

Application of Proteomics in Studying the Conditions of Phosphate Deficiency in Different Plant Species

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ABSTRACT

Phosphate is a key element required in plant nutrition. It is not easily available from natural resources. Agricultural crops and plants have to be supplied with huge quantities of phosphate fertilizers so that the required quantity of phosphate can be achieved. To solve this problem, different groups of scientists and researchers have been studying different strategies to formulate such techniques of adaptations in different plants so that the plants can thrive well and survive in phosphate deficient conditions of soil. Different biotechnological strategies and tools have aided in such studies. This article emphasizes on the proteomic study reports conducted on different plant species suffering from soil phosphate deficiency.

Keywords Phosphate, Starvation response, Proteomics, Accumulated proteins.

INTRODUCTION

Phosphorus is a key element in different biomolecules that include NADPH, ATP, nucleic acids, sugar phosphates, phospholipids. The phosphate concentration in soil is much lesser compared to the actual amount of phosphate required for the plants and seedlings. This creates a significant difference in the quantities of phosphate required and the actual quantity of phosphate that is readily available to the plants and crops. Thus phosphate can be considered as an essential, limiting nutrient in plant metabolism and growth. For the abundant and easy production of different agricultural crops, it is very important that the required amount of phosphates in plants is supplied with. Otherwise it can even lead to the death of the plants. Different groups of scientists and researchers have been working for a time period for designing some effective biotechnological techniques and strategies to bioengineer some transgenic crops which are phosphate efficient in nature and can withstand lack or starvation of phosphate for at least a certain period of time or during the time of phosphate crisis. Different study tools and strategies including genomics, proteomics and molecular biotechnology approaches can aid this research. The differentially accumulated proteins identified through proteomics analysis can further help our understanding of this topic.

Phosphate in plant nutrition: Phosphate can exist in plants as Pi (soluble inorganic phosphate anions) and organophosphate compounds. Phosphate cannot

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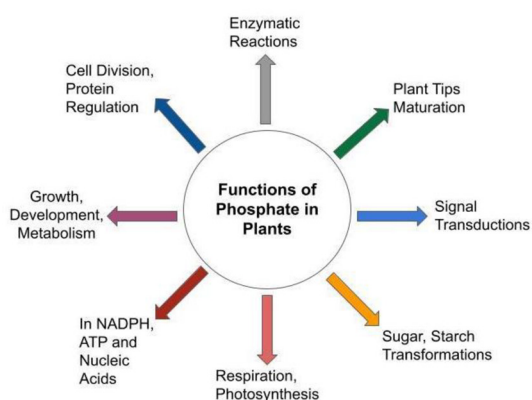


Fig. 1. Different functions of phosphate in plants.

be reduced in plants during assimilation (like that of sulphates and sulphites) but instead of that, it can remain in its oxidized state which can lead to the formation of a number of phosphate esters with a wide range of organic compounds. Phosphorus is found in every living cell of plants and has various functions (Fig. 1) in a plant body.

It plays an important role in the growth, development and metabolism of different plants and is also essential and has critical roles in almost all major processes in the plant life cycle which includes respiration, photosynthesis and other different metabolic processes like transformation of starches and sugars, enzymatic reactions, signal transduction, transfer and movement of enzymes and nutrients, within the plant (Oldroyd *et al.* 2020). In soil, phosphorus plays a central role in the development, growth and maturing of plant tips. It can also regulate different activities of a diverse array of proteins by the process of covalent phosphorylation and dephosphorylation reactions. Cell division and metabolism of the plant cells also get facilitated by phosphorus among other functions. Phosphorus is not only just a key underlying constituent of biomolecules, including deoxyribonucleic corrosive (DNA), proteins, and phospholipids, yet in addition is an important factor that can work by intervening the phosphate signaling network system (Plaxton *et al.* 2015).

Phosphate deficiency problem in plants and in soil:

In soil, the phosphate concentration is very less than

the actual amount of phosphate required by the plants. It has been found that the approximate concentration of soluble phosphate in soil ranges from 1-10 μM . However, the actual concentration or quantity of intracellular phosphate required for plant growth and metabolism ranges from about 5-20 mM . This creates a huge difference in the quantities of phosphate required and the actual quantity of phosphate that is readily available to the plants and crops. The supply of phosphate in plant nutrition depends majorly on the phosphate fertilizers. For the abundant and easy production of different agricultural crops, it is very much important that the required amount of phosphates in plants is supplied with. It relies solely on the maximum supply of the phosphate fertilizers that are being provided to the plants and crops. Phosphates from phosphate fertilized fields can sometimes run into the nearby water surfaces, pond, lakes, and lead to several environmental destructions and complications like that of eutrophication, algal bloom, blooms of different toxic cyanobacterias, destruction of the aquatic lives and aquatic cultures in the water surfaces, thereby leading to the disruption or destruction of an aquatic ecosystem and harming the biodiversity (Hallama *et al.* 2019). In most natural soils, even in the most fertile ones, phosphate is found to be the least accessible nutrient. This is because in acidic soils phosphate starts forming different complexes with aluminum and iron oxides; and in alkaline or basic soil, it leads to the formation of insoluble calcium salts. Because of this, the available quantity of phosphate in soil starts to gradually become inaccessible for uptake by the roots, which results in only about 20% (or less than 20%) of phosphorus absorption/uptake by the crops. Phosphate is not a resource that is easily available in nature. Phosphate needs to be extracted from different non-renewable phosphate reserve rocks, deposits of fossilized bones. Only after that, phosphate fertilizers can be manufactured in required quantities. Unavailability of required phosphate for its uptake by the roots due to different complex formations in different soil conditions, be it acidic or basic soil, along with the formation of different metal ions, cations, complexes for the same reason. The alarming rate in which the phosphate stocks are gradually dissolving, it might soon lead to the search for another source of phosphate extraction and acquisition. In order to reduce the overuse and

requirement of phosphate fertilizer in the field and to ensure sustainable agriculture at the same time, scientists and researchers have been working for a time period for designing some effective biotechnological techniques and strategies to encounter this problem (Byung-Kook *et al.* 2018). They can bioengineer some transgenic crops which are phosphate efficient in nature and can withstand lack or starvation of phosphate for at least a certain period of time or during the time of phosphate crisis.

Proteomics in studying plant phosphate starvation phenomenon:

Different biotechnological tools and strategies can be used to study and analyze phosphate deficiency responses in plants. In this review, proteomics analysis conducted on different plant species by different groups of scientists, have been emphasized on (Table 1). Several components of the phosphate starvation response are controlled and maintained at the transcription level. A team of researchers published a report on the signaling players of the phosphate deficient responses in plants (Rouached *et al.* 2010). It talked on the process of discovering new signaling players like that of proteins with certain SPX domains. Phosphate starved plants can remodel their proteome and transcriptome in such a way that they can cope up with the metabolic and morphological changes adapted by the plants. Another group published a study regarding the study of legumes under phosphatation deficient conditions (Abdelrahman *et al.* 2018). It was reported how transcriptomics and metabolomics played a significant role in this study. A large study data has been retrieved which talks of a plant phosphate deprivation system (mainly Arabidopsis plant). It throws light on the molecular regulations and identity of many physiological and biochemical adaptations of plants that relate to phosphate starvation systems. In Arabidopsis, it has been found that the enhanced reductions in the cytoplasmic phosphate pools that accompany a period of prolonged starvation, is actually fulfilled by a high specific response that differs in the shoots and roots of the plants. It has also been found that, in spite of the inductions of about 600-1800 genes across all of the plant tissue, only 25% approximate overlap is found between those which are specifically induced in the shoots and roots of the plants, thereby implying strong tissue specific adaptations to phosphate star-

vation. Transcriptional repression can also play an important role in determining the phosphate starvation response. About 250-700 genes possess reduced transcript accumulation in respect to phosphate starvation. Phosphate starvation inducible gene expression can be coordinated in tissue specific and temporal manner. Tissue specificity plays a critical role in Pi starvation response with only about 5-10% overlapping in the repressed gene expressions between the plant roots and shoots. Post transcriptional responses also contribute remarkably in the gene activities and expressions of the phosphate starvation inducible systems. By the process of proteomic profiling of different phosphate starved plants like maize (*Zea mays*), rice (*Oryza sativa*), Arabidopsis, it can be concluded that the transcript abundance of various different genes does not always indicate to the accumulation of proteins during phosphate starvation. One of the best examples concerning the post transcriptional response is found in Arabidopsis in respect to the phosphate starvation mechanism in the plant. In this plant, the regulatory module consists of the plant transcription factor PHR1, the E2 Ubiquitin conjugate UBC24 (also called *pho2*), miR-399 (microRNA-399) along with non coding RNA At4. When sufficient phosphate is present, UBC24 expresses and aids in the regulatory systemic phosphate homeostasis by reducing the expressions of the phosphate depriving inducible genes including the high affinity Pi transporters of plasmalemma. Again, during phosphate deprivation, transcription factor PHR1 can get induced by an unknown mechanism and leads to the activation of the expression of phloem mobile miR-399 by about 1000 times. Proteomic and Iomic studies conducted on Arabidopsis provided value inputs on the aspect of phosphate starvation (Iglesias *et al.* 2013, Watanabe *et al.* 2015). Expressions of At4 (a ribo regulator) also get strongly induced during long periods of phosphate deprivation. These factors can describe some important phosphate starvation responsive genes so that effective biotechnological techniques and strategies can be undertaken for the development of certain phosphate efficient agricultural crops. Besides the above point, differential glycosylation and reversible phosphorylation are also gaining importance in relation to various post translational modifications for controlling and maintaining the mechanisms and activities of various enzymes

