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Chapter

Understanding the Adaptive Mechanisms of Plant in Low Phosphorous Soil

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Abstract

With the rapidly increasing world population and escalating food demand in the face of changing weather patterns, it is imperative to improve our understanding of how root functional traits enhance water acquisition and nutrient foraging for improved crop yields. Phosphorous (P) is poorly bioavailable element and essential for plant growth and development. Natural P reserves are very limited, and its availability is greatly influenced by several environmental factors, e.g., due to finite natural resources, soil pH, organic matter, and soluble complexes with cations (Al, Fe, and Ca); therefore, P limitation is a major factor that adversely affects crop production. To ensure an efficient and stable agricultural system, the establishment of P efficient crop production is inevitable. Plants have evolved different adaptability mechanisms to overcome these nutrient stresses. Low P adapted responses in plants are considered as an important trait for developing new lines with improved P acquisition, water uptake efficiency, and eventually protect roots from physical impedance. Previous studies showed that, modification in root architecture is potentially correlated with water, nutrient and phosphorus uptake. During P deficit condition, plant root undergoes several phenotypic (root hair density, cluster root, and lateral root) and biochemical modifications (citrate, malate, and acid phosphates secretion) leading to the solubilization and acquisition of unavailable P complexes in soil. This chapter reveals the biochemical, physiological, and molecular mechanisms of plant adaptive responses to low P availability. Moreover, this chapter proposes how plant competes with various abiotic stresses such as P deficiency, drought, and salinity. Screening of plants with superior root hair traits would be an important approach toward the development of P efficient crop varieties.

Keywords: phosphorous deficiency, plant adaptability mechanisms, P uptake, modification in root traits, sustainable crop production

1. Introduction

Phosphorous (P) is an indispensable limiting factor for plant growth and development [1]. Agricultural land comprised on low P availability is about 67% to sustain a better crop production [2]. P is mostly absorbed by diffusion through root absorption by creating gradients force. Very little (0.05 g^{-1}) of phosphate concentration is soil moved to the roots through capillary water movement. The value of P extracted is low by P concentration at the root-soil surface, and wheat roots have to grow to come into contact with new soil from which can extract phosphate. Thus, the length of root is a major factors of absorbing surface area [3]. Organic P is not directly amenable for plant to capture to make it easily accessible for plant uptake, conversion of organic P into inorganic Pi ($H_2PO_4^-$, PO_4^{3-}, and HPO_4^{2-}) is a prerequisite [4]. Plants have adapted a range of strategies to improve Pi availability such as microbial symbiotic association [5], modification in root system architecture (RSA) [6], cluster root (CR) formation [7], organic acid exudation [8], H^+ secretion, and genetic modification [9, 10] (**Figure 1**). For instance, white lupin (*Lupinus albus*) has developed extreme tolerance to low Pi condition through forming specialized dense root structures known as cluster root [10]. Cluster root secretes large number of organic acids, protons, and acid phosphatases into the soil, that increases Pi availability [19, 20].

Another important strategy for improving Pi availability and uptake under P limited region is the exudation of organic compounds and acid phosphatase by plant roots into the rhizospheric zone. Cluster roots of white lupin are known as exudate organic acid such as citrate, malate, malonate, carboxylate, and acid phosphatase into the soil [7, 21, 22]. Several other distantly related plant families have the ability to form cluster root, and is commonly found in proteaceae family [23]. It is not mandatory that, every genus of plant family produce CR root, like some member of other families can form CR (Restionaceae, Moraceae, Myricaceae, Elaeagnaceae, Fabaceae, Casuarinaceae, Cyperaceae, Cucurbitaceae, and Betulaceae) [24].

Previous studies have shown that the exudation of PAP (purple acid phosphatase) may facilitate the use of organic P for plants [25, 26]. Membrane localized high affinity transporters (PHT1) also exhibit great contribution in improving P uptake, and have been recognized in soybean, rice, and wheat roots [27–30]. Arbuscular mycorrhizal fungi (AMF) symbiotic association plays vital role in improving plant

