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PHYSIOLOGICAL AND MOLECULAR MECHANISMS OF PHOSPHORUS UPTAKE AND UTILIZATION EFFICIENCY

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ABSTRACT

In agriculture, the excessive utilization of phosphorus (P) has increased the issues related to its sustainability due to the possible shortage of resources and its intensive use, which has raised severe environmental pollution. In soil, the minimum occurrence of phosphorus reduces the production of crops and threatens the sustainability of agriculture and food. Plants have numerous adaptive mechanisms to manage P stress by handling the alteration at different levels, such as biochemical, morphological, molecular, and physiological. A complete understanding of these adaptive mechanisms is needed to develop the efficiency of P absorption, utilization, and division with other agricultural methods that might be caused by the sustainability issues related to the transport of P for different crops. This chapter concisely covers different methods to cope with P stress and different molecular approaches, which could be utilized to improve the P uptake efficiency.

***Keywords*:** Phosphorus Use Efficiency, Nutrient Stress Adaptation, Plant Physiology, Sustainable Agriculture, Abiotic Stress Response

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1. INTRODUCTION

Phosphorus is a necessary element for agriculture because it cannot be replaced by any other element in the production of crops, nor can it be acquired from the atmosphere. It is the most important biomolecule (for instance, nucleic acid, phospholipids, and ATP) that controls the numerous biological mechanisms related to the transfer of energy reactions, protein and enzyme initiation, and regulates the cascades of cellular signal transduction (Rouached et al. 2010). Similarly, it is essential for respiration and photosynthesis. Hence, it participates in the metabolism of amino acids and carbon. In various methods for agricultural production, P is regarded as the most important limiting factor for the yield of crop, particularly in subtropics and the tropics (Ramaekers et al. 2010). Natural phosphorus sources are limited, and sedimentary residues are 80 to 90% suppliers of P production worldwide. By the report of the GPRI, globally the requirement of P will be increased hereafter for various reasons including the increasing population pressure day by day because the P reserves are controlled by some countries like Morocco, China and US and decreasing the reserves (in rock phosphates minimal amount of P_2O_5 and maximum amount of heavy metal), quality of P, huge amount is required for processing, transportation and mining of phosphate rock and rapidly enhanced raw material concentration. In 2025, the maximum demand for food grain will be approximately three hundred million tons in India. To obtain this, approximately 13.1million tons of P_2O_5 would be needed (according to the present situation), also Nitrogen and potassium, 22.4million tons, with a normal ratio like N: P_2O_5 : K_2O of 4 : 2 : 1 (Tiwari, 2001). Furthermore, 11 to 13million tons of P_2O_5 will be required for the different crops production such as potato, cotton, oilseed, sugar cane and vegetation including coconut, tea and coffee etc. With a meager 10 to 20% use efficacy of applied Phosphorus, the need for single super P and di-ammonium P may participate in huge loss of economy of INR about 7.81b (Pandey et al. 2014). The intricate role of phosphorus in regulating plant growth and development is illustrated in Fig. 1.

The bioavailability of phosphate creates a problem because of its high fixation and slow diffusion in soils causing less than 10μM amount in soil solution. Hence, all kinds of soils demand to be enriched with Phosphorus.

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From agriculture, the loss of P can occur by both non-point and point sources (Subba Rao, 2010). The point sources have polluted water of dairies, piles of manure and farms leakage. Non-point sources include specific fields where drainage, erosion of soil and surface runoff. Measures to reutilize Phosphorus from the food chain and wastewater could be another approach to conserve and environmental resources (Elser, 2012). But the plants have many adaptive mechanisms at different levels such as biochemical, molecular and physiological to manage the durable starvation of Phosphorus. Characters to improve the mining ability of phosphorus including alteration in root anatomy for instance improved root/shoot ratio, no. of lateral root, density and length of root hair (Elser, 2012; Pandey & Gahoonia, 2004). Specialized structures of root known as cluster or proteoid, in some species the roots are formed that effectively release the carboxylates (Neumann et al. 2000; Lambers et al. 2006). Increased secretion and production of enzymes and organic acids like ribonucleases in the rhizosphere and purple acid phosphatases (Singh & Pandey, 2003; Wasaki et al. 2006; Suriyagoda et al. 2012) that advantages in the phosphorus mobilization. The relationship between the roots of plant and AMF (arbuscular mycorrhizal fungi) is another source of increased attainment of phosphorus in many crops (Pandey et al. 2005). At the molecular stage, the responses of phosphorus starvation caused by the genes that induce the shortage of P but this gene encode by the enzyme which helps in the alteration of the uses of internal P and expansion of the getting of P for instance in roots the stimulation of high-affinity Pi transporter (Lin et al. 2009).

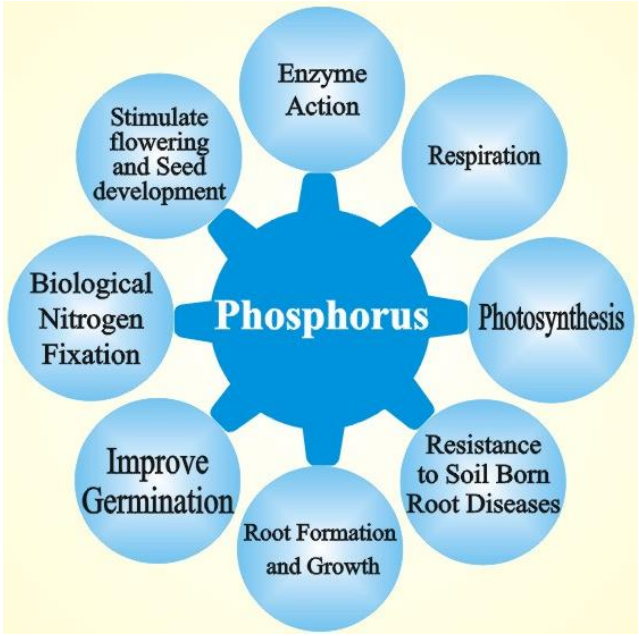

Fig. 1: Role of phosphorus in regulating plant growth and development.

In soil, the concentration of Pi is usually 0.01mM or less but it has the least mobility. Meanwhile, in sap the plants can only attain the free Pi, sometimes they suffer from the starvation of Pi. To manage the starvation of Pi, the plants have adopted several transporters that participate efficiently in the absorption of Pi from the sap to root cell, in the translocation of Pi within the organs and tissues of plant such as roots and shoots, and the subcellular phase the movement of Pi for instance in several organelles. Mostly, these transporters are the member of these subfamilies such as PHTs, SPX-EXS, SPX-MFS and SULTR-like SPDTs.

