

**Maize Kernel Development**

by Brian Larkins

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Phosphorus Uptake by Plants: From Soil to Cell

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P is an important plant macronutrient, making up about 0.2% of a plant's dry weight. It is a component of key molecules such as nucleic acids, phospholipids, and ATP, and, consequently, plants cannot grow without a reliable supply of this nutrient. Pi is also involved in controlling key enzyme reactions and in the regulation of metabolic pathways ([Theodorou and Plaxton, 1993](#)). After N, P is the second most frequently limiting

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membranes, and compartmentation and redistribution within the plant. We will concentrate on P in higher

PT UPTAKE ACROSS
THE PLASMA
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plants, although broadly similar mechanisms have been shown to apply in algae and fungi.

P IN SOIL

Although the total amount of P in the soil may be high, it is often present in unavailable forms or in forms that are only available outside of the rhizosphere. Few unfertilized soils release P fast enough to support the high growth rates of crop plant species. In many agricultural systems in which the application of P to the soil is necessary to ensure plant productivity, the recovery of applied P by crop plants in a growing season is very low, because in the soil more than 80% of the P becomes immobile and unavailable for plant uptake because of adsorption, precipitation, or conversion to the organic form (Holford, 1997).

Soil P is found in different pools, such as organic and mineral P (Fig.1). It is important to emphasize that 20 to 80% of P in soils is found in the organic form, of which phytic acid (inositol hexaphosphate) is usually a major component (Richardson, 1994). The remainder is found in the inorganic fraction containing 170 mineral forms of P (Holford, 1997). Soil microbes release immobile forms of P to the soil solution and are also responsible for the immobilization of P. The low availability of P in the bulk soil limits plant uptake. More soluble minerals such as K move through the soil via bulk flow and diffusion, but P is moved mainly by diffusion. Since the rate of diffusion of P is slow (10^{-12} to 10^{-15} m²s⁻¹), high plant uptake rates create a zone around the root that is depleted of P.

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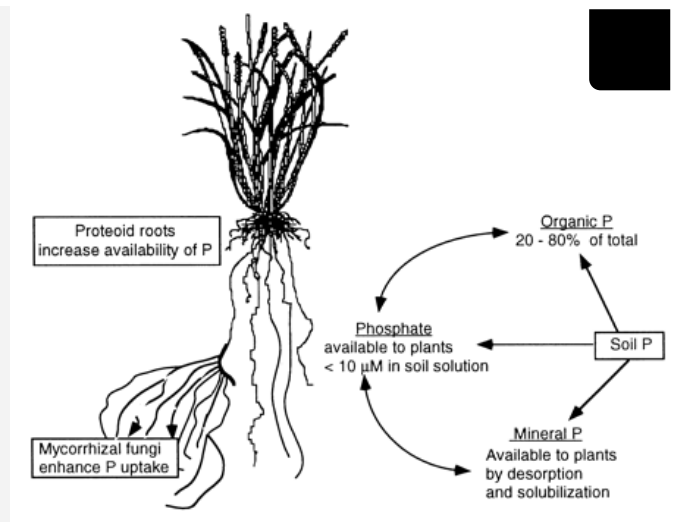


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Plant acquisition of soil P.

Plant root geometry and morphology are important for maximizing P uptake, because root systems that have higher ratios of surface area to volume will more effectively explore a larger volume of soil (Lynch, 1995). For this reason mycorrhizae are also important for plant P acquisition, since fungal hyphae greatly increase the volume of soil that plant roots explore (Smith and Read, 1997). In certain plant species, root clusters (proteoid roots) are formed in response to P limitations. These specialized roots exude high amounts of organic acids (up to 23% of net photosynthesis), which acidify the soil and chelate metal ions around the roots, resulting in the mobilization of P and some micronutrients (Marschner, 1995).

