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Conditions of Phosphate Starvation in Different Agricultural Plants for Analyzing the Significance of Purple Acid Phosphatase in Plant Phosphate Deficiency

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ABSTRACT

Phosphate is a significant component in plant nutrition. It is hard to avail from natural resources and has to be supplied externally. Plants undergo different adaptation techniques to thrive in phosphate deficient conditions of oil. These adaptations also help to extract maximum amount of phosphate from external sources while minimizing the internal phosphate usage. In this report, phosphate deficiency in different agricultural crops has been studied in brief in a number of plants. Phosphate deficiency leads to several changes and modifications in these plants. Also, there are a number of genes and factors responsible for phosphate deficiency tolerance in these plants. These genes are the PAP (purple acid phosphatase) genes. This article emphasizes on different studies conducted on the phosphate deficiency tolerance of plants in relation to the PAP genes. Identification of these PAP genes would enhance the ability of the plants to tolerate long periods of phosphate deficiency in soil.

Keywords Phosphate, Pi-starvation, purple acid phosphatase, Genes.

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INTRODUCTION

Phosphorus is found in every living cell of plants. It is a key element in different biomolecules that include NADPH, ATP, nucleic acids, sugar phosphates, phospholipids. But problem arises when phosphate concentration in soil is taken into consideration. The phosphate concentration appears to be much lesser in soil than the actual amount of phosphate required for plant nutrition, thereby creating a remarkable difference in the quantities of phosphate required and the actual quantity of phosphate that is readily available to the plants. Thus phosphate can be considered as an essential, limiting nutrient in plant metabolism and growth. The supply of phosphate in plant nutrition depends majorly on the phosphate fertilizers. Orthophosphates (HPO_4^{2-})/($H_2PO_4^{-2}$) are the most oxidized form of phosphates that are taken up primarily by the roots. It relies solely on the maximum supply of the phosphate fertilizers that are being provided to the plants and crops. Phosphate nutrition in plants is studied and determined by the root-soil interactions in

the plants. Studies have shown that about 10 million metric tons of phosphate fertilizers are being supplied to crops, each year, world wide. But it could be well understood that this quantity of phosphate will not be enough for the surplus number of crops all around the world. This gradually takes the form of a major problem. Different complexities can arise from this entire scenario. 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. We can easily calculate the expenditure behind this ample amount of phosphate fertilizers. 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 can harm the plants. 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 have conducted intense studies on the phosphate deficient conditions of soil and how they affect different plants and agricultural crops.

Phosphate starvation response in plants: Phosphate starvation or Pi-starvation response of plants (Fig. 1) refer to a compiled array of morphological and biochemical formulations adapted by the plants in order to survive in a phosphate starved or pi-deficient condition of soil. These plants have been able to gradually evolve themselves to obtain this ability of tolerating long periods of phosphate deprivation. This phosphate starvation response works on the idea of coordination between a number of phosphate starvation inducing genes that works by controlling or minimizing the internal phosphate usage along with maintaining the maximization of phosphate acquisition from external sources (Dissanayaka *et al.* 2018, Liang *et al.* 2014). Evolution of these biotechnological strategies can help the plants to survive in a Pi-deprived condition for a longer period of time. Root architecture modifications and remodeling play a significant role in periods of phosphate deficiency (Peret *et al.* 2014, Lopez-Bucio *et al.* 2003). Increase in the growth ratio of plant root to shoot is an important strategy uptaken. Changes and modifications in the size, shape, diameter and overall architecture of roots facilitate this process. Also, root hair growth is important, so that their density can be increased in the process. The top soil can be explored for finding the available phosphate facilitated by shifting from primary root growth to lateral root growth. Several hormones are also involved in root growth and remodeling (Khan *et al.* 2016, Talboys PJ *et al.* 2014). Anthocyanin accumulation is mentionworthy in this case. Anthocyanin accumulation in leaves is one of the mention worthy biochemical techniques adapted by plants to survive periods of phosphate deficiency. Accumulation of anthocyanin has been observed often in the shoots of some Pi-deficient plants. This phenomenon is also believed to protect the chloroplasts from photoinhibition activities (Chu *et al.* 2018, Mo *et al*. 2021).