To adjust the fertilization of phosphorus and decrease harmful influences within environment, several agricultural approaches have been adopted. Therefore, it will be a sustainable method to develop phosphor-effective plants by changing their adaptation strategies without harming the environment or limiting the resources of phosphorus. Improvement of Phosphorus efficiency contains efficiency of absorption and acquirement and efficiency of utilization. The fundamental technique includes the choice of cultivars and genotypes by the better Phosphorus acquirement or efficiency of utilization. At this time, it is necessary to develop the plants with enhancing phosphorus efficacy by traditional plant breeding or GE (genetic engineering). In this chapter, we will discuss several molecular, physiological and biochemical mechanisms in plants, which can be changed to effectively absorb phosphorus in the P starvation.

2. UPTAKE OF INORGANIC PHOSPHATE

2.1. Uptake of Inorganic Phosphate in Roots

In higher plants the 1st recognized Pi transporters (PTs) have been Arabidopsis AtPT1 and AtPT2 that could balance the mutant deficiency of *Saccharomyces cerevisiae* in the Pi transporter Pho84. Usually, PHT1 is determined by multi-gene family such as 9 PHT1 genes are present in Arabidopsis including AtPHT1-1 to AtPHT1-9 (Mudge, Rae, Diatloff, & Smith, 2002; Shin, Shin, Dewbre, & Harrison, 2004), in addition, thirteen PHT1 genes in rice, 15 PHT1 genes in soybean, 13 PHT1 genes in maize and 8 in tomato (Chen et al. 2014; Fan et al. 2013; Liu et al. 2011; Liu et al. 2016; Paszkowski et al. 2002; Qin et al. 2012; Wang et al. 2020). The analysis of sequence emphasized the conserved sequence of amino acids in fungal and plants PHT1 transporters. The analyses of *in-silico* have proven that every PHT1 protein has shared structure, holding twelve reputed membrane-spanning domains that are divided into two groups having six domains by hydrophilic charged loop. Both terminals like C and N are supposed to be focused within the cell (Liu et al. 2011). In *Piriformospora indica* the high-affinity crystal

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structure of Pi-PT established the expected PHT1 topology and identified that these structures are conserved in plants and fungus (Pedersen et al. 2013).

Pi absorption depends on H^+ co-transport such as 2 to 4 H^+/Pi (Sakano, 1990). For example, the ion having a negative charge, Pi is taken in the cell with approximately -120mV membrane potential and it is closely linked with the proton-ATPase activity that generates the H^+ gradient within the membrane (Gaxiola et al. 2007).

Inorganic phosphates were obtained directly from the soil, and mycorrhizal fungi were obtained indirectly (Javot et al. 2007). Inorganic phosphates are directly absorbed by the PHT1 transporters available within rhizodermal cells, particularly in trichoblast cells and cortical cells. In Arabidopsis, almost 8 to 9 AtPHT1s namely AtPHT1;1-9 are reported in root tissues (Jost et al. 2015). A minimum of 8 OsPHT1s are present in the root of rice (Chang et al. 2019; Wang et al. 2014; Ye et al. 2015). The study of deficient mutants and reverse genetics in more than one PHT1 gene has established their significant functions in the transport of Pi. In Arabidopsis, absorption of Pi is reduced about 57% by the distraction of AtPHT1;1 and 4 than the rate of wild-type in low conditions of Pi, and approximately 70% rate of wild type in high conditions of Pi, indicating that these two transporters play significant function for the absorption of Pi from the environment (Shin et al. 2004).

In Arabidopsis, the Pi absorption is decreased by the pht1;1 mutant by about 60% compared to the rate of wild type under maximum supply of Pi (Ayadi et al. 2015), demonstrating that the AtPHT1;1 has a predominant role in the take-up of Pi through the roots of Arabidopsis in high Pi conditions. On the other hand, in deficient phosphorus plants of Arabidopsis, the AtPHT1;4 plays the major function in Pi absorption, by this about 32 to 43% of Pi absorb, however, AtPHT1;1 takes part about 13 to 18% of Pi absorption, and AtPHT1;2 and 3 collectively participate in almost 30% of Pi absorption (Ayadi et al. 2015). In rice under the condition of Pi-starvation, silencing of OsPHT1; 2/3/4/6/8 decreases the absorption of Pi (Chang et al. 2019) while silencing of OsPHT1; 1/4/8 decreases the absorption of Pi in high conditions of Pi (Chen et al. 2015; Zhang et al. 2015). In double-knockdown rice plants, the OsPHT1; 9/10 decreased the Pi concentration in shoots as well as roots in both high and low conditions of Pi (Wang et al. 2014). These findings prove that PHT1 proteins have a major function in the Pi absorption from the rhizosphere in plants' roots under various environmental conditions of Pi. Genetic determinants linked to enhanced phosphorus use efficiency across various crop species are listed in Table 1

Table 1: Genes involved for higher phosphorus use efficiency in various crops

Sr. #	Crop	Gene	References
1	Soybean	GmETO1	Zhang et al. (2020)
2		GmEXPB2	Jia et al. (2014)
3		AtPAP15	Wang et al. (2009)
4		AtPAP18	Younessi-Hamzekhanlu et al. (2018)
5		OsPT2	Chen et al. (2018)
6		GmACP1	Zhang et al. (2014)
7		ZmPHR1	Wang et al. (2013)
8		GmHAD1	Cai et al. (2018)
9	Wheat	TaPT2	Guo et al. (2014)
10		TaPHO2-A1	Ouyang et al. (2016)
11	Rice	OsNRT2.3b	Feng et al. (2017)
12		OsPAP10a	Tian et al. (2012)
13		OsPAP10c	Lu et al. (2016)
14		OsPSTOL1	Chithrameenal et al. (2018)
15	Arabidopsis	GmEXLB1	Kong et al. (2019)

2.2. Transfer of Inorganic Phosphate from Root to Shoot

The root of plant absorbed Pi through PHT1 and transferred in shoots via xylem. In xylem vessels, the accumulation of Pi is held by the band of casparian, a mechanism that is used to transfer the Pi from cell to cell. This Pi export process is most probable reconciled via PHO1. The analysis of pho1 mutant determined that AtPHO1 cannot be loaded in xylem vessel for the sprouting of shoot and the protein encoded is different from the Pi-PHT transporter (Hamburger et al. 2002). AtPHO1 is comprised of 3 major areas such as (1) a large hydrophilic area comprising domain of the SPX at the N-terminal (2) the hydrophobic area containing 4 trans membranes like spirals, and (3) hydrophobic area comprising the domain of EXS at C- terminal (Wege et al. 2016). In leaf vascular network the AtPHO1 overexpression indicates that this transporter may role as an exporter of Pi exporter. Majorly, *AtPHO1* is found in trans-Golgi and Golgi networks in normal Pi conditions and is partially converted PM in leaves with the maximum extracellular penetration of Pi (Arpat et al. 2012). This subcellular arrangement indicates that *AtPHO1* can control the Pi uptake between different organelles.