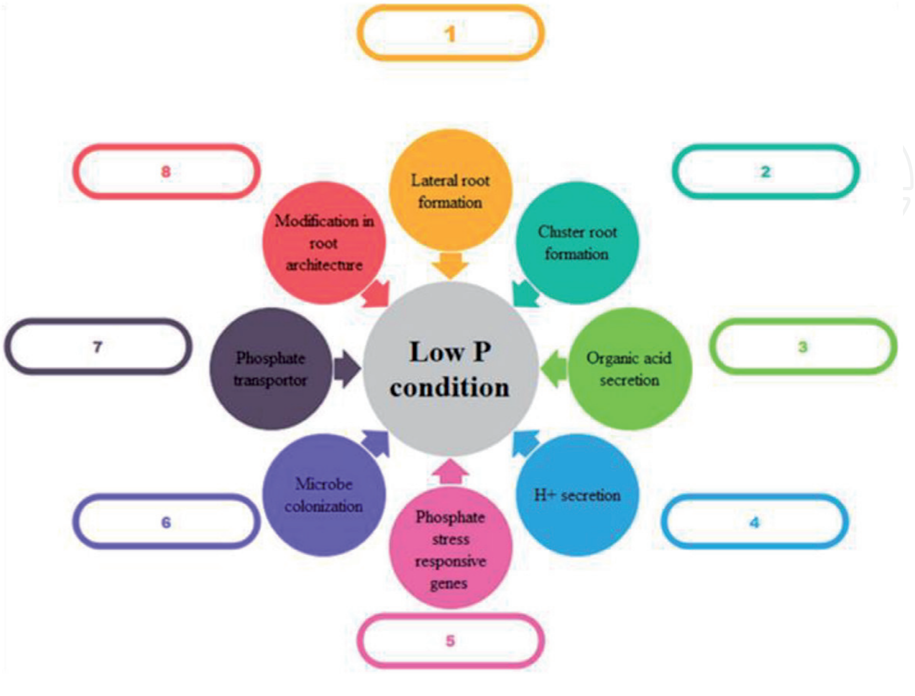

Figure 1.
Under P stress condition plant evolved multiple adaptive responses to improve Pi uptake, recycling and transportation [11–18].

ability to acquire inorganic P from rhizosphere [5]. Additionally, AMF symbiotic process activates expression of PSI genes (Pi starvation inducible), involving phosphate transporters, ATPases, and acid phosphatases, [28, 31, 32], which increases the ability of Pi acquisition in plants. Further, studies on identifying the whole genetic mechanisms underlying P adaptability mechanisms would provide a better understanding in producing modern P efficient agricultural crops, that will not only reduce fertilizer cost but also improves plant production.

2. Phosphorous concentration in soil

Most of the soils have a large reservoirs of total phosphorus, while available P is at low level [33], and it is further reported that soil total P is about 100 times higher than available P to crops plants. Phosphorous is a key determinant factor in regulating plant cell metabolism, and is a major constituent of nucleic acid, phospholipid, ATP and NADPH. It is not amenable for plant to uptake like other growth nutrient due to its high reactivity [34]. Freely available Pi can form complexes with Al and Fe under acidic and with Mg and Ca under alkaline/neutral soil, rendering the Pi inaccessible for plant to uptake [35]. Furthermore, phytic acid bounds with 60–80% of agricultural Pi and restricts its availability, that requires mineralization of Pi before assimilated by plant root [36]. This problem of Pi starvation can be solved by applying phosphate fertilizer [37]. But due to the limited availability of phosphate resources it is not a permanent solution to rely on it for future agricultural production, however, it becomes a major threating bulletin towards future agriculture system [38]. However, a deep understanding of plant adaptability and respond mechanism to low P condition would help in establishing modern strategy for efficient utilization of Pi by plants.

The whole agriculture system relies on the use of fertilizer to increase yield, and maintaining plant growth. Some ecological and economical drawbacks have provoked the interest to explore alternative approaches to fulfill the demand of global food supply [10, 39–41]. To determine the mechanism that facilitates plant growth on poor nutrient soil, scientists are learning from those plants that are extremely tolerance to nutrient deficiency condition, such as cluster root forming plant species.

2.1 Uptake vs. utilization efficiency of phosphorus

Phosphorus utilization (grain yield per unit P in the plant) is dependent on the plants P requirement. The P utilization efficiency can improve due to the increase in harvest index, P harvest index, and low P concentration in grain. Moreover, the strategy for reducing P content in grain has some limits. Therefore, in a P deficits soils, excessively low values of P concentration in grain affects seed vigor [42, 43]. To improve P utilization efficiency that selection of wheat genotypes is important, which removes small amount of P from soil due to their low P concentration in grains contributes in soil sustainability [44].

