Mycorrhizal Fungi Can Dominate Phosphate Supply to Plants Irrespective of Growth Responses[1]

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Arbuscular mycorrhizal (AM) fungi are vital components of nearly all terrestrial ecosystems, forming mutually beneficial (mutualistic) symbioses with the roots of around 80% of vascular plants and often increasing phosphate (P) uptake and growth. We present novel data showing that AM fungi can provide the dominant route for plant P supply, even when overall growth or P uptake remains unaffected. The results will change our understanding of the roles of AM fungi in agricultural and natural ecosystems; they also predict that mycorrhiza-specific plant P transporters must play a major role in plant P uptake regardless of whether the plants respond to AM colonization by taking up more P per plant or by increased dry weight, compared with non-mycorrhizal (NM) control plants.

AM associations are the outcome of 450 million years of co-evolution, which has led to adaptations in both plants and fungi that underpin their symbiotic development and function. The main physiological basis for mutualism is bidirectional nutrient transfer (Smith and Smith, 1990). Plants supply the AM fungi with sugars, and the fungi enhance the ability of the plants to scavenge for scarce and immobile nutrients, particularly P. Different AM fungus-plant combinations are functionally diverse both in effectiveness of the fungi as symbionts and in responsiveness of the plants in terms of total P uptake, growth, and/or reproduction, again compared with NM controls. This diversity has significant influences on plant interactions in ecosystems (Read, 1998; van der Heijden et al., 1998; Jakobsen et al., 2002; van der Heijden and Sanders, 2002) but is poorly understood at physiological or molecular levels.

TWO PATHWAYS OF P UPTAKE IN MYCORRHIZAL PLANTS

In an AM plant, P (as orthophosphate) can be absorbed both directly at the soil-root interface through root epidermis and root hairs and via the "mycorrhizal" pathway via external AM hyphae in soil (Fig. 1). These hyphae absorb P, translocate it rapidly to AM structures within the roots (intercellular hyphae, intracellular coils, and highly branched intracellular arbuscules; for details, see Smith and Read, 1997), from whence it is released to the interfacial apoplast adjacent to root cortical cells (Smith and Smith, 1990). Quantitative estimates of the fungal contribution to total P uptake have often assumed that the direct and mycorrhizal uptake pathways act in concert, although it is recognized that uptake directly from soil may decrease as the concentration of P in the soil solution adjacent to the roots becomes depleted (Tinker and Nye, 2000). The ability of AM hyphae to grow beyond this depletion zone and deliver P to the root is thought to be the main basis for their positive effects on P uptake and plant growth (Smith and Read, 1997). Where there is no response to symbiosis in terms of these variables (i.e. values for AM plants are not larger than NM plants growing in the same soil), it has been assumed that the mycorrhizal uptake pathway is not functioning and that all of the plant P is absorbed directly through P transporters in the root epidermis and root hairs. Increased growth or success of AM plants is then attributed to other benefits of the symbiosis, such as suppression of pathogens (West et al., 1993; Newsham et al., 1995).

FUNCTIONAL DIVERSITY IN DIFFERENT PLANT-FUNGUS COMBINATIONS

We now present results of an experiment carried out in a low-P soil/sand mix to determine the relative contributions of the direct and mycorrhizal uptake pathways in three plant species of varying responsiveness to mycorrhizas when colonized by three AM fungal species. The plants were flax (*Linum usitatissimum* L. cv Linetta), tomato (*Lycopersicon esculentum* Mill. cv Rio-Grande 76R), and medic (*Medicago truncatula* L. cv Jemalong). The AM fungi *Gigaspora rosea*

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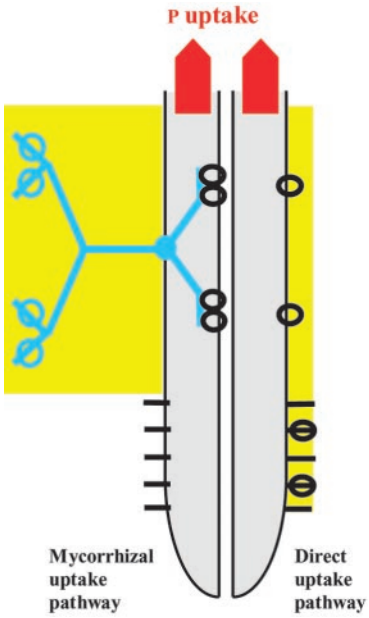

