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Review Article

Phosphorus Deficiency in Soil and its Uptake Mechanism in Crops

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ABSTRACT

Phosphorus is one of the essential elements required by all plants to complete their life cycles. It is key element in plant energy reactions, photosynthesis, genetic transfer, signal transductions and nutrient transport. Among the macro-nutrients, phosphorus is least available to the plants because major part of phosphatic fertilizers are absorbed and fixed by soil therefore in many agricultural production systems, P is considered as one of the major limiting factors for crop productivity. The visual symptoms of phosphorus deficiency are different from other nutrients which are not easily observed in field other than loss of yield. Intensive use of phosphorus in agriculture has also raised concerns about its sustainability due to potential resource scarcity. Therefore, an increased knowledge of regulatory mechanisms involved in controlling the plant's phosphorus is important for improving phosphorus uptake and utilization efficiency and thus reducing excess input of phosphatic fertilizers with appreciable levels of yield. Molecular and genetic analyses had revealed the primary mechanisms of phosphorus uptake and utilization and their relationships to phosphorus transporters, regulators, metabolic adaptation, quantitative trait loci, and microRNA. In this review, a critical insight is provided on the physiological responses of plants to phosphorus, molecular mechanisms involved in its uptake and the information available on the genes and QTLs involved in the phosphorus acquisition.

Key Words: Phosphorus deficiency; Phosphorus uptake; Phosphate transporters (genes); Phosphorus signalling; QTLs

Introduction

Phosphorus (P) is an essential macronutrient for growth and development of all living organisms. It is one of the key components of biomolecules such as ATP, nucleic acids and phospholipids, regulates many biological processes involving energy transfer reactions, photosynthesis, transformation of sugars and starch, activation of enzyme proteins, transfer of genetic characteristics from one generation to next and mediates cellular signal transduction cascades (Elanchezian, 2015; Rausch, 2002). Second to nitrogen, phosphorus is the limiting factor in agricultural production system. A global assessment of soils with P-retention properties further showed that vast areas in South America, West and Central Africa, and South-East Asia have low plant available P as a result of unfavourable soil properties, such as low pH or high concentrations of aluminium and iron (Batjes, 2011). Natural P reserves are limited and sedimentary deposits are the source of 80-90% of the world P production (Elanchezian, 2015). It has been found, nearly 5.7 billion hectares worldwide is challenged by P deficiency (Heuer, 2009), whereas in India, 49.3 % of districts and Union Territories are found low in available P, 48.8 % are medium, and 1.9 % are found having high soil phosphorus (Hasan, 1996). The only source for phosphatic fertilizers is rock phosphate, which is non renewable resource and currently, only 10% demand of phosphatic fertilizers in India is fulfilled by native deposits of rock phosphate and rest 90%, depends on imports of raw materials and processed phosphatic fertilizer products. The consistent increase in the import of phosphatic fertilizers from 243.2 thousand tons in 1970s to 1.25 million tons in 2000 is creating immense pressure on farmers as well as national economy (Sharma and

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Thaker, 2011). Annual expenditure on fertilizer subsidy for the financial year 2016-17 was Rs. 70,000 crores, out of which Rs. 19,000 crores were allocated for phosphatic and potassic fertilizers, which further increased the burden on Indian economy. P is translocated from older tissues to active meristematic tissues, which results in foliar deficiency symptoms appearing on the older (lower) portion of the plant. The visual response when P is deficient is very different than for other nutrients-which are generally expressed in terms of decreased chlorophyll production (chlorosis). Phosphorus deficient plants develop dark green or purple coloured leaves and stem. This darkening or purpling is due to the accumulation of photosynthates and anthocyanin which are being inefficiently utilized due to reduced supply of chemical energy in the plant. Purpling of leaves is frequently cited in corn and tomatoes but most of the other crops show dark colouration of leaves which can be barely differentiated from normal leaves (Hopkins, 2015). Due to less main visual symptoms, P deficiency is seldom observed in fields other than yield loss. The P bioavailability is a problem due to its slow diffusion and high fixation in soils resulting in less than 10 μM concentration in soil solution, due to which almost all types of soils need to be fertilized (Elanchezian, 2015). Insufficient amounts of phosphorus in soils with P-fixing properties results in reduced tillering, delay in flowering, reduced quality of forage, fruit, vegetable, and grain crops, and decreased disease resistance, making P an essential inorganic plant nutrient in agriculture. An alternative approach for both soils with low P content and P-fixing soils, is to enhance the plant's efficiency to acquire soil P (Ramaekers, 2010). It has therefore been suggested to increase efforts to develop crop cultivars with enhanced P efficiency.

