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Improving Phosphorus Efficiency in Crops with Focus on Purple Acid Phosphatase: Potentials and Perspective

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ABSTRACT: Low-phosphorus (P) stress as a key factor limiting plant growth and production is common in most agricultural soils. Most of the soil-applied phosphate will be rapidly immobilized and most of annually applied phosphate fertilizers are fixed in the soil in organic forms by adsorption, sedimentation and transformation. However, excess P application may lead to contamination of water sources by enriching of water bodies with nutrients that cause eutrophication. Thus understanding the mechanisms that are used by plants to cope with low-P stress will be supportive to develop more competent breeding and genetic engineering schemes for generating improved phosphorus efficient crops. To cope with P deficiency and maintenance of phosphate homeostasis, plants have developed different adaptive mechanisms, including alterations in root morphology, recycling of inorganic phosphate (Pi) and induction of acid phosphatases (APases). To establish these strategies, numerous genes are involved in alternative metabolism pathways that are regulated by complex Pi signaling networks. In this review, we intend to summarize current advances in research on the mechanisms of P efficient crops and its breeding strategies, with a particular emphasis on APase and root architecture roles in response to low-P stress.

KEYWORDS: Low-P conditions, Root system architecture, APase activity, P-efficient plants, Pi acquisition.

INTRODUCTION

Phosphorus (P) is an integral element of all living cells and organisms (104). In plants, phosphorus (P), is the second most essential nutrient after nitrogen, that is required for different biochemical processes, plant development, reproduction and growth (45, 47). Also it contributes to cellular signaling cascades by functioning as the mediators of signal transduction and its ester bond universally serves as a vital energy source for a wide range of biological functions (25). Inorganic phosphate (Pi) is the only form of P that can be assimilated by plant roots from soil. Albeit P is quite abundant in the soils, it is one of the least bio-available elements for plants, because of its high rate of fixation by metal oxides and low rate of diffusion (82, 88, 94). Therefore, large majority of total P (approximately 50–80%) fixes into organic phosphorus, of which roughly 30% is available by plant roots (32, 88). Consequently, phosphorus is not sufficient for vegetative growth and crop productivity in many types of soils. Several important crop species, including Soybean (*Glycine max*) are cultivated in tropical, subtropical and temperate areas, which their soil suffers from Pi deficiency (87). Therefore Pi deficiency frequently constrains crops productivity. However, it has

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been estimated that approximately 70% of the world's arable lands suffer from Pi deficiency, and its concentration is far below the optimum level for best plant growth (45, 85) which in turn limits crops growth and yield.

Therefore, fertilizers containing P must be supplied to meet plant P needs for better growth on low-P soils. In recent years, the annual worldwide consumption of phosphates was more than 50 million tons (51) and the world is facing a future shortage of rock phosphate, apatite, and other raw materials, which are used as P fertilizer resources (82). On the other hand even under a sophisticated Pi fertilization system, approximately 70% of the applied Pi is not accessible by plant roots, and is lost due to fixation in the soil and microbial activity. This state has led to the extreme application of fertilizers to overcome P limitations (88). However, excess P application may lead to contamination of water sources by enriching of water bodies with nutrients that cause eutrophication (96). Thus, application of Pi fertilizers is not cost effective and environmentally friendly.

To deal with P deficiency, plants have developed different adaptive mechanisms. These include: remodeling root architecture (75, 88) and Arbuscular mycorrhizal (AM) fungi and rhizobia symbioses with roots (45, 24), to increases the surface area for Pi uptake. Moreover, the secretion of organic acids (OAs) increases Pi solubility, especially in acidic soils, and the secretion of phosphatases releases Pi from soil organic matter (85, 76, 61). Activation and increase in expression levels of high affinity Pi transporters (73), biochemical and physiological alteration such as of changes in cellular P metabolism, molecular regulation (60) can also be adaptive responses.

Induction and secretion of acid phosphatases (APases) is thought to be an adaptive mechanism that helps plants survive and grow under Pi deprivation (85). These enzymes catalyze Pi hydrolysis from a broad range of phosphomonoesters that cleaves Pi from ester linkage sites. Some of them play important roles in internal P recycling by remobilization of Pi from intracellular P monoesters and anhydrides of older tissues. In contrast, extracellular or secreted APases are believed to scavenge Pi from organic phosphate compounds in the external environment, contributing to extreme P acquisition (94, 74).

