Phosphate transport and signaling
KG Raghothama

The discovery of phosphate (Pi) transporter genes has provided a basis for the molecular study of the complex pattern of Pi transport in plants. Over the past two years, a significant amount of information has been generated on the molecular regulation of phosphate transport in plants. Recent developments in plant genomics will soon allow the complete dissection of the signal transduction pathway(s) associated with plant responses to Pi limitation in the rhizosphere.

Introduction
Phosphate (Pi) is one of the essential nutrients required by plants. It is a key player in all metabolic processes including energy transfer, signal transduction, biosynthesis of macromolecules, photosynthesis and respiration [1••,2••]. Nevertheless, the interactions of Pi with soil constituents such as Al, Fe and Ca, its existence in organic forms, and its low rates of diffusion make Pi the least readily available nutrient in the rhizosphere. The low availability of Pi in the acid soils of the tropical and sub-tropical regions of the world is of serious concern to agriculture in these regions. In response to persistent Pi deficiency, plants have developed multifaceted adaptive mechanisms to acquire Pi from the soil [2••]. Enhanced uptake and efficient utilization of Pi are among the primary biochemical and molecular changes associated with Pi deficiency.

Many of the morphological and biochemical changes that are induced in roots growing in Pi-deficient conditions are geared towards enhancing Pi uptake. Root modifications include enhanced root growth, altered root architecture, and increased production and elongation of root hairs [3,4]. The root hairs are responsible for nearly 63% of Pi absorbed by Pi-deficient plants [5]. The association of mycorrhizal fungi with roots is an important symbiotic interaction that enhances Pi acquisition [6]. Mycorrhizal fungi function as an extended and highly efficient root system in that their hyphae acquire, concentrate and transport Pi from soil that would otherwise be beyond the reach of the roots. Non-mycorrhizal plants, such as white lupin, respond to Pi deficiency by producing highly branched bottlebrush-like clusters of rootlets that are covered with root hairs called proteoid roots [4,7]. Proteoid roots efficiently produce and secrete organic acids and phosphatases [8], and absorb Pi more rapidly than non-proteoid roots [7]. In many dicots, secretion of organic acids and chelating agents that enhance Pi availability from the roots is also documented (see for review [2••]).

It is becoming evident that many of the biochemical, physiological and morphological changes that occur in response to Pi deficiency are associated with altered gene expression [1••,2••,9]. These changes in gene expression are initiated as a direct and specific response to Pi starvation. Some of the induced genes are directly involved in enhancing the availability of Pi and promote its uptake. The phosphate transporters, phosphatases, and enzymes involved in organic-acid synthesis and anion channels facilitating organic acid release are examples of the proteins encoded by genes whose expression is induced by Pi deficiency. This review will provide an overview of the recent developments in our understanding of phosphate transport and signal transduction in plants experiencing Pi starvation.

Phosphate acquisition and transport in plants
Plants acquire Pi despite a steep concentration gradient across the plasma membrane: Pi concentrations within plant cells are typically 1000-times those outside. Under experimental conditions, both high and low affinity Pi-uptake mechanisms have been observed in plants [2••,10••]. Nevertheless, it is generally accepted that at Pi concentrations that are within the micromolar range (1–10 µm), which corresponds to Pi concentrations in cultivated soils, the high-affinity transporters mediate Pi uptake. An energy mediated co-transport process, driven by protons generated by a plasma membrane H+-ATPase, has been proposed as the mechanism of Pi uptake in plants [(2••,10••,11•] and references therein). Additional evidence of the involvement of protons in Pi uptake comes from the use of inhibitors that dissipate the proton gradient across membranes and that suppress Pi uptake [12•,13•]. The $K_m$ (i.e. Michaelis–Menten constant, the substrate concentration that allows the reaction to proceed at one-half its maximum rate) for high-affinity transporters varies from 1.8 to 9.9 µM [10••]. The high-affinity uptake process is induced when Pi is deficient, whereas the low-affinity transport system appears to be expressed constitutively in plants.