Phosphorus deficiency is fairly common in irrigated rice, which is the staple food crop of 70% of the world's asian population, and its damages occur throughout the growth cycle of the crop.Phosphorus deficiency is widespread in Bangladesh, India, Indonesia, Nepal, Pakistan, South China and Vietnam. Globally, more than half of all cropland is low in plant-available phosphorus. It is therefore imperative to understand how plants take up phosphorus and respond to low levels of this nutrient so that effective strategies can be employed phosphorus uptake efficiency and utilization efficiency.

This review focuses on role of phosphorus in plants, its deficiency in soils and uptake mechanism, various physiological and molecular responses involved in its acquisition and QTLs associated with phosphorus uptake.

1. Phosphorus as an essential element

Phosphorus (P) is of unambiguous importance for the production of food crops as it is the key substrate in energy metabolism in the form of adenosine tri-phosphate (ATP). It is one of the major constituents of nucleic acids in the form of sugar-phosphate backbone and membranes in the form of phospholipids bilayer. It is needed in cell division, in the formation of bio-membranes, in the transformation of starch and sugar, in seed germination, in photosynthesis, flowering and fruit formation, and in almost every phase of plant's vital processes so the demand for P fertilizer is increasing worldwide Studies using isolated chloroplasts (and other in-vitro systems) have indicated that orthophosphate (Pi) may have an important role in photosynthetic metabolism (Freeden 1990). The effects of phosphate deficiency on the rate of photosynthesis and carbon partitioning can be explained in terms of the concerted action of several regulatory mechanisms. The availability of Pi may limit ATP synthesis and also ribulose-l,5-bis- phosphate-carboxylase activity since Pi is an activator of this enzyme. It may be involved in modulation of ribulose-5-phosphate kinase, sedoheptulose-l,7-bisphosphate phosphatase, and fructose-l,6-bisphosphate phosphatase. In addition, sufficient cytoplasmic Pi must be available to transport of triose-phosphate between the chloroplast and cytosol for maintaining high rates of photosynthesis. The rate of photosynthesis in isolated intact chloroplasts is dependent on the Pi concentration of the surrounding medium with an optimum Pi concentration of about 0.2-0.5 mmol.1-1 in spinach and wheat chloroplasts. When Pi is withheld from plants, there is a substantial non-stomatal inhibition of photosynthesis (Freeden 1990; Deitz 1986).

The phosphate group has special properties that can be exploited to regulate critical biological functions when attached to proteins. A wide range of enzymes has

evolved to catalyze reactions involving phosphates, operating via a range of different mechanisms, and under a wide range of different conditions. The ability of phosphate to form esters and anhydrides that are stable at room temperatures in water made it ideal for biological molecules. The formation and cleavage of phosphate ester bonds plays a crucial role in biological signal transduction (Berg, 2010). Phosphate has almost ideal chemical properties for the formation of biological polymers and, in particular, for the modification of proteins. Phosphoryl transfer plays key roles in signaling, energy transduction, protein synthesis, and maintaining the integrity of the genetic material. The phosphate group serves as a switch to promote inducible protein-protein interactions, which allows signal transduction networks to transmit transient signals in response to extracellular stimuli (Hunter, 2012). After a signal is received, signal transduction involves altering the behavior of proteins in the cascade, in effect turning them on or off like a switch. The behaviour of proteins can be altered by adding or removing phosphates. Phosphorylation by protein kinase is one such type of important modification (Figure1). Phosphorylation may open up an enzyme's active site, allowing it to perform chemical reactions, or it may frequently generate a binding site allowing a specific interaction (may make a bulge in one side preventing the protein from fitting together) with a molecular partner. Phosphorylation of a protein can either activate or inhibit it. Phosphate hydrolysis provides a crucial source of biological energy, and, in particular the biological conversion of ATP to ADP plays a crucial role in energy transduction in life processes. Nucleoside triphosphates serve as crucial mediators of life. For instance, the regulation and control of signal transduction and transport processes relies almost exclusively on GTP. ATP, in turn, is used to drive unfavorable chemical reactions, to fuel biological machines, and to regulate key biological processes (via the phosphorylation of proteins) (Kamerlin 2013).