Among APases, purple acid phosphatases (PAPs) are primarily non-specific, the largest group and special class of APases. These enzymes exhibit distinct characteristics including a purple color in aqueous solution and they contain a bimetallic site (74, 22). PAPs release Pi from a broad spectrum of P-monoesters over a wide pH range (55) and they are commonly found in a wide range of plant species.

PAP proteins family are characterized by five conserved motifs (**D**xG-G**D**XX**Y**-G**N**H (D/E)-VXX**H**-G**H**X**H**; bold letters represent metal-ligating residues; the spacing between blocks is variable) (22, 32). PAP genes family is greatly expanded in plants: in *Arabidopsis* (*A. thaliana*), rice (*Oryza sativa*), soybean (*Glycine max*), and maize (*Zea mays*) there are 29, 26, 35 and 33 members of the PAP family, respectively (36, 101, 34, 22). The physiological impacts of plant PAPs are diverse, including improved phosphorus (P) acquisition and adaptation to biotic and abiotic stresses (59, 42, 100). The increased expressions of PAP genes in response to available Pi have been documented by several researchers (32, 87, 45). Emerging P-efficient crop varieties would be a cost effective and environmentally friendly approach in sustainable agriculture production. This review discusses the possible mechanisms for P efficiency and genetic strategies to improve P efficiency in crops through gene manipulation and root-based approaches. These studies might help scientists to gain new perceptions in developing P efficient crops, particularly through increasing root secreted PAP to reduce the consumption of chemical Pi fertilizer, maximizing the exploitation of biological potential for efficient mobilization and acquisition of soil Pi or even adding fertilizers in the forms of chemical compounds, manure or plant residual.

Root strategies in response to low-P condition

It has been known that Pi is one of the most important factors controlling primary root length (23, 30). Under low-P conditions, plant roots exhibit both morphological and physiological changes, of which the former alteration is more important to absorb more phosphate (26, 82). A variety of adaptive root characteristics (Figure 1) are crucial for phosphorus uptake in low-P conditions, including root secretory proteins (69) Root System Architecture (RSA) alteration (47). It has been well documented that phosphate tends to be more available in topsoil, because of the presence of organic matters and animal excrements (52).