The genome of Arabidopsis contains ten AtPHO1 homologs, entitled AtPHO1;H1/2/3/4/5/6/7/8/9/10, but only AtPHO1;H1 balance starvation of pho1 mutant, indicating that AtPHO1;H1 plays a major role as an exporter of Pi

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in the xylem of root (Wang et al. 2004). Whereas, AtPHO1; H3 functions as Pi export in sprouting the shoot under the condition of Zn-starvation (Khan et al. 2014). While, the rice genome contained 3 AtPHO1 homologs, named OsPHO1; 1/2/3 but only OsPHO1; 2 functions as Pi export from roots to shoots (Secco, Baumann, & Poirier, 2010). As well as, OsPHT1; 3 plays a predominant function in the Pi transfer from root to shoot at the germination stage under Pi-deficient conditions (Chang et al. 2019).

2.3. Redistribution of Inorganic Phosphate in Plants

In plants, the Pi is mobile and distributed in different regions of plants from old tissues to young leaves and in germinating seeds. In late reproductive stage and plant vegetative growth, old leaves have a significant function in nutrients for storage organs, germinating seeds and young leaves (Veneklaas et al. 2012). In leaves phloem various genes of PHT1 are expressed such as HvPHT1;6 in barley, *AtPHT1;5* in Arabidopsis, *ZmPHT1;7* in maize, and *OsPHT1;1/2/3/8* in rice (Chang et al. 2019; Nagarajan et al. 2011; Rae et al. 2003; Wang et al. 2020). ZmPHT1; 7, OsPHT1; 1/2/3/8 and AtPHT1; 5 take part in distribution of Pi in shoot from senescing tissues to younger tissues.

In addition, family proteins of PHT1 is Arabidopsis AtPHT2; 1 that a low-affinity Pi exporter located in the envelope of chloroplast, plays a role in the relocation of Pi to maintain the optimum activity of photosynthesis, and mutant pht2; 1 indicated the compact growth and regulate the transportation of Pi from senescing leaves to young leaves under Pi-deficient conditions (Shin et al. 2004). TaPHT2; 1 in *Triticum aestivum* shows a function similar to AtPHT2; 1 (Guo et al. 2013).

Pi transporter is encoded by SPDT in rice while it is expressed in part of xylem nodes. In rice, removal of OsSPDT leads to reduce the phosphorus in grains while enhanced phosphorus in leaves which demonstrating that OsSPDT plays a major role in the distribution of phosphorus in grains (Yamaji et al. 2017). Rice OsSPDT is a homolog of AtSPDT which indicates the endeavor of Pi transportation and is located in vascular cambium of various organs and phloem and xylem parenchyma tissue. In Arabidopsis, AtSPDT knockout stops the allocation of Phosphorus in immature seeds and young leaves, indicating that AtSPDT has a function in the distribution of P in immature tissues (Ding et al. 2020). Even though in rice OsPHO1;1 does not take part in the transportation of Pi from roots to shoots (Secco et al. 2010), at the reproductive phase both OsPHO1;1 & 2 are substantially articulated in node I, and are involved in the allocation of Pi in seeds (Che et al. 2020).

2.4. Transporters of Inorganic Phosphate in Tonoplast

Plant vacuoles are the primary intracellular site for Pi accumulation. In sufficient Pi status, additional Pi is absorbed and deposited in the vacuoles; however, when Pi concentration reduces in the cytoplasm, then it is supplied from the vacuole. *AtVPT1* and *SPX-MFS* protein acts as inorganic phosphate transporters in the vacuole, which facilitates the influx of Pi from the cytosol (Liu et al. 2015; Liu et al. 2016a). Certainly, the *pht5;1* is the loss-of-function mutants that show a lower Pi ratio in the vacuole and cytoplasm than controls. Rice *OsSPX-MFS1* also serves as a transporter of Pi influx in the vacuole, which harmonizes with the PHT5 mutant (Liu et al. 2016b). Furthermore, under everyday situations of Pi, AtVPT1 is mainly expressed in new tissues, while high conditions of Pi are highly expressed in mature tissues, indicating that AtVPT1 has a function in Pi accumulation in new tissues and maximum Pi detoxification in mature tissues (Liu et al. 2015). *AtVPT3* is another *VPT* protein that takes part in the transport of Pi from cytosol to vacuole, but it is majorly significant in the absence of *AtVPT1* (Luan et al. 2019).

Recently, *OsVPE1* and *OsVPE2* (Vacuolar Pi efflux) were discovered. The loss-of-function of double mutant *OsVPE1 & 2* indicates the maximum concentration of Pi in the vacuole as compared to the control, and overexpression of one or both *OsVPE1 and 2* decreases the concentration of Pi in the vacuole, which is constant as a function of OsVPE1 &2 in efflux Pi vacuolar (Xu et al. 2019).

2.5. Control of Inorganic Phosphate Transporters

Several genes, such as PHO1 and PHT, are transcriptionally activated due to the starvation of Pi and suppressed due to the excessive supply of Pi. Several transcription factors, mainly WRKYs and PHRs are investigated as important functions in the transcription regulation of PHO1 and PHT genes (Wang et al. 2020; Zhang et al. 2021). However, *AtPHO1*, the *OsPHO1* genes from rice show *cis-NAT* (cis-natural antisense transcript), and *cis-NATOsPHO1; 2* significantly activate the expression of *OsPHO1; 2* under the starvation of Pi (Jabnoune et al. 2013; Secco et al. 2010).

In rice as well as Arabidopsis, the regions of phosphorylation and dephosphorylation of *PHT1* in the C terminal, and modification of both affect the *AtPHT1;1, OsPHT1;2 & 8*, regulating the PM and Pi transporters activity, such as *AtPHT1;1* and *ZmPHT1;7* (Wang et al. 2020; Yang et al. 2020). Also, the PM site of *OsPHT1;2, AtPHT1;1,* and *OsPHT1; OsPHF1* and *AtPHF1 control 8*, and the loss of these transporters' activity leads to the maintenance of *OsPHT1;2, AtPHT1;1,* and *OsPHT1;8* in the Endoplasmic reticulum and decrease the storage in the plasma membrane (Bayle et al. 2011).

