

Improving of phosphorus use efficiency in Plant-Soil-System. A review

¹Abou Seeda M.A., ¹Yassen A.A., ²Abou El-Nour E.A. A. and ¹Sahar M. Zaghloul

¹Plant Nutrition Dept., National Research Centre, 33 El Buhouth St., 12622 Dokki, Giza, Egypt.

²Fertilization Tech. Dept., National Research Centre, 33 El Buhouth St., 12622 Dokki, Giza, Egypt.

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ABSTRACT

Phosphorus is an essential nutrient that is required for all major developmental processes and reproduction in plants. It is also a major constituent of the fertilizers required to sustain high-yield agriculture. Phosphorus form that can be assimilated by plants are suboptimal in most natural and agricultural ecosystems, and when phosphate is applied as fertilizer in soils, it is rapidly immobilized owing to fixation and microbial activity. Thus, cultivated plants can consumed approximately 20–30% of the applied phosphate fertilizers, and the rest is lost, eventually causing water eutrophication. Recent advances in the understanding of mechanisms by which wild and cultivated species adapt to low-phosphate stress and the implementation of alternative bacterial pathways for phosphorus metabolism have started to mallow the design of more effective breeding and genetic engineering strategies to produce highly phosphate-efficient crops, optimize fertilizer use, and reach agricultural sustainability with a lower environmental cost. Phosphorus dynamics in the soil plant system is a function of the integrative effects of Phosphorus transformation, availability, utilization caused by soil, rhizosphere, and plant processes. In this review, we outline the current advances in research on the complex network of plant responses to low-phosphorus stress and discuss some strategies used to manipulate genes involved in phosphate uptake, remobilization, and metabolism to develop low-phosphate-tolerant crops, which could help in designing crops that are more efficient.

Keywords: Phosphorus Dynamics-phosphorus use efficiency- management of P- uptake

1- Introduction

With increasing demand of agricultural production and as the peak in global production will occur in the next decades, phosphorus (P) is receiving more attention as a nonrenewable resource Cordell *et al.*, (2009); Gilbert, (2009). One unique characteristic of Phosphorus is its low availability due to slow diffusion and high fixation in soils. All of this means that Phosphorus can be a major limiting factor for plant growth. Applications of chemical Phosphorus fertilizers and animal manure to agricultural land have improved soil P fertility and crop production, but caused environmental damage in the past decades. Maintaining a proper Phosphorus -supplying level at the root zone can maximize the efficiency of plant roots to mobilize and acquire P from the rhizosphere by an integration of root morphological and physiological adaptive strategies. Furthermore, Phosphorus uptake and utilization by plants plays a vital role in the determination of final crop yield. A holistic understanding of Phosphorus dynamics from soil to plant is necessary for optimizing Phosphorus management and improving Phosphorus -use efficiency, aiming at reducing consumption of chemical Phosphorus fertilizer, maximizing exploitation of the biological potential of root/rhizosphere processes for efficient mobilization, and acquisition of soil Phosphorus by plants as well as recycling Phosphorus from manure and waste. Taken together, overall Phosphorus dynamics in the soil plant system is a function of the integrative effects of Phosphorus transformation, availability, and utilization caused by soil, rhizosphere, and plant processes. This Update focuses on the dynamic processes determining Phosphorus availability in the soil and in the rhizosphere, Phosphorus mobilization, uptake, and utilization by plants. It highlights recent advances in the understanding of the Phosphorus dynamics in the soil/rhizosphere-plant continuum.

2- Phosphorus Dynamics in soil

2-1 -Soil Phosphorus Transformation

Soil P exists in various chemical forms including inorganic Phosphorus and organic Phosphorus. These Phosphorus forms differ in their behavior and fate in soils Hansen *et al.*, (2004); Turner *et al.*, (2007).

Corresponding Author: Abou Seeda M.A., Plant Nutrition Dept., National Research Centre, 33 El Buhouth St., 12622 Dokki, Giza, Egypt. E-mail: mabouseeda@gmail.com

Inorganic Phosphorus usually accounts for 35% to 70% of total Phosphorus in soil (Harrison, 1987). Primary Phosphorus minerals including apatites, strengite, and variscite are very stable, and the release of available Phosphorus from these minerals by weathering is generally low to meet the crop demand though direct application of phosphate rocks (i.e. apatites) has proved relatively efficient for crop growth in acidic soils. In contrast, secondary Phosphorus minerals including calcium, iron, and aluminum phosphates which vary in their dissolution rates, depending on size particles and soil pH Pierzynski *et al.*, (2005); Oelkers and Valsami-Jones, (2008). With increasing soil pH, solubility of Fe and Al phosphates increases but solubility of Ca phosphate decreases, except for pH values above 8 Hinsinger, (2001). Phosphorus adsorbed on various clays and Al/Fe oxides can be released by desorption reactions. All these Phosphorus forms exist in complex equilibrium with each other, representing from very stable, sparingly available, to plant-available Phosphorus pools such as labile Phosphorus and solution Phosphorus Fig. (1).

