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Hormonal and Molecular Mechanism of Phosphorous Use Efficiency in Crop Improvement

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ABSTRACT: Phosphorus (P) is an essential macronutrient for all living organisms. In plants, P plays basic biological functions as a structural element in nucleic acids and phospholipids, in energy metabolism and in the regulation of enzymes. P deficiency in soils is a major limiting factor for crop growth and deficiencyis widely spread inthe countries like, Bangladesh, India, Indonesia, Nepal, Pakistan, South China, and Vietnam. The increasing demand for agricultural production poses a global challenge to improve the phosphorous use efficiency (PUE) in plants due to its low availability in a large proportion of arable lands. Phosphorus efficiency has been defined as the processes by which plants acquire, translocate, accumulate, and utilize this nutrient to better produce dry matter and/or grain under conditions of high and low supply. Food production requires application of fertilizers containing phosphorus, nitrogen and potassium on agricultural fields in order to sustain crop yields. However modern agriculture is dependent on phosphorus derived from phosphate rock, which is a non-renewable resource and current global reserves may be depleted in 50–100 years. While phosphorus demand is projected to increase, the expected global peak in phosphorus production is predicted to occur around 2030. Hence the present review is aim to understand the mechanism of PUE in relation with response of hormonal signal and molecular level. Application of this knowledge, in terms of developing crop plants having enhanced attributes for P use efficiency, along with agricultural sustainability in the face of diminishing global P supplies.

Keywords: PUE, Hormones, Crop improvement, signaling mechanism, molecular mechanism.

INTRODUCTION

Phosphorous (P) is the most problematic macronutrient in fertilizer management of rice farming because of its high fixation in the form of chelating agents. Application of chemical fertilizer is becoming very expensive intern cause highly environmental pollution. Therefore, in the current situation management of P fertilizer in the rice farming is a becoming crucial. The progress in the plant breeding is achieved by development of superior and high yielding varieties possibly by accumulation of beneficial alleles from vast plant genetic resource from worldwide. Even though significant portion of beneficial alleles were not used oversized during the process of evolution and domestication, the untapped genetic variation could be explored for genetic gain to develop agronomical superior cultivars. The increasing demand for agricultural production poses a global challenge to improve the PUE in plants due to its low availability in a large proportion of arable lands. Plants uptake P from the soil in the orthophosphate forms (Pi), which are available at low concentration in the soil solution. In a large fraction of soils, P is tightly fixed to the clay's surface, which requires high amounts of phosphate fertilizers for high-yielding farming systems, increasing production costs and hampering soil fertility management. However, low-input farmers have limited access to phosphate fertilizer, which is the second most used fertilizer for plant growth. Today, phosphorus is mostly obtained from mined rock phosphate and is often combined in mineral fertilizers with sulphuric acid, nitrogen, and potassium. Existing rock phosphate reserves could be exhausted in the next 50–100 years (Steen, 1998; Smil, 2000b; Gunther, 2005).

Historically, crop production relied on natural levels of soil phosphorus and the addition of locally available organic matter like manure and human excreta. To keep up with increased food demand due to rapid population growth in the 20th century, guano and later rock phosphate were applied extensively to food crops (Brinck, 2009; Smil, 2000b). We are entering a new and unprecedented era of global environmental change. As we are learning from climate change and global water scarcity, a long-term time frame is required to address phosphate scarcity. Decision-makers need to consider the next 50– 100 years, rather than just the next 5–10 years. IDGEC (2006) suggest that some global environmental problems occur due to the 'lack of fit between ecosystems and institutions' (IHDP, 2002). In the case of phosphorus, existing international institutional arrangements are inconsistent with the natural phosphorus cycle. This is most evident in the divide between the agricultural sector, where phosphorus is perceived as a fertilizer commodity, and the water and sanitation sector, where phosphorus is perceived as a pollutant in wastewater. This may hinder opportunities to find integrated solutions to the scarcity problem

CONCEPT OF PHOSPHOROUS USE EFFICIENCY (PUE) ?