that are enhanced and upregulated during extended periods of phosphate starvation. Upregulation and stimulation of PEP (phosphoenolpyruvate) carboxylase is a typical metabolic strategy adapted by phosphate starved plants. *In vivo* phosphorylation and activation of the phosphoenolpyruvate carboxylase isozyme AtPPC1 (besides its induction and stimulation) contributes to the metabolic adaptations and strategies of phosphate deprived Arabidopsis plants. Phosphate starvation responses have been well studied in 2010 (Yang *et al.* 2010). Many genes are involved in the phosphate deficiency tolerance strategies in different plants. Plants try to cope up with phosphate deficiency problem mainly by following two different ways, firstly by scavenging and accumulating phosphate from a number of extracellular resources that include organic phosphate monoesters and also by deploying some high affinity phosphate transporters, and secondly by the process of remobilization and scavenging of phosphate from different anhydrides and intracellular phosphate monoesters in phosphate deficient plants and crops. Phosphate is not easily available in the natural environment so scavenging and acquiring phosphate is an important strategy followed by the plants in order to survive a long period of phosphate deficiency. Another important component of phosphate starvation response in different plants and crops include the up regulation of a number of phosphate transporters with high affinity which are present in the plasma membrane (ZhaoYuan *et al.* 2009). Phosphate transporters having very high affinity can get induced when the external phosphate concentration is found to be low. These Pi transporters get activated and can start assimilating phosphate against a very steep phosphate concentration gradient. The phosphate concentration gradient actually appears to be extremely steep and abrupt since the phosphate concentration in soil can be found to be 10,000 times lower compared to what has been found in the root cells. These high affinity phosphorus transporters have been precisely cloned from a variety of plant and crop species. Arabidopsis, as noted, has been found to have a family of very high affinity phosphate transporters. It includes nine members, namely PHT1;1–9. These phosphate transporters are basically some integral membrane proteins having twelve transmembrane domains which are separated into two groups, and are also predicted to

have their N- and C-terminals located in the cytosol. The expression of the four members in this particular family is found to be in the roots. Among all of them, PHT1;1 (AtPT1) and PHT1;4 (AtPT2) are found to be the two main contributors in the high affinity phosphate transport system, which can account for about 70% of the phosphate transporting phenomenon in the roots of the plant. One of the main quantitative trait locus for the tolerance response of phosphorus deficiency condition is Pup1. It was found in Kasalath, the common aus type rice variety. The locus was first sequenced which actually shows the presence of a Pup1 specific protein kinase gene, that was ultimately named phosphorus starvation tolerance 1 or PSTOL1. Gamuyao *et al.* in (2012) explained the over expression or excess of PSTOL1 can significantly enhance the grain yield in soil lacking appropriate quantities of phosphorus (Gamuyao *et al.* 2012). In another recent study performed on sorghum plant on the genes involved in phosphate starvation response, it has been found that 2089 candidate genes were involved with the phosphate starvation response strategy and those genes were enriched and involved in 11 different pathways (Zhang J *et al.* 2019). It was also found that those candidate genes were involved in different oxido-reductase activities. Further research revealed that the number of tips and the primary root length and structure was harshly affected because of the lack of supply of required amounts of phosphate to the sorghum plants. The results obtained indicated that the acquisition of the organic phosphate from the soil medium can contribute to phosphate deficient tolerance in a number of sorghum accessions. Several plant hormones like ethylene, auxin, jasmonic acid, abscisic acid and salicylic acid signal transduction related genes and several transcriptional factors were found to be concerned with low phosphate tolerance in sorghum. In 2006, it was reported and explained that micro RNA399 (also called miR399) can control the homeostasis of inorganic phosphate (Pi) by the regulation of the expression of UBC24 by encoding of a ubiquitin conjugating E2 enzyme in Arabidopsis (Aung *et al.* 2006). This team also studied a mutant gene named *pho2* which can lead to the accumulation and increase of phosphate in the shoots of plants in a phosphate deprived medium/condition. Another plant phosphate starvation response in relation to phosphate deficiency is the

Table 1. A table of proteomics studies conducted on different plant species parts to analyze their responses to phosphate deficiency condition; (ND= Not defined).

