EPH - International Journal Of Agriculture And Environmental Research
ISSN (Online): 2208-2158
Volume 10 Issue 01 January 2024
DOI: https://doi.org/10.53555/eijaer.v10i1.97

AVAILABILITY OF PHOSPHOROUS TO THE SOIL, THEIR SIGNIFICANCE FOR ROOTS OF PLANTS AND ENVIRONMENT.

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Abstract:

In addition to being a crucial component of plant growth, phosphorus (P) is also important for preserving the sustainability of the environment. The accessibility of phosphorus in soil, its vital importance for plant roots, and the wider environmental effects of managing it are all covered in this abstract. The intricate interaction of multiple elements, including soil pH, biological material content, and microbial activity, determines the availability of phosphorus in soil. It is essential to comprehend and maximize phosphorus availability to guarantee a sufficient supply of nutrients to plant roots. Plants absorb phosphorus mostly in the form of phosphate ions (H2PO4). A deficiency of phosphorus in the soil can cause stunted growth, lower agricultural yields, and general plant health problems. Plants have developed several tactics to improve their uptake of phosphorus, such as the exudation of organic acids from their roots and as well as symbiotic relationships with mycorrhizae fungus. These adaptations demonstrate how important phosphorus is to plant life and ecological health.

Keywords: *Phosphorus, Plant Growth, Sustainability, Soil Accessibility, Environmental Effects, Microbial Activity Nutrient Supply, Phosphate Ions*

1.1. INTRODUCTION

The physical arrangement of a root structure inside the soil is termed as "root system architecture" (RSA). It is created by changing the rate of growth and angular orientation of each root that makes up the root systems, is necessary for plants to efficiently absorb water and nutrients, and it has a big influence on fertiliser use and agricultural productivity globally because of the environment's heterogeneity, an RSA is composed of very flexible nature and variety of root types with unique functionalities (Grossman JD, Rice KJ 2012) For growth and development, plants need macronutrients, which include phosphorus (P), nitrogen (N), and potassium (K). The growth, quality, and yield of crops are significantly impacted by these nutrients.(Poirier and Bucher et al., 2002).Phosphorus is a major element of biomolecules like phospholipids, proteins and nucleic acid and also involved in many metabolic processes like energy conversions and photosynthesis. Plants absorb the phosphorus directly from H_2PO_4 (Ham, B.K., Chen, and Lucas (2018). Pi content is typically higher in the top soil layers and declines with depth as a result of its slower transport as well as powerful retention in soil. (Lynch, 2007, 2013). Phosphorus is not easily available to plants due to its considerable soil mineral fixation. (Lambers H, Martinoia E, Renton M.2015). The fossil-fuel-based phosphate rock is usually used to make P fertilizer, which is utilized to circumvent the phosphorus constraint on agricultural productivity. (Wang *et al*., 2016a). The main advantage to use P fertilizer is that it provide phosphorus in very accessible form i-e H_2PO_4 and H_3PO_4 which are readily taken up by the plants (Behera *et al*., 2014).

Nevertheless, Plants only use up 20% of provided P fertilisers, with the remainder, or 80%, lost in the surroundings. (Syerset et al., 2008). Additional factors that restrict the availability of phosphorus include the soil the pH level, the immobilization process adsorption, chelating and phosphorus precipitation by iron and aluminium (Al) which are present in acidic soils, and calcium (Ca), which is present in alkaline soils. (Hanlon *et al*., 2018; Pennand Camberato *et al*., 2019). The root system architecture's responsiveness to low P situations varies significantly during development. Numerous research and analyses have been demonstrated that genotypic adaptability to phosphorus stress condition makes it easier for plants to acquire phosphorus by enabling modifications to root architecture (Roached et al. (2010), Pe'ret et al. (2011), Wang et al.(2009) Phosphorus deficient roots should express more transcriptional and post transcriptional Pi transporters to enhance phosphorus uptake from the soil. Gu et al., 2016b; Huang et al., 2013; Nussaume et al., 2011. P deficiency cause root exudates greater or lesser extent in most plant species. These exudates include RNases, Acid phosphatases, Carboxylates and proton all of which are essential for root growth during low Phosphorus condition (Wang and Lambers *et al*., 2020a). Plants can improve their phosphorus acquisition efficiency (PAE), or their capacity to absorb P from the soil, and their phosphorus usage efficiency (PUE), or their capacity for crops to use the P they have acquired to generate yield or biomass.(White et al., 2013, Wu et al., 2013, Dissanayaka et al., 2018; Rose et al., 2011; White et al., 2013). In calcareous soil localized availability of ammonium sulphate and superphosphate promote the growth of root, acidified the rhizosphere, enhance P utilization and acquisition efficiency. The root system of many plant species can be influenced by soil characteristics such as moisture content, temperature, pH, buffering ability (Fageria *et al*., 2014). Additionally, genotypes, Root length, Root hair, density of lateral roots as well as rhizobium, greatly influence P uptake from the soil (Shen *et al*., 2011; Fageria *et al*., 2013).

1.2. Phosphorus availability to soil

P-deficient soils can be of two main types: (a) soil with lower total P content and (b) Despite having a high total P concentration, the soil has limited plant P availability because P is retained well and moves more slowly.

Even in soils with high levels of P, only 1% of the P is freely accessible and soluble, while the remaining 90% is often securely bonded to soil particles in either inorganic or organic form (Jewell et al., 2010).

The soil has access to between 30 and 65 percent of the phosphorus in the soil in organic form, which is unavailable to plants, while the remaining portion is present in inorganic form. The naturally occurring forms of phosphorus in soil include decomposing plants, animal remains, and soil microorganism. (Requejo and Eichler-Löbermann *et al*., 2014).

P is only absorbed in its oxidized state by Pi, a weakly mobile and cellular ion with a strong capability to establish a connection to several organic and cations molecules in the soil. Pi resides in the pH range of 5 to 6, and plants prefer to absorb it in the form H_2PO_4 (Maharajan et al., 2018). It is the least phytoavailable nutrient because its availability greatly decreased as it is formed complexes of calcium, iron oxide and aluminum resulting in "Pi fixation" or "Pi retention" in the soil. Since most of the Pi is inaccessible to plants, soils frequently have total Pi reserves that are larger than the Pi accessible to crops Gaxiola et al.(2011). The intracellular concentration of Pi (520 mM) required for the best plant development and yield are far higher than the soluble Pi concentrations found in many soils throughout the world, which range from 1 to 10 mM (Tran et al., 2010).

Researches on the phytoavailibilty of organic P form in soil describe that it relies on environmental factors and condition as well as rhizosphere microbial activity. Plants are unable to utilize the natural P in the soil or added phosphorus from fertilizer until it is hydrolysed or digested to release P in the plants roots or in microbial soil solution. (Alori *et al*., 2017; Ali *et al*., 2019b). According to meta-analysis study crop yield would not improve by the over use of phosphorus in the soil rather it degrades the aquatic quality (Ros *et al*., 2020). The factors which affect the P availability in soil is depend upon the organic matter content, environmental factors and buffering capacity. Higher soil acidity, reduced cation exchange and greater water retention capacity are particular characteristics of soil which affect the P availability in soil (Sanderson and Sanderson *et al*., 2006). Immediately after fertilizer application more than 80% of the P might become inaccessible to plants due to adsorption, precipitation (usually caused by an interaction with Al3+ and Fe3+ in acidic soils and Ca2+ in calcareous soils or microbial inactivation (Gustafsson *et al*., 2016; Roberts and Johnston *et al*., 2015). It is very necessary to understand the long-term dynamics of phosphorus in soil which is essential for taking full advantage of legacy P (Liu et al., 2014a).

Followings are classification of the inorganic forms of P in the soil.

1-Plant available (Soil solution form) 2-SORBER phosphorus 3-Mineral phosphorus

Plant available (Soil solution phosphorus) Phosphorus in soil solutions that is easily absorbed by plants is known as plant accessible phosphorus. It is composed of inorganic phosphorus that has been dissolved into water or soil solutions. Sorber phosphorus is composed of inorganic phosphorus compounds that are bound to the clay's surface iron and aluminium oxides. Slowly released phosphorous comes from this lake. The accessibility of Phosphorus in mineral rich soil like Podzol varies depend on the soil's organic matter concentration, mineral content, buffering ability, management practises, as well environmental conditions. (Quintero *et al*., 2003; Kang *et al*., 2009).

P availability increased by 4.6 times on average across all soil types when fertilisers and charcoal were added, especially in acidic soils (pH 6.5). As compared to moderate and alkaline soil types, there is 5.1 fold greater P availability (Glaser and Lehr *et al*., 2019).Immobilization and mineralization, two methods that are predominantly mediated by soil microbes, result in substantial P fluxes between organic and inorganic Phosphate pools in the soil. (Oberson and Joner *et al*., 2005; Richardson and Simpson *et al*, 2011).

1.4. Phosphorus uptake in roots and its mobilization mechanism by soil micro organism

Plants need a variety of different mineral nutrients to carry out essential functions for healthy growth and development. A crucial nutrient for plant development and growth, phosphorus is used by plant for carrying out these processes. The majority of the Pi accessing the root is absorbed by the symplasm in the outermost cell layer or root hairs (RH). The two methods by which plants absorb Pi are known as direct uptake and AMF-mediated uptake. Direct uptake involves a direct interaction with the root system and the soil solution. (Smith 2011).

PHT1 transporters are typically used for Pi uptake, export, utilisation, and remobilization since they serve as the main route for Pi entrance into plants through soil solutions. Most PHT1 genes are highly expressed in roots., particularly in root hair cells, root caps, and outer cortex where Pi uptake was improved. (Schunmann et al., 2004a). The expression of several PHT1 gene in roots was independent no matter how much Pi is present in soil-based solutions (Shin et al., 2004; Seo et al., 2008). PHT1 proteins have also been discovered to transport other solutes, including phosphate, nitrate, arsenate, selenite, sulphate, and chloride ions. (Zhang et al., 2014; Gu et al., 2016).There are nine PHT1 genes in Arabidopsis (AtPHT1; 1 to AtPHT1; 9). (Mudge *et al*., 2002; Shin *et al*., 2004) 13 PHT1 genes present in rice (Paszkowski *et al*., 2002; Liu *et al*., 2011) and in soybean 15 PHT1 transporter genes are present (Qin *et al*., 2012; Fan *et al*., 2013).