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AtALIX controls the breakdown of *AtPHT1;1* in vacuole, and presence of *OsPHT1;1, OsPHT1;2, OsPHT1;4, OsPHT1;7, OsPHT1;8, OsPHT1;12* and *AtPHT1* can be controlled by E3 ligase ubiquitin such as *OsNLA1* and *AtNLA* and the conjugation enzyme of ubiquitin *AtPHO2* (Cardona-López et al. 2015; Yang et al. 2020). Similarly, *OsPHO2* and *AtPHO2* control the breakdown of *OsPHO1;2* or *AtPHO1* in endomembrane (Wang et al. 2020).

3. INORGANIC PHOSPHATE SIGNALING

3.1. Local Inorganic Phosphate Signaling

One of the local responses of Pi is to modify the RSA (root system architecture). Under Pi deficiency, RSA modification contains termination of development of primary root, improved the lateral root growth, and root hairs germination and development (Ma et al. 2001). RSA Modification is positively activated by the external Pi concentration that needs direct root apical interaction with the medium and it is regulated by local transportation of Pi of internal Pi concentration in the plants (Ham et al. 2018; Svistoonoff et al. 2007). The systemic responses are controlled by the condition of plant and influence the Pi absorption, P relocation and remobilization, and complete uses of phosphorus efficacy to control the metabolic maintenance of phosphorus in plants (Ham et al. 2018).

In Arabidopsis, *AtPDR2* and *AtLPR1/2* related to capture the primary growth of root in Pi starvation conditions. Locally, stress of Pi deficiency is identified at primary root apical in the Fe dependent method (Wang et al. 2018). The ferrous oxidase such as AtLPR1 oxidizes Fe^{2+} into Fe^{3+} in the apoplast that obstructs the pathway of symplastic in the niche of stem cell (Müller et al. 2015). In apical meristem, relocation of Fe^{3+} malate dependent of the primary root is important for Pi deficient induced RSA, and the secretion of malate is controlled via *AtALMT1* that is transcriptionally mediated by transcription factor *AtSTOP1* in Pi-starvation condition (Balzergue et al. 2017; Mora-Macías et al. 2017).

Current research identified that direct root illumination by blue light is essential and suitable for inhibiting the growth of primary roots of *Arabidopsis thaliana* in low Pi culture plates, and light has no obvious effect on the formation of root hairs and lateral roots induced by low Pi (Zheng et al. 2019). Therefore, in Arabidopsis, blocking the growth of primary roots by Pi deficiency in culture plates is not sustained as compared to blocking in soil, and roots of Arabidopsis should be germinated under dark conditions to achieve significant results for root growth in the soil.

3.2. Systemic Signaling

The external Pi condition is detected locally in the apical root, and Pi conditions of the complete plant is assimilated by systemic signaling and sensing. Numerous molecules (like RNAs, hormones, Pi, sugar and InsP) have been observed by systemic signals, which transfer the internal Pi status of the complete plant. Different researches by split root analyses/ Pi foliar application recommend that Pi is a systemic signaling (Balzergue et al. 2017). Pi non-metabolized analog is Phosphite (Phi) that controls the PSR (phosphate starvation response) similarly Pi acts as a signal (Jost et al. 2015; Leong et al. 2018).

Disturbance in Arabidopsis inositol *AtIPK1* decreased the InsP6 concentration in asexual parts and exaggerated Pi sensing, participating of InsP in Phosphorus signaling and sensing (Kuo et al. 2014). Molecules of InsP control the homeostasis of Pi in plants by the combination of domain of SPX having proteins (Wild et al. 2016) that are participating in Pi sensing. *OsSPX3, OsSPX 4, OsSPX 5, OsSPX6, AtSPX1* and *AtSPX2* are functional repressors of *OsPHR2* and *AtPHR1* (Zhong et al. 2018), it is the central mediators of Pi signaling and homeostasis in rice and Arabidopsis (Rubio et al. 2001). The maximum InsP concentration stimulates the *SPX* protein by interacting with *OsPHR2* or *AtPHR1*, and resulting in the reduction of InsP levels, *OsPHR2* and *AtPHR1* are secreted to control the genes expression participating in PSR (Wild et al. 2016). Similarly, the combinations of InsP and AtPHO1 domain of SPX controls the translocation of Pi and PSR in shoot (Wege et al. 2016). Currently, InsP8 was confirmed that it is an intracellular Pi signaling molecule that acts as the SPX1 ligand for modulating the homeostasis of Pi in plants (Dong et al. 2019).

The first recognized systemic stress-induced Pi singling was miR399 (MicroRNA399) in Arabidopsis. Experiments on grafting demonstrated that mature microRNA399 can transfer from shoots-to-roots via phloem under the starvation of Pi (Lin et al. 2008). MiR399 controls the outcome of mRNA *AtPHO2* that encodes the ubiquitin conjugating E2 enzyme (Aung et al. 2006). Furthermore, another vital miRNA is miR827, which is induced under Pi deficient conditions and also can transfer from shoots to roots (Hsieh et al. 2009; Huen et al. 2017). *AtNLA* is targeted by MiR827, which encodes E3 ligase ubiquitin, and AtPHT5, 1 which, encodes the Pi transporter serving in the vacuole (Lin et al. 2010).

Similarly, mRNAs translocate under the starvation of Pi almost 900 mRNAs were identified, which can transfer in grafting area of 2 Arabidopsis accessions, and about 90 mRNAs which move exclusively in Pi deficiency. More remarkably, 90 mobile mRNAs under Pi-deficiency, 37% enhanced greater than two times in low phosphorus conditions, 9% reduced greater than two-times, and more than 50% mRNAs kept constant (Thieme et al. 2015). Heterograft's experiments for *Citrullus lanatus* and *Cucumis sativus* demonstrated that stress of Pi

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prompts major and rapid modifications in the populations of mRNA in the translocation stream of phloem, and phloem mobile mRNAs of particular hundreds are distributed in particular sink tissues (Zhang et al. 2016). These findings recommended that in plants, the mobile mRNAs work as systemic signals under the deficiency of Pi. Furthermore, several hormones and sugars are shown as systemic signals (Chien et al. 2018).