Plant phosphate transporters
High-affinity Pi transporters are membrane-associated proteins that translocate Pi from an external media containing low concentrations (i.e. 1–10 µM) into the cytoplasm where Pi concentrations are much greater (i.e. mM). The availability of *Arabidopsis* expressed sequence tags has led to the isolation of several genes that encode high-affinity
Pi transporters [12•,13–18,19•,20•,21]. The functions of these isolated genes have been determined by their complementation of yeast mutants that are deficient in high-affinity Pi uptake [12•,13,14,20•,21], and by their expression in cultured tobacco cells grown in Pi-limiting media [16]. The salient features of the expression of genes encoding high-affinity phosphate transporters include: preferential expression in roots, rapid induction when Pi becomes deficient, reversibility upon resupply of Pi and a specific response to Pi deprivation [13,19•].

Recently, a gene encoding a low-affinity (high $K_m$) Pi transporter (Pht2;1) that is expressed preferentially in the leaves of *Arabidopsis* was described for the first time [22••]. Functional analysis of this gene in mutant yeast cells indicated that it is a Pi:H symporter, which has an apparent $K_m$ of 0.4 mM for Pi [22••]. Homologs of this gene are also found in other plant species including rice [22••]. The low-affinity transporters belonging to the Pht2;1 family are probably involved in loading Pi within shoots.

### Structure of plant Pi transporters

All of the high-affinity Pi transporters whose encoding genes have been cloned are integral membrane proteins. Each protein consists of 12 membrane-spanning regions that are separated into two groups of six membrane-spanning regions by a large hydrophilic charged region [23•]. Plant Pi transporters appear to have evolved by tandem intragenic duplication of the original structural unit of a six membrane-spanning protein [23•]. Interestingly, Pi:H symporters have been isolated and characterized only from fungi and plants. The remarkable similarities in the structure and function among the Pi transporters indicates that these are among the oldest and highly conserved proteins in plants. The low-affinity Pi transporter Pht2;1 is also a member of the 12-membrane-spanning-region Pi:H symporter family. Its primary structure, however, is different from that of the high-affinity phosphate transporters, suggesting that it belongs to a novel subfamily of Pi transporters [22••].

### Spatial distribution of Pi transporters

Genes encoding the high-affinity Pi transporters are preferentially expressed in Pi-starved roots [13,14,19•]. The expression of these genes in the root hairs and root epidermis indicates that these transporters are specifically targeted in those cell layers that are exposed to relatively high concentrations of Pi, thereby facilitating its uptake [12•,19•]. Recent studies show that Pi transporters are distributed along the entire length of the roots of Pi-starved plants [24••]. Moreover, a relatively uniform rate of Pi uptake was observed along the proteoid root axis [7]. These data support the hypothesis that the entire root system retains the potential to transport Pi at an increased rate in response to Pi starvation [7, 24••]. The high-affinity Pi transporters of tomato (LePT1) and potato (StPT1) are also present in organs other than roots, such as leaves, stem, tubers and flowers [13,19•]. These transporters may be involved in the transport of Pi within plants in addition to Pi acquisition by the roots. The gene encoding the low-affinity Pi transporter (Pht2;1) is constitutively expressed in leaves of *Arabidopsis* [22••].

### Complexity of Pi transport in plants

The number of Pi-transporter-encoding genes that have been cloned from barley roots [31].

### Table 1

Amino acid identity (%) among Pi transporters isolated from *Arabidopsis* shows that the high-affinity phosphate transporters are highly conserved in plants.

