Physiological and molecular approaches for improving phosphorus uptake efficiency of crops

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Intensive use of phosphorus (P) in agriculture has raised concerns about its sustainability due to potential resource scarcity and its non-judicious use which has led to serious environmental pollution. Plants possess a number of adaptive mechanisms to cope with P stress leading to changes at morphological, physiological, biochemical and molecular levels. A comprehensive understanding of these adaptive responses is required to improve P uptake efficiency, partitioning and utilization, together with other agronomic approaches, which would result in meeting the sustainability challenge of P delivery to crops. The present article briefly covers various plant responses to P stress and molecular strategies that could be used to develop plants efficient in P acquisition.

Keywords: Acid phosphatase, phosphorus starvation induced genes, phosphorus uptake efficiency, root morphology, Pi transporter.

PHOSPHORUS (P) is an indispensable element for agriculture as it can neither be substituted with any other element in crop production nor obtained from the atmosphere. It is one of the key component of biomolecules such as ATP, nucleic acids and phospholipids, regulates many biological processes involving energy transfer reactions, activation of enzyme proteins and mediates cellular signal transduction cascades[1]. It is also required for photosynthesis and respiration, thus involved in carbon and amino acid metabolism. In many agricultural production systems, P is considered as one of the major limiting factors for crop productivity, especially in the tropics and subtropics[2]. Natural P reserves are limited and sedimentary deposits are the source of 80–90% of the world P production. According to the GPRI declaration[3], the demand for P globally will increase in future due to several reasons such as the ever-increasing population pressure, control of P reserves in the hands of a few countries (such as China, US and Morocco), decreasing quality of P reserves (less concentration of P_2O_5 in rock phosphates and high concentration of heavy metals), high energy cost involved in mining, processing and transportation of phosphate rock and a sharp increase in price of raw material. In India, it is estimated that by the year 2025, total food grain requirement will be ~300 million tonnes (mt). To achieve this, about 13.1 mt of P_2O_5 would be required (based on current usage pattern) besides 22.4 mt of nitrogen (N) and potassium (K) with an average $N : P_2O_5 : K_2O$ ratio of 4 : 2 : 1 (ref. 4). In addition, another 11–13 mt of P_2O_5 will be needed for production of oilseed, vegetable, potato, sugar cane, cotton and plantation crops such as tea, coffee, coconut, etc. With a meagre 10–20% use efficiency of applied P, the demand for diammonium phosphate and single super phosphate may contribute to a huge monetary loss of INR 7.81 billion[5]. This future scenario is bound to increase the burden on Indian economy in order to make subsidized phosphatic fertilizers available to farmers.

The P bioavailability is a problem due to its slow diffusion and high fixation in soils resulting in <10 μM concentration in soil solution. Therefore, almost all types of soils need to be fertilized with P. Phosphorus loss from agriculture can come from both point and non-point sources[6]. Point sources include waste water from farms and dairies and seepage from manure piles. Non-point sources relate to individual fields from where there can be soil erosion, surface runoff and drainage. Measures to recycle P from the runoff and food chain could be an alternative strategy to protect the environment and conserve resources[7]. Plants, however, possess several adaptive strategies at physiological, biochemical and molecular levels to cope with long-term P starvation. Traits to enhance P mining ability include changes in root architecture such as increased root-to-shoot ratio, lateral root number, root hair length and density[8,9]. Specialized root structures called 'proteoid' or 'cluster' roots are formed in some species which efficiently exudate carboxylates[10,11]. Increased production and secretion of organic acids[12,13] and enzymes such as purple acid phosphatases[14] and ribonucleases in the rhizosphere helps in

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mobilization of P. Association between plant roots and arbuscular mycorrhizal fungi (AMF) is another means of improved P acquisition studied in several crops[15]. At molecular level, these P starvation responses are a result of P-starvation induced genes encoding enzymes that help in reprioritizing the internal P utilization and maximization of P acquisition such as induction of high-affinity Pi transporter in roots[16].

In order to optimize P fertilization and reduce the adverse effects on the environment, various agronomic practices are being followed. However, developing P-efficient plants by modifying their own adaptive strategies would be a sustainable approach without compromising on the environment as well as the limited P resources. Enhancement of P efficiency includes 'acquisition/uptake' efficiency and 'utilization' efficiency. The basic approach involves selection of cultivars/genotypes with an enhanced P acquisition or utilization efficiency. Developing plants with improved P efficiency through conventional plant breeding or genetic engineering is the need of the hour. In this article, we discuss the various physiological, biochemical and molecular plant processes which could be modified for efficient P uptake under P stress.