Pi UPTAKE ACROSS THE PLASMA MEMBRANE AND TONOPLAST

The uptake of P poses a problem for plants, since the concentration of this mineral in the soil solution is low but plant requirements are high. The form of P most readily accessed by plants is Pi, the concentration of which rarely exceeds $10 \mu\text{M}$ in soil solutions (Bielecki, 1973). Therefore, plants must have specialized transporters at the root/soil interface for extraction of Pi

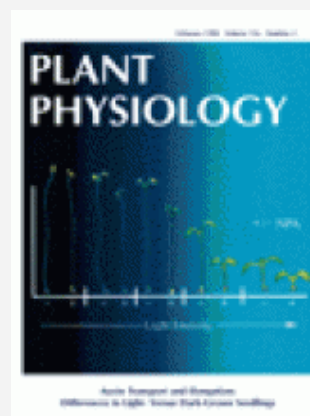
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from solutions of micromolar concentrations, as well as other mechanisms for transporting Pi across membranes between intracellular compartments, where the concentrations of Pi may be 1000-fold higher than in the external solution. There must also be efflux systems that play a role in the redistribution of this precious resource when soil P is no longer available or adequate.

The form in which Pi exists in solution changes according to pH. The pKs for the dissociation of H_3PO_4 into H_2PO_4^- and then into HPO_4^{2-} are 2.1 and 7.2, respectively. Therefore, below pH 6.0, most Pi will be present as the monovalent H_2PO_4^- species, whereas H_3PO_4 and HPO_4^{2-} will be present only in minor proportions. Most studies on the pH dependence of Pi uptake in higher plants have found that uptake rates are highest between pH 5.0 and 6.0, where H_2PO_4^- dominates (Ullrich-Eberius et al., 1984; Furihata et al., 1992), which suggests that Pi is taken up as the monovalent form.

Under normal physiological conditions there is a requirement for energized transport of Pi across the plasma membrane from the soil to the plant because of the relatively high concentration of Pi in the cytoplasm and the negative membrane potential that is characteristic of plant cells. This energy requirement for Pi uptake is demonstrated by the effects of metabolic inhibitors, which rapidly reduce Pi uptake. The precise mechanics of membrane transport are still not clear, although cotransport of Pi with one or more protons is the favored option based on the following observations.

The addition of Pi to starved roots results in both depolarization of the plasma membrane and acidification of the cytoplasm (Ullrich and Novacky, 1990). The depolarization indicates that Pi does not enter simply as H_2PO_4^- or HPO_4^{2-} , both of which would lead to membrane hyperpolarization. From these results it is likely that Pi is co-transported with positively charged ions. Cotransport of Pi with a cation involving a

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stoichiometry of more than 1 $C^+/H_2PO_4^-$ or more than 2 C^+/HPO_4^{2-} would result in a net influx of positive charge and hence lead to the observed membrane depolarization. The cytoplasmic acidification associated with Pi transport would suggest that the cation is H^+ , but acidification would occur regardless of the nature of the cation if the transported species were $H_2PO_4^-$, since it would undergo a pH-dependent dissociation in the cytoplasm to HPO_4^{2-} and H^+ . To verify H^+ cotransport requires simultaneous or at least comparable measurements of Pi influx and the change induced in cytoplasmic pH. Estimates of the cytoplasmic buffering capacity would then allow calculation of the Pi-associated H^+ flux, from which the stoichiometry could be deduced.

Pi uptake across the plasma membrane in animal cells normally involves cotransport with Na^+ . Na-energized, high-affinity Pi uptake systems have also been found in cyanobacteria and green algae. In some organisms, such as *Saccharomyces cerevisiae*, both Na^+ - and H^+ -dependent Pi uptake systems have been described (Roomans et al., 1977). Dependence of Pi uptake on Na^+ has not yet been demonstrated in higher plants, but this may be partly because few studies have actually tested this possible mode of energized Pi uptake.

Transfer of Pi from the cytoplasm to the vacuole involves a different set of thermodynamic parameters to those applying to the plasma membrane, mainly because of the millimolar concentrations in the cytoplasm and vacuole compared with the micromolar concentrations in the soil. Few estimates of cytosolic and vacuolar Pi concentrations are available. However, when maize was grown at Pi concentrations similar to those found in soils (i.e. 10 μM), the root cell cytoplasmic Pi concentration was estimated to be higher than the vacuolar concentration (Lee and Ratcliffe, 1993). Soybean leaf cell cytoplasmic Pi concentrations were also found to be higher than

concentrations in the vacuole when plants were grown in solutions containing 50 to 100 μM Pi (Lauer et al., 1989). Since the membrane potential of the vacuole is usually slightly positive with respect to the cytoplasm under these realistic conditions, Pi transfer to the vacuole need not be energized.