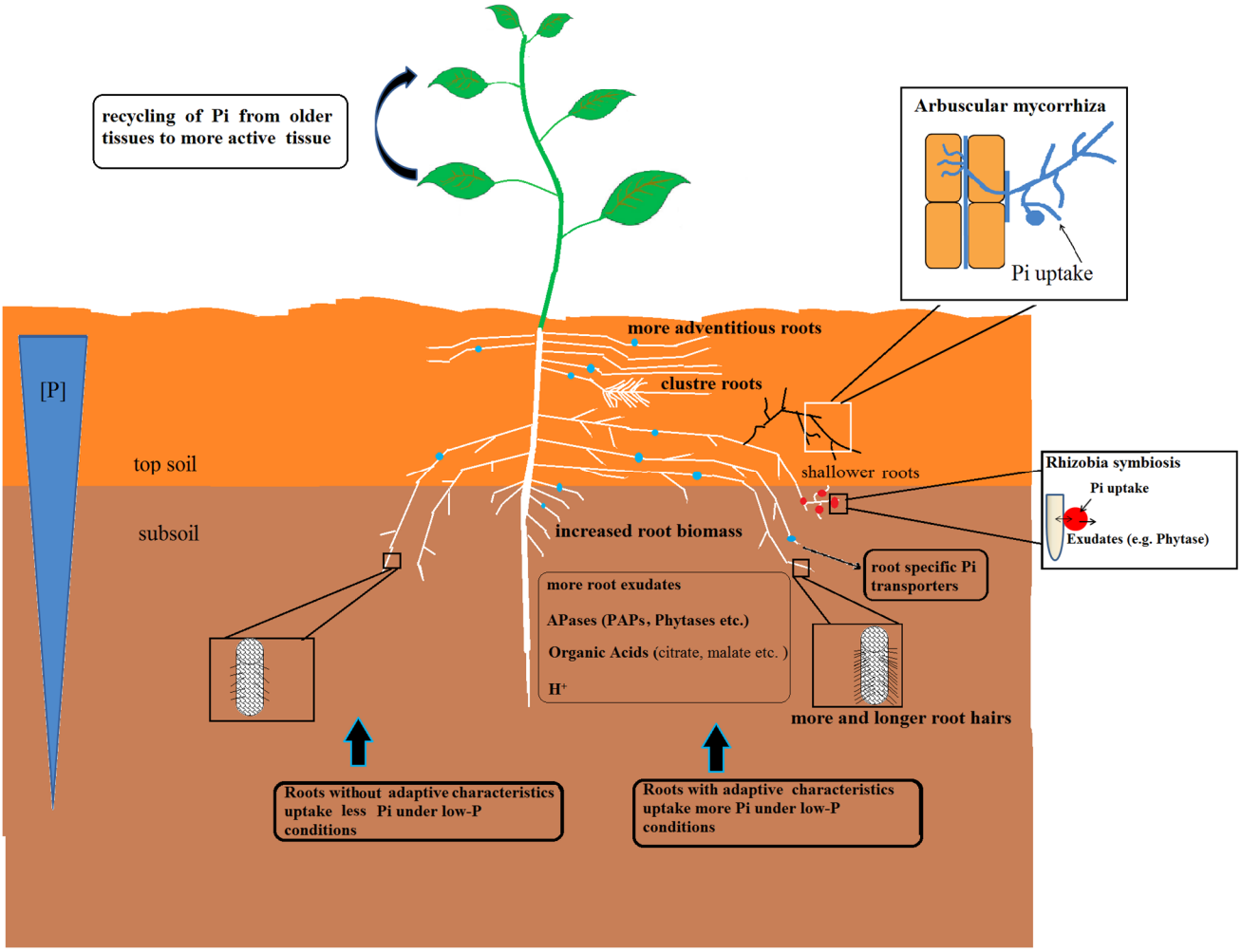

Figure 1. Schematic strategies associated with adaption to low-P conditions in crop roots. Enhanced phosphate (Pi) availability in the soil is achieved by remodeling of root system architecture, creating symbiotic with rhizosphere microorganisms, the production and secretion of organic acids (OAs) and APases and inducing high-affinity Pi transporters. The induced high-affinity Pi transporters in the root–soil and AM and rhizobia symbiosis interfaces, facilitates the acquisition and translocation of Pi into different plant organs.

Thus, inhibition of primary root growth and enhanced production of cluster and lateral roots are important to uptake more P from topsoil (86).

Root growth

Root/shoot ratio is increased by allocating more biomass to root system (88), which is a common response of plants to P-deficiency, resulting from a greater inhibition of shoot growth than root growth. Therefore, the capacity of plants to find an adequate phosphate supply depends on developing root architecture traits that promote topsoil foraging (45). Primary Root (PR) growth response in monocot species is more complex and in some crops including maize, Pi deficiency slightly motivates PR growth (38). It has been suggested this phenomenon may be due to more abundant phosphorus reserves in their seeds (9).

Auxin as a regulator for root growth under low-P conditions

It has been revealed that auxin receptor TIR1 (Transport Inhibitor Response 1) lever is higher in low-P (54). Changes in auxin transport and sensitivity to auxin are proposed to be the key mechanisms to modulate primary root development and to increase lateral root formation in Pi deficiency conditions (48). To increase lateral root

formation mediated by TIR1, the presence of ARF7 (Auxion Response Factor 7) transcription factor, which transduce increased auxin response is necessary. This phenomenon in turn leads to the formation of new lateral roots (54).

Root Pi transporters

High-affinity Pi transporters may play a crucial role to absorb Pi under low-P conditions. This system is capable at low Pi concentrations (Km ranging from 3-10 μM), whereas the low-affinity system acts at high Pi concentrations (Km ranging from 50-300 μM) (65). Therefore, plants with high-affinity Pi transporters are suitable for growing in low-P conditions. There are four families of phosphate transporter (*Pht*) gene (*Pht1, Pht2, Pht3,* and *Pht4*) in *Arabidopsis* (57). In other plants, several members of *pht1* encode Pi transporters, including in soybean, rice, *Medicago truncatula* and maize there are 14, 13 (OsPT1–13), 5 (*MtPT1- MtPT5*) and 5 (ZmPht1; 1–5) members of *pht1* genes, respectively (18, 1, 43, 50). In *M.truncatula* and rice two out of five members (*MtPT1* and *MtPT2*) and four out of 13 members (*OsPT2, OsPT3, OsPT6,* and *OsPT7*) respectively, are highly expressed and play an important role in low-P conditions (45). Maize inorganic phosphate transport factors 1 and 2 (ZmPT1 and ZmPT2) are involved in transporting lipid transfer protein (LTP) and amino acid carrier protein as regulators of the root-meristem response to Pi-starvation. *LaPT1* is a Pi transporter gene in lupin, and secretion of this gene and acid phosphatase *LaSAP1* gene are upregulated by exogenous sucrose in Pi-sufficient seedlings grown in darkness and are suppressed in cluster roots in dark-adapted plants grown in Pi-deficient conditions (44).