Figure 1. Diagrammatic representation (not to scale) of direct and mycorrhizal uptake pathways into plant roots. In the direct pathway, high-affinity plant P transporters (black circles) located in the epidermis and root hairs are involved in uptake of orthophosphate from the soil solution directly into plant cells. If the rate of uptake exceeds the rate of diffusion of P in the soil solution, the concentration of P is reduced leading to 1- to 2-mm zones of depletion (narrow yellow band) close to the root surfaces, which limit the rate of uptake. The mycorrhizal pathway involves uptake of P from the soil solution by AM fungal transporters (blue circles) located in external hyphae. P is then translocated rapidly over considerable distances (1–15 cm) and is delivered to fungus-plant interfaces in the root cortex. Plant P transporters located at these interfaces (black circles) absorb P into root cortical cells.

Nicolson and Schenck (Banque Européen des Glomales, BEG 9), *Glomus intraradices* Schenck and Smith (BEG 87), and *Glomus caledonium* (Nicol. and Gerd.) Trappe and Gerdemann (BEG 20) were grown in pot cultures of *Trifolium subterraneum* to provide inoculum, because AM fungi are unculturable and must be propagated on host plants. All plant-fungus combinations plus noninoculated, NM plants of each species were grown, to give a total of 12 treatments. A novel compartmented pot system was used to determine the contribution of the mycorrhizal uptake pathway to total plant P uptake (Fig. 2). The experimental plants (two per pot) were grown in compartmented, non-draining pots. The main root + hyphal compartment (RHC) contained 1,100 g of soil/sand mix, with or without incorporated AM inoculum (80 g kg^{-1}) containing colonized roots, spores, and soil. The hyphal compartment (HC) was a small plastic tube containing 25.3 g of the same soil mix (2.3% of the total) without inoculum, capped with 25-μm nylon mesh, which allowed hyphae of AM fungi, but not roots, to penetrate from the RHC and absorb P. The HC was placed horizontally, 5 cm below the soil surface with the mesh toward the center of the pot. The soil for the HCs was well mixed with ^{33}P-labeled orthophosphate of very high specific activity to provide a specific activity of 69.2 kBq mg^{-1} bicarbonate-extractable P (Olsen et al., 1954). The small size of the HC meant that quantities of P available to NM and mycorrhizal plants were almost equal, and results were not biased in favor of the fungal pathway, as in some previous compartmented pot designs with large HCs (e.g. Li et al., 1991). The location of the HC within the RHC ensured that no fungi were disadvantaged because of poor growth or P uptake at a distance from roots (Smith et al., 2000). Thus ^{33}P in the HC could only reach the plants via the hyphae of AM fungi (mycorrhizal pathway); unlabeled P could be absorbed from the RHC via both direct and mycorrhizal pathways. The soil used and the general experimental procedures were as described previously, and the P level in the soil was growth limiting (Pearson and Jakobsen, 1993; Smith et al., 2000). Plants were harvested at 6 weeks.

Compared with NM plants without additional P, flax grew better, but to different extents, when colonized by each of the three fungi tested (*G. rosea* < *G. caledonium* < *G. intraradices*; Table I). Medic responded positively to the two *Glomus* spp. in terms of dry weight production, but showed a small growth depression (lower dry weight) with *G. rosea*, compared with NM plants. Tomato did not respond positively to any of the fungi (Table I). The changes in growth are presented as mycorrhizal growth dependency (MGD) in Figure 3a. P uptake also varied between the different plant-fungus combinations (Table I), and mycorrhizal P dependencies (MPDs) were similar to MGDs, allowing for small increases in plant P concentrations in some cases (Fig. 3b). All inoculated plants became colonized by AM fungi

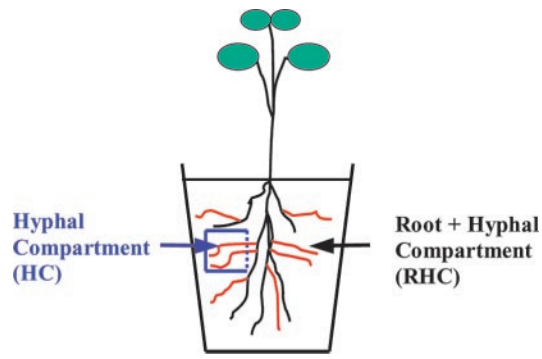

Figure 2. Diagrammatic representation (not to scale) of the compartmented pot design used in the experiment. The main RHC was a non-draining plastic pot containing 1,100 g of soil/sand mix. For mycorrhizal treatments, this mix included 80 g of pot culture inoculum of the appropriate fungus (see text). NM treatments received no inoculum. The HC was a small plastic tube containing 25.3 g of the same soil/sand mix without inoculum and capped with 25-μm nylon mesh, which allowed hyphae (shown in red) but not roots (shown in black) to grow into the HC. The soil in the HC was well mixed with ^{33}P-labeled orthophosphate of high specific activity. There were two plants per pot; for simplicity, only one is illustrated.