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AtPT1 to AtPT6 [14,15,17,18]; tomato LePT1 and 2 [12•,19•]; *Medicago*, MtPT1 and 2 [20•]; *Catharanthus*, CrPT1 [21]; potato, StPT1 and 2 [13]; *Triticum*, TaPT1 (Accession No. AF110180); tobacco, NtPT1 (Accession No. AB020061) was calculated by using the FASTA algorithm software of the Genetics Computer Group (GCC, Madison WI). Three more *Arabidopsis* Pi transporter homologs, AtPT7 (BAC F9H16.16), AtPT8 (Accession No. AC015460) and AtPT9 (Accession No. AC007551) showing 40–55% amino-acid identity are also reported. In addition, several Pi transporters have also been cloned from barley roots [31].
The existence of multiple high-affinity Pi transporters is certainly a reflection of the complexity of the Pi transport process within plants (Figure 1). Evidence of the existence of Pi transporters that are involved in xylem loading within roots comes from a well-characterized Arabidopsis mutant (pho1) which lacks the ability to load Pi into the xylem [25]. The phosphate is unloaded from the xylem into actively photosynthesizing leaf tissues. Phloem loading and unloading are important components of the internal movement of Pi within plants. In addition, the pho2 mutants of Arabidopsis provides genetic evidence of the involvement of Pi transporters in phloem loading of Pi. The uncontrolled uptake of Pi in pho2 phenotype may be caused by alterations in the function of Pi transporter(s) or
by the involvement of a regulatory gene that controls Pi loading in the shoot [26•]. Even though nine phosphate transporter homologs have been identified in Arabidopsis, none of them is allelic with pho1 and pho2 mutants. Interestingly, AtPT1 and AtPT2 are the only major transcripts that have been detected by Northern analysis [14,15,17]. This could be explained either by the low expression levels of other transporters or by the existence of high sequence similarity among some of the nine homologues. Detailed analysis of gene expression at various developmental stages using gene-specific probes (i.e. 3′ or 5′ untranslated regions of cDNA), in situ hybridization and immunolocalization studies should help to describe complex processes involved in the expression of genes encoding Pi transporter.

Intricately regulated movement of Pi across the tonoplast, in addition to Pi uptake and efflux, regulates cellular Pi homeostasis. The cytoplasmic Pi concentration (which is in the mM range) is generally maintained at a constant level under varying levels of Pi supply, whereas the vacuolar Pi levels change significantly when Pi is deficient [10••]. The transport of Pi across the tonoplast requires ATP and cytoplasmic alkalization [10••,11•]. The bi-directional flux of Pi across the tonoplast takes place whether Pi concentrations are high (i.e. mM) in the vacuole, the cytoplasm or both, indicating that transport systems that have fast uptake rates (i.e. high $V_{\text{max}}$) are operating at the tonoplast. The tonoplast H-ATPase or pyrophosphatase could provide the energy required to maintain an electrochemical gradient across the tonoplast thereby facilitating Pi transport. The tonoplast-associated Pi transporters have, however, yet to be isolated and analyzed in plants. Pi efflux is another important mechanism for regulating Pi concentrations in the cytoplasm. When Pi is present in sufficient concentrations, high rates of Pi efflux almost compensate for Pi influx, supporting the hypothesis that when Pi availability is non-limiting the Pi homeostasis is primarily controlled by Pi efflux [10••]. As further evidence of the complexity of Pi transport, significant amounts of Pi are recycled in plants during Pi deficiency or senescence.

Transcriptional regulation of phosphate transporters
Transcriptional activation of Pi transporters in response to Pi starvation seems to be a major regulatory mechanism for Pi uptake. It is becoming apparent that Pi deficiency rapidly induces the expression of genes that encode Pi transporters leading to increased transcription and protein synthesis, the assembly of the proteins in the plasma membrane of the outer cell layers of roots, and enhanced Pi uptake [24••]. Recent studies in our laboratory have shown that expression of the luciferase reporter gene driven by the $\text{AtPT2}$ promoter is strongly induced in roots of Pi-starved seedlings (KG Raghothama, unpublished data). Our studies also show that the disappearance of negative DNA-binding protein factors may be associated with expression of genes in Pi-starved plants (U Mukatira, D Varadarajan, KG Raghothama, Amer Soc Plant Physiol Abstr 1999:189). These results further substantiate the hypothesis that Pi transporters are transcriptionally regulated in response to Pi deficiency.

Signal transduction during Pi starvation
Plants probably have at least two different signaling mechanisms that maintain Pi homeostasis, one operating at the cellular level and another involving multiple organs and most probably arising from the shoots [2••]. At the cellular level, movement of Pi from and to the vacuole, and regulated efflux and influx are the primary mechanisms that maintain Pi homeostasis. Changes in cytosolic or vacuolar Pi concentrations could trigger a signal transduction pathway leading to the activation of Pi-starvation rescue systems similar to those found in microorganisms [2••]. The whole plant response is much more complex. The transport of Pi from old to young tissues, or from root to shoot and back to roots, is likely to affect Pi-stress signaling.