In plants supplied with higher concentrations of P, Pi appears to be close to electrochemical equilibrium across the tonoplast. In one of the few studies in which tonoplast transport has been examined, Pi uptake into vacuoles isolated from P-sufficient barley leaves was shown to follow a monophasic, almost linear concentration dependence up to at least 20 μM , and was independent of ATP supply (Mimura et al., 1990). However, in vacuoles isolated from Pi-starved cells, Pi uptake rates were found to be much higher and ATP dependent, despite the fact that the lower Pi concentrations in the vacuoles would favor passive Pi accumulation. This suggests the de-repression or activation of a second transporter in the tonoplast in response to Pi starvation.

The concentration dependence of Pi uptake in vacuoles from Pi-starved cells has not been reported; a biphasic response would support the presence of a second transporter that might play an important role in maintaining Pi homeostasis when the Pi supply is limited. The process of vacuolar Pi mobilization following Pi starvation is likely to require energy-dependent transport across the tonoplast, the mechanism of which is not understood, although an $\text{H}^+/\text{H}_2\text{PO}_4^-$ symport would be thermodynamically feasible. There is clearly a great deal more to understand about the specific mechanisms of vacuolar Pi transport in higher plants and the role these mechanisms play in buffering cytoplasmic Pi concentration.

MULTIPLE Pi TRANSPORTERS

The question of whether there are several Pi transporters with different functional characteristics in plant cell membranes or only one transporter with characteristics that vary with internal Pi status or external concentration has been addressed using kinetic analysis of uptake. In this type of analysis a transporter's affinity (K_m) for a particular mineral is estimated by measuring the rate of uptake at different external concentrations of an ion. Results from kinetic studies have been variously interpreted to support the existence of only one uptake system in barley roots (**Drew and Saker, 1984**) or up to seven in maize roots (**Nandi et al., 1987**). The most common interpretation of these kinetic studies is that two Pi uptake systems exist, one with a high affinity and activity that is either increased or de-repressed by Pi starvation, and one with a lower affinity and activity that is constitutive. Estimates of the K_m for high-affinity uptake range from 3 to 7 μm , whereas for low-affinity transporters the K_m estimates are more variable, from 50 to 330 μm in several different tissues and plant species (**Ullrich-Eberius et al., 1984**; **McPharlin and Bieleski, 1987**; **Furhata et al., 1992**).

Recent advances in the molecular biology of putative plasma membrane and tonoplast Pi transporters confirm that plants have multiple transporters for Pi. Thus far, four different transporter genes have been cloned from Arabidopsis, three from potato, and two from tomato. Putative plasma membrane or tonoplast phosphate transporters in higher plants were cloned by probing the database of translated expressed sequence tags with fungal phosphate transporter peptide sequences. This approach identified at least three expressed sequence tags from randomly sequenced Arabidopsis cDNAs with translational products that were similar to the fungal phosphate-transporter proteins. Using the expressed sequence tags, full-length clones have been isolated from cDNA and genomic libraries

([Muchhal et al., 1996](#); [Leggewie et al., 1997](#); [Smith et al., 1997](#)). One putative phosphate transporter gene was expressed in tobacco cells ([Mitsukawa et al., 1997](#)). High-affinity Pi uptake was detected in the cells in which this gene was overexpressed, demonstrating that at least one member of this gene family encodes a high-affinity plasma membrane Pi transporter.

The proteins encoded by these genes contain large regions that are identical to each other (Table I). The gene family appears to be clustered in the Arabidopsis genome with at least three members (*APT1*, *APT2*, and *AtPT4*) mapping to a specific region of chromosome 5 ([Lu et al., 1997](#); [Smith et al., 1997](#)). These multiple Pi-transporter genes are differentially expressed. Some are strongly up-regulated by Pi starvation, whereas the expression of others is constitutive ([Leggewie et al., 1997](#)). In the cases of *APT1* and *APT2*, the deduced amino acid sequences are 99% identical, which suggests that the proteins have the same functional characteristics. Although these proteins are almost identical, the promoter regions are completely different and may contain specific information that controls the spatial expression of these genes in different cell types, such as epidermal or cortical cells in the roots.