Table I. *Plant growth (dry wt) and P uptake (mg P)[a] per pot (two plants) of flax, medic, and tomato in symbiosis with three arbuscular mycorrhizal fungi, G. rosea, G. caledonium,* or *G. intraradices. Values are means and* SEs *of means of three replicate pots, except for NM flax and tomato for which there were four replicates.*

Plant	NM		*G. rosea*		*G. caledonium*		*G. intraradices*	
	Dry Wt	P	Dry Wt	P	Dry Wt	P	Dry Wt	P
	g	*mg*	*g*	*mg*	*g*	*mg*	*g*	*mg*
Flax	0.4 ± 0.0	0.4 ± 0.03	0.8 ± 0.1	1.2 ± 0.1	4.8 ± 0.1	4.7 ± 0.2	6.1 ± 0.1	7.8 ± 0.1
Medic	1.5 ± 0.1	2.1 ± 0.2	1.0 ± 0.1	2.2 ± 0.1	4.8 ± 0.2	6.3 ± 0.3	4.8 ± 0.3	8.2 ± 0.1
Tomato	7.5 ± 0.4	9.0 ± 0.35	5.1 ± 0.4	6.6 ± 0.5	6.6 ± 0.2	8.1 ± 0.3	6.1 ± 0.1	8.6 ± 0.2

[a] Dried ground plant material was digested in nitric:perchloric acid (4:1, v:v). Total P content of the extracts was measured by the molybdate blue method (Murphy and Riley, 1962) on a Technicon Autoanalyser II (Analytical Instrument Recycle, Golden, CO).

(Table II), but the variations in growth and in P uptake from the pots as a whole were not directly related to the percentage of root length colonized (compare Tables I and II). There was no colonization in noninoculated (NM) controls.

THE MYCORRHIZAL PATHWAY CAN DOMINATE PLANT P UPTAKE

By supplying ^{33}P in small HCs to which only the fungal hyphae had access (Fig. 2), we demonstrated large differences in the relative contributions of the direct and mycorrhizal pathways of P uptake via different fungi. Specific activities of ^{33}P (kBq mg^{-1} P) in the different plant-fungus combinations were very variable (Fig. 3c), showing that the mycorrhizal pathway made different contributions to total P uptake. We calculated the contributions of the mycorrhizal pathway to P uptake into the plants; these are directly proportional to the specific activities of ^{33}P. Values slightly higher than the theoretical maximum of 100% (indicated by the horizontal dotted line in Fig. 3c) suggest either that (a) AM fungal hyphal densities were higher in the HCs than RHCs or (b) bicarbonate extraction underestimates the specific activity of ^{33}P available to the hyphae. These uncertainties do not invalidate the conclusion that the quantitative contribution of P transfer via the mycorrhizal pathway was extremely high in five out of the nine individual plant-fungus combinations and was not correlated with percentage of colonization or MPD. The calculations suggest that when *G. intraradices* was the fungal partner, all of the P was delivered via the mycorrhizal pathway to all three plants (Fig. 3c). Other fungi showed different patterns of P delivery. Flax and medic colonized by *G. caledonium* also received P exclusively via the mycorrhizal pathway, but in tomato, only approximately 70% was absorbed by this route. *G. rosea* was a poor symbiont with all three plants and delivered much less P, even to flax, which showed positive growth and P responses to this fungus. Interestingly, although medic did receive approximately 40% of the P from *G. rosea*, it, like tomato, showed a growth depression compared with NM controls (Fig. 3a). It appears that *G. rosea*