Gene manipulation strategies for improving root Pi uptake

Overexpression of *GmEXB2* caused a significant increase in root cell division and elongation, more growth and higher Pi uptake at both low and high external P levels in Arabidopsis and soybean (24). *GmACP1* is an acid phosphatase encoding gene that is 86% identical to a common bean acid phosphatase (*PvPS2*) and 70% identical to a tomato acid phosphatase (*LePS2*). The transgenic soybean hairy roots overexpressing *GmACP1* exhibited 11.4 to 22.8% increase in root dry weight (100). Similar results have been revealed by overexpression of protein phosphatase *PvS2:1* in bean hairy roots and *Arabidopsis* (40). According to the literatures, there are several mutants with altered root growth under Pi deficiency conditions. However, for most of them, the root development is not completely suppressed in low-P conditions. Thus, although some of their phenotypes are caused by an alteration in the local low Pi-triggered signaling or stress response, others are probably a simple consequence of reduced metabolic activities (53). The PHO1 family protein which acts as Pi exporter plays an important role in the transfer of Pi from roots to shoots in several plant species, including *Arabidopsis* and rice (66). While overexpression of *PHO1* results in an intense efflux of Pi out of cells and into the xylem vessel, which in turn increases shoot Pi level and reduces shoot growth, it has been shown that reduced *PHO1* expression in roots is sufficient to maintain shoot growth and to suppress the expression of P starvation-responsive genes in Arabidopsis, despite the strongly P deficient leaves. These findings indicate that reduced shoot growth is a result of genetic reprogramming by P deficiency, rather than a direct consequence of P deficiency.

PAP genes roles in root architecture alteration

It has been documented that transgenic plants overexpressing PAP genes show altered root architecture under various P levels (32, 86). In addition, some of these genes participate in root growth, including mutation in *AtPAP10*, and *pap12*/*pap26* double mutant (mutation in both *PAP12* and *PAP26*) lead to attenuated root growth (52). *PAP12* and *PAP26* are the two closest paralogs of *PAP10* and the predominant PAPs secreted by roots of Pi-deficient *Arabidopsis* (80). Overexpressing the soybean PAP gene *GmPAP4* results in significantly more and longer lateral roots than wild type (WT) *Arabidopsis* plants. However, further investigations are needed to clarify direct or indirect effect of GmPAP4 on lateral root growth (32). Results on the root development characteristic of *pap10/12/26* triple mutant line in *Arabidopsis* showed that under low-P conditions, root biomass was lower than for the WT. *AtPAP10*, *AtPAP12,* and *AtPAP26* overexpressing lines gained more shoot and root biomass than the WT under Pi-deficient condition (85). Moreover, similar results reported by other researches about roles of APase genes in

root development, including overexpression of AtPAP15 and *AtPAP18* in soybean and tobacco respectively, result in significant increases in root growth (99, 88, 94). The above results indicated that the reduced acquisition of Pi in the external environment because of the impaired of acid phosphatase activity can directly affect plant growth (52, 87, 99). Inhibition of primary root growth and increased number and length of lateral roots (89, 46) together with the enhanced production of root hairs are thought to increase the surface area for Pi acquisition. .

Table 1. Major genes and transcription factors involved in root architecture and growth response to phosphate deficiency in different plant species