4. ENHANCE THE EFFICIENCY OF PHOSPHORUS ACQUISITION

4.1. Morphological and Physiological Methods to Enhance the Efficiency of Phosphorus Acquisition

This section provides an in-depth exploration of the various morphological and physiological factors that influence phosphorus acquisition. It highlights the intricate adaptations of plant structures and functions that facilitate the effective uptake of this essential nutrient, shedding light on the complex interplay between plant morphology and the surrounding soil environment (Fig. 2).

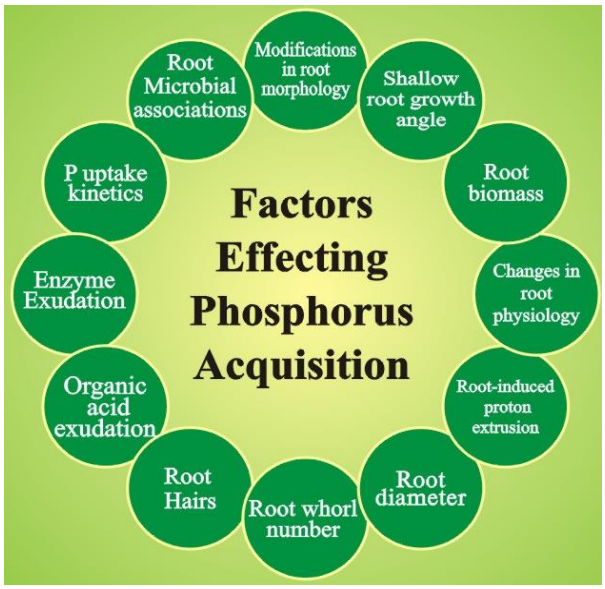

Fig. 2: Factors affecting on phosphorus acquisition.

4.1.1. **Modifications in root morphology:** Roots architecture like root volume, diameter, length, surface area, root hairs along with length of root hairs are the reasons of intraspecific and interspecific modification under the transportation of phosphorus. Maximum root contact with soil delivers maximum area for absorption, which is attained by a greater network of roots and is vital for adequate absorption of immobile nutrients like phosphorus. In black-gram, significant impact of root surface area, volume, length and lateral roots number was identified by the maximum absorption of phosphorus in 1.5 months after sowing (Jakkeral et al. 2009).

4.1.2. **Root hairs:** Root hairs' existence enhances significantly the surface area of root without participating in biomass of root. In deficient phosphorus conditions, absorption is closely linked with length of root (Løes & Gahoonia 2004), surface area of root (Pandey, 2001), length and density of root hair (Bates & Lynch 2000). In genotypes of barely longer root hairs were identified to maintain the maximum yield of grains in phosphorus deficiency (Gahoonia & Nielsen 2004). Furthermore, genotypic variations in root and root hair length in lentil (Tara et al. 2006) and chickpea (Tara et al. 2007) and surface area of root in wheat (Pandey et al. 2003) in deficient phosphorus were reported. According to Mendelian pattern, trait of root hair is inherited as noted between the cross of wild type barely and barely root hairless mutant (brb) indicating that it is regulated through single gene (Gahoonia et al. 2001). This might be useful for genetic study related to development of root hair in cereals.

4.1.3. ***Root diameter:*** The diameter of root indicates the volume of soil infiltrated by roots per unit of photosynthate participated. However, calculation of root diameter is not a common procedure; it is noted that cultivars having fine roots may uptake the phosphorus efficiently. Fine roots cover the maximum volume of soil per unit of surface area of root. While fine roots need to be exchanged regularly, more total carbon is required to produce them.

4.1.4. ***Root whorl number****:* Basal root whorl and node quantity differs among annual legumes genotypes for example bean that shows the enhanced exploration of soil by enhanced the number of whorls root. Among bean genotypes, the basal roots developed at various whorls by different numbers like 1 to 4. In the population of a recombinant inbred line (RIL) the wild type bean with three whorls in which greater than 60% biomass deposited as compared to two whorls (Lynch, 2011).

4.1.5. ***Shallow root growth angle:*** The subsoil strata have lower available Phosphorus as compared to topsoil strata due to accumulation by passage of time by the residues of plants and fertilizers. Under these conditions, traits related to root enhance the foraging of topsoil that will support getting the maximum phosphorus. Maize and beans proficient genotypes have thin roots in topsoil. Development of thinner axial root angle or seminal roots enhances the foraging of topsoil so it provides a better opportunity to acquire the phosphorus (Zhu et al. 2005). Though, this character may not be appropriate for the cultivation of crops in drought circumstances. Similarly, adventitious roots with the development of thinner root angels may enhance the requirement of phosphorus. But, excess adventitious roots development improves the need for carbohydrates that consecutively consequences in the imbalance of source to sink and reduced the requirement of phosphorus (Lynch, 2011).

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4.1.6. Root biomass: under the stress of phosphorus conditions, the biomass of roots is enhanced because it is common practice caused by the greater ratio of root/shoot. It is considered that from a general assimilation network produced on the ground; about 50% carbon is distributed underground in barley and wheat (Swinnen, 1994). Therefore, the absorption of phosphorus be determined by not only on the size of root but also on the size of shoot. Crops varieties with a wide network of root linked with an extensive system of shoot would be Phosphorus efficient, participating in the stability of yield under phosphorus deficiency.

4.2. Changes in Root Physiology

Responses of physiological and biochemical found during phosphorus stress such as extrusion of proton (Shen et al. 2006), carboxylates and phosphatases exudation (Ligaba et al. 2004; Pandey, 2006) parameters related to kinetic (Pandey et al. 2007), cluster root formation (Lambers et al. 2006) and mycorrhizal symbiosis (Pandey et al. 2005). All these biochemical and physiological modifications in roots that help in efficient phosphorus mobilization from fractions of organic Phosphorus (P_{org}) and mineral bound in soil (Hinsinger, 2001).

4.2.1. Root-induced proton extrusion: In phosphorus starvation, the roots of plants release protons that cause rhizosphere acidification (Gollany & Schumacher, 1993). In rhizosphere, an increase of 2 to 3 units of pH as compared to bulk soil aids in the suspension of sparingly soluble Phosphorus. Greater diversity in crop genotypes has been noted for proton efflux; however, the roots that stimulated the modification in pH do not always lead to increase in the absorption of phosphorus. When the pH of the rhizosphere was changed, barley and wheat indicated significant variations among genotypes in the uptake capacity of inorganic Phosphorus (Pi), which shows that, besides the extrusion of protons, other processes may be involved in the modification of the uptake of P in cereals. The alteration of pH in roots is caused by the imbalance of anion and cation in plants, which indicating that genetic regulation of balance of cation–anion would increase the plant ability to change the rhizospheric pH (Gollany & Schumacher, 1993).