Table I.

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Comparison matrix of phosphate transporter polypeptides

A cDNA encoding a Pi transporter from potato, which is expressed in roots under conditions of Pi starvation, was characterized in the *pho84* yeast mutant ([Leggewie et al., 1997](#)). The K_m for Pi uptake was 130 μm , much higher than would be expected if it were involved in Pi uptake from soils, where concentrations rarely exceed 10 μm . Various reasons were suggested ([Leggewie et al., 1997](#)) for the high K_m values, but perhaps the most interesting is that phosphate transporters may contain a number of different protein subunits. The normal function of phosphate transporters may require subunits

that are absent when this plant cDNA is expressed in yeast. Genetic evidence from *Saccharomyces cerevisiae* indicates that several proteins containing putative membrane-spanning domains may interact to form a Pi-transporter complex (Bun-ya et al., 1991, 1996; Yompakdee et al., 1996). Although the association between these proteins has not been directly demonstrated, and one protein (Pho84) has been shown to be sufficient to catalyze phosphate transport in proteoliposomes (Berhe et al., 1995), the genetic evidence supports the idea that phosphate transporters are comprised of multiple subunits.

In summary, kinetic and molecular data show that higher plants have multiple transporters for Pi across cellular membranes. The molecular data show that there are at least four genes that encode Pi transporters, and the kinetic data suggests the presence of two types of transporters with different affinities for Pi. The recent advances in the molecular biology of these transporters provide powerful tools for understanding how their function is integrated into plant physiological processes. More work will be required to gain a comprehensive picture of the location (cellular and subcellular) and precise function of the multiple phosphate transporters in plants.

COMPARTMENTATION OF P

Maintenance of stable cytoplasmic Pi concentrations is essential for many enzyme reactions. This homeostasis is achieved by a combination of membrane transport and exchange between various intracellular pools of P. These pools can be classified in a number of different ways. First, according to their location in physical compartments such as the cytoplasm, vacuole, apoplast, and nucleus. The pH of these compartments will determine the form of Pi. The second pKa for H_3PO_4 is 7.2, so Pi in the cytoplasm will be approximately equally partitioned between the ionic

forms H_2PO_4^- and HPO_4^{2-} , whereas in the more acidic vacuole and apoplast, H_2PO_4^- will be the dominant species. Second, by the chemical form of P, such as Pi, P-esters, P-lipids, and nucleic acids. The proportion of the total P in each chemical form (except P in DNA) changes with tissue type and age and in response to P nutrition. Third, according to physiological function, as metabolic, stored, and cycling forms.

Our knowledge of the distribution of P into metabolic pools and physical compartments comes from three types of studies. Before 1980, information about P compounds and their distribution within tissues was derived from the analysis of isolated organelles or from the partitioning of the radioactive tracer ^{32}P between different chemical fractions (Bielecki, 1973). Other information came from studies on the rate at which ^{32}P is incorporated into or lost from tissues, commonly referred to as compartmental analysis (Macklon et al., 1996). A major advance in mapping intracellular pools came with the application of NMR spectroscopy in plant tissues. This technique allowed analysis in vivo of Pi and other important P-metabolites (Ratcliffe, 1994), as well as the monitoring of time-dependent changes in the amounts of these compounds. Figure 2 shows a typical ^{31}P -NMR spectrum, such as is observed from samples of root tips or suspension-cultured cells, and indicates where the observed compounds are found within the cell.