2.2 P-solubilizing microbes improves plant growth

The availability of soluble P uptake by plant is due to PS microbes, and the release of important nutrients can also improve growth and development of plants [45]. Therefore, due to symbiotic and asymbiotic the change in the concentration of phytohormones, e.g., indole acetic acid also gave the positive results about the increase in growth and development of plants [46, 47]. This mechanism is active at different growth stages; however, PS microbes have the ability for synthesizing plant growth promoting nutrients at different climatic conditions [48].

3. Plant low P adaptability mechanisms

Naturally, plants have evolved several different mechanisms to cope with nutrient limiting (Pi stress) conditions, either by acquiring more phosphate from soil or by maintain Pi homeostasis within plant body. These adaptive mechanisms could be appearing as biochemical, physiological, or molecular responses to low P conditions.

3.1 Biochemical

In a Pi stress condition, the plant roots undergo a range of phosphate stress responses, involving modification in root system architecture (RSA), increasing/inducing expression of Pi transporters, secretion of large amount of organic acid and acid phosphatases. Root exudates are below ground substances released by the plant root which plays multiple role in plant defense and nutrient uptake such as attractants, stimulator, signaling molecules, and also as an inhibitor against toxic pathogen. Root exudates are continuing source of fixed carbon to carry out plant's photosynthetic activity. Major differences in the root exudation type, exudation levels, and root architecture system distinctly varies from plant species to species. It is speculated that, nutrient influx and efflux by plant root is heterogeneous among time and space [49]. Mucilage exuded by the roots, with its high water holding capacity [50], may increase water holding capacity of the rhizosphere (area around plant root).

Mucilage has positive effects on root water and nutrient uptake, it has the potential to increase the capability of young root segments to capture water from soils, particularly under drought condition. Such characteristics potentially help plants to use soil resources and survive drought spells [51]. However, the role of root exudates and the rhizosphere on nutrient uptake and drought tolerance has not yet been demonstrated and remains largely hypothetical. Plant roots exude several compounds such as phenolic, amino acids, sugars, and organic acids [52]. Major organic acids e.g. citrate, malate, and oxalate are implicating in regulating nutrient acquisition, and stimulating toxic metal detoxification mechanisms [53–55].

There is an evidence, indicating direct role of organic acid in mobilizing phosphorous for plant uptake and detoxification of Al^{3+}, Fe, and Mn^{2+} [56, 57]. It is noteworthy to mention that, from total P fraction exist in soil only Pi (inorganic P) and is directly available to capture by plant root [58]. A number of plant species respond to low P condition by secreting large amount of organic acids such as *Lupinus albus, Glycine max, Zea mays, Triticum aestivum, Cajanus cajan, Phaseolus vulgaris; Cassia tora, Hordeum vulgare* and *Solanum tuberosum* [55, 59–65]. For example, *Lupinus albus* cluster root forming plant were shown to secrete citric acid, and proposed that citrate greatly improved Pi acquisition by forming ferric-hydroxy-phosphate compound diffused to the root and release Pi in to the rhizosphere [59]. Similarly, *Cajanus cajan* exudates malonic and piscidic acid that solubilized fixed P to directly available Pi form [63, 66].

3.2 Physiological

Plants survive in heterogeneous environment, are exposed to various abiotic factors such as; high temperature, salinity, drought, and nutrient deficiency etc. Phosphorous deficient soil is one of the major abiotic factors compromising plant growth status, particularly by reducing crop yield. Drought is a major stress on plants that partially limit nutrient availability, acquisition and remobilization [67]. Under low P availability plants adapted various physiological responses such as anthocyanin accumulation [68, 69], inhibition of primary root elongation, massive production of lateral and cluster root development [68]. Root tip serves as entry point for P sensing, modification in root system potentially contribute to nutrient uptake for maintaining plant survival under P starvation [70–72]. It is suggested that well developed root architecture is an important adaptive strategy for plants to acquire more Pi from soil. It has been revealed that, *Phaseolus vulgaris* genotype having highly branched root architecture showed efficient P acquisition ability [73].