Morpho-physiological approaches to improve P acquisition efficiency

Modifications in root morphology

Root morphology such as root length, diameter, surface area, volume, presence of root hairs, and length of root hairs are the causes of inter- and intra-specific variation in P uptake. Greater root–soil contact provides greater absorptive area achieved with larger root systems and is important for uptake of relatively immobile nutrients such as P. Significant contribution of root length, volume, number of lateral roots and root surface area were reported towards total P uptake at 45 days after sowing blackgram (*Vigna mungo*)[17].

Root hairs: Presence of root hairs increases the effective root surface area considerably without contributing to the root biomass. Under low P, uptake is closely related to root length[18], root surface area[19], root hair length and root hair density[20]. Long root hairs in barley genotypes were reported to sustain high grain yields under low P[21]. Similarly, genotypic differences in root length and root hair length in lentil[22] and chickpea[23] and root surface area in wheat[24] under low P were noted. The root hair trait is inherited in a Mendelian fashion as shown by a cross between root hairless mutant of barley (*brb*) and wild type suggesting that it is governed by a single gene[25]. This could be helpful in genetic analysis of root hair development in cereals.

Root diameter: Root diameter denotes the volume of soil penetrated by roots per unit of photosynthate invested. Though measuring root diameter is not a common practice, it is observed that genotypes with thin roots may absorb P more effectively. Thin roots explore larger soil volume per unit of root surface area. Since thin roots have to be replaced more frequently, the maintenance carbon cost to produce them would be higher[26]. High heritability (0.54) of root diameter has been reported in white clover[27].

Root whorl number: Basal root whorl or node number varies among genotypes of annual legume such as bean which exhibits enhanced soil exploration by increased number of root whorls. Among genotypes of bean, the basal roots developed at distinct whorls with numbers varying from one to four. In recombinant inbred line (RIL) population of common bean with three whorls, more than 60% biomass accumulated than those with two whorls[28].

Shallow root growth angle: The topsoil strata has higher available P than the subsoil strata owing to deposition by plant and fertilizer residues over time. Under these circumstances, root traits that increase topsoil foraging will aid in acquiring more P. Efficient genotypes of beans and maize have shallow roots in the top soil[29]. Shallower root growth angle of axial or seminal roots increase the topsoil foraging and thereby better P acquisition[29]. However, this trait may not be suitable for crops grown under drought condition. Adventitious roots with shallow root growth angle may also increase P acquisition. However, excess growth of adventitious roots increases carbohydrate demand, which in turn results in a source–sink imbalance and decreased P acquisition[28].

Root biomass: Besides above traits, increases in root biomass under P stress are common phenomena resulting in greater root-to-shoot ratio. It is estimated that out of the total net assimilates produced above ground, almost 50% of carbon is partitioned below ground in wheat and barley[30]. Thus, P uptake depends, not only on root size, but also on shoot size. Crop genotypes with extensive root systems coupled with a large shoot system would be P efficient, contributing to yield stability during P starvation.

Changes in root physiology

Physiological and biochemical responses observed under P stress include proton extrusion[31], exudation of carboxylates[32] and phosphatases[33], kinetic parameters[34], mycorrhizal symbiosis[15] and formation of cluster roots[11]. All these physiological and biological changes induced in roots, help in efficient mobilization of P from mineral-bound or organic P (P_{org}) fractions in soil[35].

Root-induced proton extrusion: Plant roots release protons under P deficiency leading to acidification of the

rhizosphere[36]. Two to three units increase in rhizoshpere pH relative to the bulk soil helps in dissolution of sparingly soluble P. Large variation among crop genotypes has been observed for efflux of proton[37], however, root-induced pH change is not always responsible for enhanced P uptake. When rhizosphere pH was unaltered, wheat and barley showed significant genotypic variation in terms of inorganic P (P_i) absorption capacity[37]. This indicates that in addition to proton extrusion, other mechanisms might also be engaged in causing variation in P acquisition in cereals. The root-induced pH change is the result of overall imbalance between cation and anion in plants[38] suggesting that genetic manipulation of cation–anion balance would enhance the ability of plants to modify rhizospheric pH.

Organic acid exudation: A major fraction of exudates released by plant roots during P starvation comprises the organic acids (OA) such as citrate and malate[32]. These mobilize both P_{org} and P_i by displacing phosphate from soil matrix through ligand exchange[11]. OA exudation is also induced under low soil moisture levels due to reduced mobility of soil P_i during water deficit condition[39]. Besides OA, phenolics and mucilages are also released under low P, which also act in the same manner as the OA[11].