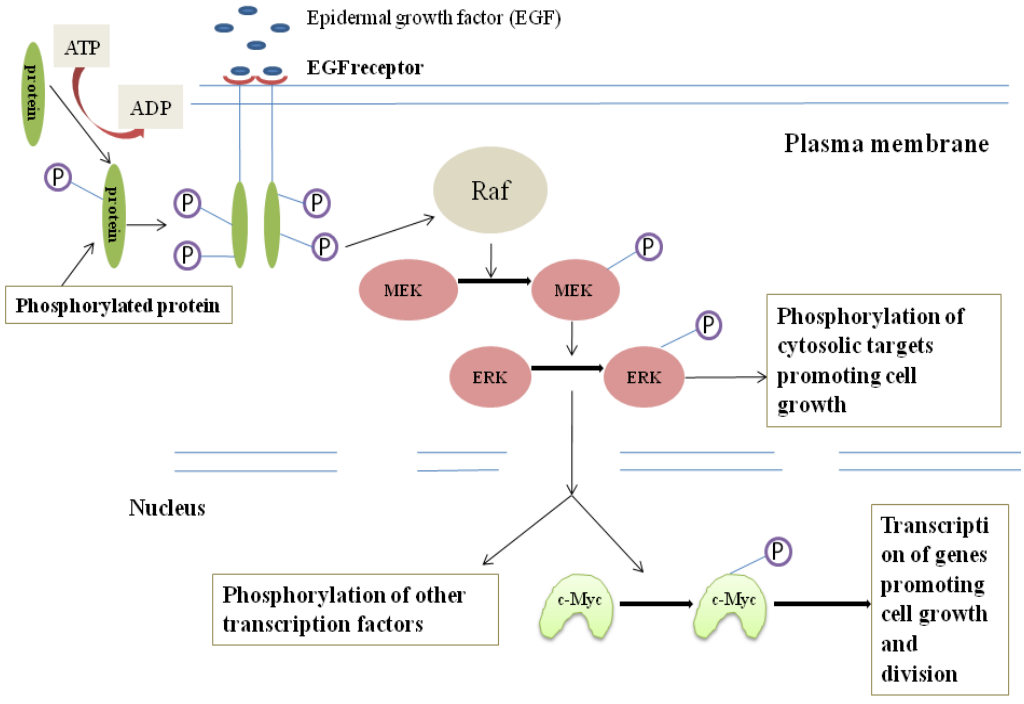

Figure 1 (1) Phosphorylated receptors trigger a series of events which activate the kinase Raf (Rapidly activated fabrosarcoma). (2) Active Raf phosphorylates and activates MEK (Mitogen activated protein kinase kinase), which phosphorylates and activates the ERKs (Extracellular signal-regulated kinases). (3) The ERKs phosphorylate and activate a variety of target molecules which include transcription factors, like c-Myc, as well as cytoplasmic targets. The activated targets promote cell growth and division.Together, Raf, MEK, and the ERKs make up a three-tiered kinase signaling pathway called a **mitogen-activated protein kinase** (**MAPK**) cascade.

2.Phosphorus deficiency in soil and plants

Phosphorus (P) is one of the essential nutrients necessary for the growth of all forms of life. The native soil P reserves are limited and are exhaustible under intensive agriculture. The economic as well as the environmental implications of P escaping from farm lands is driving increased interest in bringing improved P use efficiency in focus. World Rock Phosphate (RP) availability, the only economic source of P is estimated to peak by 2030 (Cordell et al., 2009) and thereafter a steep decline is predicted. With changes in economics and technology, the estimates of RP reserves are subject to change. Irrespective of the estimates, world RP reserves will exhaust sooner or later, therefore addressing future P supply should be one of the most urgent priorities for the future sustainability of agriculture and humanity. About 95% of the phosphate rock mineral is used to produce fertilizer, animal feeds and pesticides. Rock phosphate reserve across the globe is estimated at 71,000 million tonnes (as P2O5) (United States Geological Survey 2012). The total resources of rock phosphate in India as per United Nations Framework Classification (UNFC) are placed at 305.3 million tonnes. The production of the rock phosphate in 2007-08 was 1.86 million tonnes. Rajasthan continued to be the principal producing state, contributing 94% of the total production followed by Madhya Pradesh with 6%. Grade-wise about 43% of the total production of rock phosphate was about 30-35% P2O5, 4% of 25-30% P2O5 and 53% of 15-20% P2O5 (Geological Survey of India, 2011). Closer look into the fertility of Indian soils reveals that Indian soils do not have the ability to meet the demands for phosphorus of today's high-yielding crops. Soils of more than 80% of the districts represented low to medium P fertility categories indicating the necessity of P fertilization to produce optimum crop yields (Muralidharudu et al., 2011). Based on nutrient-wise index of P, available P are found low, medium and high in soils of 165, 47 and 8 districts of Northern-Western Indian states (Table 1). Stunted dark green plants with erect leaves and reduced tillering signal P deficiency. Leaves are narrow, short, very erect, and 'dirty' dark green. Stems are thin and spindly, and plant development is retarded. The number of leaves, panicles, and grains per panicle also reduced. Young leaves may appear to be healthy, but older leaves turn brown and die. Red and purple colors develop in leaves if the variety has a tendency to produce anthocyanin. A plant shows intervienal chlorosis as P deficiency symptom if it has no tendency to produce anthocyanin (www.knowledgebank.irri.org).