4.2.2. **Organic acid exudation*:*** The exudates' main part secreted by roots of plant in phosphorus deficiency including organic acids (OA) like malate and citrate (Ligaba et al. 2004). Both mobilize such as P_{org} and P_i by transferring phosphate from sap of soil via exchange of ligand (Lambers et al. 2006). Also, exudation of OA is promoted in low levels of soil moisture because of the reduction of P_i soil mobility in drought circumstance (Liebersbach et al. 2004). In addition OA, mucilage and phenolic are also secreted in phosphorus deficiency and its effect is similar to OA (Lambers et al. 2006).

4.2.3. Enzyme exudation: In rhizophere different enzymes like phytases and phosphatases are secreted by roots of plant where they hydrolyze P_{org} pools in the soil. It is noted that in rhizosphere the acid phosphatases are plentiful in P deficiency (Taraafdar & Claassen, 2005). Except for the presence of phytate dephosphorylating microorganisms, most plants have a very limited ability to absorb phytate (Taraafdar & Claassen, 2005). Some transgenic plants that overexpress extracellular phytase are more likely to obtain phytic acid when grown on sterile laboratory media. Therefore, it has been found that these phytases reproduce rapidly when grown in the soil, which limits their capacity to link with phytate. This shows that phytase-mediated dephosphorylation of phytate only available after the mobilization of phytate in soil sap.

4.2.4. Phosphorus uptake kinetics: Related to enzyme kinetics for measuring the chemical reaction rate, the kinetics nutrient absorption can also be studied for the rate of nutrient uptake by membrane transporters. In the environment, limiting the absorption rate of nutrients can be indicated by rectangular hyperbola, like the equation of Michaelis–Menten for kinetics of enzyme. Therefore in plants, this equation has been changed for measuring the mean net phosphorus influx (I_n) in the roots of plant and can be demonstrated that $I_n = [I_{max}(C_o - C_{min})]/[K_m + C_o - C_{min}]$, here I_{max} is denoted the maximum mean influx (mol cm^{-1} s^{-1}) while C_o is represented the phosphorus concentration in surface of root (mol cm^{-3}), as well as C_{min} is denoted the concentrations at which $I_n = 0$ (mol cm^{-3}) and K_m represent the constant of Michaelis–Mentes (mol cm^{-3}) (Nielsen, 1976). Like kinetics of enzyme, $I_n = 1/2$, when $C_o = K_m + C_{min}$. It was noted that the rates of Phosphorus absorption kinetic parameters, namely I_{max}, C_{min} and K_m varied expressively among barley and wheat genotypes (Nielsen & Schjørring, 1983). To improve the efficiency of phosphorus absorption, the genotypes with low C_{min}, high I_{max} and K_m values should be preferred. The plants having lower C_{min} can efficiently uptake the phosphorus available in low concentration, which participates in the development of low-input agricultural methods.

4.2.5. Root-microbial associations: The most common terrestrial symbiosis of AMF associations occurs in 70 to 80% of terrestrial plant species (Smith et al. 2011). However, the increasing evidence that several endophytes can make a special association with some host plants but the AMF is non-host specific (Bagyaraj 2011). It is noted that in maize the demand for phosphorus enhanced in phosphorus starvation although it reduced in excess phosphorus (Kaeppler et al. 2000). Variation in genotypes in the sense of AM infection rate was noted especially in wheat and different other crops (Pandey et al. 2005). From the species of cereal, maximum productivity of AM symbiosis for the absorption of phosphorus was observed in rye and triticale many traits inherited from wheat instead of rye (Løes & Gahoonia 2004). The mycorrhizal response is inversely proportional to biomass of shoot, demonstrating that

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there are different genotypic responses to mycorrhizal associations that require further research.

4.3. Improvement of Phosphorus Acquisition Efficiency by Molecular Approaches

Research on microarray makes it possible to identify the comprehensive profile of gene expression under the deficiency of phosphorus in Arabidopsis (Chen et al. 2011) and different species of crop for example maize (Calderon-Vazquez et al. 2008), potato (Hammond et al. 2011) bean (Hernández et al. 2007) and rice (Park et al. 2012). These experiments demonstrated that modifications in various biochemical and signaling mechanisms lead to change at different levels such as metabolic, protein and gene. Today, advanced technology such as RNA-seq has been used to identify the extensive-expression of the gene in *Lupinus albus* in which 2128 differentially expressed sequences were reported in which twice or more modification under phosphorus starvation (O'Rourke et al. 2013). The gene expression resulting in phenotypic changes is under complicated regulation and is usually up-regulated by the deficiency of phosphorus leads to accumulation of transcript for maximum time (Hammond et al. 2003). The studies of transcriptome showed that the rapid modifications in different gene expression encoding phosphatases, RNases and Pi transporters and different other genes participated in reprogramming of metabolic pathways of lipid recycling, carbohydrate mobilization and nitrate assimilation (Hernández et al. 2007). Therefore, change in the expression of gene that controls the carbohydrates, photosynthesis and secondary metabolism were not changed when Phosphorus was resupplied (Hammond et al. 2011).

The study of proteomics has been utilized to detect the proteins with modified profiles in phosphorus deficiency. Profiling of protein in soybean (Chen et al. 2011), maize (Li et al. 2007), *Arabidopsis* (Lan et al. 2012) and *Brassica napus* (Yao et al. 2011) indicated that not all differentially expressed proteins were directly linked with phosphorus metabolism in phosphorus deficiency conditions. Proteins that participated in C- metabolism is mostly up-regulated although several proteins involved in the metabolism of amino acid, signaling and transcription factors are generally down-regulated under phosphorus deficiency. These experiments indicate that specific pathways are developed in specific plant species to survive under phosphorus stress conditions.

4.4. Molecular approaches for the Regulation of Root System Architecture

Modification in root growth pattern under phosphorus deficiency is a complicated character; however, a couple of genes involved in this mechanism have been detected in different species of the plant. The genes involved in hormones and developments function as a mediator in controlling the architecture system of root (Pérez-Torres et al. 2009). Root development genes for example NAC, *APETALA1*, *APETALA2 ENHANCER OF* GLABRA3, and *TRANSPARENT TESTA1* (Hardtke, 2006) were detected to be affected by deficient phosphorus. Moreover, the transcripts involved in hormones for example auxin (auxin-responsive factor and *AUX/IAA* gene families) and abscisic acid were observed under phosphorus level (Vieten et al. 2007). It was observed that the growth of meristem roots is controlled in Arabidopsis by *PDR2*, *LPR1* and LPR2 that also play an important function in phosphorus sensing through root cap in phosphorus deficiency (Ticconi et al. 2009).