Enzyme exudation: Enzymes such as phosphatases and phytases are released by plant roots into rhizosphere where they hydrolyse soil P_{org} pools[40]. It is reported that acid phosphatases are more abundant in the rhizosphere under P starvation[41]. Most plants have very limited capacity for phytate uptake except in the presence of microbes that dephosphorylate phytate[11]. There was greater access to phytate by few transgenic plants overexpressing extracellular phytases when grown under sterile media in laboratories. However, these phytases were found to be rapidly immobilized when grown in soil, thereby, limiting its ability to interact with phytate. This indicates that phytase-mediated dephosphorylation of phytate occurs only after the latter has been mobilized into soil solution.

P uptake kinetics: Similar to enzyme kinetics where the rate of a chemical reaction is assessed, nutrient uptake kinetics can also be analysed in terms of the rate of nutrient influx through membrane transporters. The uptake rate of a limiting nutrient in the environment can be described by a rectangular hyperbola, similar to the Michaelis–Menten equation for enzyme kinetics. However in plants, this equation has been modified to calculate the mean net influx (I_n) of P into plant root and can be expressed[42] as $I_n = [I_{max}(C_o - C_{min})]/[K_m + C_o - C_{min}]$, where I_{max} is the mean maximum influx (mol cm^{-1} s^{-1}); C_o is the concentration of P at root surface (mol cm^{-3}); C_{min} is the concentration at which $I_n = 0$ (mol cm^{-3}); K_m is the Michaelis–Mentes constant (mol cm^{-3}). Similar to enzyme kinetics, $I_n = 1/2$, when $C_o = K_m + C_{min}$.

It was observed that the values of P uptake kinetic parameters, viz. I_{max}, K_m and C_{min} differed significantly among genotypes of wheat[34] and barley[43]. For improving P uptake efficiency, the genotypes should be selected for high I_{max} and for low C_{min} and K_m values. Plants with lower C_{min} may be able to efficiently absorb the P present at lower concentration, thereby, facilitating low input farming systems.

Root-microbial associations: Terrestrial symbiosis, the most widespread of the AMF associations, is found in 70–80% of the land plant species[44]. AM fungi are non-host specific although evidence is growing that certain endophytes may form preferential association with certain host plants[45]. It is reported that P acquisition of maize crop increased under low P while it decreased under high P conditions[46]. Genotypic variation in terms of degree of AM infection was reported in wheat[15] and other crops. Among cereal species, high efficiency of AM symbiosis in terms of P uptake was reported in rye and most of these traits in triticale seem to be inherited from wheat rather than rye[18]. The mycorrhizal responsiveness has inverse relationship with shoot biomass, indicating that there is differential genotypic responsiveness towards mycorrhizal associations, which needs further studies.

Molecular approaches to improve P acquisition efficiency

Microarray studies have made it possible to explore the global gene expression profiles under P deprivation in *Arabidopsis*[47,48] and crop species such as maize[49], potato[50], bean[51] and rice[52]. These studies revealed alterations in several biochemical and signalling pathways resulting in changes at the gene, protein and metabolite levels. Recently, the RNA-seq technology has been employed to study the global gene expression in *Lupinus albus* wherein 2128 differentially expressed sequences were identified in response to P deficiency with a two-fold or greater change[53]. The expression of genes causing alternations in phenotype, is under complex regulation and is generally up-regulated by P starvation resulting in transcript accumulation over longer periods[54]. Transcriptome analyses indicated rapid changes in the expression of several genes encoding Pi transporters, phosphatases and RNases and other genes involved in the reprogramming of metabolic pathways of lipid recycling, nitrate assimilation and carbohydrate mobilization[47,50,51,55]. However, altered gene expression regulating photosynthesis, carbohydrate and secondary metabolism were not reversed when P was resupplied[50].

The proteomics approach has also been used to identify proteins with altered profiles under P starvation. Protein profiling in maize[56], *Brassica napus*[57], soybean[48] and

Arabidopsis[58] revealed that not all differentially expressed proteins were directly related to P metabolism under P starvation. Proteins involved in carbon metabolism are generally up-regulated while a number of proteins of amino acid metabolism, transcription and signalling factors are mostly down-regulated in response to P starvation. These studies suggest that specific mechanisms are evolved in particular plant species to cope with P stress.