3. Phosphorus uptake mechanism in crops

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 Phosphate ion {(H2PO4)2− or (HPO4)2−}. The form in which Pi exists in solution changes according to pH. 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, which suggested that dihydrogen form of orthophosphates (H2PO4−) is most readily transported into the plant. In plants, uptake of Pi occurs by diffusion (Clarkson 1981). Pi absorption is accompanied by H+ influx with a stoichiometry of 2 to 4 H+ per H2PO4− transported. The Pi acquired by roots is rapidly loaded on to xylem and then transported to different parts of the plant according to the metabolic need (Sakano et al., 1992; Ullrich-Eberius et al., 1981 and Ullrich-Eberius et al., 1984). Within the plant, most phosphorus is stored in the vacuole. However, phosphate efflux from the vacuole is insufficient to balance the cytosolic phosphate concentration during phosphorus starvation which leads to insufficient phosphate efflux from the vacuole, triggering plant adaptive responses to facilitate phosphorus acquisition and translocation. Two categories of transporters are expressed for phosphate transport across the plant. These are Low-affinity transporters and high affinity transporters. The Pi transporters are actually proton/phosphate (H+/H2PO4−) symporters. The low-affinity transporters are active in vascular loading and unloading, internal distribution and remobilisation of acquired P (Smith et al., 2001) whereas, the high-affinity Pi transporters play an important role in acquisition of P. Recent advances in the molecular biology of putative plasma membrane and tonoplast Pi transporters confirm that plants have multiple transporters for Pi. So far, nine transporter genes have been cloned from *Arabidopsis*, at least five from potato, two from tomato and up to eight from barley.

3.1 Phosphate transporters

(A) Pht1 family of phosphate transporters: The Pht1 family of Pi transporters is pivotal for Pi uptake from the soil and the transport of Pi from the root to the shoot. Pi transporters encoded by members of the Pht1 gene family, are predominantly expressed in epidermal

cells and in the outer cortex of the root. (Mudge et al., 2002; Schunmann et al., 2004). These proteins are part of direct Pi uptake pathway and transport P as Pi anions, mainly $H2PO^{-}4$ and $HPO2^{-}4$, against a concentration gradient between the soil solution and the cytoplasm of the root epidermal cell.

Table 1 State wise Nutrient Index in Northern-Western States

S. No.	State	Category	Districts
1.	Utter Pradesh	Low (48)	Hardoi, Lakhimpur Kheri, Sitapur, Barabanki, Aligarh, Allahabad, Mainpuri, Bulandshar, Muzaffar Nagar, Ghaziabad, Fatehpur, Etah, Moradabad, Agra, Lucknow, Faizabad, Shahjahanpur, Varanasi, Gorakhpur, Raibareilly , Santkabir Nagar , Mahamaya Nagar , Lalitpur , Sultanpur , Rampur Azamgarh, Unnao, Badaun, Jhansi, J. P . Nagar, Ferozabad, Mathura, Kushinagar, Kannoj, Kaushambi, Auraiya, Jalaun, Maharajganj, Mau, Saharanpur, Pilibhit, Pratapgarh, Chandauli, Mirzapur, Kashiram Nagar, Gonda, Sidharth Nagar, Bahraich.
		Medium (8)	Etawah, Farrukhabad, Meerut, Bareilly, Kanpur, Deoria, Ambedkarnagar, Ghazipur.
		High (0)	Nil.
2.	Punjab	Low (4)	Ferozepur, Mansa, Muktsar, Barnala.
		Medium (16)	Gurdaspur, Ropar, Fatehgarh Sahib, Kapoorthala, Mohali, Patiala, Ludhiana, Sahid Bhagat Singh Nagar, Sangrur, Jalandhar, Hoshiarpur, Bathinda, Faridkot, T aran - Taran, Amristar, Moga.
		High (1)	Mohali.
3.	Rajasthan	Low (29)	Jaipur, T onk, Dausa, Sriganganagar, Hanumangarh, Churu, Banswara, Bikaner, Jodhpur, Jhalawar, Sikar, Bhilwara, Alwar, Swai Madhopur, Baran, Udaipur, Chittorgarh, Kota, Bundi, Barmer, Pali, Sirohi, Jhunjhunu, Bharatpur, Jaisalmer, Karauli, Nagaur, Jalour, Pratapgarh
		Medium (4)	Ajmer, Rajsamand, Dungarpur, Dholpur
		High (0)	Nil.
4.	Haryana	Low (14)	Hisar, Rohtak, Sirsa, Faridabad, Rewari, Fatehabad, Jhajjar, Yamunagar, Ambala, Bhiwai, Gurgaon, Palwal, Mewat, Panchkula
		Medium (7)	Karnal, Kurukshetra, Kaithal, Mahendragarh, Panipat, Jind, Sonipat
		High (0)	Nil
5.	Madhya Pradesh	Low (26)	Ujjain, Gwalior, Khargone, Mandsaur, Hoshangabad, Ratlam, Raisen, Bhopal, Bhind, Dewas, Dhar, Shajapur, Harda, Sehore, Chhindwara, Shivpuri, Guna, Datiya, Jabalpur, Burhanpur , Sheopur , Ashoknagar, Tikamgarh, Damoh, Sagar, Seoni
		Medium (5)	Indore, Morena, Neemuch, Khandwa, Barwani
		High (0)	Nil
6.	Jammu & Kashmir	Low (9)	Baramulla, Shopian, Anantang, Budgam, Kupwara, Kulgam, Ganderbal, Srinagar, Bandipora.
		Medium (1)	Phulwara
		High (0)	Nil