According to in silico investigations,PHT1 proteins all share the same structure and arrangement having 12 putative membrane-spanning sections split into two distinct sets of six domains that are connected by a charged hydrophilic loop,On the interior of the cell, both N- and C-terminus ought to be in line. (Rausch and Bucher *et al*., 2002; Liu *et al*., 2011). Pi absorption in Arabidopsis reduced by approximately 57% under low P conditions when AtPHT1; 1 and AtPHT1;4 are disturbed. AtPHT1;4 plays a significant function in acquiring phosphorus in P-starved plants , approximately 32%–43% of The mineral phosphorus uptake and an overall 32%–43% of Pi uptake from the soil through AtPHT1;2 and AtPHT1;3. Ayadi et al., 2015; Shin et al., 2004; Misson et al., 2004.) Phosphorus distribution into the plant's aerial portions and xylem loading are the responsibility of transporters.Pi is transported through the root cortex to the xylem via phosphate 1 (PHO1). It also contributes to Pi export from the cell and a drop Pi concentrations in the vacuole, along with root-to-shoot Pi export. The expression of (AtPHO1) A. thaliana PHO1 in shoot led to an increase in shoot Pi content and a strong release of Pi into the extracellular medium, further demonstrating its function.Stefanovic et al., 2011; Arpat et al., 2012).

Through a variety of mechanisms microorganism can increase the plant capacity to enhance P acqusition that can be summed up as follows: 1-By Increasing root growth, either by extending roots (e.g., through mycorrhiza associations) or hormonally stimulate root growth, lateral root branching, or roots hair production ; and through Phytostimulating (Richardson et al., 2009a; Hayat et al., 2010). 2- By changing the way of absorption, the soil solution contains more orthophosphate ions, and the movement of organic phosphorus is either directly or indirectly promoted. (Seeling and Zasoski *et al*., 1993) 3- By incorporating metabolic pathways which are thought to be effective in mineralizing and solubilizing of Phosphorus (Richardson *et al*., 2009a). Phosphorus (P) may be more easily soluble from minerals when it is released by microbes in the form of LMWOAAs, protons and other secondary organic compounds (Jones and Oburger, 2011). In actuality, P-solubilizing microorganisms can be categorised as 0.5-0.1% of the soil's fungi and 1-50% of soil bacteria. (Gyaneshwar et al., 2002). The rhizosphere is a type of bacterium known as Plant-growth-promoting rhizobacteria (PGPR). which may enhance PAE mainly by influencing the accessibility of nutrients, such P, or by tangentially generating phytohormones or developmental regulators for plant development and growth. (Richardson et al., 2009).

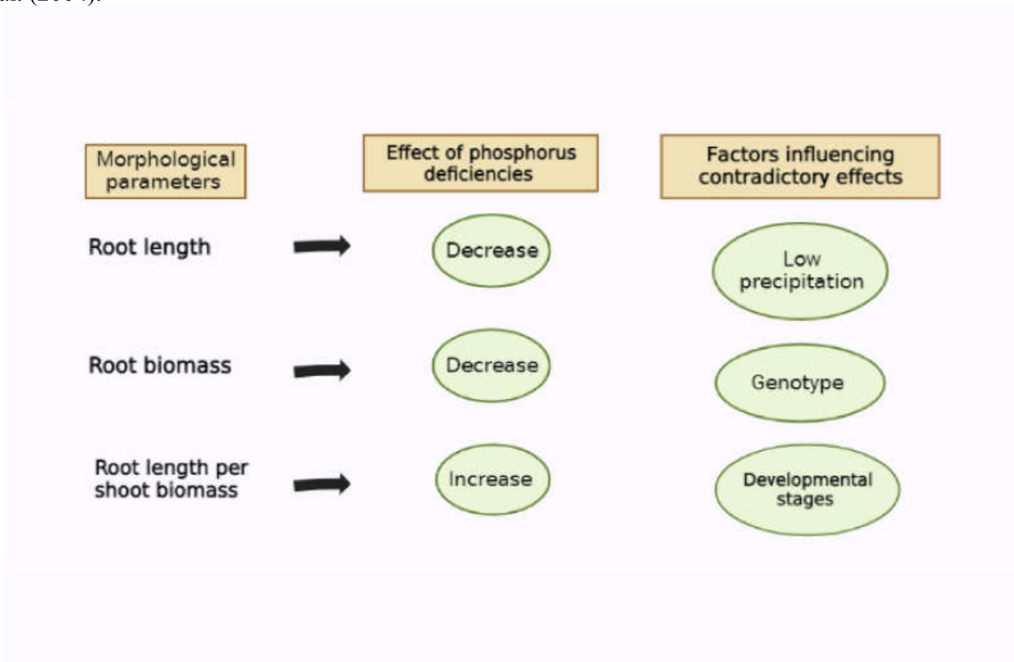
Serial number	***Gene***	***Major function***	***References***

1-	GmACP1	The Overexpression of this gene increase phosphorus efficiency by 11–20% in soybean hairy roots.	Zhang D et al.,2014
2-	ZmPTF1	Enhances maize's ability to tolerate low phosphorus levels by controlling root development and carbon metabolism.	Li Z et al., 2011
3-	OsPTF1	Increases the phosphorus content of transgenic plants by 30%.	Yi K et al.,2005
4-	OsPht1-8	Distribution and remobilization of phosphorus	Jia H et al.,2011
5-	AtPHR1, OsPHR1, OsPHR2	Increase the content of phosphate in the shoot and the expression of different phosphorus transporters.	Wu P, Xu JM .2010
6-	OsPT1, OsPT6	uptake of phosphorus and increase phosphorus accumulation	Zhou J et al.2008 Seo HM et al.,2008
7-	LaGPX-PDE1 , LaGPX-PDE2	control the growth of root hair and promote glycerophosphodiester breakdown	Cheng L et al., 2011
8-	AtPHO, AtPHO1-H1, AtPHO1-H10	During phosphorus starvation the overexpression of this gene increase phosphorus acquisition	Stefanovic A , et al.,2007
9-	GmEXPB2	The expression of this gene increases lateral root elongation, which increases phosphorus uptake.	Guo WB et al., 2011
10-	AtPAP15	Enhances the leaf's intracellular APase activity, which in turn improves phosphorus usage effectiveness and yield.	Wang X ., .2007
11-	PvPS2-2	Increase roots dry mass, root hair densities and phosphorus concentration as a means of increasing the efficiency of phosphorus acquisition in stem hair.	Liang CY et al., 2012
12-	LASAP2, OsPAP10a (NC_008394.4)	Under phosphorus-deficient environments, increase production of dry matter and phosphorus accumulation.	Wasaki J et al., 2009
13-	AtAVP1OX, LeAVP1D-1, LeAVP1D-2	When there is a phosphorus shortage, the concentration of root hairs increases.	Yang H et al.2007
14-	At2g01060	irrespective of phosphorus availability, increases the accumulation of phosphorus in the shoot	Lundmark M et al.,.2011
15-	GmEXPB2 (β-expansin)	Improved response of the root system to Pi shortage, which improved soybean PE	(Guo et al. 2011)

1.5. Phosphorous use efficiency

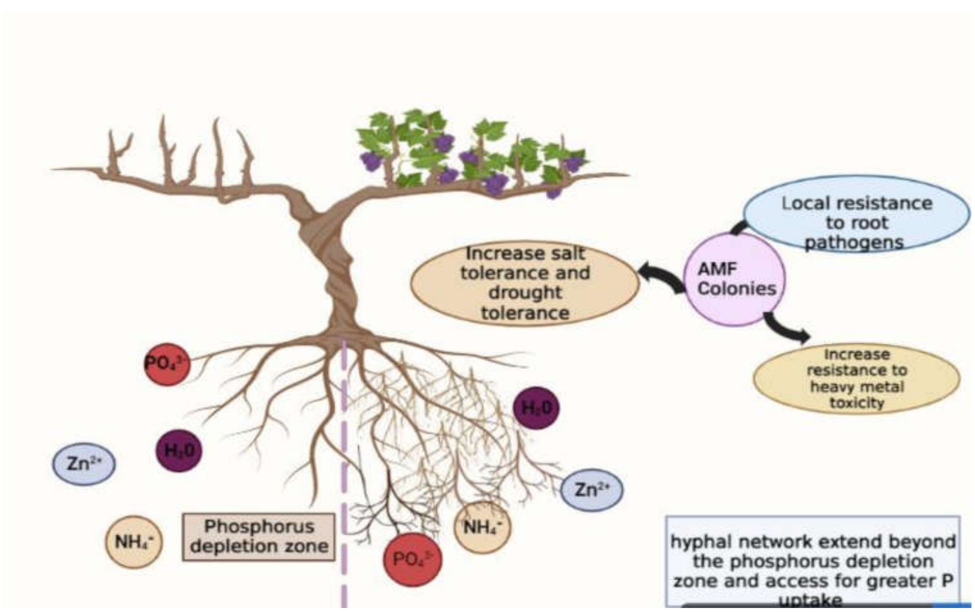
The poor availability of phosphate (Pi) and its limited flexibility to plants hinder plant growth and agricultural production. Sun et al. (2018), Kochian (2012), Shen et al. (2011), etc. Plants only absorb 20 to 30 percent of the provided P (Vance et al., 2003; Richardson and Simpson, 2011). In many agroecosystems P containing fertilizers are used to ease these limits. In aquatic settings, this state causes eutrophication and dangerous algal blooms, results from phosphorus (P) discharge from soils, which leads to the phosphorus (P) enrichment of water bodies (Zak *et al*., 2018). Plants can increase phosphorus use efficiency by improving their P acquisition efficiency (PAE, or their capacity to absorb P from the soil) or P utilization efficiency (PUE, or their ability to use the P acquired to produce biomass or yield) (Hammond et al., 2009; Rose et al., 2011; White et al., 2013; Wu et al., 2013; Dissanayaka et al., 2018). The emphasis on improving PAE has grown over the past few decades which includes increasing root density and increasing the number of lateral root branches (Hammond *et al*., 2009; George *et al*., 2011; White *et al*., 2013; Sun *et al*., 2018; Wang *et al*., 2019). The solubilization of soil P is facilitated by increased root exudation of protons, organic anions, and enzymes (Pang et al., 2018; Robles-Aguilar et al., 2019; Wen et al., 2019).