Gene/ Transcription Factor (TF)	Species overexpressing (OE)/ species identified (SI)/mutant (M)	Main effects	Reference
AtPht;5	*Arabidopsis*(OE)	Increases number and length of root hairs, Pi uptake and an the transcript levels of Pi scavenging genes	(49)
PSTOL1	Rice (SI)	Responsible for root system architecture alteration and early establishment of the root system	(19)
HPS7	*Arabidopsis* (mutation)	Remodeling of RSA, increased expression of Pi starvation-induced genes	(61)
GLK	*Arabidopsis*(OE)	inhibition of root growth under Pi deficiency	(61)
H^+-PPases	*Arabidopsis*, tomato, rice, alfalfa and cotton (OE)	Important role in root system patterning and foraging Pi from soils	(20)
(*LPR1*) and *LPR2*	*Arabidopsis*	Control of the PR Response to Low Phosphate	(72,79)
APSR1	*Arabidopsis* (M)	Coordinate cell process (e. g. root meristem maintenance) for good root growth in low-P	(21)
*NRR*a and *NRRb*	Rice (knockdown by RNAi and OE)	negative regulatory roles in rice root growth	(103)
OsARF12	Rice and *Arabidopsis* (SI)	Partial controlling root system alteration and Pi-induced auxin response	(54)
*PHR1*TF	*Arabidopsis* (SI)	regulates P starvation-responsive genes, including *AtIPS1*, lateral root formation or anthocyanin accumulation	(78)
GmEXPB2	Soybean (OE)	increased root and shoot growth, improved Pi acquisition under low-Pi stress	(94)
AtBHLH32	*Arabidopsis (*M*)*	Regulates P starvation-induced genes, and suppress root hair cell differentiation	(10)
PDR2	*Arabidopsis* (M)	Proper expression of SCARECROW (SCR), a key regulator of root patterning in Pi-deprived roots	(77)
OsPHR2 , *OsARF16*, *OsMYB2P-1*	Rice (SI)	Remodulation of root system architecture and regulation of phosphate-starvation responses	(91,68)
GbWRKY1(TF)	Cotton (OE in *Arabidopsis*)	Remodulation of root system architecture by alteration of auxin sensitivity	(95)
TaPHR1(TF)	Wheat (SI)	Remodulation of root system architecture	(84)
*ZmPTF*1(TF)	Maize (SI)	controlling of root system architecture and regulating carbon metabolism	(37)
OsPTF1(TF)	Rice (OE)	Increased tillering, root and shoot biomass and improved P acquisition.	(98)
ZAT6 and WRKY75	*Arabidopsis* (SI)	P acquisition and homeostasis that is mediated through alterations in root structure	(83, 14)

Modulation of root system architectures mediated by the overexpression PAP genes in turn can improve plant Pi status. This process begins with a reduction in cell elongation followed by progressive loss of meristematic cells (61). Increased root biomass, particularly increased root hairs, are important for plant P absorption from the soil by expanding the absorptive root surface area and increasing the soil volume explored by the roots.

The effect of other root growth regulator genes on low Pi-mediated stress

In addition to *PAPs*, other genes and transcription factors involving in the Primary Root (PR) growth response to low Pi are well understood and there are clear evidences for their role in modulating plant root system architectures, morphology and physiology in response to Pi deficiency. Transgenic plants overexpressing these genes may exhibit more improved root characteristics to cope with low-P conditions. They play central roles in different aspects of the metabolic, architectural and morphological responses of roots to Pi deficiency, which have been identified and demonstrated in several plant species. Overexpression of these kinds of genes may lead to increased root growth under P deficiency, supporting plant Pi status. Besides, some transcription factors are induced in response to low-P conditions. They may contribute in response to P deficiency through alterations in root system architectures and structures (Table 1).

Root exudates: organic acid exudation

Several plant roots under Pi deficiency conditions, including maize, rapeseed, rice, alfalfa, chickpea, wheat, soybean, triticale and rye OA (Organic Acid exudation), like citrate, malate, oxalate tartrate, acetate, succinate, lactate upturns and H^+ ions (31), release inorganic P from Al^{3+},Fe^{3+},and Ca^{2+}, which are abundant in the topsoil. Soybean genotypes with different P efficiency differed in the type and quantity of organic acids exude from the roots under low-P condition (16). In soybean exudation of oxalate and malate are induced by low- P conditions (41). OA transporters such as ALMT (aluminum-activated malate transporter) channels (64) and MATE (multidrug and toxic compound extrusion) are required for malate and citrate exudation, respectively. In addition, it is believed that other exudates such as Acid phosphatases (APases), RNases, and protons (H^+) intricately are involved in P releasing from insoluble P pools in the rhizosphere (56).