S. No.	State	Category	Districts
7.	West Bengal	Low (0)	Nil
		Medium (4)	South 24 Parganas, Bankura, Murshidabad, East Medinipur.
		High (5)	Burdwan, Malda, Howarh, Hooghly, South Medinipur.
8.	Assam	Low (0)	Nil
		Medium (0)	Nil
		High (1)	Barpeta
9.	Himachal Pradesh	Low (1)	Kullu
		Medium (0)	Nil
		High (0)	Nil
10.	Gujarat	Low (19)	Surat, Gandhinagar, Navsari, Sabarkantha, Mehsana, V alsad, Vijaypur, Bhavnagar, Vadodara, Rajkot, Kheda, Junagarh, Banaskantha, Narmada, Surendranagar, Amreli, Jamnagar, Porbandar, Bharuch.
		Medium (2)	Ahmedabad, Anand
		High (0)	Nil
11.	Chhattisgarh	Low (10)	Kanker, Raigarh, Raipur, Dhamtari, Durg, Bilaspur, Surguja, Bastar, Mahasamandh, Jajgir
		Medium (0)	Nil
		High (0)	Nil
12.	Uttarakhand	Low (4)	Udham Singh Nagar, Haridwar, Nainital
		Medium (0)	Nil
		High (0)	Nil

Although the majority of Pht1 transcripts have been located in root epidermal cells and root hairs, many of them have also been detected in leaves, stems, cotyledons, pollen grains, seeds, flowers, and potato tubers, suggesting their involvement not only in Pi uptake by roots but also in internal root-to-shoot distribution (Ai et al., 2009; Fan et al., 2013). In soybean, 14 members of the Pht1family encode high-affinity Pi transporters predominantly expressed in roots under low-Pi conditions (Fan et al., 2013). In Medicago truncatula, 5 transporters encoded by Pht1genes are inducible by low Pi, of which MtPT1 (Medicago truncatula PHOSPHATE TRANSPORTER 1) and MtPT2 plays an important role in Pi uptake; MtPT4 plays a role in Pi translocation from mycorrhizal fungi into the roots (Harrison et al., 2002; Liu et al., 2008; Xiao et al., 2006). In rice, the Pht1gene family is composed of 13 members (OsPT1–13); 4 of these (OsPT2, OsPT3, OsPT6, and OsPT7) are highly expressed in Pi-deprived roots, but several (such as OsPT6) apparently plays a dual role in Pi uptake from the soil and Pi translocation inside the plant (Ai et al., 2009; Goff et al., 2002; Paszkowski et al., 2002) (Table 2). In maize, five Pht1 genes (ZmPht1;1-5) are induced by Pi limitation not only in roots but also in other tissues, such as young and old leaves, anthers, pollen, and seeds (Nagy et al., 2006). Therefore, at least some members of the Pht1gene family play an important role in Pi uptake from the soil solution, particularly when this nutrient is present in limiting amounts.

(B) Pht2, Pht3 and Pht4 family of phosphate transporters: Members of the Pht2, Pht3, and Pht4 gene families have been associated mainly with Pi distribution within subcellular compartments, and their gene products are specifically located in the plastid inner membrane, mitochondrial inner membrane, and the golgi compartment, respectively (Cubero et al., 2009; Guo et al., 2008; Versaw and Harrison 2002.). In *Arabidopsis*, the

low-affinity transporter PHT2;1, encoded by a member of the Pht2 family, is located in chloroplasts, and a pht2;1 mutation reduces Pi transport into the chloroplast and decreases Pi allocation throughout the whole plant.