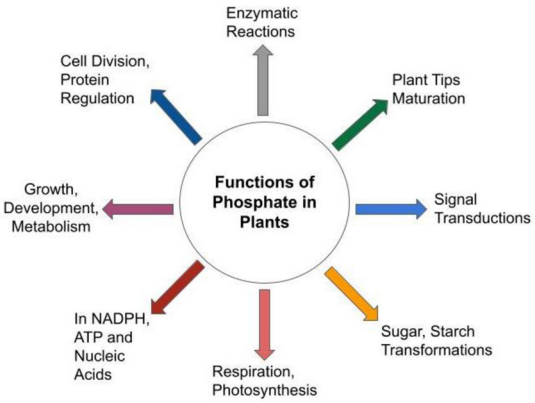

Fig. 1. Different functions of phosphate in plants,

Phosphate scavenging can be done to obtain phosphate from some non-essential phosphate esters by phosphate starvation inducible hydrolase like acid phosphatases, ribonucleases, phospholipases. Some bypass or alternative enzymes to the adenylate dependent or phosphate dependent reactions of glycolysis and mitochondrial respiration, can also be counted. This can be done by the reorganization of cellular metabolism in such a way that it can conserve, maintain and ultimately regulate the limited amounts of phosphates and adenylates. This requirement can be achieved by the alteration of the organization of mitochondrial respiration, glycolysis and tonoplast

hydrogen pumps which can allow phosphate and adenylate dependent reactions to be altered or bypassed during the long periods of Pi-starvation. Due to Pi-starvation, increased starch content and diminished sucrose content were noticed in the leaves of most plants. Secretion of organic acids can help in the chelating of metal cations that can further help in the immobilization of phosphate, thereby increasing the phosphate concentration in soil by 10 to 1000 times. Besides these, organic acid secretion also helps to increase the scavenging of phosphates from organic phosphate esters in local soils. Root associated Purple Acid Phosphatase (PAP) can hydrolyze the organic phosphate forms. Thus, acid phosphatase secreted in the plant roots help to facilitate this process (Dissanayaka *et al.* 2018, Chen and Liao 2016). The upregulation or induction of high affinity phosphate transporters is another biochemical adaptive strategy formulated by the Pi-deprived plants. Increase in high affinity phosphate transporters of the plasma membrane can be helpful in maintaining the lack of required phosphate amounts in plants. When the external phosphate concentration lowers down, induction of these transporters come into action and they start assimilating phosphate actively against an abrupt steep of Pi gradient, since the concentration of phosphate in the soil is found to be 10000 times lower than that of what is found in the root cells. Pi deficiency also significantly affects the leaves of plants thereby triggering leaf remodeling. Leaf angles, their inclination, erectness, tilt have been found to be regulated in different plants, including rice (Umehara *et al.* 2010, Ruan *et al.* 2018). It has also been found that, phosphate deprived plants can use their membrane phospholipids as a significant hotspot for internal phosphate supply by supplanting phospholipids in their membranes with the non-phosphorus galactolipid and digalactosyldiacylglycerol. Redesigning of this membrane lipid has drawn a lot of consideration as a model of metabolic change from phospholipids to the galactolipid (Nakamura 2013). Under the states of phosphate starvation, phospholipids which represent about 30% of all organophosphate in plants, can be replaced by some non-phosphorus lipids like sulfoquinovosyl diacylglycerol or SQDG. In Arabidopsis leaves, proteins like lipoxygenase, 3-phosphoglycerate dehydrogenase and lipid-transfer proteins were observed to be up-regulated (Wang *et al.* 2018). Various such studies have been conducted in different plants to study the phenomenon of Pi-deficiency.