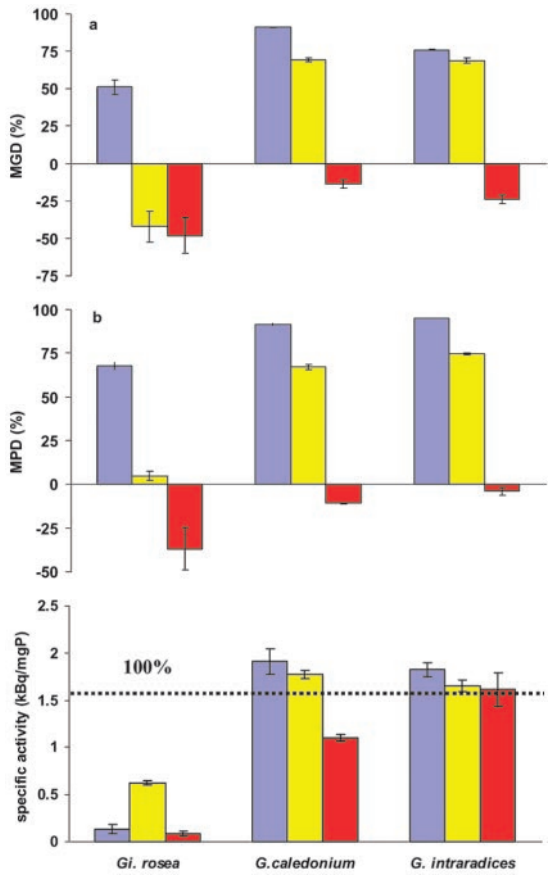

Figure 3. Mycorrhizal effects on growth, total P uptake, and specific activities of ^{33}P in flax (blue bars), medic (yellow bars), and tomato (red bars). a, Percentage MGD; b, percentage MPD; and c, specific activity of ^{33}P in the plants. Mycorrhizal dependencies were calculated as follows: MGD (or MPD) = 100 (value for M plant − mean value for NM plants)/value for M plant. In c, the dotted horizontal line indicates the predicted specific activity of ^{33}P in the plants if 100% of P was derived via the mycorrhizal pathway. This percentage was calculated using values for specific activities of ^{33}P in the plants and bicarbonate-extractable P in the HC and the total P available in the pots and in the HC. It assumes that the densities of hyphae (meters per gram of soil) were the same in the HC and RHC. Values are means and SEs of means of three replicate pots. ^{33}P was measured in the same extracts as those used for determination of total P (Table I) in a liquid scintillation counter (TR 1900, Packard Instrument, Meriden, CT).

Table II. *Percent mycorrhizal colonization*[a] *by three AM fungi in roots of flax, medic, and tomato*

Plant	*G. rosea*	*G. caledonium*	*G. intraradices*
Flax	40 ± 2	20 ± 4	53 ± 5
Medic	84 ± 1	77 ± 3	99 ± 0
Tomato	32 ± 5	44 ± 2	82 ± 2

[a] Percent colonization was determined by a line intercept method (McGonigle et al., 1990) following clearing in 10% (w/v) KOH and staining with Trypan blue (Smith et al., 2000). Means and SES of means of three replicate pots.

requires relatively high amounts of organic C from the plants.