Acid Phosphatase

It has been confirmed by all array studies that production and secretion of acid phosphatases are a universal response to P-starvation in higher plants (85), which allows them to cope with this challenge and restore their growth in low-P conditions. There are two kinds of Pi - starvation induced (PSI) acid phosphatase; first are the intracellular APases, which are likely to be involved in the remobilization and recycling of Pi from intracellular P monoesters and anhydrides of older tissues to more active photosynthetic tissue, while the second ones, extracellular or secreted APases are believed to scavenge Pi from organophosphate compounds in the external environment (67). As mentioned above, the majority of total P fixes into organic phosphorus, of that roughly 30% is available by plant roots re-mobilization of P to more active photosynthetic tissues. Therefore, the production and secretion of APases from plant roots may increase the availability of Pi in the external environment for root absorption; consequently this may improve P efficiency, which results in improved plant growth under low-P conditions. In recent years, important achievements in terms of improved P efficiency crops mediated by overexpression of APas genes have been achieved via genetic engineering. They can release Pi from a broad spectrum of P-monoesters. For example, AtPAP10, AtPAP12 or AtPAP26 release Pi from ADP, glycerol-3-P ADP, Fru-6-P, phosphoenopyruvate or DNA in *Arabidopsis* (85), while PvPAP1 and PvPAP3 release Pi from dNTPs in common bean (*Phaseolus vulgaris*) (39).

The roles of PAPs in increasing P availability under low-P conditions

Purple acid phosphatases (PAPs) are members of the metallo-phosphoesterase family and have been known to play important roles in phosphorus (P) acquisition and recycling in plants (34, 63). Plant tolerance to P starvation is, in part, attributed to released acid phosphatases. PAPs can 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 (24). Out of three Pi starvation-responsive PAPs, two are secreted acid phosphatases (SAP1 and SAP2), while the third one is an intracellular acid phosphatase (IAP).

The phosphate-starvation-inducible (PSI) secreted PAPs can be assigned to two groups. One is released into the growth medium, and the other is tightly associated with the root surface after secretion (85). *AtPAP10, AtPAP12* and *AtPAP26* are predominant PSI-secreted PAP genes, which form a clade, separate from the other 29 *Arabidopsis* PAPs, designated group Ia-2. It has been suggested that Ia-2 subgroup plays more central role in response to P deficiency. It has been shown that AtPAP12 and AtPAP26 release into the rhizosphere, while AtPAP10a is a cell wall bound PSI-secreted PAP associated with the root surface. (80, 85, 79). In addition, PAPs facilitate re-mobilization of P from other subcellular compartments in source tissues, such as old leaves or seeds toward more active photosynthetic tissues (67).

PAPs in different plants

Plant genomes contain several putative PAP encoding genes. It has been shown that the majority of PAP proteins are secretory proteins, also some of them are localized in mitochondria and only few of them are localized in chloroplast. Variation in subcellular localization of PAPs indicates functional differences (22). They 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 (101) (Table 2).

Other roles of PAPs

Besides, PAPs may also play other crucial roles in plants, which may be involved in tolerance to the biotic and abiotic stresses (59) by playing a role in other biological functions, including peroxidation (11), ascorbate recycling (102) and regulation of cell wall carbohydrate biosynthesis (28). For instance, a soybean *PAP* gene (*GmPAP3*) is inducible under NaCl and oxidative stress but not under low-P conditions (42). Its expression also increases significantly under drought stress in soybean (70). *GmPAPs* expression (e.g. *GmPAP15* and *GmPAP23*) increases in leaves and roots of soybean under P-deficient conditions (34, 42). In addition, they are involved in response to environmental stress. For example, ectopic expression of *GmPAP3* in rice not only improves plant growth traits, but also aid restoration of oxidative state by increasing the superoxide dismutase (SOD), catalase (CAT), and proline content (12), which in turn reduce oxidative damage under salt stress conditions. In addition to the primary function of PAP genes, such as *AtPAP15* and *AtPAP17*, which is to catalyze Pi hydrolysis from phosphomonoesters, its overexpression in *Arabidopsis* also enhances salt stress through increasing foliar ascorbate content (102, 11). AtPAP17 can also be induced by abscisic acid (ABA), salt stress, senescence and hydrogen peroxide during exposure to oxidative stress. Thus, AtPAP17 may be involved in P mobilization and in the metabolism of reactive oxygen species (ROS) under stresses or in senescent plant material. Transgenic soybean overexpression *AtPAP15* with phytase activity showed significantly increased phytase secretion from soybean roots, which in turn improved soybean P utilization (25).

Table2. Physiological roles of some APase and PAP genes in different plant species.