Phosphate deficiency studies conducted in different plants: Effects of phosphate deficiency have been studied in a number of plants. Meng X and team conducted studies on *Citrus grandis* on the absorbance of different mineral nutrients, its antioxidant metabolism and photosynthetic performance of the plant system (Meng *et al.* 2021)(Table 1.).The results showed that phosphate deficiency significantly lowers the photosynthetic performance of the plant and affects its nutrient absorption at the same time. It ultimately results in the stunted growth of *Citrus grandis.* Malhotra H and team studied the growth of some plants in response to the scarcity and excessity of phosphorus in them (Malhotra *et al*. 2018). They studied and analyzed different biochemical, morphological and physiological adaptations undergone by the plants in response to phosphorus deficiency, while there was barely any phosphorus toxicity reported in the plants. Aziz T and team conducted similar studies on phosphate deficiency (Aziz *et al.* 2014). Due to low phosphorus content, soybean plant production and growth decreases significantly (Yang *et al.* 2020). Through reversible protein phosphorylation, some studies were conducted on soybean and the report was published in 2021 (Jiang *et al.* 2021). The acquisition and accumulation of phosphate by mycotrophic plants have been found to get remarkably enhanced by the presence of the *Arbuscular mycorrhizae* which are present between the roots of most vascular plants (exception *Cyperaceae, Cruciferae, Proteaceae, Cheonpodiaceae* and *Junaceae* families) and soil-living fungi of order *Glomales*. A report published by Lambers *et al*. (2015) studied phosphate nutrition in Proteaceae and explored different traits for enhancing the phosphate efficiency of agricultural crops (Lambers *et al.* 2015). Disruption of different beneficial mycorrhizal associations due to phosphate fertilization besides soil tilling has been an unwanted consequence of modern agriculture. It is noteworthy that many non-mycotrophic plants like harsh hakea (*Hakea prostrata)*, buckwheat (*Fagopyrum esculentum*), white lupin (*Lupinus albus*) are famous for their potential to survive on phosphate deficient medium and soil conditions. This reflects a proof that the

non-mycotrophic plants have adapted themselves with different strategies to survive in phosphate deprived soil conditions, compared to the mycotrophic plants who cannot do the same. Phosphate uptake can be facilitated by proteoid roots, a bunch of short lateral roots that have the ability to uptake phosphate much faster compared to the non proteoid roots. The Proteaceae family's non mycotrophic members like white lupin, harsh hakea can lead to the formation of proteoid roots when they are cultivated in phosphate deprived conditions of soil. These proteoid roots can improve root-soil interactions to facilitate the process of acquiring high quantities of phosphate from the soil (Lambers *et al.* 2011). Arabidopsis (a member of the Cruciferae family) does not form any kind of mycotrophic association. This is the reason why it is considered an ideal model plant for analyzing and studying the biochemical and molecular adaptations of phosphate deprivation in non-mycotrophic plants.

A group of scientists reported a study on the levels of phosphate tolerance on a number of chickpea genotypes (Gülüt and Ozdemir 2021). 'Diyar. 95′, 'İzmir', 'ER. 98′, 'Çağatay', 'ILC.482′, 'Gülümser', 'Gökçe', 'Damla', 'Yaşa.05′ were the 9 chickpea genotypes studied under greenhouse conditions. This study provided valuable information regarding these chickpea genotypes which might enhance its breeding in future and further studies on the same. A group of scientists published a report in 2018 on the cellular patterns of the roots of *Arabidopsis thaliana* under conditions of phosphate deficiency (Janes *et al.* 2018). They observed distinct changes in the roots, root hairs, cortex of Arabidopsis due to phosphate deficiency. Another report on *Arabidopsis thaliana* published in 2020 talked on the growth of the primary roots in Arabidopsis due to a phosphate dependent condition. According to this study, blue light can regulate the growth of these phosphate dependent

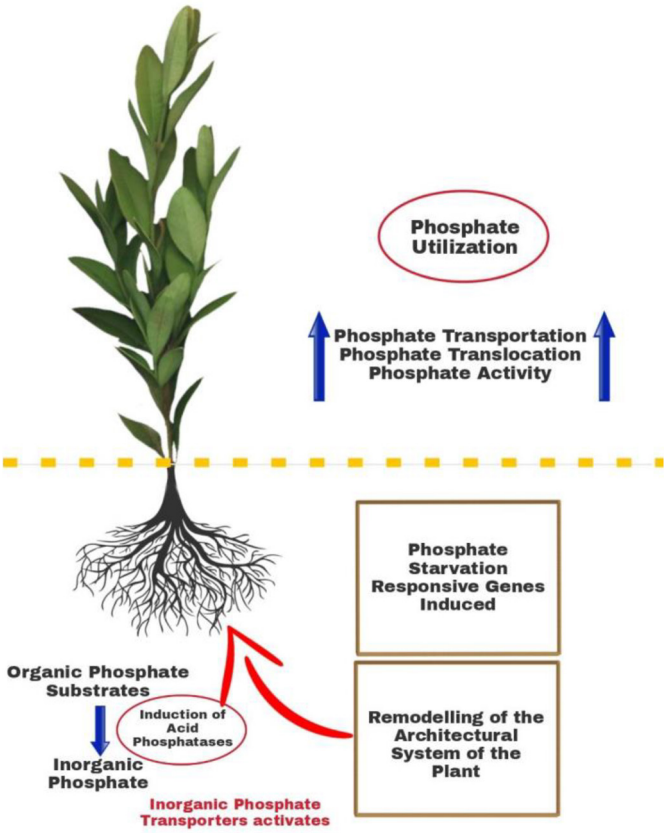

Fig 2. Phosphate starvation in plants.