Microbes and their interactions which include arbusclar mycorrhizae fungi that increase the soil volume used to acquire phosphorus. Since shallowness root system may affect P uptake because the top layer of soil typically rich in phosphorus as a result, plant adaptation in root structure may help to boost phosphorus acquisition efficiency (PAE) (Van de Wiel *et al*., 2016). Additionally, modifications in root architecture that include basal root horizontal growth, shallower growth angles, longer lateral roots, more root hair, and adventitious axial root lengths are crucial for P acquisition. (Lynch and Brown, 2001; Vance et al., 2003;Richardson et al., 2011; van de Wiel et al., 2016). PUE (Plant use efficiency) could be classified into PAE (Plant acquisition efficiency) and IPUE (White and Veneklaas, 2012).By improving PAE Efficiency of phosphorus utilization (PUE) in P-deficient soils can be increased, This might be accomplished by picking crop species with improved root system, higher hairy production in roots, phosphate transporter, root exudates, and root symbiosis, as well as genetic make-up, uptake, and internal utilisation efficacy. A shallow root design allows for the enlargement of the roots inside a Phosphate-fertilized soil containing an inorganic P pool, as opposed to a deep root architecture that promotes root proliferation deep within an uncultivated or low P soil. P acquisition through the rhizosphere is favored by axially roots, especially basal roots, which extend close to the soil's surfaces and permit other roots axes to be closer to topsoil. Fujita et al. (2004).



1.8. Symbiotic microbial interactions improve soybean phosphorus efficiency (PE).

More than 65% of all land plant species that are known to exist (n > 200,000) form the mycorrhiza (AM) symbiosis, considered most important symbiosis on the planet, because of its beneficial effects on soil's fertility. All legumes are included in this, along with numerous other essential agronomic crop species like rice, maize, and wheat (Uddin et al., 2011). Pi is released into plant cells by the AMF from pools of Pi that remain inaccessible to plant roots. Fungi that intimately grow between and within the cells of the roots and form heavily branching hyphae are associated with AMF. Arbuscules then form at the hyphal ends and are encircled by the plasma membrane of root forming effective interface for communication and nutrition exchange between two species. Outside of the roots, fungus hyphae are widely dispersed and easily pass through small soil pores to access nutrients like phosphorus. (Yang et al., 2012). Using phosphorus transporters found in cortical cells, fungi absorb carbon from host and transfer phosphate for host uptake to the periarbuscular interface (Smith at al., 2008). In higher phosphorus conditions (HPC), the beneficial effects of AMF colonisation were significantly diminished (Paszkowski et al., 2002). Lower phosphorus conditions have resulted in an up to 30-fold increase in AMF-regulated Pi absorption. (Guimil€ et al., 2005).

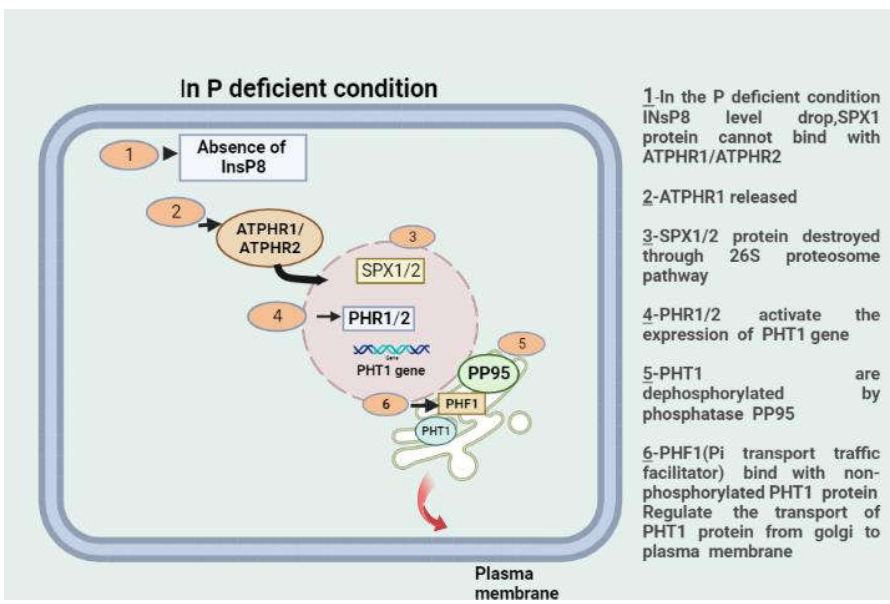


In a symbiotic system rice absorbs more than 70% of phosphorus by AMF (Yang et al., 2012). In agricultural contexts, Auxin and ethylene concentrations influence the host plant's development of lateral roots and hairy roots. (Rubio at al., 2009).

It is very important for cereal crops to have the proper AMF that decreases the need for phosphorus fertiliser, environmental pollution, carbon consumption, and provides a greater amount of to the host. In an extremely low P soil condition, field treatment of soybean with efficient rhizobia has resulted in a 95% rise in tissue P content. (Qin et al. 2012).Rhizobia led to a shallow and broad root system because of nodule development, enhanced total length of the root, root surface area. (Yang et al. 2017) Rhizobia-soybean symbiosis affect the expression of Pi transporter genes (GmPT1 to GmPT14) in the Pht1 group. (Wang et al. 2016b)High-affinity Pi transporter GmPT5, displayed significant expression to physiological response of soybean roots during condition of low phosphorus. Further research revealed the key role of GmPT5 which is situated in plasma membrane of root that facilitate the transfer of Pi to the nodules across the membrane. Through transformation of the hairy root the usage of Agrobacterium rhizogenic has proved effective, used to enhance symbiotic interaction between roots and microbial populations present in the rhizosphere (Yamada et al. 2012; Kereszt et al. 2007). The hairy roots transformation approach promoted nodulation, which increased the symbiosis between soybean and rhizobia. (Yang et al. 2010).

Phosphate transport and signalling systems that contribute to Pi homeostasis at the cellular level

In order to adjust to the decreased supply of Pi, plants have developed extensive regulatory systems. These regulatory mechanism involve both internal and outer sensing, concentrations of phosphorus along with systemic and local signalling pathways. Plant's phosphorus metabolic balance is controlled by systemic reactions, which are based on the whole plant's Pi state, Pi acquiring capability, P transfer, remobilization, and net Phosphorus usage efficiency Ham et al. (2018); Zhang et al. (2014).



The systemic indicators Pi, RNAs, InsP, sugars, and hormones have all been found to internally interact with the Pi state of the entire plant. (Balzergue et al., 2011).The disruption of AtIPK1 gene in Arabidopsis decreased the amount of InsP6 in vegetative tissues, also have an effect on Pi sensing. Pi homeostasis is regulated through the interaction of InsP molecules with the domain containing protein SPX (Wild et al., 2016), that play a role in Pi sensing. OsSPX3/4/5/6 and AtSPX1/2 are the basic and functional repressors of OsPHR2 and AtPHR1 Shi, 2014; Wang, 2014c; Zhong, 2018; Lv et al., 2014; 2014; Wang et al., 2014c) the key controllers of Pi signalling and homeostasis in rice and Arabidopsis (Zhou et al., 2008; Rubio et al., 2001).

Increase level of InsP encourage combination of SPX protein through OsPHR2 and AtPHR1 (Wild et al., 2016). When InsP levels fall, OsPHR2 and AtPHR1 cannot bind to SPX protein. In order to regulate the expression of PSR-related genes, OsPHR2 and AtPHR1 are released. A 26S proteasome pathway is used to degrade SPX4/6; this releases PHR2 into the nucleus and causes PHO1:H1 and PSR genes to be produced. Due to WRKY6 degradation being controlled by the ubiquitin E3 ligase PRU1, PHO1 expression is unrepressed. PHT1 gene expression is activated when PHR1 and PHR2 connect to PIBS.PHT1 proteins (OsPHT1; 8and OsPHT1; 2) are dephosphorylated by phosphatase PP95, and PHF1 (Pi transport traffic facilitator) helps PHT1 migrate from the ER to the PM by binding with non-phosphorylated PHT1 proteins.

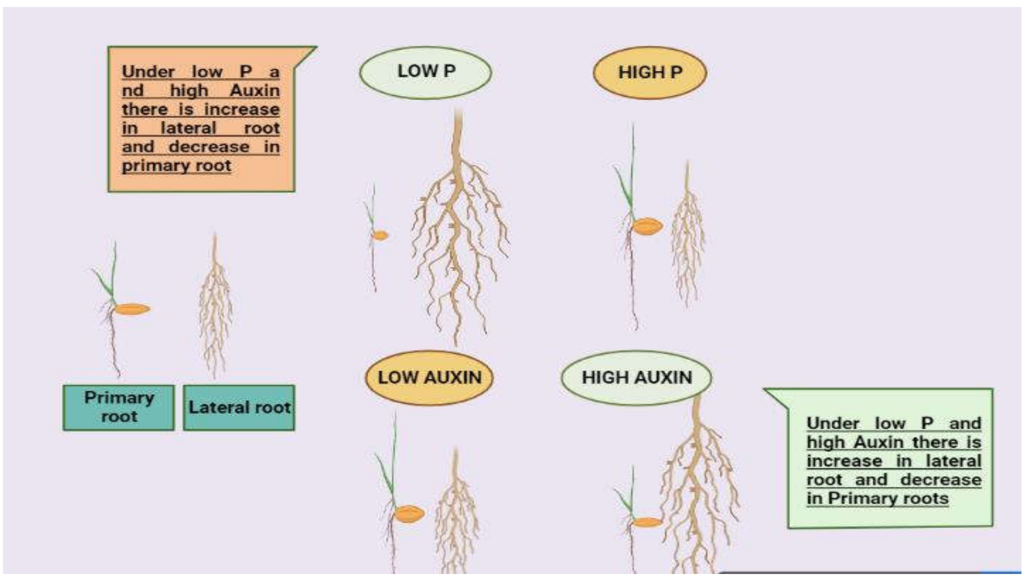
2.0. Root system architecture is affected by limited P availability

The configuration of the roots, their depth, the dimension and quantity of their external roots and hairs on the roots, as well as how they spread out throughout the soil, all contribute to the root system's architecture. Additionally, the management of fertilisers and the pH level of the rhizosphere have a significant impact on how roots and phosphorus are distributed in the soil profile. (Jing and co.2010)

2.1. Development of primary roots in responses to low P:

Species and genotype differences affect the primary root's adaptation response to low P. Substantial P deficiency situation reduces the growth of primary roots as its initial reaction. (Williamson et al., 2001; Jain et al., 2007; Tyburski et al., 2010, 2012; Pe'rez-Torres et al., 2008). A primary root, which emerges first in both dicots as well and monocots, is made of meridional tissue that is formed during embryogenesis. The primary root's growth becomes restricted after getting into contact with the low-P medium; In the region of root extension, this is associated with an overall reduction in differentiation of cells and proliferation (Ticconi et al., 2004; Sa 'nchez-Caldero 'n et al., 2005 ; Svistoonoff et al., 2007). In low phosphorus soil condition, shallow roots that effectively utilize topsoil elementary resources (Lynch and Ho, 2005; Ho et al., 2004).)