Root hairs are also quite important for the uptake of poorly mobile growth factor such as P by improving soil exploration. It was reported that, under P deficient condition root hairs regulates almost 63% of the total P uptake [17]. Therefore, different plant species or genotypes with different root hairs/length may exhibit different P uptake efficiency [74]. Cluster root excretes large number of citrate, malonate, and phosphatases, that help in solubilization of fixed P to available form that is easily accessible for plant to capture [75]. Many studies elaborated that root hairs exhibit primary role in P acquisition under low P soil [17, 68]. It is concluded that root hairs showed strong correlation in phosphorus acquisition [76].

3.3 Molecular

Generally, plants employ a range of molecular mechanisms to confer resistance against multiple abiotic and biotic stresses that influence nutrient availability, uptake, and recycling. The ability of plant to sense and transduce signals is regulated by multiple genes or transcription factor. A growing body of evidence from mammals and yeast proposes that role of chromatic structure governs by metabolic signals [77], while the identification of molecular players involved in crosstalk of signal transduction pathways remains largely unknown [78]. Understanding the molecular mechanism behind belowground root traits would help to identify genetic markers to improve abiotic/biotic stress tolerance and environmental variability. Plants exposed to P starvation conditions evolved different adapted responses controlled by phosphorous starvation and root development related genes. For example, AtPHR1 and OsPTF1 genes are considered to be central regulator for P starvation responses [79, 80], upregulation of these genes may improve P availability, which is important for plant root growth, and development. This is indirect evidence that, root hairs and length are major key determinant and positively correlates with nutrient uptake.

A clear understanding of molecular mechanism of root system architecture (RSA) is necessary to improve nutrient acquisition, and plant productivity. OsFH1 plays critical role in root hair development and elongation [80, 81]. Phosphorous is an essential macronutrient for plant survival, due to its limited reservoirs the establishment of phosphorous efficient crops is needed. Pup1 phosphorous deficiency tolerance locus has been identified in rice (Kasalath variety). Pup1 is protein kinase gene later named as phosphorous starvation tolerance-1 (PSTOL1) (**Table 1**) [28]. The overexpression of PSTOL1 gene in rice which naturally lacks PSTOL1 showed greatly increased grain yield in P deficient soil. It also triggered root growth initiation, and resulting the nutrients and P uptake ability from soil. Thereby, PSTOL1 confer tolerance to drought and P deficient soil [82].

Collectively it is suggested that, all root development/elongation related genes play critical role in increasing P acquisition and bioavailability. However, to understand candidate genes involved in development of root would enable farmers and breeders to screen out cultivars with better adapted root system through marker assisted selection tool.

No.	Genes/transcription factors	Plants	Function	Reference
1.	*OsPTF1*	*Oryzae sativa*	Contribute to P availability	[79]
2.	*OsPSTOL1*	*Oryzae sativa*	Confer tolerance to drought and increased crop yield	[82]
3.	*OsFH1*	*Oryzae sativa*	Improves root hairs growth and elongation	[81]
4.	*DRO1*	*Oryzae sativa*	Develop deeper root system	[83]
5.	*OsEXPA17*	*Oryzae sativa*	Involved in root elongation	[84]
6.	*OsSNDP1*	*Oryzae sativa*	Promotes root hair elongation	[85]
7.	*OsSAPK10*	*Oryzae sativa*	Increases root hair length	[86]
8.	*AtPHR1*	*Arabidopsis thaliana*	Contribute to P availability, important role in regulating PSRs	[79, 80]
9.	*PHO1 and AVP1*	*Arabidopsis thaliana*	Improved resistance to drought, and maintain Pi homeostasis, plant productivity	[87, 88]
10.	AVP1	*Solanum lycopersicum*	Increased Pi transport and root/shoot dry weight, resistant to P deficient soil	[89]

Table 1.
The phosphorous starvation induced genes and transporters involved in promoting plant growth and development.

4. "Omics" approaches contribute to Pi adaptation mechanism

The prime objective for future crop production is the development of well adapted lines to Pi starvation condition. Identification of key genes are upregulated under Pi deficient soil could be a useful tool for understanding plant development responses, and use as marker selection for crop improvement, and reported in various plant species transcriptomic and metabolomics approaches had identified bunch of genes and metabolites involved in regulating plant developmental responses and cluster root formation, and provides deep insight in identifying Pi acquisition pathway and network [90, 91]. Genetic engineering has great potential