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 rotein	Reference
Arabidopsis thaliana	Leaves	SCX iTRAQ LC-MS/MS	5106	156	106	50	Wang ZQ *et al.* 2011
Arabidopsis thaliana	Roots	2-DE iTARQ LC-MS	13298	356	199	157	Lan *et al*. 2011
Arabidopsis thaliana	Suspension cells	2-DE MALDI` TOF MS	110	46	26	6	Tran *et al*. 2008
Oryza sativa	Roots	2-DE MALDI-TOF MS	140	10	2	8	Kim *et al.* 2011
Glycine max	Leaves	2D-IEF/SDS-PAGE MALDI-TOF MS	55	17	7	10	Chu *et al.* 2018
Glycine max	Leaves	SDS-PAGE Gel Digestion LC -MS/MS	4219	707	267	440	Cheng *et al.* 2021
Glycine max	Roots	iTRAQ	ND	427	213	214	Jiang *et al.* 2021
Glycine max	Roots	iTRAQ LC-MS/MS	ND	71	30	41	Wu *et al.* 2018
Glycine max	Roots	2-DIGE	325	105	61	44	Vengavasi *et al.* 2017
Glycine max	Nodules	2-DE MALDI TOF MS	ND	44	17	27	Chen *et al.* 2011
Brassica napus	Roots/ Leaves	2-DE MALDI TOF MS	1000	32	4/12	13/3	Yao *et al.* 2011
Hordeum vulgare	Roots	SDS PAGE LC MS/MS	ND	697	ND	ND	Wang *et al*. 2021
Hordeum vulgare	Roots/ Leaves	2-DE MALDI-TOF/TOF-MS	ND	31	ND	ND	Nadira *et al.* 2016
Triticum aestivum	Roots	iTRAQ	6842	323	ND	ND	Wang *et al.* 2021
Solanum lycopersicum	Leaves	2-DE MALDI-TOF MS/MS/MS	600	46	31	15	Muneer *et al.* 2015
Pinus massoniana	Seedlings	2-DE MALDI-TOF/TOF MS	ND	98	44	54	Fan *et al.* 2016
Zea mays	Leaves	2-DE MALDI TOF MS/TOF	1342	200	ND	ND	Deng *et al.* 2014
Zea mays	Roots	2-DE MALDI TOF MS	1300	254	76	30	Li *et al*. 2007
Zea mays	Roots	2-DE MALDI-TOF-MS	850	91	ND	ND	Li *et al.* 2014

roots in Arabidopsis thaliana (Yeh *et al.* 2020). Reports of a study conducted on upland rice on its nutrition deficiency due to soil phosphate deprivation is important in this aspect and was published in 2011 (Mghase *et al.* 2011).

Purple Acid Phosphatases: Phosphatases or phosphomonoesterase are hydrolytic enzymes that have the ability to cleave the ester bonds present between the phosphate groups and the remaining organic residues found in the organic phosphates. Different phosphatases require different optimum pH for their activities. Phosphatases can be categorized into two types, acid phosphatases and alkaline or basic phosphatases. P-nitrophenyl has been found to work as a substrate for both the kinds of phosphatases, that is, it can be a substrate to both acid and alkaline phosphatases. So when it is hydrolyZed by either of the two enzymes, p-nitrophenyl is yielded as a result. Acid phosphatases are a family of enzymes found widespread in nature and natural sources. It can be found in several plant and animal species. Acid phosphatase is basically a lysosomal enzyme that has the capability to hydrolyze organic phosphates at an acidic pH.