With the discovery of numerous genes and gene transcription factors (TFs), it is now known that P uptake, transport, and the remobilization in addition to the regulation of primary elongation of roots in an environment of low P availability are all crucial processes. Seventy percent of all root phosphorus transport activity is accounted for by PHT1; 1 -9 (PHOSPHATE TRANSPORTER 1; 1 - 9) group of nine high-affinity Pi transporters (Shin et al., 2004). PHT1; 5 has recently been found to negatively affect the growth of primary roots as a result of decline in P availability (Nagarajan et al., 2011).



2.2. Low P concentrations cause lateral roots to grow.

Additionally, decrease Pi availability encourages lateral root synthesis and lengthening, root hair development and length of roots, and drastically alters the roots system's spatial layout. As soil exploration is increased by lateral roots, it increases the absorptive surface to absorb more P (Zhu et al., 2005a).and solubilisation of phosphorus (Lynch, 1995, 2007). Increased lateral root density results from the relocation of mitotic activity to the site of lateral root development under reduced concentration of phosphorus (Tyburski et al., 2012).However, there are species- and genotype-specific differences in how lateral roots respond to P deficiency.

Lines that carried the "many short lateral roots" genotype demonstrated higher shoot biomass and a greater P-acquisition efficiency in low-P conditions than lines having "a few lengthy lateral roots." Compared to genotypes with limited lateral roots, the genotypes having greater lateral root density revealed higher growth rates, biomass residue, and P uptake. (Zhu et al., 2005a, 2005b). Relationship among root system architecture and P-acquisition efficiency in different crop species has also been research. Role of LRs for uptake of the nutrients and growth in rice was assessed when wild type is compared with the mutant deficient in LR production. (Liu et al., 2013). Findings demonstrated that, in nutrient-sufficient conditions, LRs are important for acquiring elements with a lower mobility, such as phosphorus, magnesium, and Copper. However, in the pot trials, when soil P availability increased, LRs' apparent contribution to shoot and root biomass increased. Recent research of elevated rice cultivated under condition of Large LRs are more significant than tiny LRs for overall phosphorus absorption in dehydrated conditions, as demonstrated by phosphorus deprivation. A Upland rice produced in P-deficient soil recently proved this in a study that under dry circumstances, LRs having large area considered more important than short LRs for total P absorption. (De Bauw et al., 2020).

2.4. Root hair development in adaptation to low phosphorus levels :

When P levels are low, a plant's initial response is to produce more root hair.. (Jain et al., 2007; Ma et al., 2001). a tubular-shaped roots cell termed as trichoplast, is the site of root hair production a root architectural feature and are crucial to the acquisition of vital plant nutrients. Root hair is an essential architectural feature to obtain essential plant nutrients from soil and easy way to investigate a broad rhizosphere region.

In model plant, Arabidopsis, Approximately more than seventy percent of the root surface regions are covered with root hair. (Parker et al. (2000). Cells in the lateral root cap and xylem progressively assemble auxin as a result of local signalling of Low P in the soil (Bhosale et al., 2018; Wendrich et al., 2020). The TMO5/LHW gene transcription factor (TF) complex promotes the synthesis of cytokinin in response to auxin that has accumulated in the xylem. In this case, cytokines functions as a mobile signal, increasing the root hair density.

Increased density of root hair and the growth of lateral roots contribute to greater phosphorus acquisition efficiency. (Gilroy and Jones, 2000; Wang et al., 2016). The growth of root hairs is influenced by auxin, sucrose, and ethylene Song and Liu (2015); Niu et al. (2013). According to certain reports, auxin homeostasis is essential for the extension of root hairs when there is little exogenous P available. Song and Liu (2015); Niu et al. (2013). For conserving P intake and stability in yield in low P soil areas, RH characteristics may be effective strategies.

2.5. Conclusion:

In summary, the amount of phosphorus existing in soil is an essential element that influences the development and growth of the roots of plants and has a big impact on the ecosystem. The availability of phosphorus, its significance for development of plant roots, and its effects on the surrounding ecosystem have all been covered in detail in this review article. An important mineral for plant growth, phosphorus is especially important for the development and maintenance of root systems. Sufficient availability of phosphorus promotes strong root growth, which in turn improves nutrient intake, water absorption, and general plant health. On the other hand, a lack of phosphorus can result in decreased plant output, slowed root growth, and eventually financial losses in agriculture.

A balance must be struck between supplying plants with enough phosphorus and avoiding overusing it, which can result in environmental issues such soil erosion, eutrophication of aquatic environments, and water pollution. Mitigating these environmental issues requires sustainable phosphorus management techniques, such as accurate fertilizer application, organic matter recycling, and the use of phosphate-efficient crop cultivars.

In summary, soil phosphorus availability is a complex problem with significant effects on agricultural productivity, plant root growth, and environmental sustainability. A comprehensive strategy that incorporates environmental stewardship, agricultural efficient methods, and scientific research is needed to address these issues. By doing this, we can make sure that the nutritional requirements of plants are met, the environment is protected, and our food supply is secure for future generations.

References

[1]. Ai, P., Sun, S., Zhao, J., & Xu, G. (2009). Regulation and function of Pht1 family phosphate transporters in rice.

[2]. Alori, E. T., Glick, B. R., & Babalola, O. O. J. F. i. m. (2017). Microbial phosphorus solubilization and its potential for use in sustainable agriculture. *8*, 971.

[3]. Arpat, A. B., Magliano, P., Wege, S., Rouached, H., Stefanovic, A., & Poirier, Y. J. T. P. J. (2012). Functional expression of PHO1 to the Golgi and trans-Golgi network and its role in export of inorganic phosphate. *71*(3), 479-491.

[4]. Ayadi, A., David, P., Arrighi, J.-F., Chiarenza, S., Thibaud, M.-C., Nussaume, L., & Marin, E. J. P. P. (2015). Reducing the genetic redundancy of Arabidopsis PHOSPHATE TRANSPORTER1 transporters to study phosphate uptake and signaling. *167*(4), 1511-1526.

[5]. Balzergue, C., Puech-Pagès, V., Bécard, G., & Rochange, S. F. J. J. o. E. B. (2011). The regulation of arbuscular mycorrhizal symbiosis by phosphate in pea involves early and systemic signalling events. *62*(3), 1049-1060.

[6]. Bates, T., Lynch, J. J. P., cell, & environment. (1996). Stimulation of root hair elongation in Arabidopsis thaliana by low phosphorus availability. *19*(5), 529-538.

[7]. Behera, M., Bhattacharyya, S., Minocha, A., Deoliya, R., Maiti, S. J. C., & materials, b. (2014). Recycled aggregate from C&D waste & its use in concrete–A breakthrough towards sustainability in construction sector: A review. *68*, 501-516.

[8]. Bhosale, R., Giri, J., Pandey, B. K., Giehl, R. F., Hartmann, A., Traini, R., . . . Swarup, K. J. N. c. (2018). A mechanistic framework for auxin dependent Arabidopsis root hair elongation to low external phosphate. *9*(1), 1409.

[9]. Bicharanloo, B., Salomon, M. J., Cavagnaro, T. R., Keitel, C., Brien, C., Jewell, N., . . . Soil. (2023). Arbuscular mycorrhizae are important for phosphorus uptake and root biomass, and exudation for nitrogen uptake in tomato plants grown under variable water conditions. 1-18.

[10]. Brown, L., George, T., Thompson, J., Wright, G., Lyon, J., Dupuy, L., . . . White, P. J. A. o. B. (2012). What are the implications of variation in root hair length on tolerance to phosphorus deficiency in combination with water stress in barley (Hordeum vulgare)? *, 110*(2), 319-328.

[11]. Brown, L. K., George, T. S., Barrett, G. E., Hubbard, S. F., White, P. J. J. P., & Soil. (2013). Interactions between root hair length and arbuscular mycorrhizal colonisation in phosphorus deficient barley (Hordeum vulgare). *372*, 195-205.