Root system architecture regulated at molecular level

Alteration of root growth pattern in response to P starvation is a complex trait; however, a few genes associated with this process have been identified in several plant species. The genes related to development and hormone action act as mediators in regulating root system architecture[59]. Genes involved in root development such as NAC (for NAM, no Apical Meristem; ATAF1/2, Cup-shaped Cotyledons2), TRANSPARENT TESTA1, ENHANCER OF GLABRA3, APETALA1 and APETALA2[60,61] were reported to be influenced by P starvation. Similarly, the transcripts responsive to hormones such as auxin (auxin-responsive factor and AUX/IAA gene families) and abscisic acid were found to be influenced by P level[49,62]. Development of root meristem was found to be under the control of PDR2 (phosphate deficiency response 2), LPR1 (low phosphate root 1) and LPR2 in *Arabidopsis*[63,64], which also has a role in sensing P by root cap under P starvation[64]. In cereals, members of the gene families GRAS (named after the first three members: GIBBERELLIC-ACID INSENSITIVE (GAI), REPRESSOR of GAI (RGA) and SCARECROW (SCR)), COBRA (COB glycosylphosphatidyl inositol-anchored protein) and LOB (lateral organ boundary), domains have been found to be associated with root development[65–67].

In maize, six genes were reported to control root morphology, viz. *Rtcs* (rootless concerning crown and seminal roots), *Bk2* (brittle stalk-2), *Bk2-L3* (brittle stalk2-like protein-3), *Rth1* (root hairless-1), *Rth3* (roothairless-3) and *Scr* (scarecrow), were studied under P stress. Expression of *Scr* controlling endoderm and cortex formation was not influenced by P starvation. Efficient lines exhibited higher expression of the genes *Rtcs*, *Bk2* and *Rth3* relative to P inefficient line[68]. Transcriptome analysis of lateral root primordium zone revealed that the auxin signalling is responsible for causing modification in root morphology under P stress. This may be attributed to localized changes in auxin concentration due to biosynthesis and transport, in which, LOB domain proteins play an intermediary role[69]. Transcription factors such as SHORTROOT and SCARECROW identified in maize determine meristem identity and hence, root morphology[70,71]. Expression patterns of these transcription factors are also altered in response to P starvation[49].

A recent landmark development was the identification and functional analysis of *PSTOL1* (P starvation tolerance1) gene in rice (*Indica* cv. Kasalath) which regulates root development and growth under P stress[72]. However, elucidation of the molecular mechanisms and downstream targets of *PSTOL1* need to be further studied. This gene can be used to improve P efficiency in rice crops by use of targeted inter-variety breeding[73]. Progress made so far in deciphering the molecular and genetic control of root system development enriches our understanding of root morphogenesis in response to phosphate stress.

High affinity P_i transporters induced by P stress

The P_i transporters belong to Pht1 (high-affinity) and Pht2 (low-affinity) families expressed under low and high external P concentration respectively[16]. The Pht1 genes are involved in P uptake against a sharp concentration gradient, as the root cells may contain 10,000-fold higher soluble P concentration than the soil solution. These transporters consist of 12 transmembrane domains and proton (H^+)/P symporter, a large hydrophilic loop between transmembrane domains 6 and 7 with both N and C termini located in the cytoplasm[16]. The members of Pht1 family are more abundant in roots than shoots and enhanced transcripts are noted under P starvation[74]. In *Arabidopsis*, nine members of Pht1 (AtPht1.1–AtPht1.9) family have been identified and all are responsive to P nutrition[75]. Significant roles of AtPht1.1 and AtPht1.4 are observed in plant P_i acquisition, under both deficient and sufficient P_i conditions. Each member of Pht1 exhibits a tissue-specific expression, such as in root epidermal, root hair or stellar cells, whereas others were expressed in Golgi apparatus or endoplasmic reticulum. AtPht1.9 and AtPht1.8 were expressed in roots, in response to P starvation. Analysis of the double mutant (*pht 1.9/pht1.8*) revealed that Pht1.9 and Pht1.8 transporter proteins function together to sustain plant P supply under low P[76]. Other members of Pht1 family need to be characterized and functionally validated.