In animals, it has been found that the postpubertal prostatic epithelial cells have a precisely high concentration of acid phosphatases. This enzyme is also found in the cells and cellular components of bone, liver, spleen, intestine, kidney, blood. In plants, the acid phosphatases or APases generally do not exhibit any particular or absolute specificity for substrates. Acid phosphatases help to catalyze the process of hydrolysis of phosphate from a very widespread and broad range of phosphate monoesters having an optimum acidic pH and also helps in the function of production, acquisition, transporting and recycling of phosphates in the plants (Tran *et al.* 2010).

The vacuolar acid phosphatases present in the phosphate deprived plant cells are very likely to remobilize and recycle phosphate from several disposable intracellular phosphate anhydrides and phosphate monoesters. This phenomenon is followed and marked by reductions in the cytoplasmic phosphate metabolites during periods of extended phosphate starvation and deprivation. The extracellular acid phosphatases typically belong to a group of phosphate deprivation inducible hydrolases which are secreted by phosphate starved plants. They have the potential to hydrolyze phosphate from the external organophosphates that are capable of comprising up to 80% of total phosphate quantity present in the soil. Acid phosphatase present in the leaves can be used as biochemical markers for the genetic analysis of germplasm of rice plants. They can be grouped into four different types depending on the context of their isoform patterns. Acid phosphatases have also been found in the aleurone particles of rice grains along with their roles of being associated with the hydrolysis of several phosphate reserves. In rice, acid phosphatase activity in the roots of plants and the secretion of acid phosphatases from the roots can help in increasing the response to phosphate deficiency. It was also found that the roots of white lupin (*Lupinus albus* L. cv. Kievskij mutant) when grown under the conditions of low phosphate in the surroundings and leads to phosphate starvation, can secrete acid phosphatase called S-APase or Secreted acid phosphatases. Secreted acid phosphatases have the ability to hydrolyze organic phosphate compounds in the rhizosphere and thereby supply required inorganic phosphate to the plants. Two distinctive categories of plant acid phosphatases can be identified on the basis of their relative substrate selectivities. The first category of plant acid phosphatase includes the truly 'non-specific' enzymes that show very little or no substrate specificity. These nonspecific acid phosphatases can occur in a broad range of species and tissues and can feature a considerable amount of diversity with some regards to their physical properties. These enzymes actually appear to have some importance in the production, acquisition, transport and recycling of phosphate. The second category of plant acid phosphatases are the specialized enzymes like that of the 3-Phosphoglycerate (3-PGA) phosphatase enzyme obtained from maize leaves and the phosphoenolpyruvate (PEP) phosphatase of black mustard (*Brassica nigra*) cell cultures suspension which can display a very clear and specific non-absolute substrate specificity. These acid phosphatases are hypothesized to have several distinct metabolic functions. The Purple acid phosphatases (Fig. 2) belong to the acid phosphatase group. Purple acid phosphatases (PAPs) are, in general, some metallo enzymes that have the ability to hydrolyze the phosphate anhydrides and phosphate esters under acidic conditions. It appears purple in color in a solution in their oxidized form. This happens due to the presence of a dinuclear iron center. A tyrosine residue is connected to this dinuclear iron center through the transfer of charge. This metallic center comprises of M and Fe^{3+}, where M can be Mg^{2+} or Fe^{3+} or Zn^{2+} or Mn^{2+}. The conserved Fe^{3} gets stabilization in its ferric form, on the other hand, M may undergo a reduction reaction. If treated with some mild reductants, purple acid phosphatases can be converted to their pink form from their oxidized purple form. This pink form of PAP is enzymatically active in nature. Again if it is treated with some strong reducing agents, it leads to the dissociation of the metallic ions and ends up rendering the enzyme inactive and colorless. All purple acid phosphatases can contain a binuclear metal site. Also, they are tartrate-resistant in nature. The appearance of the pink or purple color of the concentrated water solution is the result of a transition of charge-transfer between the chromophoric ferric ion and the tyrosine residues. The second non chromophoric metal ion which occupies the binuclear site, is manganese or zinc in plant enzymes, and iron in mammalian purple acid phosphatases (Schenk *et al.* 2013). Several studies