[12]. Burak, E., Quinton, J. N., & Dodd, I. C. J. A. o. B. (2021). Root hairs are the most important root trait for rhizosheath formation of barley (Hordeum vulgare), maize (Zea mays) and Lotus japonicus (Gifu). *128*(1), 45-57.
[13]. Calderón-Vázquez, C., Alatorre-Cobos, F., Simpson-Williamson, J., & Herrera-Estrella, L. J. H. o. m. I. b. (2009). Maize under phosphate limitation. 381-404.
[14]. Carminati, A., Passioura, J. B., Zarebanadkouki, M., Ahmed, M. A., Ryan, P. R., Watt, M., & Delhaize, E. J. N. P. (2017). Root hairs enable high transpiration rates in drying soils. *216*(3), 771-781.
[15]. Cheng, L., Bucciarelli, B., Liu, J., Zinn, K., Miller, S., Patton-Vogt, J., . . . Vance, C. P. J. P. p. (2011). White lupin cluster root acclimation to phosphorus deficiency and root hair development involve unique glycerophosphodiester phosphodiesterases. *156*(3), 1131-1148.
[16]. Chiou, T. J., Liu, H., & Harrison, M. J. J. T. P. J. (2001). The spatial expression patterns of a phosphate transporter (MtPT1) from Medicago truncatula indicate a role in phosphate transport at the root/soil interface. *25*(3), 281-293.
[17]. De Bauw, P., Mai, T. H., Schnepf, A., Merckx, R., Smolders, E., & Vanderborght, J. J. A. o. b. (2020). A functional–structural model of upland rice root systems reveals the importance of laterals and growing root tips for phosphate uptake from wet and dry soils. *126*(4), 789-806.
[18]. Dissanayaka, D., Plaxton, W. C., Lambers, H., Siebers, M., Marambe, B., Wasaki, J. J. P., Cell, & Environment. (2018). Molecular mechanisms underpinning phosphorus-use efficiency in rice. *41*(7), 1483-1496.
[19]. Eriksson, A. K., Hesterberg, D., Klysubun, W., & Gustafsson, J. P. J. S. o. t. T. E. (2016). Phosphorus dynamics in Swedish agricultural soils as influenced by fertilization and mineralogical properties: Insights gained from batch experiments and XANES spectroscopy. *566*, 1410-1419.
[20]. Fageria, N., Santos, A., Reis Jr, R. J. C. i. s. s., & analysis, p. (2014). Agronomic evaluation of phosphorus sources in lowland rice production. *45*(15), 2067-2091.
[21]. Fageria, N. K. (2013). *Mineral nutrition of rice*: CRC press.
[22]. Fan, X.-D., Wang, J.-Q., Yang, N., Dong, Y.-Y., Liu, L., Wang, F.-W., . . . Sun, Y.-P. J. G. (2013). Gene expression profiling of soybean leaves and roots under salt, saline–alkali and drought stress by high-throughput Illumina sequencing. *512*(2), 392-402.
[23]. Föhse, D., Claassen, N., Jungk, A. J. P., & Soil. (1991). Phosphorus efficiency of plants: II. Significance of root radius, root hairs and cation-anion balance for phosphorus influx in seven plant species. *132*, 261-272.
[24]. Franco-Zorrilla, J. M., Martin, A. C., Solano, R., Rubio, V., Leyva, A., & Paz-Ares, J. J. T. P. J. (2002). Mutations at CRE1 impair cytokinin-induced repression of phosphate starvation responses in Arabidopsis. *32*(3), 353-360.
[25]. Fujita, K., Kai, Y., Takayanagi, M., El-Shemy, H., Adu-Gyamfi, J. J., & Mohapatra, P. K. J. P. S. (2004). Genotypic variability of pigeonpea in distribution of photosynthetic carbon at low phosphorus level. *166*(3), 641-649.
[26]. Gahoonia, T., Nielsen, N. J. P., Cell, & Environment. (2003). Phosphorus (P) uptake and growth of a root hairless barley mutant (bald root barley, brb) and wild type in low-and high-P soils. *26*(10), 1759-1766.
[27]. Gaxiola, R. A., Edwards, M., & Elser, J. J. J. C. (2011). A transgenic approach to enhance phosphorus use efficiency in crops as part of a comprehensive strategy for sustainable agriculture. *84*(6), 840-845.
[28]. George, T. S., Brown, L. K., Ramsay, L., White, P. J., Newton, A. C., Bengough, A. G., . . . Thomas, W. T. J. N. P. (2014). Understanding the genetic control and physiological traits associated with rhizosheath production by barley (H ordeum vulgare). *203*(1), 195-205.
[29]. George, T. S., Fransson, A.-M., Hammond, J. P., & White, P. J. J. P. i. a. b. p. i. s. p. c. (2011). Phosphorus nutrition: rhizosphere processes, plant response and adaptations. 245-271.
[30]. Gilroy, S., & Jones, D. L. J. T. i. p. s. (2000). Through form to function: root hair development and nutrient uptake. *5*(2), 56-60.
[31]. Glaser, B., & Lehr, V.-I. J. S. r. (2019). Biochar effects on phosphorus availability in agricultural soils: A meta-analysis. *9*(1), 9338.
[32]. Gomez-Ariza, J., Balestrini, R., Novero, M., Bonfante, P. J. B., & Soils, F. o. (2009). Cell-specific gene expression of phosphate transporters in mycorrhizal tomato roots. *45*, 845-853.
[33]. Grossman, J. D., & Rice, K. J. J. E. A. (2012). Evolution of root plasticity responses to variation in soil nutrient distribution and concentration. *5*(8), 850-857.
[34]. Grunwald, U., Guo, W., Fischer, K., Isayenkov, S., Ludwig-Müller, J., Hause, B., . . . Franken, P. J. P. (2009). Overlapping expression patterns and differential transcript levels of phosphate transporter genes in arbuscular mycorrhizal, P i-fertilised and phytohormone-treated Medicago truncatula roots. *229*, 1023-1034.
[35]. Gu, B.-W., Lee, C.-G., Lee, T.-G., & Park, S.-J. J. S. o. t. T. E. (2017). Evaluation of sediment capping with activated carbon and nonwoven fabric mat to interrupt nutrient release from lake sediments. *599*, 413-421.
[36]. Gu, R., Chen, F., Long, L., Cai, H., Liu, Z., Yang, J., . . . Genomics. (2016). Enhancing phosphorus uptake efficiency through QTL-based selection for root system architecture in maize. *43*(11), 663-672.
[37]. Güimil, S., Chang, H.-S., Zhu, T., Sesma, A., Osbourn, A., Roux, C., . . . Descombes, P. J. P. o. t. N. A. o. S. (2005). Comparative transcriptomics of rice reveals an ancient pattern of response to microbial colonization. *102*(22), 8066-8070.
[38]. Guo, W., Zhao, J., Li, X., Qin, L., Yan, X., & Liao, H. J. T. P. J. (2011). A soybean β-expansin gene GmEXPB2 intrinsically involved in root system architecture responses to abiotic stresses. *66*(3), 541-552.
[39]. Gyaneshwar, P., Naresh Kumar, G., Parekh, L., Poole, P. J. P., & soil. (2002). Role of soil microorganisms in improving P nutrition of plants. *245*, 83-93.

[40]. Haling, R. E., Brown, L. K., Bengough, A. G., Valentine, T. A., White, P. J., Young, I. M., & George, T. S. J. P. (2014). Root hair length and rhizosheath mass depend on soil porosity, strength and water content in barley genotypes. *239*, 643-651.
[41]. Haling, R. E., Simpson, R. J., Delhaize, E., Hocking, P. J., Richardson, A. E. J. P., & Soil. (2010). Effect of lime on root growth, morphology and the rhizosheath of cereal seedlings growing in an acid soil. *327*, 199-212.
[42]. Ham, B.-K., Chen, J., Yan, Y., & Lucas, W. J. J. C. O. i. B. (2018). Insights into plant phosphate sensing and signaling. *49*, 1-9.
[43]. Hammond, J. P., Broadley, M. R., White, P. J., King, G. J., Bowen, H. C., Hayden, R., . . . Spracklen, W. P. J. J. o. e. b. (2009). Shoot yield drives phosphorus use efficiency in Brassica oleracea and correlates with root architecture traits. *60*(7), 1953-1968.
[44]. Hanlon, M. T., Ray, S., Saengwilai, P., Luthe, D., Lynch, J. P., & Brown, K. M. J. J. o. e. b. (2018). Buffered delivery of phosphate to Arabidopsis alters responses to low phosphate. *69*(5), 1207-1219.
[45]. Hayat, R., Ali, S., Amara, U., Khalid, R., & Ahmed, I. J. A. o. m. (2010). Soil beneficial bacteria and their role in plant growth promotion: a review. *60*, 579-598.
[46]. Hirsch, J., Marin, E., Floriani, M., Chiarenza, S., Richaud, P., Nussaume, L., & Thibaud, M. J. B. (2006). Phosphate deficiency promotes modification of iron distribution in Arabidopsis plants. *88*(11), 1767-1771.
[47]. Ho, M. D., McCannon, B. C., & Lynch, J. P. J. J. o. T. B. (2004). Optimization modeling of plant root architecture for water and phosphorus acquisition. *226*(3), 331-340.
[48]. Holz, M., Zarebanadkouki, M., Kuzyakov, Y., Pausch, J., & Carminati, A. J. A. o. B. (2018). Root hairs increase rhizosphere extension and carbon input to soil. *121*(1), 61-69.
[49]. Huang, W., Liu, J., Wang, Y. P., Zhou, G., Han, T., Li, Y. J. P., & Soil. (2013). Increasing phosphorus limitation along three successional forests in southern China. *364*, 181-191.
[50]. Jain, A., Poling, M. D., Karthikeyan, A. S., Blakeslee, J. J., Peer, W. A., Titapiwatanakun, B., . . . Raghothama, K. G. J. P. P. (2007). Differential effects of sucrose and auxin on localized phosphate deficiency-induced modulation of different traits of root system architecture in Arabidopsis. *144*(1), 232-247.
[51]. Jia, H., Ren, H., Gu, M., Zhao, J., Sun, S., Zhang, X., . . . Xu, G. J. P. P. (2011). The phosphate transporter gene OsPht1; 8 is involved in phosphate homeostasis in rice. *156*(3), 1164-1175.
[52]. Jing, J., Rui, Y., Zhang, F., Rengel, Z., & Shen, J. J. F. C. R. (2010). Localized application of phosphorus and ammonium improves growth of maize seedlings by stimulating root proliferation and rhizosphere acidification. *119*(2-3), 355-364.
[53]. Jones, D. L., & Oburger, E. J. P. i. a. b. p. i. s. p. c. (2011). Solubilization of phosphorus by soil microorganisms. 169-198.
[54]. Jungk, A. J. J. o. P. N., & Science, S. (2001). Root hairs and the acquisition of plant nutrients from soil. *164*(2), 121-129.
[55]. Kabir, Z., Koide, R. J. A., ecosystems, & environment. (2000). The effect of dandelion or a cover crop on mycorrhiza inoculum potential, soil aggregation and yield of maize. *78*(2), 167-174.
[56]. Kang, S.-M., Joo, G.-J., Hamayun, M., Na, C.-I., Shin, D.-H., Kim, H. Y., . . . Lee, I.-J. J. B. l. (2009). Gibberellin production and phosphate solubilization by newly isolated strain of Acinetobacter calcoaceticus and its effect on plant growth. *31*, 277-281.
[57]. Karthikeyan, A. S., Varadarajan, D. K., Mukatira, U. T., D'Urzo, M. P., Damsz, B., & Raghothama, K. G. J. P. p. (2002). Regulated expression of Arabidopsis phosphate transporters. *130*(1), 221-233.
[58]. Kereszt, A., Li, D., Indrasumunar, A., Nguyen, C. D., Nontachaiyapoom, S., Kinkema, M., & Gresshoff, P. M. J. N. p. (2007). Agrobacterium rhizogenes-mediated transformation of soybean to study root biology. *2*(4), 948-952.
[59]. Kirkby, E. A., & Johnston, A. E. J. T. e. o. p.-p. i. (2008). Soil and fertilizer phosphorus in relation to crop nutrition. 177-223.
[60]. Klamer, F., Vogel, F., Li, X., Bremer, H., Neumann, G., Neuhäuser, B., . . . Ludewig, U. J. A. o. b. (2019). Estimating the importance of maize root hairs in low phosphorus conditions and under drought. *124*(6), 961-968.
[61]. Kochian, L. V. J. N. (2012). Rooting for more phosphorus. *488*(7412), 466-467.
[62]. Kohli, P. S., Maurya, K., Thakur, J. K., Bhosale, R., Giri, J. J. P., Cell, & Environment. (2022). Significance of root hairs in developing stress-resilient plants for sustainable crop production. *45*(3), 677-694.
[63]. Kuo, H. F., Chang, T. Y., Chiang, S. F., Wang, W. D., Charng, Y. y., & Chiou, T. J. J. T. P. J. (2014). Arabidopsis inositol pentakisphosphate 2-kinase, A t IPK 1, is required for growth and modulates phosphate homeostasis at the transcriptional level. *80*(3), 503-515.
[64]. Lambers, H., Albornoz, F., Kotula, L., Laliberté, E., Ranathunge, K., Teste, F. P., . . . Soil. (2018). How belowground interactions contribute to the coexistence of mycorrhizal and non-mycorrhizal species in severely phosphorus-impoverished hyperdiverse ecosystems. *424*, 11-33.
[65]. Li, M., Qin, C., Welti, R., & Wang, X. J. P. p. (2006). Double knockouts of phospholipases D ζ 1 and D ζ 2 in Arabidopsis affect root elongation during phosphate-limited growth but do not affect root hair patterning. *140*(2), 761-770.
[66]. Li, Z., Gao, Q., Liu, Y., He, C., Zhang, X., & Zhang, J. J. P. (2011). Overexpression of transcription factor ZmPTF1 improves low phosphate tolerance of maize by regulating carbon metabolism and root growth. *233*, 1129-1143.

