegetable agriculture, especially those that follow organic agriculture practices, as a means to reduce pest and disease pressures and to maintain soil fertility. Growing crops in sequence according to their MD could help to maintain the indigenous AM fungal population and improve the yields of subsequent crops. Non-mycorrhizal or low-mycotrophic crops such as beetroots and cabbage will lower the indigenous AM fungal population when grown in succession (Plenchette et al. 1989; Karasawa & Takebe 2012) and thereby decrease AM fungus colonization of roots in successive mycorrhizal host crops (Ryan & Angus 2003; Karasawa & Takebe 2012). Conversely, mycorrhizal host crops succeeding other mycorrhizal hosts in rotation show an overall increase in AM fungus colonization of roots, growth and nutrient uptake (Karasawa et al. 2002). For example, corn planted after crops that had high relative MD, i.e. sunflower or soyabean, had a higher rate of AM fungus colonization of roots and higher yield than corn following crops with lower relative MD, i.e. canola or wheat (Arihara & Karasawa 2000; Karasawa et al. 2002). Producers of mixed vegetable operations could adopt rotations that favour AM fungus colonization of roots by avoiding non-mycorrhizal crops and by interspersing highly mycorrhizal crops throughout the rotation. Practically, this will prove challenging because there are many factors influencing a producers' growing decisions and planting non-mycorrhizal crops in sequence is unavoidable at times.

Cover cropping with mycorrhizal crops is another strategy to maintain the AM fungal population in non-cultivated sections of the field or between plantings of short-season crops (Galvez et al. 1995). Introducing cover crops after non-mycorrhizal crops was reported to improve the growth and AM fungus colonization of roots of the following crop (Karasawa et al. 2002). Sufficient time must be allowed for a cover crop to boost the soil AM fungi population following the harvest of a non-mycorrhizal crop; for instance, a cover crop of sunflowers, a mycorrhizal host, required at least 3 months to raise the AM fungi population and deliver growth benefits to the succeeding corn crop (Karasawa et al. 2002). In intensively cropped systems and in northern growing climates, time and space constraints may not allow for the establishment of a cover crop between plantings of marketable crops. Intercropping mycorrhizal crops with the main non-mycorrhizal crop is a possible solution. Karasawa and Takebe (2012) intercropped clover and vetch between rows of cabbage, a non-mycorrhizal crop, and found a 15% increase in AM fungus colonization of roots in the succeeding winter wheat crop in the same year, compared with winter wheat following cabbage. Green manure and winter cover crops with mycorrhizal hosts can be incorporated into rotations to maintain or enhance the AM fungal population in "resting" sections as an alternative to fallowing, which is known to reduce the indigenous AM fungus population (Plenchette et al. 2005).

Selective inoculation of vegetable seedlings before transplanting can also be considered. Allium crops show consistent, positive responses to inoculation. For example, Welsh onion inoculated with *Glomus* species at the seedling stage had 94% AM fungus colonization of roots and achieved marketable yields under field conditions without additional P fertilizer inputs (Tawaraya et al. 2012). Inoculation of seedlings establishes the AM fungi symbiosis and allows rapid expansion of the hyphal network following transplanting, providing early growth benefits to the host. However, care must be taken in selecting the growth media for vegetable seedlings, considering that plant P status may

control the AM fungus colonization of its roots (Balzergue et al. 2013). For example, high AM fungus colonization of roots from commercial strains was achieved in leek grown on peat-based substrates, but there was no gain in shoot dry matter, N and P concentrations (Perner et al. 2006). Although a growth response is not necessary in the greenhouse phase of vegetable production, high nutrient supply in the substrate could prove detrimental to the AM fungus symbiosis.

AM fungi can also be inoculated in soils where mycorrhizal populations are very low, as is the case in some high-input cropping systems (Plenchette et al. 2005), but this is not recommended without knowledge of the soil test P status in case the lack of AM fungus colonization of roots in these fields is related to historical P over-fertilization. If indigenous AM fungi are scarce on the farm in the first place, the reasons why should be determined, as it could be difficult or impossible to re-establish a population from inocula (Tawaraya et al. 2012). Strains of *G. fasciculatum* and *G. etunicatum* perform better in soils that are rich in nutrients and organic matter and could be appropriate inocula, but it is difficult to detect plant responses to AM fungal strains in soils with a history of high input agriculture (Herrera-Peraza et al. 2011). Cultivating host crops may be a more reliable and cost-effective method of boosting the indigenous AM fungus population in such a situation (Plenchette et al. 2005). Although on-farm production of mixed-species AM fungal inocula is generally economical, at the end of a 7-year on-farm trial with bell pepper, Douds et al. (2012) concluded that there was no guarantee of gains in growth and yield that could be attributed to the AM fungus when the fields receiving these inocula had high soil test P levels.