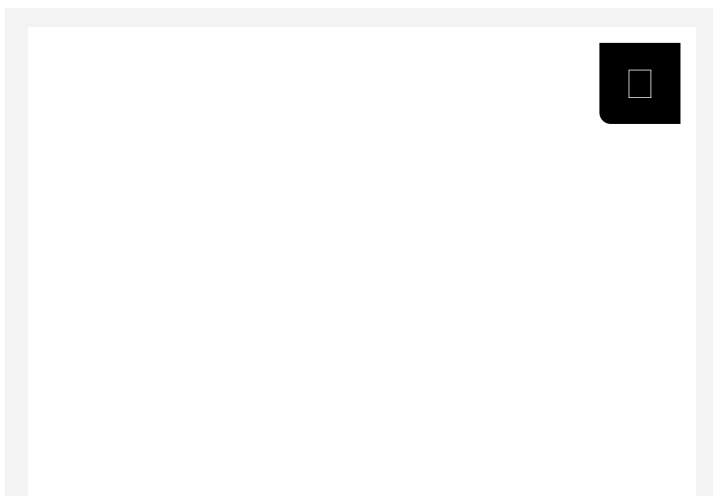


Fig. 2. [Download figure](#) | [Open in new tab](#) | [Download powerpoint](#)

³¹P-NMR of carrot cells. The assignments of the labeled resonances are: 1, several P-monoesters including Glc-6-P and phosphocholine; 2, cytoplasmic Pi; 3, vacuolar (vac) Pi; 4, γ-P of nucleoside triphosphates, principally ATP; 5, α-P of NTPs; 6, NDP-hexose and NAD(P)H; 7, NDP-hexose; and 8, β-P of NTPs. (Spectrum redrawn from [Carroll et al., 1994](#).)

Separate signals are detectable for Pi and other soluble-P compounds located in the near-neutral cytoplasm or in the acidic vacuole (Fig.2). ³¹P-NMR is at present the only way to measure directly the cytoplasmic and vacuolar pools of Pi in vivo. In an NMR spectrum the intensity of the resonances, reflected in the peak areas, provides an immediate representation of the relative amounts of the different soluble-P fractions present. The peak areas represent the content of Pi from which concentrations can be derived (see [Lee and Ratcliffe, 1993](#)). NMR studies confirmed that a small, rapidly turning over pool of Pi (representing 1–5% of total Pi) is located in the cytoplasm and a larger storage pool is located in the vacuole ([Ratcliffe, 1994](#)). NMR studies have made a major contribution to our knowledge of the behavior of the cytoplasmic and vacuolar pools of Pi within the plant.

REGULATION OF Pi UPTAKE

Cytoplasmic Pi is maintained at constant concentrations (5–10 mM), more or less independently of external Pi concentrations, except under severe P depletion ([Lee et al., 1990](#); [Lee and Ratcliffe, 1993](#); [Mimura, 1995](#)). In contrast, vacuolar Pi concentrations vary widely; under conditions of P starvation, vacuolar Pi may be almost undetectable. Pi in the vacuole also increases more readily than other P fractions in response to improved P status. However, it does not seem to

increase above about 25 mm ([Lee et al., 1990](#); [Lee and Ratcliffe, 1993](#); [Mimura, 1995](#)).

When the supply of Pi is limited, plants grow more roots, increase the rate of uptake by roots from the soil, retranslocate Pi from older leaves, and deplete the vacuolar stores of Pi. In addition, mycorrhizal fungi may more extensively colonize the roots. Conversely, when plants have an adequate supply of Pi and are absorbing it at rates that exceed demand, a number of processes act to prevent the accumulation of toxic Pi concentrations. These processes include the conversion of Pi into organic storage compounds (e.g. phytic acid), a reduction in the Pi uptake rate from the outside solution ([Lee et al., 1990](#)), and Pi loss by efflux, which can be between 8 and 70% of the influx ([Bielecki and Ferguson, 1983](#)). Any or all of these processes may be strategies for the maintenance of intracellular Pi homeostasis.

It is clear from both kinetic and molecular studies that the capacity to transport Pi across cellular membranes involves several different transporters and is in some way regulated by the external supply of Pi. [Furihata et al. \(1992\)](#) showed differential expression of phosphate transporters using kinetic techniques in which the high-affinity, but not the low-affinity, system was repressed by high concentrations of Pi. The expression of certain members of the putative plasma membrane or tonoplast phosphate-transporter gene family increases during periods of Pi starvation. In Arabidopsis at least three genes encoding phosphate transporters are expressed in roots and are up-regulated by Pi starvation. Similarly, in potato one gene was specifically induced in roots and stolons by starving the plants of Pi, whereas a second gene was expressed throughout the plant under conditions of high or low phosphate.