Gene	Plant	Roles of the genes under low-P conditions	Reference
MtPAP1	Alfalfa	improving P utilization in natural soils	(93)
GmPAP4	Soybean	Catalyze the phytate in rhizosphere to maintain plant growth and development under low-P conditions.	(32)
GmPAP1 and *GmPAP2*	Soybean	only induction under low-P conditions	(42)
PvPAP3	bean	bean hairy roots overexpressing PvPAP3 showed increase in both growth and P absorption	(97)
OsPAP10a and *OsPAP2*	Rice	specially induced by Pi-deprivation and plants overexpressing *OsPAP10a* gene show much more increase of APase activity	(75, 27)
LEPS2	Tomato	play a role in signaling transduction through protein dephosphorylation	(4)
StPAP2	Potato	only express and exudate from Pi-deprived roots	(105)
NtPAP12	Tobacco	decreases the activity levels of the glycosidases and increases levels of xyloglucanoligosaccharides and cello-oligosaccharides	(29)

PAPs could have several functions in the phenomena of plant cells due to various substrate preferences. It has been suggested that the cellulose and callose synthase activities are promoted by the increase in the oligosaccharides caused by the action of PAP. For example, tobacco (*Nicotiana tabacum*) NtPAP12 can be involved in the deposition of beta glucan (28, 62), also its increased activity enhances cellulose and callose synthases (28), which can catalyze the dephosphorylation of phosphorylated tobacco wall proteins (29).

A diphosphonucleotide phosphatase/phosphodiesterase (PPD1) from yellow lupin (*Lupinus luteus*) seeds, which belongs to a novel group of high-molecular-weight plant PAPs involved in plant growth and pathogen defense, since they are able to generate reactive oxygen species (2) In *Arabidopsis* plants, loss of PAP5 leads to increased susceptibility to virulent *Pseudomonas syringae*. Furthermore, *pap5* plants failed to accumulate H2O2 in response to infection. It has been shown that optimal level of *PAP5* is critical for mounting appropriate defense responses and prolonged expression of *PAP5* could negatively affect basal resistance against virulent *Pseudomonas syringae* (58).

Phytase activity of PAPs

Phytases, which are special subgroup of PAPs, play important role in phosphorus efficiency improvement in plants; like PAPs. They can hydrolyze P monoesters from organic phosphate compounds like phytic acid and its derivatives to a series of lower phosphate esters of myo-inositol and phosphate, which in turn release Pi (33). Phytases are of particular importance during seed germination where they mobilize phosphate from phytate, also they can secrete into the rhizosphere, which they hydrolyze phytin reserves to release Pi for the rapidly growing seedling and plants under low-P conditions (35). For example, OsPAP15 acts as a phytase during rice seed germination (15). Previously, a lot of phytase genes have been characterized in diverse plants and overexpression of these genes such as *PhyA*, *MtPHY1* and *OsPHY1* may lead to significant improvement of crop production on low-Pi soils (92). It has been shown that phytase PAP (*PAPhy*) is active in the mature grain of wheat and barley while it is not present in mature grain of maize and rice. It has been indicated that the PAP-derived phytase potential of a cereal grain comprises two different pools, one pool being synthesized and stored during grain filling and the other one being synthesized during germination (17).

The roles of APases in roots of N2-Fixing plants

It has been documented that legumes species develop a symbiosis relationship between their roots and rhizobia to fix N2. In addition, it has been shown that N2-Fixing nodules contribute to activation of several number of APases genes for their tolerance in low-P conditions (3, 5), indicating that acid phosphatases might strongly establish an adaptive mechanism of the rhizobia–legume symbiosis to low-P environments (33). There is considerable need for P in legume N2 -fixing nodules to maintain their N2-fixation process (81). Therefore, low-P conditions are thought to be an important constraint for legume crop production. The stabilization of P levels in the symbiotic tissues can be achieved through several mechanisms, including higher P allocation to nodules, formation of a strong P sink in nodules, direct P acquisition via nodule surface and P remobilization from organic-P containing compounds (71). Phytase activity in nodules would contribute to the adaptation of rhizobia–legume symbiosis to low-P environments. It has been shown that increased phytase activity in bean nodules is an adaptive mechanism in response to P-deficient conditions and may be involved in the tolerance of rhizobial symbiosis to P deficiency (3) thus the increase in activity of APase in leguminous plants indicates their physiological role in the regulation of nitrogenase activity in connection with the nodule-P status, which may expand the availability of Pi for both plant and bacteria. The expression of *GmPAP* gene family is highly induced in the nodules of soybean in response to P deprivation (34), indicating that the excretion of acid phosphatases from nodules may be stimulated by low P availability. Acid phosphatase not only contributes to optimal intracellular P foraging ability but also is involved in multiple functions during the N2 fixation, including carbon metabolism, regulation of nodule permeability to O2 diffusion (7) and alleviation of oxidative stress (6).