are going on for identification of the PAP genes in various crops and plants. The number of putative PAP isozymes have been predicted to be 26 in rice, 35 in soybean, 33 in maize and 25 in chickpea, 29 in Arabidopsis, 25 in physic nut (Zhang *et al.* 2011, González-Muñoz *et al.* 2015, Bhadouria *et al.* 2017, Venkidasamy *et al.* 2019). It's been documented that Pi-deficiency complements the expression stages of maximum plant PAPs. For instance, in rice, 10 out of 26 pap individuals, OsPAP1a, 1d, 3b, 9b, 10a, 10c, 20b, 21b, 23, and 27a have been found to be upregulated within the roots underneath the phosphate scarcity conditions (Zhang *et al.* 2011). In the same way, Pi deficiency enhanced transcripts of the PAP isozymes have also been found at least in 11 out of 33 PAP isozymes in maize, in 11 out of 29 PAP isozymes in Arabidopsis, 12 of 25 PAP isozymes in chickpea, in about 20 out of 25 PAP isozymes in physic nut and in 23 out of 35 PAP isozymes in soybean (González-Muñoz *et al.* 2015, Bhadouria *et al.* 2017, Venkidasamy *et al.* 2019). These PAP enzymes help to represent the largest group of acid phosphatases and are characterized by the purple or pink color they give out in water solution. It happens because of a charge transfer transition between the *Tyrosine resid*ue to Fe (III) in a binuclear metal center. In accordance to their protein size, purple acid phosphatases can be differentiated into two different forms: The low molecular mass one (called LMM, size about 35 kDa) and the one having high molecular mass (called HMM, with size 55–60 kDa) PAPs. The monomeric low molecular mass proteins can carry only the catalytic domain. On the other hand, the high molecular mass purple acid phosphatases are either homodimeric or heterodimeric proteins in nature, where each of the subunits has an unknown functional N-terminal domain and a C-terminal domain in which the active site is present (Schenk *et al*. 2013). A phylogenetic tree of purple acid phosphatase in plants (Fig. 3 and 4) can well depict its characteristic properties.

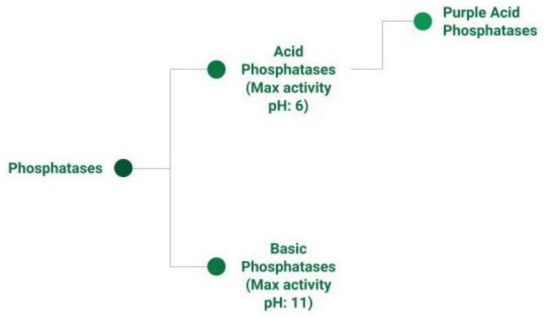

Fig. 3. Purple acid phosphatase, an acid phosphatase.

The acid phosphatase activity and the external secretion in lentils is found to be genotypic dependent as also observed in other crops. ILL6002 does not show significantly greater acid phosphatases like other PD tolerant genotypes implying this genotype might have some strong other means of adaptation. PAPs like AtPAP15, AtPAP23, NtPAP, OsPHY1, GmPhy have been found to exhibit increased activity on phytate. Further attempts are being made to identify the phosphate deficient responsive purple acid phosphatase (PAP) genes in various plants and agricultural crops. In a study related to *Arabidopsis thaliana,* two PAP genes of Arabidopsis, AtPAP26 and AtPAP17 were studied in relation to phosphate deficiency and concentration of phosphate in the soil. The study results demonstrated the activation of AtPAP26 and AtPAP17 genes to compensate for the loss of function of each other, which further facilitates the growth and development of Arabidopsis (Farhadi *et al.* 2020). These two genes are also involved in the salt tolerance activity of Arabidopsis (Abbasi-Vineh *et al.* 2021). In the case of soybean, about 38 GmPAP isozymes could be identified in its genome. The transcripts of 19 GmPAP contributors within the leaves and 17 in the roots were upregulated at about 16 days of Pi-deficiency in spite of the dearth of a response for any GmPAP contributors to Pi-starvation at 2 days (Zhu *et al.* 2020). In another stud, MtPHY1, a phytase gene along with a purple acid phosphatase gene MtPAP1, were isolated from *Medicago truncatula* and were then introduced into white clover (*Trifolium repens* L.) via Agrobacterium-mediated transformation. The transgenes were triggered by the root-specific MtPT1 promoter or the constitutive CaMV35S promoter. The study results concluded that the transgenic expressions of MtPHY1 or MtPAP1 in the white clover plants enhanced their abilities of organic phosphorus utilization in response to Pi-starvation (Ma *et al.* 2009). Another interesting study reported the high level of production of the secondary metabolite chicoric acid through intracellular phosphate supply and extracellular phosphate limitation in *Echinacea*