[67]. Liang, C. Y., Chen, Z. J., Yao, Z. F., Tian, J., & Liao, H. J. J. o. i. p. b. (2012). Characterization of two putative protein phosphatase genes and their involvement in phosphorus efficiency in Phaseolus vulgaris F. *54*(6), 400-411.
[68]. Liu, R., & Lal, R. J. S. r. (2014). Synthetic apatite nanoparticles as a phosphorus fertilizer for soybean (Glycine max). *4*(1), 5686.
[69]. Liu, T.-Y., Aung, K., Tseng, C.-Y., Chang, T.-Y., Chen, Y.-S., & Chiou, T.-J. J. P. P. (2011). Focus Issue on Phosphorus Plant Physiology: Vacuolar Ca2+/H+ Transport Activity Is Required for Systemic Phosphate Homeostasis Involving Shoot-to-Root Signaling in Arabidopsis. *156*(3), 1176.
[70]. Liu, X., Zhao, X., Zhang, L., Lu, W., Li, X., & Xiao, K. J. F. P. B. (2013). TaPht1; 4, a high-affinity phosphate transporter gene in wheat (Triticum aestivum), plays an important role in plant phosphate acquisition under phosphorus deprivation. *40*(4), 329-341.
[71]. López-Bucio, J., Hernández-Abreu, E., Sánchez-Calderón, L., Nieto-Jacobo, M. F., Simpson, J., & Herrera-Estrella, L. J. P. p. (2002). Phosphate availability alters architecture and causes changes in hormone sensitivity in the Arabidopsis root system. *129*(1), 244-256.
[72]. Lundmark, M., Nilsson, L., Kørner, C. J., & Nielsen, T. H. J. F. P. B. (2011). Overexpression of the MYB-related transcription factor GCC7 in Arabidopsis thaliana leads to increased levels of Pi and changed P-dependent gene regulation. *38*(2), 151-162.
[73]. Lv, X., Pu, X., Qin, G., Zhu, T., & Lin, H. J. A. (2014). The roles of autophagy in development and stress responses in Arabidopsis thaliana. *19*, 905-921.
[74]. Lynch, J. P., Brown, K. M. J. P., & Soil. (2001). Topsoil foraging–an architectural adaptation of plants to low phosphorus availability. *237*, 225-237.
[75]. Lynch, J. P., Ho, M. D., Phosphorus, L. J. P., & soil. (2005). Rhizoeconomics: carbon costs of phosphorus acquisition. *269*, 45-56.
[76]. Lynch, J. P. J. A. J. o. B. (2007). Roots of the second green revolution. *55*(5), 493-512.
[77]. Ma, Z., Bielenberg, D., Brown, K., Lynch, J. J. P., cell, & environment. (2001). Regulation of root hair density by phosphorus availability in Arabidopsis thaliana. *24*(4), 459-467.
[78]. Macrae, M., Ali, G., King, K., Plach, J., Pluer, W., Williams, M., . . . Tang, W. J. J. o. e. q. (2019). Evaluating hydrologic response in tile-drained landscapes: Implications for phosphorus transport. *48*(5), 1347-1355.
[79]. Maharajan, T., Ceasar, S. A., Ajeesh krishna, T. P., Ramakrishnan, M., Duraipandiyan, V., Naif Abdulla, A. D., & Ignacimuthu, S. J. P. B. (2018). Utilization of molecular markers for improving the phosphorus efficiency in crop plants. *137*(1), 10-26.
[80]. Marin, M., Feeney, D., Brown, L., Naveed, M., Ruiz, S., Koebernick, N., . . . Puértolas, J. J. A. o. B. (2021). Significance of root hairs for plant performance under contrasting field conditions and water deficit. *128*(1), 1-16.
[81]. Misson, J., Thibaud, M.-C., Bechtold, N., Raghothama, K., & Nussaume, L. J. P. m. b. (2004). Transcriptional regulation and functional properties of Arabidopsis Pht1; 4, a high affinity transporter contributing greatly to phosphate uptake in phosphate deprived plants. *55*, 727-741.
[82]. Mudge, S. R., Rae, A. L., Diatloff, E., & Smith, F. W. J. T. P. J. (2002). Expression analysis suggests novel roles for members of the Pht1 family of phosphate transporters in Arabidopsis. *31*(3), 341-353.
[83]. Nagarajan, V. K., Jain, A., Poling, M. D., Lewis, A. J., Raghothama, K. G., & Smith, A. P. J. P. P. (2011). Arabidopsis Pht1; 5 mobilizes phosphate between source and sink organs and influences the interaction between phosphate homeostasis and ethylene signaling. *156*(3), 1149-1163.
[84]. Niu, Y. F., Chai, R. S., Jin, G. L., Wang, H., Tang, C. X., & Zhang, Y. S. J. A. o. b. (2013). Responses of root architecture development to low phosphorus availability: a review. *112*(2), 391-408.
[85]. Nussaume, L., Kanno, S., Javot, H., Marin, E., Pochon, N., Ayadi, A., . . . Thibaud, M.-C. J. F. i. p. s. (2011). Phosphate import in plants: focus on the PHT1 transporters. *2*, 83.
[86]. Oberson, A., & Joner, E. J. J. O. p. i. t. e. (2005). Microbial turnover of phosphorus in soil. 133-164.
[87]. Pang, J., Bansal, R., Zhao, H., Bohuon, E., Lambers, H., Ryan, M. H., . . . Siddique, K. H. J. N. P. (2018). The carboxylate-releasing phosphorus-mobilizing strategy can be proxied by foliar manganese concentration in a large set of chickpea germplasm under low phosphorus supply. *219*(2), 518-529.
[88]. Parker, J. S., Cavell, A. C., Dolan, L., Roberts, K., & Grierson, C. S. J. T. P. C. (2000). Genetic interactions during root hair morphogenesis in Arabidopsis. *12*(10), 1961-1974.
[89]. Paszkowski, U., Kroken, S., Roux, C., & Briggs, S. P. J. P. o. t. N. A. o. S. (2002). Rice phosphate transporters include an evolutionarily divergent gene specifically activated in arbuscular mycorrhizal symbiosis. *99*(20), 13324-13329.
[90]. Pausch, J., Loeppmann, S., Kühnel, A., Forbush, K., Kuzyakov, Y., Cheng, W. J. S. B., & Biochemistry. (2016). Rhizosphere priming of barley with and without root hairs. *100*, 74-82.
[91]. Penn, C. J., & Camberato, J. J. J. A. (2019). A critical review on soil chemical processes that control how soil pH affects phosphorus availability to plants. *9*(6), 120.
[92]. Péret, B., Clément, M., Nussaume, L., & Desnos, T. J. T. i. p. s. (2011). Root developmental adaptation to phosphate starvation: better safe than sorry. *16*(8), 442-450.
[93]. Pérez-Torres, C.-A., Lopez-Bucio, J., Cruz-Ramírez, A., Ibarra-Laclette, E., Dharmasiri, S., Estelle, M., & Herrera-Estrella, L. J. T. P. C. (2008). Phosphate availability alters lateral root development in Arabidopsis by modulating auxin sensitivity via a mechanism involving the TIR1 auxin receptor. *20*(12), 3258-3272.