Changes in Pi-transport activity and phosphate-transporter gene expression show that plant cells respond to changes in the Pi concentration of the

external medium or in the vacuole. However, the intracellular signals and the factors that modify gene expression in the nucleus while cytoplasmic concentrations of Pi remain relatively constant are unknown. Progress at the molecular level may eventually provide insight into the processes that regulate phosphate uptake through the isolation of genes encoding proteins that interact and regulate phosphate-transport mechanisms.

P TRANSLOCATION IN WHOLE PLANT

Recent studies (Mimura et al., 1996; Jeschke et al., 1997) provide a picture of patterns of Pi movement in whole plants. In P-sufficient plants most of the Pi absorbed by the roots is transported in the xylem to the younger leaves. Concentrations of Pi in the xylem range from 1 mM in Pi-starved plants to 7 mM in plants grown in solutions containing 125 μ M Pi (Mimura et al., 1996). There is also significant retranslocation of Pi in the phloem from older leaves to the growing shoots and from the shoots to the roots. In Pi-deficient plants the restricted supply of Pi to the shoots from the roots via the xylem is supplemented by increased mobilization of stored P in the older leaves and retranslocation to both the younger leaves and growing roots. This process involves both the depletion of Pi stores and the breakdown of organic P in the older leaves. A curious feature of P-starved plants is that approximately one-half of the Pi translocated from the shoots to the roots in the phloem is then transferred to the xylem and recycled back to the shoots (Jeschke et al., 1997). In the xylem P is transported almost solely as Pi, whereas significant amounts of organic P are found in the phloem.

A number of mutants that show altered Pi accumulation in leaves have been identified. These may help us to understand the processes controlling the allocation of Pi within the plant. One Arabidopsis mutant (*pho1*) was

isolated based on reduced total phosphate concentrations in the leaf tissue ([Poirier et al., 1991](#)) and was shown to have root Pi uptake rates that were the same as the wild type, but reduced translocation rates to the shoot. In the *pho1* mutant, it is not known whether a gene encoding a transporter or regulatory molecule has been mutated; however, the phosphate-transporter genes that have been cloned do not map to the *pho1* (or *pho2*) locus. This mutation highlights the importance of specialized mechanisms for the transfer of Pi to the xylem. Another *Arabidopsis* mutant, *pho2*, accumulates P in its leaves to toxic concentrations, which is indicative of a defect in the regulation of Pi concentrations in shoots ([Delhaize and Randall, 1995](#)) and illustrates the significance of regulating intracellular concentrations.

MYCORRHIZAE IN P UPTAKE

There is a general perception that Pi uptake by plants occurs as a direct consequence of uptake from the soil by root cells. However, in more than 90% of land plants, symbiotic associations are formed with mycorrhizal fungi. In these plants the fungal hyphae play an important role in the acquisition of P for the plant ([Bolan, 1991](#); [Smith and Read, 1997](#)). Mycorrhizae can be divided into two main categories: ectomycorrhizae and endomycorrhizae, of which vesicular arbuscular mycorrhizae are the most widespread in the plant kingdom ([Smith and Read, 1997](#)). The mycorrhizal symbiosis is founded on the mutualistic exchange of C from the plant in return for P and other mineral nutrients from the fungus. Influx of P in roots colonized by mycorrhizal fungi can be 3 to 5 times higher than in nonmycorrhizal roots (rates of $10^{-11} \text{ mol m}^{-1} \text{ s}^{-1}$; [Smith and Read, 1997](#)).

The few published studies of the kinetics of Pi uptake indicate that mycorrhizal roots and isolated hyphae have P-uptake systems with characteristics similar to

those found in nonmycorrhizal roots and other fungi (**Thomson et al., 1990**; **Smith and Read, 1997**). Germ tubes of the vesicular arbuscular mycorrhizal fungus *Gigaspora margarita* have two Pi-uptake systems (K_m 2–3 μm and 10,000–11,000 μm) (**Thomson et al., 1990**). A recent molecular study (**Harrison and van Buuren, 1995**) identified the gene *GvPT*, which encodes a high-affinity fungal phosphate transporter ($K_m = 18 \mu\text{m}$) in external hyphae that is similar in both structure and function to high-affinity transporters in plants (Table I).