DISCUSSION

Many studies highlighted the importance of Pi as a critical element in plant and agricultural sustainability. According

to the low bioavailability, high rate fixation by metal oxides and low rate of diffusion of Pi in soils, root architecture system is a key trait for optimizing Pi acquisition in crops. Approximately only 20% of the topsoil is explored by roots during plant growth; therefore, enhancing topsoil foraging is essential to improve Pi usage. Among the adaptive root characteristics for phosphorus uptake in P deficiency circumstances, a variety of those are crucial, including root/shoot ratio, root secretory proteins, root surface binding proteins, root hair formation, and formation of cluster roots. However, evaluating the phenotypes of roots in soil is a major challenge, and the use of *in vitro* systems that can enable prediction of root system phenotypes under different soil conditions or the use of nondestructive methods will be helpful. In addition to root system architecture, plants have developed several strategies todeal with low-P conditions and maintain Pi homeostasis. It has been suggested that multi-dimensional gene regulation networks are involved in response to low-P conditions.

The previous studies have helped us to gain new insight into the plant adaptive responses under low-P conditions, describing the structural features, expression patterns, intermolecular relations, subcellular localizations and biochemical characteristics, functions and roles of the related genes, transcriptional factors and pathway network. Among these genes and networks, root exudates including APases and high affinity transporter are important. These data could be used in both the theory and the practice for genetic improvement of crop varieties. Taken together, screening germplasms in order to identify P efficient genotypes and developing transgenic plants overexpressing appropriate genes (e.g. PAP genes), will be much more helpful in crop production under low-P conditions. Plants with increased Apase activity may exhibit an improved root morphology and physiology to capture much more Pi in low-P conditions. In this situation the use of P fertilizers will be reduced. It is worthy to note that heavy application of these fertilizers in crop production lead to environmental contamination. However, more studies and collaborations between plant breeders and physiologists are needed to develop P efficient crops. In addition, supplementary applied and theoretical research are still necessary to understand the regulatory network for maintenance of Pi homeostasis and adaptive response under low-P conditions to design more appropriate breeding scheme to improve P efficiency in crops. Such P efficient crops will help us to achieve sustainable agriculture.

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بهبود کارایی فسفر در گیاهان با تمرکز بر روی اسید فسفاتاز ارغوانی: پتانسیل‌ها و دورنما

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چکیده

تنش کمبود فسفر به عنوان فاکتور محدود کننده کلیدی رشد و تولید گیاهان در اغلب خاک‌های کشاورزی متداول می‌باشد. اغلب فسفات به کار برده شده در خاک به سرعت تثبیت شده و اغلب کودهای فسفاته که سالانه به زمین‌های زراعی اضافه می‌شود توسط فرآیندهایی مانند جذب سطحی، رسوب و ترانسفورماسیون به شکل آلی تثبیت می‌شود. به هر حال کاربرد بیش از حد فسفر می‌تواند توسط غنی سازی آب‌های زیر زمینی با عناصر غذایی منجر به آلودگی منابع آبی شود که باعث به وجود آمدن پدیده یوتریفیکاسیون می‌شود. بنابراین درک مکانیسم‌هایی که توسط گیاهان برای مقابله با تنش کمبود فسفر استفاده می‌شود، می‌تواند برای توسعه برنامه‌های مناسب مهندسی ژنتیک و به‌نژادی گیاهان با بهبود کارایی فسفر کمک کند. برای مقابله با کمبود فسفر و حفظ همئوستازی فسفات، گیاهان مکانیسم‌های سازگاری متفاوتی را توسعه داده‌اند که از جمله می‌توان به تغییر در مورفولوژی ریشه، بازیافت فسفات معدنی و القای اسید فسفاتازها اشاره کرد. برای تثبیت این استراتژی‌ها، ژن‌های متعددی در مسیرهای متابولیسمی جایگزین درگیر می‌باشند که توسط شبکه‌های پیچیده پیام رسان فسفر تنظیم می‌شوند. در این مقاله، ما می‌خواهیم پیشرفت‌های اخیر در تحقیقات مربوط به مکانیسم‌های گیاهان با بهبود کارایی فسفر و استراتژهای اصلاحی آنها را جمع بندی کنیم که تأکید مخصوصی روی نقش اسید فسفاتاز و معماری ریشه در پاسخ به کمبود فسفر خواهیم داشت.

کلمات کلیدی: شرایط کمبود فسفر، معماری سیستم ریشه، فعالیت اسید فسفاتاز، گیاهان با کارایی موثر P، جذب Pi