3.2 Role of Mycorrhizae in phosphate uptake: Mycorrhizae is present in symbiotic relationship with plant. As the Arbuscular Mycorrhizae fungi (AMF) colonize plant root cortical cells, extraradical hyphae operate as an extension of the root system and acquire Pi from regions of the soil beyond the Pi-depletion zone close to the root and in return obtain food from plant. Rice takes up more than 70% phosphorus via AMF in a symbiotic system. OsPHT1.11 is the first AM-specific phosphors transporter in rice. Pht1 Pi transporter genes have been identified in tomato, potato, Medicago, and rice that is specifically expressed in mycorrhizal roots and mediate Pi transport across the periarbuscular membrane (Glassop et al., 2007; Harrison et al., 2002; Nagy et al., 2005; Rausch et al., 2001). Some of these transporters, such as OsPT11 and OsPT13, are indispensable for establishing this association and contribute 70% of the symbiotically acquired Pi (Yang et al., 2012).

3.3 Role of PHO1 family proteins: The PHO1 family proteins plays an important role in the transfer of Pi from roots to shoots in several plant species, including *Arabidopsis* and rice (Secco et al., 2010). PHO1 is expressed in the vascular cylinder and is slightly up-regulated by P starvation (Hamburger et al., 2002) (Figure 1). Recently, the critical role of PHO1 as Pi exporter has been reported (Stefanovic et al., 2011). Overexpression of PHO in leaves leads to efflux of Pi out of cells and into the xylem vessel, resulting in high shoot Pi level and reduced shoot growth.

3.4 Role of Purple acid phosphatases: Purple acid phosphatases (APases) or PAPs comprise the largest class of plant APases. Purple acid phosphatases (PAPs) catalyze Pi hydrolysis from a broad range of phosphomonoesters. The PAP-encoding genes are highly induced by P starvation and can be secreted or located in the cellular organelles to utilize externally available Pi in the soil or to recycle it from intracellular P sources for metabolic processes (Li et al., 2012). The *Arabidopsis* genome encodes for 29 putative PAP isozymes, which are transcriptionally expressed under various developmental and environmental factors. The first purified and characterized PAP was AtPAP17 from *Arabidopsis*. AtPAP26, this is one of the 29 acid phosphatases in *Arabidopsis*, exhibits major phosphatase activity during P starvation and leaf senescence and possesses dual-functionality in a secreted or vacuolar-localized form (Hurley et al., 2010; Robinson et al., 2012). Even though AtPAP26 expression is not up-regulated, its activity and protein levels are up-regulated under P starvation (Veljanovski et al.,., 2006). Therefore, it is possible to considerably improve the P uptake efficiency by overexpressing the secreted PAPs in crop plants.

4. Phosphate sensing and molecular responses to phosphate deficiency

(1) Local phosphate sensing: The PDR2 (Phosphate Deficiency Response 2), LPR1 (Low Phosphate Root 1), and LPR2 genes, which encode an endoplasmic reticulum-resident protein (Ticconi et al., 2009) and multicopper oxidases (Svistoonoff et al., 2007), respectively, have been identified as important regulators of meristem responses to low Pi availability in the *Arabidopsis* primary root. PDR2 functions together with LPR1 in regulating root meristem activity through an endoplasmic reticulum–located pathway that regulates SCR (Scarecrow) levels by restricting the movement of SHR (Short-Root) from the endodermis to adjacent cell layers under Pi-deficient conditions (Nakajima et al., 2001).

(2) Long distance phosphate signaling: Plant metabolic acclimations to Pi deficiency involves sensing the nutrient status in the shoot and is dependent on photosynthesis, the transport of sugars, and their further distribution between sources and sink tissues (Liu et al., 2005). For example, in white lupin, the Pi transporter gene LaPT1 and the secreted acid phosphatase LaSAP1gene are upregulated by exogenous sucrose in Pi-sufficient seedlings grown in darkness and are repressed in cluster roots in dark-adapted plants grown in Pi-deficient conditions (Liu et al., 2005). Together with sugars, long-distance movement of microRNAs (miRNAs) acts in systemic Pi sensing (Pant et al., 2008; Vance 2010). The best-characterized example of systemically transported miRNAs involved in the regulation of Pi responses is miR399. miR399 is a microRNA upregulated by low-Pi conditions that mediates the cleavage of the PHO2 mRNA. PHO2

(PHOSPHATE 2) is a ubiquitin-conjugating E2 enzyme that controls PHO1 activity and whose transcript levels are finely tuned by miR399. PHR1 (PHOSPHATE STARVATION RESPONSE 1) is a MYB-type transcription factor that plays a central role in transcriptional regulation under low-Pi conditions. In addition to PHR1, other Pi-responsive transcription factors that play important roles in different aspects of the metabolic and morphological responses to Pi limitation have been identified in several plant species (Dai et al., 2012; Devaiah et al., 2007; Zhou et al., 2008) (Table 3).