Conclusions

Increasing cost of P fertilizers due to dwindling reserves of non-renewable phosphate rock and the negative impacts on water quality in areas where excessive P fertilization occurred are compelling vegetable producers to adopt integrated nutrient management strategies. Applying less P fertilizer is an obvious solution, but may appear to be a risky option for producers of high-value vegetable and horticultural crops. One of the consequences of lowering soil test P levels is that mycorrhizal plants will naturally associate with AM fungi, which could compensate for lower P fertilizer inputs. Because this review focused on AM fungi-induced P uptake, other benefits of AM fungi for vegetable crops were not considered but could include (1) enhanced water uptake (Augé 2001; F.A. Smith & S.E. Smith 2011; S.E. Smith & F.A. Smith 2011), (2) solubilization and uptake of other mineral nutrients such as Zn (Jansa et al. 2003) and (3) protection against plant diseases through physical and biochemical mechanisms (Abdel-Fattah et al. 2011). The multiple advantages of AM fungi for vegetable crops hold promise for reducing costs associated with irrigation, fertilizer and agrochemical use, although producers will want to verify AM fungus effects on growth and marketable yield on a crop-specific and site-specific basis.

Still, there are a number of questions concerning the practicality and advisability of reducing P fertilizer inputs to vegetable crops and expecting that crop P requirements could be met by AM fungi. For instance, what level of AM fungus inocula is required in agricultural fields to provide adequate AM fungus colonization of roots of mycorrhizal crops and achieve the maximum AM fungi-induced P uptake that is possible for a particular crop? What AM fungus species or strains must be present in the field to ensure that the mycorrhiza is able to scavenge enough plant-available P from the soil solution, or solubilize and mineralize additional plant-available P, to meet the crop requirements? Is manipulation/modification of the indigenous AM fungus community possible/practical?

Assessment of the soil P supplied to the crop from mycorrhiza is required because the magnitude and pattern of P uptake vary not only between crop species, but also among cultivars. These questions have implications for integrated nutrient management strategies that include AM fungi. It might be revealed, for instance, that inorganic P fertilizer should not be applied at the beginning of the growing season to avoid inhibiting the early-season AM fungus colonization of roots, but that a targeted, post-emergence P fertilizer application will sustain crop P nutrition while the hyphal network of AM fungi develops to the point that it can access soil P reserves and supply the balance of crop P requirements for the growing season.

Scientific studies are needed to provide the fundamental knowledge and justification for including AM fungi in integrated nutrient management strategies for P fertilization of vegetable crops, focusing on the mechanisms that control P uptake by mycorrhiza. The ^{32}P radiotracer is a powerful tool to determine what proportion of plant P nutrition is derived from mycorrhiza. As noted by Li et al. (2006), more than 50% of P uptake by plants was derived from AM fungi, even when soluble P fertilizer was applied, indicating the presence of a functional AM pathway for P transfer to the plant that could only be detected by such tracer methods. Areas for future research could be: (1) Confirming the taxonomy of AM fungi considered in P uptake studies with molecular genetic data for accurate species identification (e.g. see revised nomenclature of Schüßler and Walker (2010) and Krüger et al. (2012); (2) Developing a better understanding of the underlying mechanisms for plant-derived regulation of the P uptake pathways (direct uptake vs. AM fungi-mediated P uptake); (3) Relating mechanisms of mycorrhizal P uptake to specific plant families, based on their morphological and physiological characteristics; (4) Relating the mycorrhizal phenotype to the plant host, and the underlying mechanisms that control plant/fungal compatibility; (5) Establishing kinetic models describing P uptake and transfer by individual AM fungus species, and determine how they are influenced by the plant host and soil environment; (6) Establishing the relationship between AM fungal morphotype and P uptake efficiency; (7) Selecting compatible host/fungal pairs for inoculation; (8) Developing population-level models of AM fungi to assess whether species of AM fungi are increasing, persisting or declining in agricultural fields; and (9) Developing process-level models to select agronomic practices for optimal health and performance of AM fungal species.

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