In maize, 6 genes have been observed that mediate the morphology of root namely *Rtcs*, *Bk2*, *Bk2-L3*, *Rth1*, *Rth3* and *Scr* were analyzed in phosphorus stress. The expression of *Scr* that regulates the formation of endoderm and cortex was not induced by phosphorus deficiency. The effective lines showed the higher gene expression namely *Rtcs*, *Rth3* and *Bk2* as compared to Phosphorus inefficient line[68]. Analysis of the transcriptome of the primordium region of lateral roots indicated that the signal of auxin controls the alteration in root architecture in phosphorus stress conditions. This may be as a local modification in the concentration of auxin because of transport and biosynthesis, in which domain of LOB proteins has an intermediary function (Li et al. 2012). In maize, different transcription factors (TFs) like SCARECROW and SHORTROOT were observed that revealed the identity of root morphology and meristem (Lim et al. 2005). Similarly, expression patterns of these TFs are changed under phosphorus deficiency.

In rice, the most recent significant development was the analysis of functional and identification of *PSTOL1* gene (P starvation tolerance1) that mediates the growth and development of root in phosphorus stress conditions (Gamuyao et al. 2012). Therefore, molecular processes clarification and targets of *PSTOL1* downstream must be more analyzed. In rice, *PSTOL1* gene can be utilized to enhance the efficiency of phosphorus with the help of selected inter-variety breeding (Kochian, 2012)Up to now, the advancement in deciphering and controlling the genetic and molecular mechanisms of root system development enhances our knowledge about root morphogenesis under P stress conditions.

4.5. High Affinity P_i Transporters Induced by P Stress

P_i transporters are a member of Pht1 and Pht2 families that expressed in the low and high external concentrations of phosphorus respectively (Lin et al. 2009). The *Pht1* genes are participating in phosphorus absorption under high concentration gradient, such as root cells may have 10,000 times higher soluble phosphorus content than soil solution. In Arabidopsis, 9 members of *Pht1* family such as *AtPht1.1-9* have been recognized and

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all of which are responding to phosphorus nutrition (Mudge et al. 2002). Important functions of *AtPht1.1* and *AtPht1.4* are found in the plant for the absorption of P_i in both high and low P_i conditions. Every member of *Pht1* shows an expression of tissue-specific for example in the epidermis of root, stellar cells and root hair, while others were displayed in ER or Golgi apparatus. But, *AtPht1.9* and *AtPht1.8* were exhibited in roots under phosphorus deficiency. Double mutant studies such as *pht1.9/pht1.8* indicated that these transporter proteins work collectively to maintain the supply of phosphorus in plants under deficient phosphorus condition (Remy et al. 2012). Other *Pht1* family members must be recognized and functionally authorized.

In crops, the P_i transporter of high-affinity genes has been observed under phosphorus deficiency. In maize, 5 *Pht1* genes (Nagy et al. 2006) while in rice 13 putative *Pht1* genes such as OsPT1 to OsPT13 (Goff et al. 2002) were found that participating in the absorption and allocation of phosphorus. The *OsPT11* and *OsPT13* were stimulated under AM-inoculation entirely in roots (Glassop et al. 2005). While *OsPT8* (OsPht1.8) is observed in several organs as compared to the tissue under phosphorus conditions, it participated in the homeostasis of P_i (Jia et al. 2011). In shoots and roots the expression of *OsPT2* (OsPht1.2) and *OsPT6* (OsPht1.6) under phosphorus deficiency, indicated that *OsPT6* is played a role in the translocation and absorption of phosphorus in plant, while *OsPT2* is a low-affinity transporter that plays a function in stored phosphorus translocation (Ai et al. 2009). In barely, 8 *Pht1* genes have been identified out of which *HvPHT1.1* and *HvPHT1.2* were expressed in cortex, vascular tissues of root, root hairs and epidermal cells (Glassop et al. 2005). *HvPHT1.1* a high-affinity P_i transporter that plays a role in the absorption of P (Preuss et al. 2011), while *HvPHT1.6* was found in phloem tissue of leaf and expressed in roots as well as shoots (Huang et al. 2008), with significant functions in re-translocation of P_i in plants (Preuss et al. 2010).

Currently, Liu et al. (2013) categorized and functionally indicated as a high-throughput P transporter, such as *TaPht1.4* in wheat, fully expressed in roots under P starvation. It exhibited a 35.3 μM K_m with yeast complementation analysis. Another gene, *TaPHT2.1*, a member of the *Pht2* family, was upregulated by deficient phosphorus and clearly expressed in leaves. Its occurrence in the envelope of the chloroplast indicated a vital function in controlling the translocation of P_i from cytosol to the chloroplast (Guo et al. 2013). In wheat, this gene can play a role in enhancing phosphorus utilization efficiency. Furthermore, a high-affinity P_i transporter such as *GmPT5* recognized in soybean, is expressed in an interchangeable region between young nodules and roots and controls the Pi influx from roots to nodules (Karthik et al. 2014). In several crops the transport proteins have a vital role in enhancing the phosphorus absorption efficiency; however, a genotypic variant in expression configuration and adjustment of P transporters needs to be further studied.

4.6. Phosphorus Starvation Resulted in Purple Acid Phosphatases

PAPs or APases contain the largest class of plant APases. Many PAPs are non-specific APases that catalyze the P_i from phosphomonoesters in an extensive range of pH. The PAPs encoding genes are significantly induced under phosphorus deficiency and are exuded in rhizosphere to use the existing P_i in soil or transferred to other organelles to reprocess the P_i (Li et al. 2012). The genome of Arabidopsis is encoded by 29 PAP putative isozymes that are expressed transcriptionally under several environmental and developmental factors (Tran et al. 2010). First isolated, characterized and purified PAP was *AtPAP17* from Arabidopsis. It has about 34kD low molecular mass monomeric protein, transcriptionally prompted in leaves and roots in phosphorus deficiency. In its promoter region, there is a consensus PHR1-binding site and is found in plasma membrane and cell wall. It does not only affect the mobilization of phosphorus but also participated in ROS metabolism in the response to oxidative, senescence and salinity stresses. Other APase such as *AtPAP26* has an important role in phosphatase activity and is located in vacuole. *AtPAP26* recycles Pi within the cell and also Pi remobilizes from the organic pool under phosphorus deficiency (Robinson et al. 2012).