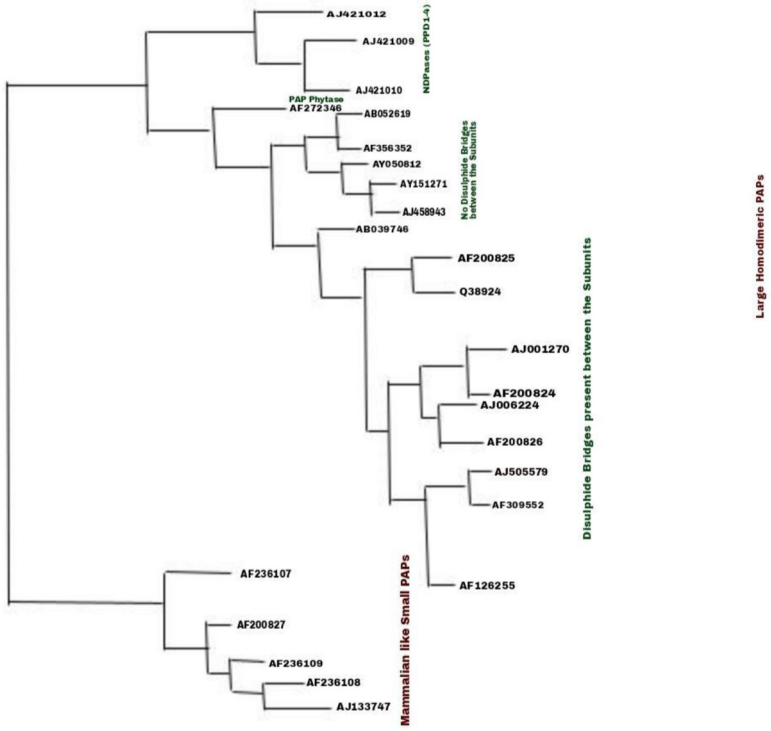

Fig. 4. Modified phylogenetic tree of purple acid phosphatase in plants, from the studies of Olczak and Watorek 2003.

purpurea hairy roots (Salmanzadeh M *et al.* 2019). Cloning of the PAP genes and their respective roles in secretion of purple acid phosphatase in a number of plants, along with their abiotic stress tolerance tactics are in full progress in different studies. It might help in improving the abiotic stress including phosphate deficiency tolerance in the far future.

DISCUSSION

The idea of the brief study conducted in this report was for studying the conditions and results of phosphate deficiency in different plants and agricultural crops, thereby emphasizing on purple acid phosphatase genes in those plants which can help in phosphate acquisition and its recycling in the plants. Being a key ingredient in facilitating plant growth, development and metabolism, the deficiency of phosphate in the soil abruptly affects the plants. Either phosphate fertilizers have to be supplied from an external source or the internal phosphate usage has to be limited by the plants. Some plants scavenge phosphate from external sources to fight with this adverse situation. Many plants adapt a series of biochemical and morphological adaptations to effectively protect themselves from the periods of phosphate deficiency in soil. The acid phosphatases play an important role in this part. Acid phosphatases help to catalyze the hydrolysis of phosphate from a broad range of phosphate monoesters having an optimum acidic pH, thereby helping the plant in the acquisition, transporting and recycling of phosphates. Purple Acid Phosphatase or PAP is a type of acid phosphatase which is extremely relevant in this topic. Different groups of scientists have been working on different plants to identify the PAP genes of interest which would lead them to find a solution to the problems faced by the plants due to phosphate deficiency in the soil and the ways they can efficiently manage this situation. PAP genes have been identified in a number of plants till date including soybean, arabidopsis, maize, rice. A number of biotechnological studies like proteomics, genomics, genetical analysis have been also implemented to mark these genes. According to the researchers, if

they can successfully identify and mark the putative purple acid genes in different plants, they would be able to scientifically modify and design the genes in such a manner that the plants would be able to tolerate long periods of phosphate deficiency. Also, the problems faced by the plants (stunted growth, root modification) could be reduced simultaneously. With the advancement of scientific technologies, we can soon hope to find a solution to this problem by designing some transgenic crops to tolerate this long period of soil phosphate deficiency.

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