Progress in the genetic improvement of PUE is generally hampered because of there is no generally agreed way of defining this PUE. Here different authors or researchers or scientist they have used the different criteria's (Table 1) like, increase in yield per unit of P applied, increase in grain yield per unit of nutrient supplied, increase in shoot biomass per unit of P uptake and increased P uptake in tops per unit of root dry weight as a calculation of agronomic PUE, P use efficiency 1, P use efficiency 2 and root efficiency ratio respectively. Ozturk *et al.* (2005) they have reported varietal difference in the P efficiency ratio, similarly Jones *et al.* (1989); Manske *et al.* (2002) these researchers used the criteria of increase in the grain yield per unit P uptake as a calculation of P utilization efficiency, Liao *et al.* (2008) used the criteria of total P accumulated per unit of root weight and root length as a P uptake efficiency. Phosphorous uptake efficiency (PAE) is the ability of plants to uptake Pi from the rhizosphere. Phosphorous use efficiency (PUE) is referred as the efficiency of allocation/ mobilization of P within the plant for sustaining biomass production. (Internal PUE).

Table 1: Common terms used to assess PUE.

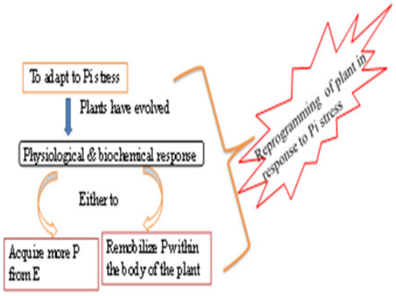
Sr. No.	Term	Description	Reference
1.	Agronomic PUE	Yield increase per unit P applied	(Hammond *et al.,* 2009)
2.	P use efficiency (I)	Grain yield/ nutrient supplied	(Manske *et al*., 2001)
3.	P use efficiency (II)	Shoot biomass/unit P uptake	(Wissuwa *et al*., 1998)
4.	P uptake efficiency (I)	Total above ground nutrient per unit P applied	(Osborne and Rengel 2002a)
5.	P uptake efficiency (II)	Total P accumulated per unit root weight or length	(Liao *et al*., 2008)
6.	P acquisition efficiency	Total P in the plant per unit P applied	(Osborne and Rengel 2002a)
7.	P utilization efficiency	Grain yield per unit P uptake	(Manske *et al*., 2002)
8.	Shoot P utilization efficiency (I)	Shoot biomass /unit P uptake	(Su *et al*., 2006)
9.	Shoot P utilization efficiency (II)	Shoot biomass per unit P uptake (shoots and roots minus seed P reserve)	(Osborne and Rengel 2002a)
10.	Biomass utilization efficiency	Biomass yield per unit P uptake	(Su *et al*., 2009)
11.	P harvest index	Grain P concentration/ total P uptake	(Batten 1992)
12.	P efficiency ratio (I)	Grain yield /unit P uptake	(Jones *et al*.,1989)
13.	P efficiency ratio (II)	Shoot growth at low P relative to shoot growth at high P	(Ozturk *et al*., 2005)
14.	Relative grain yield	Grain yield at low P relative to grain yield at high P	(Graham 1984)
15.	Root efficiency ratio	P uptake in tops unit root dry weight	(Jones *et al*., 1992)

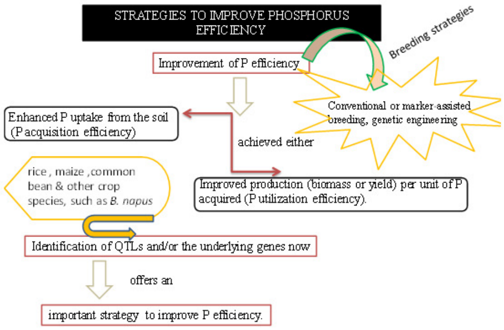
NEED TO IMPROVE (PUE) IN FARMING SYSTEMS