[94]. Poirier, Y., & Bucher, M. J. T. A. b. A. S. o. P. B. (2002). Phosphate transport and homeostasis in Arabidopsis. *1*.
[95]. Poirier, Y., Thoma, S., Somerville, C., & Schiefelbein, J. J. P. p. (1991). Mutant of Arabidopsis deficient in xylem loading of phosphate. *97*(3), 1087-1093.
[96]. Qin, L., Zhao, J., Tian, J., Chen, L., Sun, Z., Guo, Y., . . . Liao, H. J. P. p. (2012). The high-affinity phosphate transporter GmPT5 regulates phosphate transport to nodules and nodulation in soybean. *159*(4), 1634-1643.
[97]. Quintero, C. E., Boschetti, N. G., Benavidez, R. A. J. C. i. s. s., & analysis, p. (2003). Effect of soil buffer capacity on soil test phosphorus interpretation and fertilizer requirement. *34*(9-10), 1435-1450.
[98]. Raghothama, K., Karthikeyan, A. J. P., & Soil. (2005). Phosphate acquisition. *274*, 37-49.
[99]. Ramaekers, L., Remans, R., Rao, I. M., Blair, M. W., & Vanderleyden, J. J. F. C. R. (2010). Strategies for improving phosphorus acquisition efficiency of crop plants. *117*(2-3), 169-176.
[100]. Rausch, C., & Bucher, M. J. P. (2002). Molecular mechanisms of phosphate transport in plants. *216*, 23-37.
[101]. Requejo, M. I., & Eichler-Löbermann, B. J. N. C. i. A. (2014). Organic and inorganic phosphorus forms in soil as affected by long-term application of organic amendments. *100*, 245-255.
[102]. Richardson, A. E., & Simpson, R. J. J. P. p. (2011). Soil microorganisms mediating phosphorus availability update on microbial phosphorus. *156*(3), 989-996.
[103]. Richardson, A. E. J. P., & soil. (2009). Regulating the phosphorus nutrition of plants: molecular biology meeting agronomic needs. *322*(1-2), 17-24.
[104]. Roach, T., Beckett, R. P., Minibayeva, F. V., Colville, L., Whitaker, C., Chen, H., . . . Environment. (2010). Extracellular superoxide production, viability and redox poise in response to desiccation in recalcitrant Castanea sativa seeds. *33*(1), 59-75.
[105]. Roberts, T. L., Johnston, A. E. J. R., conservation, & recycling. (2015). Phosphorus use efficiency and management in agriculture. *105*, 275-281.
[106]. Robertson-Albertyn, S., Alegria Terrazas, R., Balbirnie, K., Blank, M., Janiak, A., Szarejko, I., . . . Hedley, P. E. J. F. i. p. s. (2017). Root hair mutations displace the barley rhizosphere microbiota. *8*, 1094.
[107]. Robles-Aguilar, A. A., Pang, J., Postma, J. A., Schrey, S. D., Lambers, H., Jablonowski, N. D. J. P., & soil. (2019). The effect of pH on morphological and physiological root traits of Lupinus angustifolius treated with struvite as a recycled phosphorus source. *434*, 65-78.
[108]. Ros, M. B., Koopmans, G. F., van Groenigen, K. J., Abalos, D., Oenema, O., Vos, H. M., & van Groenigen, J. W. J. S. R. (2020). Towards optimal use of phosphorus fertiliser. *10*(1), 17804.
[109]. Rose, T. J., Rose, M. T., Pariasca-Tanaka, J., Heuer, S., & Wissuwa, M. J. F. i. P. S. (2011). The frustration with utilization: why have improvements in internal phosphorus utilization efficiency in crops remained so elusive? *, 2*, 73.
[110]. Rouached, H., Stefanovic, A., Secco, D., Bulak Arpat, A., Gout, E., Bligny, R., & Poirier, Y. J. T. P. J. (2011). Uncoupling phosphate deficiency from its major effects on growth and transcriptome via PHO1 expression in Arabidopsis. *65*(4), 557-570.
[111]. Rubio, M. C., Becana, M., Kanematsu, S., Ushimaru, T., & James, E. K. J. N. P. (2009). Immunolocalization of antioxidant enzymes in high-pressure frozen root and stem nodules of Sesbania rostrata. *183*(2), 395-407.
[112]. Sánchez-Calderón, L., López-Bucio, J., Chacón-López, A., Gutiérrez-Ortega, A., Hernández-Abreu, E., & Herrera-Estrella, L. J. P. p. (2006). Characterization of low phosphorus insensitive mutants reveals a crosstalk between low phosphorus-induced determinate root development and the activation of genes involved in the adaptation of Arabidopsis to phosphorus deficiency. *140*(3), 879-889.
[113]. Sanderson, K. R., & Sanderson, J. B. J. C. j. o. p. s. (2006). Prince Edward Island growers can reduce soil phosphorus buildup while maintaining carrot crop yield. *86*(Special Issue), 1401-1403.
[114]. Schneider, K. D., Thiessen Martens, J. R., Zvomuya, F., Reid, D. K., Fraser, T. D., Lynch, D. H., . . . Wilson, H. F. J. J. o. E. Q. (2019). Options for improved phosphorus cycling and use in agriculture at the field and regional scales. *48*(5), 1247-1264.
[115]. Schunmann, P. H., Richardson, A. E., Vickers, C. E., & Delhaize, E. J. P. P. (2004). Promoter analysis of the barley Pht1; 1 phosphate transporter gene identifies regions controlling root expression and responsiveness to phosphate deprivation. *136*(4), 4205-4214.
[116]. Seeling, B., Zasoski, R. J. J. P., & Soil. (1993). Microbial effects in maintaining organic and inorganic solution phosphorus concentrations in a grassland topsoil. *148*, 277-284.
[117]. Seo, H.-M., Jung, Y., Song, S., Kim, Y., Kwon, T., Kim, D.-H., . . . Nam, M.-H. J. B. L. (2008). Increased expression of OsPT1, a high-affinity phosphate transporter, enhances phosphate acquisition in rice. *30*, 1833-1838.
[118]. Shen, J., Yuan, L., Zhang, J., Li, H., Bai, Z., Chen, X., . . . Zhang, F. J. P. p. (2011). Phosphorus dynamics: from soil to plant. *156*(3), 997-1005.
[119]. Shi, J., Hu, H., Zhang, K., Zhang, W., Yu, Y., Wu, Z., & Wu, P. J. J. o. E. B. (2014). The paralogous SPX3 and SPX5 genes redundantly modulate Pi homeostasis in rice. *65*(3), 859-870.
[120]. Shin, H., Shin, H. S., Dewbre, G. R., & Harrison, M. J. J. T. P. J. (2004). Phosphate transport in Arabidopsis: Pht1; 1 and Pht1; 4 play a major role in phosphate acquisition from both low-and high-phosphate environments. *39*(4), 629-642.
[121]. Singh, R., & Yadav, M. J. J. o. F. L. (2008). Effect of phosphorus and biofertilizers on growth, yield and nutrient uptake of long duration pigeonpea under rainfed condition. *21*(1), 46-48.