Phosphate transporters are induced rapidly in response to Pi starvation. The expression of Pi-transporter mRNA in cell cultures was evident 3–6 h after transfer to medium that contained no Pi (DH Kim, U Muchhal, KG Raghothama, Amer Soc Plant Physiol Abstr 1998:136). Both the transcripts of Pi transporter mRNA and concentrations of the transporter proteins themselves increased within 12–24 h of the onset of Pi starvation in tomato [19•,24••]. A rapid increase in the number of Pi transporters occurs before the appearance of any visible Pi-deficiency symptoms, suggesting that signals are initiated as a consequence of subtle changes in some cellular Pi pools. Divided-root studies support the existence of internal signaling mechanisms that lead to Pi-starvation-induced gene expression [19•]. Uptake studies in the $\text{pho2}$ Arabidopsis mutant, a hyperaccumulator of Pi in shoots, also support this mechanism [26•]. In addition, the formation of proteoid roots in white lupin is also linked to changes in internal Pi concentrations [7]. This evidence together suggests that signals that result in the induction of gene expression are initiated in response to changes in internal concentration of Pi in higher plants.

In Pi-deficient plants, changes in cellular Pi concentrations are accompanied by the translocation of considerable amounts of carbohydrate to the roots. It is possible that information about the nutrient status of the shoot is transmitted to the root via certain carbon assimilates or changes in Pi fluxes. A close relationship between altered root growth and Pi deficiency suggests that phytohormones may be involved in the response to low Pi availability [27]. Phytohormones, such as auxin and ethylene, must be involved in altering root growth, the elongation of root hairs, and the formation of proteoid roots. Nevertheless, at present there is no direct evidence of a role for phytohormones as primary signals in the response to Pi starvation. The expression of genes encoding Pi transporters in tomato cells not experiencing Pi starvation did not change significantly in response to the auxin NAA (alpha-naphthylacetic acid) or the ethylene
precursor ACC (1-aminocyclopropane-1-carboxylic acid), indicating that these hormones are not directly involved in regulating Pi uptake (DH Kim, U Muchhal, KG Raghothama, Amer Soc Plant Physiol Abstr 1998:136). In addition, abscisic acid (ABA) may not play a major role in the Pi-stress-induced response [28]. Although no direct evidence is available at present, it is likely that ethylene and auxin have roles in altering root architecture and promoting root hair elongation in response to Pi starvation [27]. One can also envision a role for calcium in Pi-starvation-induced signal transduction. There is evidence of increased Ca^{2+}-ATPase transcript accumulation in the roots of Pi-starved tomato [29]. Cytosolic calcium levels and their modulation through the activity of specific Ca^{2+}-ATPases are thought to play a role both in the response and the adaptation of plants to Pi starvation. Direct evidence for the involvement of calcium in Pi-starvation-induced signaling is, however, still lacking.

At present, the information about signal transduction in Pi-starved plants is rather sketchy at best. The discovery of Psr1 (phosphorus starvation response 1), a regulatory protein in Chlamydomonas may shed some light on the signal transduction pathway involved in the Pi-starvation response [30••]. The Psr1, a putative transcriptional activator, is crucial for acclimation of the unicellular green alga, Chlamydomonas, to Pi starvation. Homologs of this gene are present in vascular plants, and they may be involved in a similar type of regulation as has been observed in algal cells.

Conclusions
In recent years, significant progress has been made in isolating and characterizing molecular determinants of Pi acquisition and transport. We now know that the ‘simple process’ of Pi transport is regulated by multiple transporters that are expressed and controlled in a spatial and temporal manner. It is becoming clear that changes in the intracellular concentrations of Pi could initiate signal transduction pathway(s) leading to the adaptation of plants to Pi deficiency. Nevertheless, the task of understanding how plants sense and respond to the amount of available Pi in the rhizosphere is still a challenging and ongoing area of research. New genomics tools such as expressed sequence tags, sequence-tagged mutants, gene-chips, microarrays and the nearly completed Arabidopsis genome sequence will allow researchers to dissect the molecular complexities of Pi transport and signaling. This will certainly lead to a better understanding of the complex physiological and biochemical responses observed in Pi-starved plants, and ultimately to the development of molecular strategies to improve Pi efficiency and crop productivity.