- ✓ Many soils have intrinsically low available P
- ✓ Natural reserves of P are being depleted & price (2007-08) increases are likely in the future
- ✓ The effects of P pollution on water quality are attracting legislative regulation.
- ✓ The concept of 'peak P' has gained some attention in the media, due to limited P reserves

MOLECULAR MECHANISM AND BREEDING STRATERGIESFOR PUE

To adapt to P stress plants have evolved with physiological and biochemical response (plants have reprograming its mechanism) either by acquiring more phosphorous from surrounding environment or by remobilize phosphorous within the body of the plant.

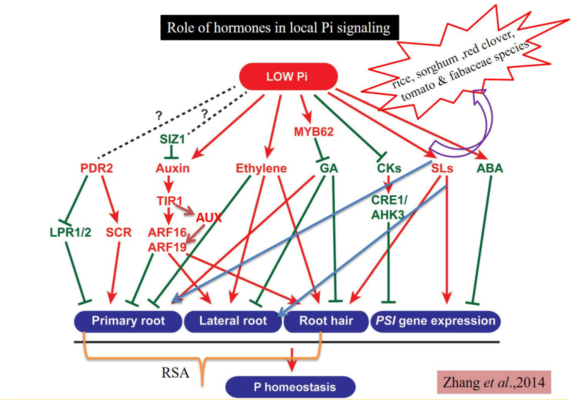




Molecular and genetic analyses have revealed the primary mechanisms of phosphorus uptake and utilization and their relationships to P-transporters, regulators, root architecture, metabolic adaptations, QTLs, hormonal signaling and micro-RNA. Improvement of P efficiency can be achieved either by enhanced P uptake from the soil (P acquisition efficiency) and/or by improved production (biomass or yield) per unit of P acquired (P utilization efficiency). Substantial genetic variation in relation to plant P efficiency has been well documented, and numerous QTLs encoding traits for crop P efficiency have been identified in rice, maize, common bean, soybean and other crop species, such as *Brassica napus.* Identification of QTLs and/or the underlying genes now offers an important strategy to improve P efficiency. This could be achieved by conventional or marker assisted breeding, genetic engineering with direct gene transformation, or a combination of these strategies (Zhang *et al*., 2014). Substantial genetic variation in relation to plant P efficiency has been well documented, and numerous QTLs encoding traits for crop P efficiency have been identified in rice (Ni *et al.,* 1998; Wissuwa *et al.,* 1998; Wissuwa and Ae 2001), maize (Chen *et al*., 2008, 2009a; Kaeppler *et al.,* 2000), common bean (Liao *et al.,* 2004; Yan *et al.,* 2004; Beebe *et al.,* 2006), soybean (Liang *et al.,* 2010a, 2010b), and other crop species, such as *Brassica napus* (Yang *et al.,* 2010, 2011; Ding *et al.,* 2012). Identification of QTLs and/or the underlying genes now offers an important strategy to improve P efficiency. This could be achieved by conventional or marker-assisted breeding, genetic engineering with direct gene transformation, or a combination of these strategies. However, it is unfortunate that very few examples of successful improvement for P efficiency in crops have been reported using any of the above-mentioned approaches. The progress that has been achieved relates to improvements in P uptake efficiency, rather than P use efficiency.

Conventional breeding approaches that target P efficiency have made some progress. One example is soybean breeding in South China, where several P-efficient soybean varieties having better root architectural traits have been nationally certified and commercially released. Compared to conventional breeding, the achievements from marker-assisted breeding for P efficiency have been generally limited. This situation is probably due to significant environmental effects on P efficiency traits, which results in most P-related QTLs making very small contributions to overall P efficiency. As yet, the only P-related QTL available to marker-assisted breeding is Pup1 (Phosphorus uptake 1) in rice. Pup1 was introgressed into several rice varieties through a marker-assisted backcrossing approach (Chin *et al.,* 2011), and these lines exhibited a dramatic increase in rice P uptake efficiency, especially on P-deficient soils. Furthermore, over expression of PSTOL1, the rice gene responsible for the Pup1 QTL, also enhanced grain yield on P-deficient soils (Gamuyao *et al*., 2012), clearly confirming the significant potential for employing Pup1 or PSTOL1in rice breeding for P use efficiency.