From Arabidopsis, other PAP genes such as *AtPAP10*, 12, and *15* are also up-regulated under phosphorus deficiency. *AtPAP10* is mainly related to the surface of root and stimulated by the deficiency of P_i, while *AtPAP12* is exuded to use the organic phosphate (Haran et al. 2000). However, *AtPAP15* has dual properties such as phytase and APase activity. In the germination of seeds and pollen, *AtPAP15* acts predominantly in the mobilization of Pi from the supplies of phytate. In genetically modified soybean, *AtPAP15* overexpression enhanced the phosphorus uptake and improved the growth in culture media having phytate. Functional study of *AtPAP23* genes displayed its major expression in flowers (Wang et al. 2009). Many PAPs have been detected and categorized according to species of crop like *LaSAP2* in white lupin, in tomato *LePS2*, in soybean *GmPAP*, in mung bean *VrPAP1*, in mustard APase, in kidney beans *PvPS2.1* and in tobacco *NtPAP12* (Liang et al. 2012; Wongkaew et al. 2013). In GM tobacco, the expression of *NtPAP12* changed the composition of cell wall and enhanced the synthase activity of β-glucan representing its role to control the protein phosphatase biosynthesis of cell wall (Kaida et al. 2009). PAPs play an important function in Pi scavenging and recycling, so these are the evident selection for transgenic crops under high phosphorus. Application of external phosphatic fertilizers affects the Pi and P_{org} content of agricultural soils, so changing the available concentration

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of P_{org} for the hydrolysis of PAP (Richardson et al. 2009). Hence, by overexpressing the secretion of PAPs in crops, the absorption efficiency of phosphorus can be significantly improved.

4.7. Efflux Transporters Involved in Organic Acid Exudation

Major strategies are the secretion of organic acids for the plants by the cause of the acidification of rhizosphere. Two independent mechanisms lead to the organic anions efflux in rhizosphere, namely *active efflux of proton* that takes part in H^+-ATPase of plasma membrane, while *passive efflux* via channel such as transporters (Diatloff et al. 2004). The main strategy for efficient uptake of phosphorus is the efflux of organic anion via channels induced in phosphorus deficiency. Therefore, the efflux organic anion transporters are significantly promoted in the response of aluminum (Al) toxicity as compared to phosphorus deficiency in various crops. Yang et al. (2013) review about exudations of organic anions has been published. Studies on the interactions of P and Al roots showed that the starvation of phosphorus induces the malate and oxalate exudation, whereas Al stimulates roots to exude citrate in *Glycine max*. In *Lolium pilosus*, *efflux of proton* and citrate happened mainly under phosphorus starvation, but not the toxicity of Al (Ligaba et al. 2004). The starvation of phosphorus induced of citrate exudation from the mature root clusters of *Lupinus albus*, while Al activated exudation of citrate was confined in the 5-10 mm sub-apical region of lateral cluster roots (Wang et al. 2007). Al^{3+} activated anion channels (ALAACs) permeable to citrate and malate were mainly expressed in maize and wheat root tips (Mi et al. 2008). In wheat, the 1st detected gene was *TaALMT1* which provides tolerance against the toxicity of Al, which was overexpressed in extremely Al-sensitive tobacco (Mi et al. 2008) and seedlings of GM barley (Delhaize et al. 2004).

Overexpression of *HvAACT1* in barley gene responsible for Al-induced citrate exudation in tobacco, increased the secretion of citrate and tolerance of Al (Furukawa et al. 2007). This is valid proof for the function of organic acid root exudation in the tolerance of plants against Al. In addition, various transgenics have been produced in many crops by detecting *TaALMT1* homologs and overexpressing them (Yang et al. 2013). The Arabidopsis plants overexpressing *GmALMT1*, malate transporter, located in plasma membrane of root showed the efflux of malate under phosphorus deficiency in an extracellular Al-independent manner and pH-dependent (Liang et al. 2013). While the stresses related to P and Al co-occur in acid soils, many genes provide the tolerance against Al toxicity and phosphorus deficiency.

5. STRATEGIES TO DEVELOP PHOSPHORUS EFFICIENT CROP PLANTS

Ultimately, 3 methods (such as genetic engineering, marker-assisted and conventional breeding) are used to produce crops that can efficiently uptake the phosphorus from the soil. In soybean, the conventional approaches like recurrent selection and backcross breeding have developed the superior traits of root and other significant agricultural traits that helped them to perform better in acidic soils under phosphorus deficiency (Cheng et al. 2011). Recently, molecular marker-assisted breeding has become popular after identifying various QTLs for several traits under phosphorus stress conditions. QTLs have been found in various crops like maize (Lynch, 2011), rice (Wissuwa et al. 2005), soybean (Zhang et al. 2009), *Brassica oleracea* (Hammond et al. 2009) and common bean (Beebe et al. 2006) that develop the resistance against phosphorus stress. Many traits were developed on root characters that were utilized for QTLs mapping related to phosphorus efficiency. Although except for the *Pup1* locus in rice, no other QTLs have been recognized (Gamuyao et al. 2012). However, the method for combining the analysis of transcriptome and fine mapping can promote the early detection of the genes for producing the phosphorus stress-resistant genotypes. SUB-1 introgressed *HYVs* of rice showed better results with suboptimal phosphorus fertilization in submergence conditions of stress (Elanchezhian et al. 2015). These warrants observed in other tolerant genes of abiotic stress associated with phosphorus deficiency induced genes for better performance in problematic soils.

Efforts to develop genetically modified plants with low phosphorus tolerance through genetic engineering. The genes contain TFs, protein kinases, PAPs and high-affinity P_i transporters and those that take part in the production of organic acids were selected. The 1st GM soybean was developed by the *AtPAP15* overexpression that leads to a significant enhancement in yield and phosphorus efficiency (Wang et al. 2009). Two TFs such as PTF1 and PHR1 overexpressed in rice (OsPHR2) and maize (ZmPTF1, OsPTF1) that lead to increase in the production of root, improve the phosphorus utilization efficiency and production of biomass (Zhou et al. 2008).

6. CONCLUSION

However, in cultivated soil, a large amount of fixed phosphorus is still not available for plants without specific root characters, while the global phosphorus resources are rapidly depleting. In this context, developments of phosphorus efficient crops that may survive in phosphorus deficiency and with minimum depends on chemical phosphorus fertilizers are essential for the future sustainable production of crops because of depleting the phosphorus natural resources. Also, it covers the second green revolution, which ensures the security of food globally as the populations grow in the future.

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