The high affinity P_i transporter genes have been identified in crop plants in response to P starvation. Five Pht1 genes in maize[77] and thirteen putative Pht1 genes (OsPT1–OsPT13) in rice[78] were identified which contributed to P uptake and allocation. The OsPT11 and OsPT13 were induced in response to AM-inoculation exclusively in roots[79]. OsPT8 (OsPht1.8) that is expressed in various organs irrespective of tissue P status, is involved in P_i homeostasis[80]. Expression of OsPT2 (OsPht1.2) and OsPT6 (OsPht1.6) in roots and shoots under P starvation, suggests that OsPT6 is involved in P uptake and translocation throughout the plant, whereas OsPT2, a low-affinity transporter plays a role in translocation of stored P[81]. Eight Pht1 genes have been described in barley out of which HvPHT1.1 and HvPHT1.2 were found to be

expressed in root hairs, cortex and epidermal cells and root vascular tissues[79]. HvPHT1.1, a high affinity P_i transporter involved in P uptake[82], whereas HvPHT1.6 was reported to be localized in leaf phloem tissue and expressed in both shoots and roots[83], with important roles in P_i re-translocation in plants[84].

Recently, Liu *et al.*[85] isolated and functionally characterized a high affinity P transporter in wheat, TaPht1.4, exclusively expressed in roots under P deficiency. It showed a K_m of 35.3 μM with yeast complementation studies. Another gene, TaPHT2.1, belonging to Pht2 family was up-regulated by low P and strongly expressed in leaves. Its presence in the chloroplast envelope suggested a crucial role in mediating P_i translocation from cytosol to chloroplast[86]. This gene can function in the improvement of P use efficiency in wheat. A high affinity P_i transporter, GmPT5, identified in soybean expressed in the junction area between roots and young nodules and regulates the entry of P_i from roots to nodules[87]. Transport proteins are key targets for improving P uptake efficiency in various crops; however, genotypic variation in the expression pattern and regulation of P transporters is yet to be explored.

Purple acid phosphatases induced by P starvation

Purple acid phosphatases (APases) or PAPs comprise the largest class of plant APases. Most PAPs are non-specific APases and catalyse P_i from phosphomonoesters over a wide pH range. The genes encoding PAPs are highly induced in response to P starvation and are secreted into the rhizosphere to utilize available P_i in the soil or transported to organelles to recycle P_i[47,69]. The *Arabidopsis* genome encodes for 29 putative PAP isozymes, which are transcriptionally expressed under various developmental and environmental factors[88]. The first purified and characterized PAP was AtPAP17 from Arabidopsis. It is a 34 kD low-molecular mass monomeric protein, transcriptionally induced in roots and leaves under low P. It has consensus PHR1-binding sites in its promoter region and is localized in the cell wall or plasma membrane[89]. Besides influencing P mobilization, it is also involved in the metabolism of reactive oxygen species during incidence of salinity, senescence and oxidative stresses. Another APase, AtPAP26, with a major phosphatase activity is localized in the vacuole. AtPAP26 recycles intracellular P_i and also remobilizes P_i from the organic pool during P starvation[90].

Other PAP genes from *Arabidopsis*, AtPAP10, AtPAP12 and AtPAP15, are also up-regulated by P starvation. AtPAP10 is predominantly associated with the root surface and induced by P_i deprivation, whereas AtPAP12 is secreted to utilize P_{org} (ref. 91). On the other hand, AtPAP15 is the only member of AtPAP family that possesses both APase and phytase activity. During pollen or seed germination, AtPAP15 plays an important role in P_i mobilization from the phytate reserves. Overexpression of AtPAP15 in transgenic soybean plants improved P acquisition and enhanced growth on culture media containing phytate[92]. Functional analysis of AtPAP23 genes showed its predominant expression in the flowers[93].

Several PAPs have been identified and characterized from crop species such as LaSAP2 in lupin (*Lupinus albus*), LePS2 in tomato (*Solanum lycopersicum*), GmPAP in soybean (*Glycine max*), VrPAP1 in mungbean (*Vigna radiata*), APase in *Brassica juncea*, PvPS2.1 in bean (*Phaseolus vulgaris*) and NtPAP12 in tobacco[91,94–97]. In transgenic tobacco, NtPAP12 expression altered cell wall composition and increased *β*-glucan synthase activity indicating its function as a protein phosphatase controlling cell wall biosynthesis[97]. PAPs play a vital role in recycling and scavenging of P_i, therefore are obvious targets for engineering P-efficient crops. It is observed that the external application of phosphatic fertilizers influences the P_{org} and P_i content of agricultural soils, thereby altering the amount of P_{org} available for PAP hydrolysis[98]. Therefore, it is possible to considerably improve the P uptake efficiency by overexpressing the secreted PAPs in crop plants.