Species	Plant part	Protein separation method	Total protein	No. of DAP	Up regulated protein	Down regulated protein	Reference
<i>Arabidopsis thaliana</i>	Leaves	SCX iTRAQ LC-MS/MS	5106	156	106	50	Wang <i>et al.</i> 2018
<i>Arabidopsis thaliana</i>	Roots	2-DE iTRAQ LC-MS	13298	356	199	157	Lan <i>et al.</i> 2011
<i>Arabidopsis thaliana</i>	Suspension cells	2-DE MALDI TOF MS	110	46	26	6	Tran <i>et al.</i> 2008
<i>Oryza sativa</i>	Roots	2-DE MALDI-TOF MS	140	10	2	8	Kim <i>et al.</i> 2011
<i>Glycine max</i>	Leaves	2D-IEF/SDS-PAGE MALDI-TOF MS	55	17	7	10	Chu <i>et al.</i> 2018
<i>Glycine max</i>	Leaves	SDS-PAGE Gel Digestion LC-MS/MS	4219	707	267	440	Cheng <i>et al.</i> 2021
<i>Glycine max</i>	Roots	iTRAQ	ND	427	213	214	Jiang <i>et al.</i> 2021
<i>Glycine max</i>	Roots	iTRAQ LC-MS/MS	ND	71	30	41	Wu <i>et al.</i> 2018
<i>Glycine max</i>	Roots	2-DIGE	325	105	61	44	Vengavasi <i>et al.</i> 2017
<i>Glycine max</i>	Nodules	2-DE MALDI TOF MS	ND	44	17	27	Chen <i>et al.</i> 2011
<i>Brassica napus</i>	Roots/Leaves	2-DE MALDI TOF MS	1000	32	4/12	13/3	Yao <i>et al.</i> 2011
<i>Hordeum vulgare</i>	Roots	SDS PAGE LC-MS/MS	ND	697	ND	ND	Wang <i>et al.</i> 2021
<i>Hordeum vulgare</i>	Roots/Leaves	2-DE MALDI-TOF/TOF-MS	ND	31	ND	ND	Nadira <i>et al.</i> 2016
<i>Triticum aestivum</i>	Roots	iTRAQ	6842	323	ND	ND	Wang <i>et al.</i> 2021
<i>Solanum lycopersicum</i>	Leaves	2-DE MALDI-TOF MS/MS/MS	600	46	31	15	Muneer <i>et al.</i> 2015
<i>Pinus massoniana</i>	Seedlings	2-DE MALDI-TOF/TOF MS	ND	98	44	54	Fan <i>et al.</i> 2016
<i>Zea mays</i>	Leaves	2-DE MALDI TOF MS/TOF	1342	200	ND	ND	Deng <i>et al.</i> 2014
<i>Zea mays</i>	Roots	2-DE MALDI TOF MS	1300	254	76	30	Li K <i>et al.</i> 2007
<i>Zea mays</i>	Roots	2-DE MALDI-TOF-MS	850	91	ND	ND	Li K <i>et al.</i> 2014

secretion of acid phosphatases in plants. The regulation and stimulation of the secreted intracellular acid phosphatase activity has been long identified and marked as a biochemical hallmark of phosphate deprivation in plants. It was found from a reporter system, driven by a high affinity phosphate starvation induced promoter called PHR1 or Phosphate starvation responsive⁻¹, that it has the ability to expand and stimulate a particular group of phosphate responsive genes through the GNATATNC cis element by encoding a MYB transcription factor. In soybean,

proteomics study identified GmENO2 proteins being involved in Pi-starvation (Cheng *et al.* 2021). With the help of proteomics study, a number of differentially accumulated proteins or DAPs could be identified in different plant species in response to the scarcity of phosphate in soil. That table has been presented in this report. lycopersicum

Discussion: Phosphate being a significant component of overall plant nutrition, is essentially required for plant growth, development, metabolism. A number

of biotechnological studies including proteomics, genomics, genetical analysis have been also implemented to mark the phosphate soil deficient condition in various crops and plants. With the use and implementation of various biotechnological approaches, different research groups have aimed to design phosphate deficient agricultural crops in such a manner that the plants would be able to tolerate long periods of phosphate deficiency. Also, the strategies implemented by the plants including root architecture modification, could be reduced simultaneously. With continuous studies and research in this area, we can hope to see genetically modified plants and agricultural crops in near future that would be efficient enough to tolerate the complications of phosphate deficiency in soil without getting affected or getting restricted in their proper growth and development.

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