LOSS OF FUNCTION OF THE DIRECT P UPTAKE PATHWAY AND KEY ROLES FOR MYCORRHIZA-SPECIFIC P UPTAKE MECHANISMS

Our results clearly indicate loss of function of the direct uptake pathway in roots colonized by AM fungi, which can apparently be complete in some AM symbioses. This confirms and extends one previous report (Pearson and Jakobsen, 1993), indicating a similar effect of *G. caledonium* in reducing the direct uptake capacity of cucumber (*Cucumis sativus*) roots, but the extent of the effect was not determined, and the significance has not been widely appreciated. Two processes may contribute to the loss of function of the direct uptake pathway. First, plant genes encoding P transporters expressed in the epidermis and root hairs may be down-regulated in response to AM colonization (Liu et al., 1998b; Rosewarne et al., 1999; Chiou et al., 2001). This may be analogous to the down-regulation of high-affinity P transporters in NM plants with improved P supply (Daram et al., 1998; Liu et al., 1998a). Both mycorrhizal and P effects have been shown to be much greater in medic than tomato and to vary with fungal species (Burleigh et al., 2002). No information on P transporter gene expression in flax is available. Second, the contribution of direct uptake may also be affected by the concentration of available P in the soil solution at the root/soil interface, declining as the P concentration is reduced at the surface of actively absorbing roots (Li et al., 1991). As direct uptake declines, its replacement by the mycorrhizal pathway will depend on the expression of P transporters in the external mycelium of the fungi (Harrison and van Buuren, 1995; Maldonado-Mendoza et al., 2001) and in plant cells adjacent to fungal structures in the root cortex (see Fig. 1). These plant cells absorb P released from the fungus into the interfacial apoplast (Rosewarne et al., 1999; Rausch et al., 2001; Harrison et al., 2002; Paszkowski et al., 2002). "Mycorrhiza-induced" P transporters, demonstrated recently (Rausch et al., 2001; Harrison et al., 2002; Paszkowski et al., 2002), are likely to play important roles in this process. These transporters are exclusively expressed in mycorrhizal roots: *MtPT4* in medic colonized by *Glomus versiforme* or *Gigaspora gigantea* (Harrison et al., 2002); *StPT3* in potato (*Solanum tuberosum*; Rausch et al., 2001) and *OsPT11* in rice (*Oryza sativa*; Paszkowski et al., 2002), both colonized by *G. intraradices*. Only three species of AM fungi have been tested thus far for their effects on the expression of mycorrhiza-specific P transporters, and our physiological results lead us to predict that there will be considerable diversity in the ability of different fungi to induce these mycorrhiza-specific genes, leading to the differences in contribution of the mycorrhizal pathway as reported here. At the same time, differential effects of AM fungi in regulating plant transport genes expressed in epidermis and root hairs must be considered. Most of our results are consistent with down-regulation. However, in flax colonized by *G. rosea*, there was a 60% MPD (increase in P uptake in mycorrhizal plants; Fig. 3b), but the mycorrhizal uptake pathway contributed only 9% of total P (Fig. 3c). This suggests that *G. rosea* increased P uptake via the direct uptake pathway in flax roots, presumably due to up-regulation of genes in epidermis and root hairs. Similar and tantalizingly suggestive effects of *Scutellospora calospora* on P uptake by both cucumber (Pearson and Jakobsen, 1993) and medic (Smith et al., 2000) have also been observed. Differences in gene expression and function of the mycorrhizal pathway, unrelated to P nutrition or extent of colonization as we have demonstrated, indicate differences in molecular cross-talk between different plant and fungal species, extending previous indications from P uptake experiments (Pearson and Jakobsen, 1993) and differential colonization of a tomato mutant by different fungal species (Gao et al., 2001).

IMPLICATIONS FOR ECOLOGY AND AGRICULTURE

Confirmation that mycorrhizal uptake can replace direct uptake, even in tomato, which showed no response to AM colonization, compels re-evaluation of estimates of mycorrhizal contributions to P nutrition based on total plant uptake in AM and NM plants (e.g. Smith et al., 1994). Furthermore, we can no longer say that lack of a positive change in growth or P nutrition as a result of AM colonization (i.e. no "mycorrhizal dependency") indicates that the symbiosis is nonfunctional in terms of pathways of P uptake. When colonized by AM fungi in the field, plants showing little or no growth response (including some crop plants) may depend for efficient exploitation of scarce soil P on a suite of P transporters that are different from those expressed when the plants are not mycorrhizal, as when they are grown in experiments with sterilized soil or with the application of fungicides. Most AM fungal species, including those used in our investigation, are widespread in terrestrial ecosystems. They exist in mixed communities of typically up to 20 or more species (based on identi-

fication of spore types in soil), with *Glomus* spp. particularly prevalent in agricultural systems. Most AM fungi are believed to be unspecific with respect to their ability to colonize different species of plants, although there may be exceptions (Helgason et al., 2002; Sanders, 2002). The unrelated AM fungi that we used can be considered as representative of those likely to be found in a mixed field community (e.g. Johnson et al., 1991).

Effective genetic manipulation of plant P uptake will depend on identifying which transporters actually operate under field conditions. It follows that the search for mechanisms and genes contributing to plant "P efficiency" should no longer ignore the modifying effects of mycorrhizal symbionts (Zhu et al., 2001). Furthermore, if mycorrhizal P uptake can be effectively "silent," mycorrhizal uptake of other nutrients, until now considered unimportant because colonization had little or no effect on whole-plant uptake, may also be significant. It is as yet unclear whether assemblages of co-occurring AM fungi in plant ecosystems will mirror the range of nutrient transport capacities and modifications to root function we have shown here using AM fungi from laboratory cultures. Because there is no reason to believe otherwise, the ecological consequences for growth of competing plant species of different responsiveness will be highly complex. Unraveling the complexities will require the concerted and collaborative efforts of physiologists and molecular biologists as well as ecologists.

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