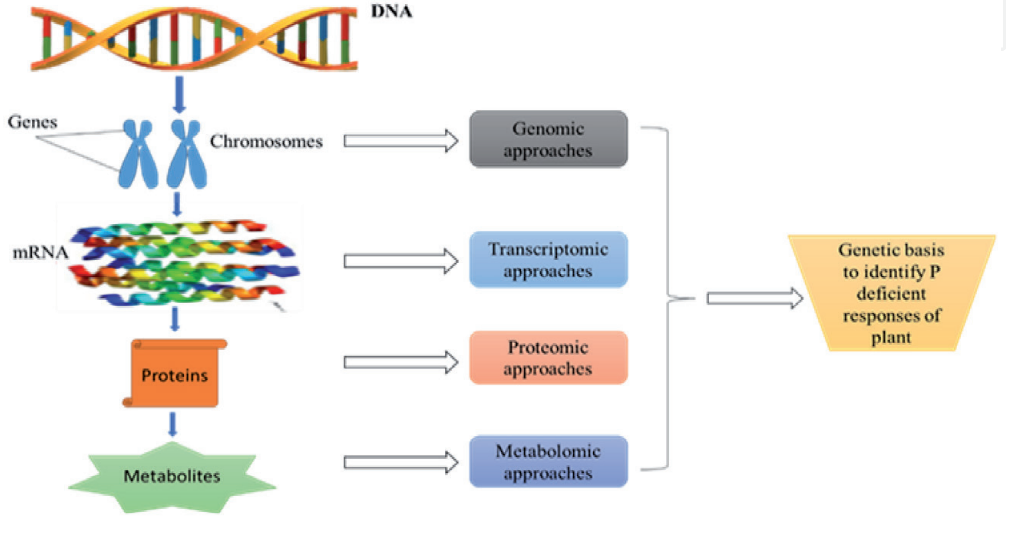

Figure 2.
Omics approaches can reveal molecular basis of plant developmental adaptation to poor nutrient soil.

to revolutionize functional analysis of gene (**Figure 2**), particularly in those plants which have developed stable transformation method.

5. Generation of phosphorous efficient crops

Molecular engineering is a useful approach for breeding and production of transgenic, efficient P uptake plants. It has been shown in rice and Arabidopsis studies that, overexpression of PSTOL1 in rice increases P uptake efficiency under low P availability condition [82], and overexpression of AVP1 also improves P uptake in Arabidopsis and several other plant species [92], suggesting that molecular approaches can significantly improves P uptake efficiency.

Overexpression strategy has also been reported to change exudation rate of acid phosphatase and H^+ secretion in tomato root, that promotes the solubilization of soil fixed P to Pi form [93]. Contrastingly, knockout approaches can also be used for altering Pi homeostasis, for example, OsPHT1.8 and OsPHF1 reduces P uptake and translocation [94, 95].

6. Concluding remarks

P deficiency is an important limiting factor in terms of plant nutrition and growth in cultivated soils. Although the exogenous application of chemical P fertilizer is extensively exploited to fulfill crop nutrition demands. The overuse of chemical fertilizer is not a permanent solution due to finite P reserves and imposes serious threats to environment safety. The excessive use of P fertilizer adversely affects soil biota (microbes, earthworms) and its physical or mechanical properties, eventually reduces crop productivity. As a consequence, soil compactness serves as a major constraint that restricts root growth and elongation. Despite of reduction in root length, root hairs endure as a unique trait for enhancing P acquisition ability under highly compacted low P soil. An efficient uptake of nutrients is a cornerstone towards crop improvement and productivity. Improved phosphorous use efficiency will be arising as a demanding approach in the future to achieve higher crop productivity. Root hairs and density significantly contribute to improve P availability under diverse soil constraints. In future, a clear understanding of molecular mechanism underlying root system architecture (RSA) is necessary to improve nutrient acquisition, and plant yield. More studies in a wide range of plants at the genetic level would provide breeders with molecular markers useful for improving nutrient uptake in plants growing in soils having heterogeneous P levels. The recurring theme is that potential importance of P efficient crops in improving agricultural yield under limited resources is still poorly identified. Such studies will provide important clues for potential targets that can be utilized to engineer biofertilizers which can increase phosphorus use efficiency by changes root trait modification in poor nutrient availability soil.

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Conflict of interest

There is no conflict of interest exist to declare.

Author's contribution

MA conceived the first idea and prepared the first draft, KA helped in improving writing. MA, KA, and JK critically reviewed the final draft. All author(s) read and approved the final draft.

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