Efflux transporters involved in organic acid exudation

Exudation of organic acids is one of the important strategies adopted by plants resulting in rhizosphere acidification. There are two separate transport processes causing efflux of organic anions into the rhizosphere, viz. an *active H^+ efflux* which involves a plasma membrane H^+-ATPase, and the *passive efflux* through channel-like transporters[99,100]. An important strategy for efficient P acquisition is the organic anion efflux through channels induced during P starvation[101]. However, the organic anion efflux transporters are greatly induced under aluminium (Al) toxicity than P starvation in several crops. A recent review on organic anion exudation has been published by Yang *et al.*[102]. Studies on root Al and P interactions provided evidence that P deficiency induces exudation of oxalate and malate, while Al activated roots exude citrate in soybean. In *Lolium pilosus*, citrate and H^+ efflux occurred primarily in response to P deficiency but not Al-toxicity[32]. P deficiency induced citrate exudation from the mature cluster roots of white lupin (*Lupinus albus*) whereas Al stimulated citrate exudation was localized to the 5- to 10-mm sub-apical root zones of lateral cluster roots[103]. Al^{3+}-activated anion channels (ALAACs) permeable to malate and/or citrate were predominantly expressed in the root tips of wheat and maize[104,105].

The first gene, TaALMT1, identified in wheat conferring tolerance to Al-toxicity was overexpressed in highly Al-sensitive transgenic barley seedlings[106] and tobacco[105].

Overexpression of barley gene (HvAACT1) responsible for Al-induced citrate secretion in tobacco enhanced citrate secretion and Al resistance[107]. This provided a direct evidence for the role of root organic acid exudation in plant Al tolerance. Further, many transgenics have been developed in various crops by identifying the homologues of TaALMT1 and overexpressing them[102]. Other genes, encoding type I H^+-pyrophosphatase (AVP1, Arabidopsis vacuolar pyrophosphatase 1) and a type II H^+-pyrophosphatase (AVP2)[108,109] also play a role in organic acid exudation. Overexpression of AVP1 in Arabidopsis enhanced the citrate and malate secretion from roots, enabling plants to tolerate Al toxicity[108,109]. Arabidopsis plants overexpressing the malate transporter (GmALMT1) localized to root plasma membrane exhibited malate efflux in response to P starvation in an extracellular pH-dependent and Al-independent manner[110]. Since Al and P stresses co-exist in acid soils, most of the genes conferring tolerance towards Al toxicity might also provide tolerance against P starvation.

Strategies to develop P efficient crop plants

Basically, there are three approaches to develop crops which can efficiently acquire P from soil, viz. conventional breeding, marker-assisted breeding and genetic engineering. Conventional methods such as backcross breeding and recurrent selection have resulted in soybean varieties with superior root traits and other agronomically important traits that helped them outperform in acid soils with low P[111]. In recent years, molecular marker-assisted breeding has gained popularity after the identification of several quantitative trait loci (QTLs) for various traits in response to P stress. QTLs imparting tolerance to P stress, have been identified in crops such as rice[112], common bean[113], soybean[114], *Brassica oleracea*[115] and maize[28]. Most of the traits used to map the QTLs associated with P efficiency were based on root characters. Although, QTLs are known, challenge still lies in utilizing these QTLs in marker-assisted selection because the genes underlying these QTLs have not been identified except the *Pup1* locus in rice[72]. Therefore, a strategy combining fine mapping and transcriptome analysis may facilitate earlier gene identification for development of P stress tolerant cultivars. SUB-1 introgressed HYVs of rice performed better with suboptimal P fertilization under submergence stress conditions[116]. This warrants looking into other abiotic stress tolerant genes in conjunction with P starvation induced genes for better management of problem soils.

Attempts have been made to produce transgenic plants, tolerant to low P by genetic engineering. The genes encoding PAPs, transcription factors, high affinity P_i transporters, protein kinases and those involved in the production of organic acids were targeted. The first transgenic soybean was produced by overexpressing AtPAP15 leading to a significant improvement in P efficiency and yield[92]. Two transcription factors, PTF1 and PHR1, overexpressed in maize (ZmPTF1, OsPTF1) and rice (OsPHR2) resulted in improved root production, enhanced P use efficiency and biomass production[117,118].

Conclusions

On the one hand, substantial amounts of P fixed in agricultural soils remain inaccessible to plants lacking specific root traits, and on the other global P reserves are being rapidly depleted. 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 is indispensable for the future sustainable crop production in the light of ever diminishing natural P reserves. This also paves way for a second green revolution that assures a food secure world amidst growing population in the near future.

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