A number of factors may contribute to the increased rate of Pi uptake measured in mycorrhizal plants (**Smith and Read, 1997**). An extensive network of hyphae extends from the root, enabling the plant to explore a greater volume of soil, thereby overcoming limitations imposed by the slow diffusion of Pi in the soil. Several studies have shown that the depletion zone around plant roots, which is caused by plant uptake and the immobile nature of Pi, is larger in mycorrhizal than in nonmycorrhizal plants (**Bolan, 1991**). Mycorrhizal fungi may also be able to scavenge Pi from the soil solution more effectively than other soil fungi because C (which may be limiting in the soil) is provided to the fungus by the plant. The plant/fungus association could therefore enable the plant to compete more effectively with soil microorganisms for the limited amount of available soil Pi. Mycorrhizal fungi may also be able to acquire P from organic sources that are not available directly to the plant (e.g. phytic acid and nucleic acids) (**Jayachandran et al., 1992**).

Little is known about the transport of P compounds within mycorrhizae or the mechanism of P efflux from the fungus. Pi and organic P (such as polyphosphate) could be carried within the fungus by cytoplasmic streaming or by bulk flow to the plant root from external hyphae located in the soil. The current view is that Pi is the major form effluxed by the fungus across the

interfacial membranes. However, there is also evidence in higher plants that phosphocholine can be broken down outside cells to release Pi. It is possible that phosphocholine is also effluxed by the fungus to the plant; Pi would then be taken up by the plant via an H⁺ cotransporter, as in nonmycorrhizal roots. Since it is known that the phosphate transporter cloned from *Glomus versiforme* (*GvPT*) is not expressed in fungal structures inside the plant, it cannot be a candidate for the fungal P efflux mechanism. Efflux of P must depend on a different transporter of unknown structure.

The role of P in the regulation of symbiosis is still poorly understood, in part because of conflicting experimental results. In mycorrhizal roots demand for P by the plant may regulate the activity of P transporters in the fungus, with efflux from the fungus being the limiting step.

However, NMR studies of ectomycorrhizal roots of *Pinus resinosa* (MacFall et al., 1992) showed that although there was an increase in polyphosphate P in mycorrhizal roots, the vacuolar Pi content of mycorrhizal and nonmycorrhizal roots was similar. The mycorrhizal plants did not accumulate Pi in the vacuoles, which suggests that the fungus (*Hebeloma arenosa*) may be able to limit the efflux of P to the plant.

Mycorrhizal roots are able to take up Pi from solutions containing up to 100 mM Pi (Smith and Read, 1997), concentrations far above that likely to be encountered in the soil. High external Pi concentrations (up to 16 mM) had little adverse effect on germination and growth of germ tubes in the vesicular arbuscular mycorrhizal fungus *G. margarita* (Tawaraya et al., 1996). These results suggest that the low levels of colonization seen in plants growing in soils with high P status may not be the result of direct regulation of the activity of the fungus by soil Pi, but, rather, that specific signals from the plant regulate the activity of the fungus.

CONCLUSIONS

Considering that P is an essential and often limiting nutrient for plant growth, it is surprising that many aspects of P uptake and transport in plants are not thoroughly understood.³¹P-NMR studies have provided a picture of where Pi is distributed in a living cell, kinetic studies have elucidated the general functional characteristics of plasma membrane and tonoplast Pi transporters, and molecular studies have confirmed the presence of multiple genes encoding phosphate transporters that are differentially expressed. Perhaps the next important leap in our conceptual understanding in this area will come from the integration of these techniques to provide a comprehensive picture of the function of phosphate transporters and how the control of their spatial and temporal expression allows the plant to cope with changing environmental conditions.

A final issue to raise is that the soil Pi concentration has often been ignored by plant physiologists. It is common to find experiments in which plants were grown in 1 mM Pi, which may be 100-fold higher than the Pi concentrations plants encounter in agricultural or natural ecosystems. To fully understand how plants acquire Pi from soils and regulate internal Pi concentrations, future studies on Pi uptake by plants must more closely mimic soil conditions, in which the concentration of Pi is always low and soil microflora influence both acquisition and mobilization.

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Footnotes

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