[122]. Smith, S. E., Jakobsen, I., Grønlund, M., & Smith, F. A. J. P. p. (2011). Roles of arbuscular mycorrhizas in plant phosphorus nutrition: interactions between pathways of phosphorus uptake in arbuscular mycorrhizal roots have important implications for understanding and manipulating plant phosphorus acquisition. *156*(3), 1050-1057.
[123]. Song, G., & Liu, S. J. A. O. S. (2015). Phosphorus speciation and distribution in surface sediments of the Yellow Sea and East China Sea and potential impacts on ecosystem. *34*, 84-91.
[124]. Stefanovic, A., Arpat, A. B., Bligny, R., Gout, E., Vidoudez, C., Bensimon, M., & Poirier, Y. J. T. P. J. (2011). Over-expression of PHO1 in Arabidopsis leaves reveals its role in mediating phosphate efflux. *66*(4), 689-699.
[125]. Stefanovic, A., Ribot, C., Rouached, H., Wang, Y., Chong, J., Belbahri, L., . . . Poirier, Y. J. T. P. J. (2007). Members of the PHO1 gene family show limited functional redundancy in phosphate transfer to the shoot, and are regulated by phosphate deficiency via distinct pathways. *50*(6), 982-994.
[126]. Sun, D., Hale, L., Kar, G., Soolanayakanahally, R., & Adl, S. J. C. (2018). Phosphorus recovery and reuse by pyrolysis: Applications for agriculture and environment. *194*, 682-691.
[127]. Svistoonoff, S., Creff, A., Reymond, M., Sigoillot-Claude, C., Ricaud, L., Blanchet, A., . . . Desnos, T. J. N. g. (2007). Root tip contact with low-phosphate media reprograms plant root architecture. *39*(6), 792-796.
[128]. Szarejko, I., Janiak, A., Chmielewska, B., & Nawrot, M. J. B. G. N. (2005). Genetic analysis of several root hair mutants of barley. *35*, 36-38.
[129]. Ticconi, C. A., Delatorre, C. A., Lahner, B., Salt, D. E., & Abel, S. J. T. P. J. (2004). Arabidopsis pdr2 reveals a phosphate-sensitive checkpoint in root development. *37*(6), 801-814.
[130]. Tran, H. T., Qian, W., Hurley, B. A., SHE, Y. M., Wang, D., Plaxton, W. C. J. P., cell, & environment. (2010). Biochemical and molecular characterization of AtPAP12 and AtPAP26: the predominant purple acid phosphatase isozymes secreted by phosphate-starved Arabidopsis thaliana. *33*(11), 1789-1803.
[131]. Tyburski, J., Dunajska-Ordak, K., Skorupa, M., & Tretyn, A. J. J. o. B. (2012). Role of ascorbate in the regulation of the Arabidopsis thaliana root growth by phosphate availability. *2012*.
[132]. Tyburski, J., Dunajska, K., Tretyn, A. J. P. s., & behavior. (2010). A role for redox factors in shaping root architecture under phosphorus deficiency. *5*(1), 64-66.
[133]. Uddin, M. J., Ahmed, S., Rashid, M., Hasan, M. M., & Asaduzzaman, M. J. J. o. A. R. (2011). Effect of spacing on the yield and yield attributes of transplanted aman rice cultivars in medium lowland ecosystem of Bangladesh. *49*(4), 465-476.
[134]. van de Wiel, C. C., van der Linden, C. G., & Scholten, O. E. J. E. (2016). Improving phosphorus use efficiency in agriculture: opportunities for breeding. *207*, 1-22.
[135]. Vance, C. P., Uhde-Stone, C., & Allan, D. L. J. N. p. (2003). Phosphorus acquisition and use: critical adaptations by plants for securing a nonrenewable resource. *157*(3), 423-447.
[136]. Wang, Q., Wang, J., Yang, Y., Du, W., Zhang, D., Yu, D., & Cheng, H. J. B. g. (2016). A genome-wide expression profile analysis reveals active genes and pathways coping with phosphate starvation in soybean. *17*, 1-11.
[137]. Wang, X., Wang, Y., Tian, J., Lim, B. L., Yan, X., & Liao, H. J. P. P. (2009). Overexpressing AtPAP15 enhances phosphorus efficiency in soybean. *151*(1), 233-240.
[138]. Wang, Y., Lambers, H. J. P., & Soil. (2020). Root-released organic anions in response to low phosphorus availability: recent progress, challenges and future perspectives. *447*, 135-156.
[139]. Wang, Y., Thorup-Kristensen, K., Jensen, L. S., & Magid, J. J. F. i. p. s. (2016). Vigorous root growth is a better indicator of early nutrient uptake than root hair traits in spring wheat grown under low fertility. *7*, 865.
[140]. Wang, Z., Ruan, W., Shi, J., Zhang, L., Xiang, D., Yang, C., . . . Yu, Y. J. P. o. t. N. A. o. S. (2014). Rice SPX1 and SPX2 inhibit phosphate starvation responses through interacting with PHR2 in a phosphate-dependent manner. *111*(41), 14953-14958.
[141]. Wasaki, J., Maruyama, H., Tanaka, M., Yamamura, T., Dateki, H., Shinano, T., . . . nutrition, p. (2009). Overexpression of the LASAP2 gene for secretory acid phosphatase in white lupin improves the phosphorus uptake and growth of tobacco plants. *55*(1), 107-113.
[142]. Wen, T. J., & Schnable, P. S. J. A. j. o. b. (1994). Analyses of mutants of three genes that influence root hair development in Zea mays (Gramineae) suggest that root hairs are dispensable. *81*(7), 833-842.
[143]. Wen, Z., Li, H., Shen, Q., Tang, X., Xiong, C., Li, H., . . . Shen, J. J. N. P. (2019). Tradeoffs among root morphology, exudation and mycorrhizal symbioses for phosphorus-acquisition strategies of 16 crop species. *223*(2), 882-895.
[144]. Wendrich, J. R., Yang, B., Vandamme, N., Verstaen, K., Smet, W., Van de Velde, C., . . . Arents, H. E. J. S. (2020). Vascular transcription factors guide plant epidermal responses to limiting phosphate conditions. *370*(6518), eaay4970.
[145]. White, P. J., George, T. S., Dupuy, L. X., Karley, A. J., Valentine, T. A., Wiesel, L., & Wishart, J. J. F. i. p. s. (2013). Root traits for infertile soils. *4*, 193.
[146]. White, P. J., Veneklaas, E. J. J. P., & soil. (2012). Nature and nurture: the importance of seed phosphorus content. *357*, 1-8.
[147]. Wild, M., Davière, J.-M., Regnault, T., Sakvarelidze-Achard, L., Carrera, E., Diaz, I. L., . . . Achard, P. J. D. C. (2016). Tissue-specific regulation of gibberellin signaling fine-tunes Arabidopsis iron-deficiency responses. *37*(2), 190-200.

[148]. Williamson, L. C., Ribrioux, S. P., Fitter, A. H., & Leyser, H. O. J. P. p. (2001). Phosphate availability regulates root system architecture in Arabidopsis. *126*(2), 875-882.
[149]. Wu, P., Shou, H., Xu, G., & Lian, X. J. C. o. i. p. b. (2013). Improvement of phosphorus efficiency in rice on the basis of understanding phosphate signaling and homeostasis. *16*(2), 205-212.
[150]. Wu, P., & Wang, Z. J. F. i. B. (2011). Molecular mechanisms regulating Pi-signaling and Pi homeostasis under OsPHR2, a central Pi-signaling regulator, in rice. *6*, 242-245.
[151]. Yamada, T. M., Sueitt, A., Beraldo, D., Botta, C., Fadini, P., Nascimento, M., . . . Mozeto, A. J. W. R. (2012). Calcium nitrate addition to control the internal load of phosphorus from sediments of a tropical eutrophic reservoir: microcosm experiments. *46*(19), 6463-6475.
[152]. Yang, H., Knapp, J., Koirala, P., Rajagopal, D., Peer, W. A., Silbart, L. K., . . . Gaxiola, R. A. J. P. b. j. (2007). Enhanced phosphorus nutrition in monocots and dicots over-expressing a phosphorus-responsive type I H+-pyrophosphatase. *5*(6), 735-745.
[153]. Yang, K., Jeong, N., Moon, J.-K., Lee, Y.-H., Lee, S.-H., Kim, H. M., . . . Jeong, S.-C. J. J. o. H. (2010). Genetic analysis of genes controlling natural variation of seed coat and flower colors in soybean. *101*(6), 757-768.
[154]. Yang, S.-Y., Grønlund, M., Jakobsen, I., Grotemeyer, M. S., Rentsch, D., Miyao, A., . . . Salamin, N. J. T. P. C. (2012). Nonredundant regulation of rice arbuscular mycorrhizal symbiosis by two members of the PHOSPHATE TRANSPORTER1 gene family. *24*(10), 4236-4251.
[155]. Yang, Y., Shi, X., Ballent, W., & Mayer, B. K. J. W. E. R. (2017). Biological phosphorus recovery: Review of current progress and future needs: Yang et al. *89*(12), 2122-2135.
[156]. Yi, K., Wu, Z., Zhou, J., Du, L., Guo, L., Wu, Y., & Wu, P. J. P. p. (2005). OsPTF1, a novel transcription factor involved in tolerance to phosphate starvation in rice. *138*(4), 2087-2096.
[157]. Yu, H., Xie, W., Wang, J., Xing, Y., Xu, C., Li, X., . . . Zhang, Q. J. P. o. (2011). Gains in QTL detection using an ultra-high density SNP map based on population sequencing relative to traditional RFLP/SSR markers. *6*(3), e17595.
[158]. Zak, D., Goldhammer, T., Cabezas, A., Gelbrecht, J., Gurke, R., Wagner, C., . . . McInnes, R. J. J. o. A. E. (2018). Top soil removal reduces water pollution from phosphorus and dissolved organic matter and lowers methane emissions from rewetted peatlands. *55*(1), 311-320.
[159]. Zhang, C., Ding, S., Xu, D., Tang, Y., Wong, M. H. J. E. M., & Assessment. (2014). Bioavailability assessment of phosphorus and metals in soils and sediments: a review of diffusive gradients in thin films (DGT). *186*, 7367-7378.
[160]. Zhang, D., Song, H., Cheng, H., Hao, D., Wang, H., Kan, G., . . . Yu, D. J. P. g. (2014). The acid phosphatase-encoding gene GmACP1 contributes to soybean tolerance to low-phosphorus stress. *10*(1), e1004061.
[161]. Zhang, H., Kovar, J. J. M. o. p. a. f. s., sediments, residuals,, & waters. (2009). Fractionation of soil phosphorus. *2*, 50-60.
[162]. Zhang, J. L., Zhao, S., Han, C., Wang, Z., Zhong, S., Sun, S., . . . Yuan, K. D. J. N. l. (2016). Epitaxial growth of single layer blue phosphorus: a new phase of two-dimensional phosphorus. *16*(8), 4903-4908.
[163]. Zhang, L., Hu, B., Li, W., Che, R., Deng, K., Li, H., . . . Chu, C. J. N. P. (2014). Os PT 2, a phosphate transporter, is involved in the active uptake of selenite in rice. *201*(4), 1183-1191.
[164]. Zhang, T., Hu, Y., Zhang, K., Tian, C., Guo, J. J. I. C., & Products. (2018). Arbuscular mycorrhizal fungi improve plant growth of Ricinus communis by altering photosynthetic properties and increasing pigments under drought and salt stress. *117*, 13-19.
[165]. Zhang, Y.-Q., Deng, Y., Chen, R.-Y., Cui, Z.-L., Chen, X.-P., Yost, R., . . . Soil. (2012). The reduction in zinc concentration of wheat grain upon increased phosphorus-fertilization and its mitigation by foliar zinc application. *361*, 143-152.
[166]. Zhang, Y., Xu, F., Ding, Y., Du, H., Zhang, Q., Dang, X., . . . Environment. (2021). Abscisic acid mediates barley rhizosheath formation under mild soil drying by promoting root hair growth and auxin response. *44*(6), 1935-1945.
[167]. Zhong, Y., Wang, Y., Guo, J., Zhu, X., Shi, J., He, Q., . . . Lv, Q. J. N. P. (2018). Rice SPX6 negatively regulates the phosphate starvation response through suppression of the transcription factor PHR2. *219*(1), 135-148.
[168]. Zhou, Q. Y., Tian, A. G., Zou, H. F., Xie, Z. M., Lei, G., Huang, J., . . . Chen, S. Y. J. P. b. j. (2008). Soybean WRKY-type transcription factor genes, GmWRKY13, GmWRKY21, and GmWRKY54, confer differential tolerance to abiotic stresses in transgenic Arabidopsis plants. *6*(5), 486-503.
[169]. Zhu, J., Kaeppler, S. M., Lynch, J. P. J. P., & Soil. (2005). Mapping of QTL controlling root hair length in maize (Zea mays L.) under phosphorus deficiency. *270*, 299-310.