Acknowledgements
Research in my laboratory is supported by a grant from the US Department of Agriculture. I thank U Mukatira, a graduate student, for compiling the data presented in Table 1. My sincere thanks are due to my colleague M Jenks for critical reading of the manuscript. I apologize to those colleagues whose work is not directly cited because of space limitations.

References and recommended reading
Papers of particular interest, published within the annual period of review, have been highlighted as:
• of special interest
•• of outstanding interest

1. Plaxton WC, Carswell MC: Metabolic aspects of the phosphate starvation response in plants. In Plant Responses to Environmental Stresses: From Phytohormones to Genome Reorganization. Edited by Lerner HR. New York: Dekker; 1999:349-372. An excellent review of biochemical changes occurring during phosphate starvation. This article addresses the effect of Pi starvation on photosynthesis, energy transfers, glycolysis and respiration among the other biochemical changes.

2. Raghothama KG: Phosphate acquisition. Annu Rev Plant Physiol • Plant Mol Biol 1999, 50:685-693. This informative review provides a comprehensive overview of the physiological and biochemical adaptations of plants that enable them to acquire and utilize Pi in Pi-deficient conditions. A special emphasis is placed on the recent developments in the molecular biology of Pi acquisition.


12. Daram P, Brunner S, Amrhein N, Bucher M: Functional analysis and cell-specific expression of a phosphate transporter from tomato. Planta 1998, 206:225-233. In an elegant piece of work, the tomato phosphate transporter was functionally characterized in the yeast mutant that lacks the high-affinity Pi transporter. This study also provides evidence of the expression of Pi transporters in the epidermal and root hair cells of tomato.


Muchhal US, Raghothama KG: unique to plants and fungi.

This paper describes the cloning and characterization of phosphate transporters from tomato. Studies show that the epidermal layers of Pi-starved roots are enriched in Pi transporters. The authors also provide evidence of the regulation of gene expression by internal signals in response to Pi starvation.

Liu C, Muchhal US, Mukatira U, Kononowicz AK, Raghothama KG:


This paper describes the cloning and characterization of phosphate transporters from *Medicago truncatula* roots. Regulation in response to phosphate and to colonization by arbuscular mycorrhizal (AM) fungi. *Mol Plant Microbe Interact* 1998, 11:14-22.

An interaction between mycorrhizal colonization and the expression of the genes encoding two plant phosphate transporters is examined in this interesting paper. The fungal colonization results in down-regulation of plant Pi transporters. The transcripts of both the transporter genes are present in roots, and transcript levels increase in response to Pi starvation.


This paper describes the cloning and characterization of the first low-affinity phosphate transporter from plants. The gene that encodes this transporter is constitutively expressed in leaves and, interestingly, the transport is driven by a proton:phosphate symport process.

Pao SS, Paulsen IT, Saier MH: Major facilitator superfamily.


The authors have done an excellent job of compiling extensive data on the major facilitator superfamily (MFS) in an easy to understand review. An informative discussion on the origin and functional significance of the MFS is presented: these H+Pi symporters are presumed to be of ancient origin and unique to plants and fungi.


This is the first report to describe the transcriptional regulation of any major nutrient transporter in plants. In addition, this study also shows that the plasma membranes of Pi deficient roots are enriched in Pi transporters, a physiologically relevant location for the high-affinity Pi transporters.


In this study, the Pi acquisition and transport by the *pho2* mutant, which accumulates excessive Pi in its shoots, and wild-type *Arabidopsis* plants were compared. The Pi uptake rate of *pho2* is nearly twice that of wild-type plants. Interestingly, Pi uptake rates of isolated roots of the mutant and wild-type plants are similar. These data support the hypothesis that the shoot influences Pi uptake by the roots. It is presumed that the *pho2* mutation may lead to a defect in the phloem transport of Pi or lack of regulation of internal Pi levels in the shoot.


This paper is of special interest because it describes the characterization of a regulator of phosphorus metabolism in a photosynthetic organism. *Psr1* is a Pi-starvation-induced regulatory gene isolated from *Chlamydomonas*, which plays an important role in acclimation of the organism to Pi starvation. This putative transcriptional activator is localized in the nucleus under Pi-deficient and sufficient conditions. The existence of homologs of *Psr1* in vascular plants suggests a role for similar proteins in the adaptation of plants to Pi-limiting conditions.