ROLE OF HORMONES FOR P SIGNALING



Hormone-mediated Pi signalling pathways controlling RSA and PSI gene expression in response to Pi-stress conditions

P deficiency can change hormone production, sensitivity and transport to regulate expression of PSR genes and RSA. Here the problems is that hormones can act as both locally and systemically, the hormones like Auxins, ethylene, cytokines, gibberellic acid and Abscisic acid have all been implicated in the regulation of RSA and PSR genes.

Auxins (A): this hormone has been shown to play an important role in changing RSA in plants grown under

P deficiency conditions, this hormone also play an important role in the p starvation induced changes of root development. From the study of this hormone in relation to P starvation here it is concluded that low P availability modifies local auxins concentrations within the root systems through change in auxin transport rather than auxin synthesis.

P-deficiency induces the expression of TIR_1 (Transport inhibitor response1), the auxin receptor which stimulates degradation of auxin response repressor proteins (AUX), induction of this degradation process could then allow the auxin response factor 19 (ARF19) and ARF2 to activate or repress a set of auxin response genes thereby promoting lateral root growth.

Ethylene: Ethylene has also been shown to regulate P deficiency induced RSA remodeling, under P deficiency conditions the enhancement of both ethylene synthesis and responsive in roots has been observed. This hormone play role in enhancement of lateral root and root hair density, rather than the primary roots under low P conditions.

Gibberellic acid (GA): GA modulates the P starvation induced changes in RSA and anthocyanin accumulation *via.*, a GA- DELLA signaling pathway, more recent study reported that P starvation induced transcription factor (MYB62) regulates P homeostasis and GA biosynthesis in Arabidopsis, here MYB62 expression was detected in leaves and flowers but P starvation only induced its expression in leaves, suggesting MYB62 mainly functions in shoots not roots.

Cytokines (CKs): CKs are well documented as negative regulators of PSR genes here, endogenous CK levels decrease under P deficiency conditions, exogenous CK application represses the induction of many phosphate starvations induced (PSI) genes. Similarly, a microarray analysis conducted on rice indicated that CK treatment repress the induction of many PSI genes. Mutation in CRE1 (cytokinin response 1) or AHK3 (Arabidopsis histidine kinase 3) both encoding CK regulators they restore the PSI gene induction under P starvation conditions. The negative regulation of CKs under P deficiency has been observed in crops like, rice, sorghum, red clover, tomatoes and fabaceae species.

Strigalactones (SL): A new class of plant hormones, SLs are shown to involved in control of shoot branching and root development, numerous studies have confirmed that the biosynthesis of SL is greatly increased in P stressed roots of number of plants including (rice, sorghum, red clover *etc*..). This hormone inhibits primary root growth and adventitious root formation and promotes root hair elongation. Overall the auxin, ethylene, SL levels are induced under low P conditions and act as a positive regulators of P starvation signaling pathways. Similarly, GA and CK levels are decreased by low P availability and act as negative regulators of P starvation signaling pathways.

CONCLUSIONS

P as an essential plant macronutrient, the low availability of phosphorus (P) in most soils imposes serious limitation on crop production. Plants have evolved complex responsive and adaptive mechanisms for acquisition, remobilization and recycling of phosphate (Pi) to maintain P homeostasis. Spatio-temporal molecular, physiological, and biochemical Pi deficiency responses developed by plants are the consequence of local and systemic sensing and signaling pathways. Pi deficiency is sensed locally by the root system where hormones serve as important signaling components in terms of developmental reprogramming, leading to changes in root system architecture.

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