5. QTLs identified for phosphorus uptake in various crops

Modifications to the root system architecture can be crucial for a plant to adapt to low-Pi stress. Quantitative trait loci (QTLs) that associate root traits such as lateral root length and lateral root number with phosphate acquisition efficiency (PAE) and phosphate utilization efficiency (PUE) have been identified in rice, common bean, and maize. In the low-Pi-tolerant maize genotype Mo17, QTLs associated with lateral root branching and length and root hair length have been reported (Zhu et al., 2005). In rice, qREP-6 (Root Elongation under Phosphorus Deficiency 6), a QTL associated with lateral root length, produces a positive correlation between Pi shoot content and tiller number in low-Pi soils (Shimizu et al., 2008). Through the use of Pi-inefficient and Pi-efficient Brassica napus genotypes, two low-Pi-specific QTLs that respectively accounted for 9.4% and 16.8% of the phenotypic variations in plant dry weight, Pi uptake, root system architecture, and root volume in low-Pi soils were detected (Yang et al., 2011). In common bean, QTL analysis showed the importance of basal roots and adventitious roots for Pi acquisition (Liao et al., 2004; Ochoa et al., 2006) and also the importance of root hair density and length for Pi efficiency in the field. Beebe et al., (2006) identified 26 individual QTLs for P accumulation and associated root characters using composite interval mapping (CIM) analysis.

In addition, some QTLs associated with other root traits of Pi-efficient genotypes, such as basal root whorl number, adventitious root formation, and root hair length, have been identified. The basal root whorl number is associated with three major QTLs, explaining 58% of the phenotypic variation in the acquisition of Pi efficiency in common bean (Lynch 2011; Miguel et al., 2011). Root hair length and density and root exudation

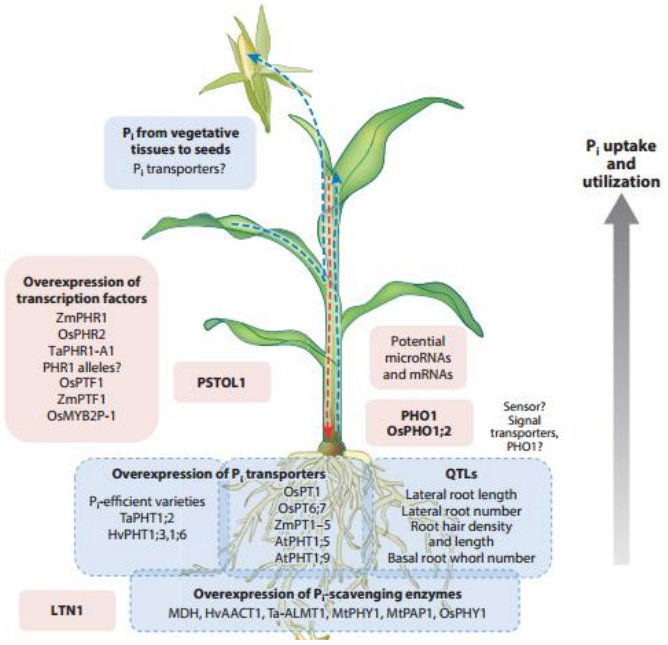

Figure 2 Transcription factors, Pi transporters, and Pi-scavenging enzymes as well as the quantitative trait loci (QTLs) associated with Pi acquisition and utilization efficiencies in maize.

correlated with higher yield in Pi-limited soils, and 19 and 5 QTLs associated with these traits were identified in bean and maize, respectively (Yan et al., 2004; Zhu et al., 2005), suggesting that all of these root traits should be considered targets to improve Pi efficiency in crops. In soybean thirty-four additive QTLs were detected on nine linkage groups, with corresponding contribution ratios of 6.6–19.3% which can be used in breeding soybean for improved phosphorus- deficiency tolerance. In rice, the low-Pi tolerance naturally present in wild cultivars can be used to improve PAE and PUE in modern varieties (Gamuyao et al., 2012). The low-Pi-tolerance QTL Pup1was identified by crossing the indica landrace Kasalath (tolerant of Pi deficiency) with the japonica cultivar Nipponbare (intolerant of Pi deficiency). Introgression of Pup1 into modern rice varieties increased Pi uptake by 170%and grain yield by 250% in low-Pi soils (Gamuyao et al., 2012; Wissuwa and Ae, 2001). Recently, Gamuyao et al., sequenced the gene responsible for the Pup1 QTL and identified it as PSTOL1 (Phosphorus Starvation Tolerance 1), encoding the Pup1 protein kinase. Expression of PSTOL1 in low-Pi-intolerant varieties demonstrated that it acts as an enhancer of early root growth, thereby enabling plants to acquire more Pi and other nutrients (Figure 2).

CONCLUSION

Phosphate (Pi) plays a central role as reactant and effector molecule in plant cell metabolism. Research on phosphorus nutrition has traditionally received little attention when compared with other essential plant nutrients. Nevertheless, the importance of phosphates is well known, and phosphate-containing compounds are the focus of a great body of both academic and pharmaceutical interest. The central role of P in plants in bioenergetics made P, an irreplaceable requirement in all energy-requiring reactions in living organism. In addition, P modifies enzyme activity in phosphorylation, activates proteins, regulates metabolic processes, and is involved in cell signaling and division (Dubetz and Bole, 1975). Furthermore, P is a structural component of nucleic acids, nucleotides, phospholipids, coenzymes, and phosphoproteins. Phosphates, inorganic or organic, also serve as cellular pH buffers. From a cellular perspective, P has widespread involvement in virtually every physiological process in plant. Despite of its huge requirement, phosphorus remains inaccessible to plants because of its fixation in agricultural soils. Also, the depletion of global phosphorus reserves aggravated the problem. To meet the future demands for higher yields and more efficient crop production, a fundamental understanding of the regulatory processes in plant Pi acquisition and adaptive responses to Pi availability is necessary. In this regard, development of P-efficient crops which can survive on low available P concentration in soil solution and with less dependency on chemical P fertilizers will reduce environmental impacts associated with P fertilizers and P waste, increase the nutritional value of grains, and improve farm economies. Tremendous genetic variation for adaptation to P deficiency exists among food crops. The study and use of this variation are pivotal for the development of crop plants with better growth rates and higher yields on P deficient soils. Efforts are being made to increase the uptake of a number of major nutrients, including phosphate, by over-expressing genes encoding nutrient transporter proteins. The identification and molecular characterisation of numerous Pi transporters has led to a better understanding of P nutrition in plants. The detailed study of the regulatory mechanisms of Pi-repressible Pht1 gene expression could reveal how intracellular signaling networks receive and process information to control the Pi starvation response in plants. Attempts have also been made to produce transgenic plants, tolerant to low P by genetic engineering. The genes encoding PAPs, transcription factors, high affinity Pi transporters, protein kinases and those involved in the production of organic acids were targeted. The first transgenic soybean was produced by over-expressing AtPAP15 leading to a significant improvement in P efficiency and yield. Two transcription factors, PTF1 and PHR1, over-expressed in maize (ZmPTF1, OsPTF1) and rice (OsPHR2) resulted in improved root production, enhanced P use efficiency and biomass production. The ultimate goal will be to generate crops with high yield in low-P soils to allow low input of P fertilizer. A more complete understanding of Pi uptake and utilisation in plants will thus eventually have significant implications with respect to both the environment and world agriculture.

Table 2 Phosphate (Pi) transporters to improve phosphate acquisition and utilization efficiencies

Over expressed Pi transporter	Species	Main effects
HvPht1;1 and HvPht1;6	Rice	Improved Pi uptake
OsPT1 (OsPht1;1)	Rice	Twofold increase in shoot Pi content, a larger number of tillers, and 20% more panicles at harvesting per plant. Enhanced Pi transport to shoot at the beginning of the grain-filling stage. Increased production of root hairs.
OsPT8 (OsPht1;8)	Rice	Stunted growth and 50% less shoot and root biomass under P-sufficient conditions.
AtPht1;5	*Arabdiopsis*	Increased shoot biomass and total leaf area as well as lower Pi and higher Pi in shoot and root, respectively

Table 3 Major transcription factors involved in phosphate (Pi) sensing and molecular responses to phosphate deficiency in different plant species

Transcription factors	Species	Main effects
PHR1 (OsPHR2, PvPHR1, ZmPHR1, TaPHR1)	Rice, maize, wheat, bean, white lupin	Overexpression in rice improved root architecture. Overexpression in wheat stimulated lateral branching, improved Pi uptake and increased grain yield
PTF1 (OsPTF1, ZmPTF1)	Rice, maize and white lupin	Overexpression in rice increased the number of tillers, biomass, Pi content, and Pi uptake. Overexpression in maize improved root development, increased the number of tassel branches, increased kernel size, and increased levels of soluble sugars in roots.
MYB2P-1 (OsMYB2P1)	Rice, maize and white lupin	Overexpression in rice enhanced tolerance to Pi deficiency, whereas suppression by RNAi in rice increased sensitivity to Pi deficiency
WRKY75	Rice, common bean, white lupin and *Arabdiopsis*	Positively regulates low-Pi responses but negatively regulates lateral root and root hair growth

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Conflict of Interest

The authors declare that they have no conflict of interest.

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