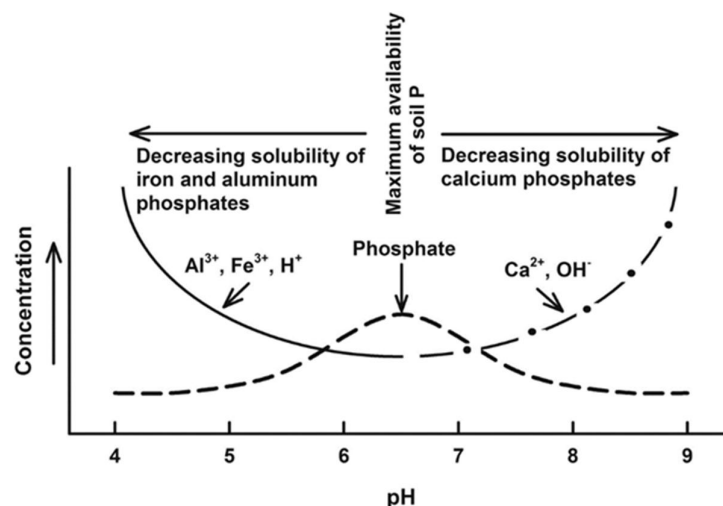


Fig. 1: Diagram illustrated general qualitative representation of soil phosphorus availability as impacted by pH after Price (2006)

In acidic soils, Al/Fe oxides and hydroxides, such as gibbsite, hematite, and goethite can dominantly adsorb phosphorus Parfitt, (1989). Phosphorus adsorbed on the surface of clay minerals and Fe/Al oxides. The nonprotonated and protonated bidentate surface complexes may coexist at pH 4 to 9, while protonated bidentate inner sphere complex is predominant under acidic conditions Luengo *et al.*, (2006); Arai and Sparks, (2007). Clay minerals and Fe/Al oxides have large specific surface areas, which provide large number of adsorption sites. The adsorption of soil phosphorus can be enhanced with increasing ionic strength. With further reactions, phosphorus may be occluded in nanopores that frequently occur in Fe/Al oxides, and thereby become unavailable to plants Arai and Sparks, (2007).

In neutral-to-calcareous soils, phosphorus retention is dominated by precipitation reactions Lindsay *et al.*, (1989), although phosphorus can also be adsorbed on the surface of Ca carbonate Larsen, (1967) and clay minerals Devau *et al.*, (2010). Phosphate can precipitate with Ca, generating di-calcium phosphate (DCP) that is available to plants. Ultimately, DCP can be transformed into more stable forms such as Octocalcium phosphate and hydroxyapatite (HAP), which are less available to plants particularly under alkaline condition Arai and Sparks, (2007). HAP accounts for more than 50% of total inorganic phosphorus in calcareous soils from long-term fertilizer experiments. HAP dissolution increases with decrease of soil pH Wang and Nancollas, (2008) Fig. (2).

Acidification rhizosphere may be an efficient strategy to mobilize soil phosphorus from calcareous soil. Organic phosphorus generally accounts for 30% to 65% of the total P in soils Harrison, (1987). Soil organic phosphorus mainly exists in stabilized forms as inositol phosphates and phosphonates, and active forms as orthophosphate diesters, labile orthophosphate monoesters, and organic polyphosphates Turner *et al.*, (2002); Condon *et al.*, (2005). The organic phosphorus can be released through mineralization processes mediated by soil organisms and plant roots in association with phosphatase secretion. These processes are highly influenced by soil physicochemical properties

of soils; transformation of organic phosphorus forms has a great influence on the overall bioavailability of Phosphorus in soil (Turner *et al.*, 2007).

Therefore, Phosphorus availability in soil is extremely complex and needs to be systemically evaluated because it is highly associated with Phosphorus dynamics and transformation among various Phosphorus pools Fig. (3).

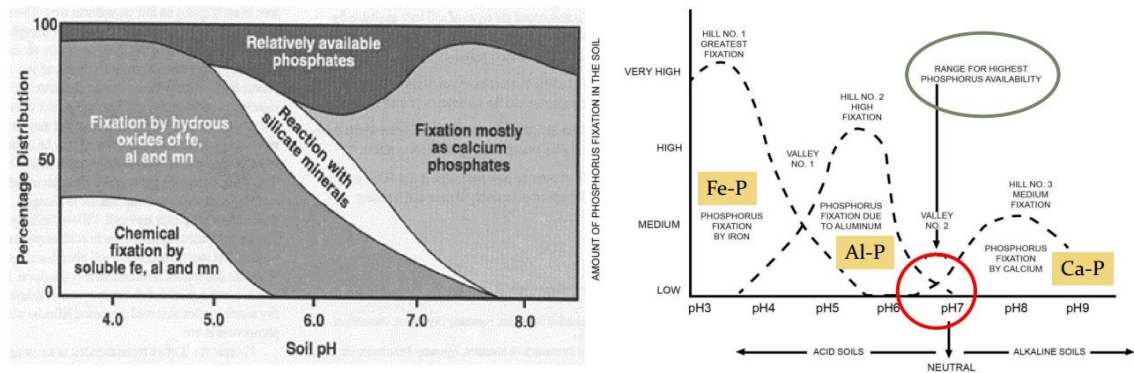


Fig. 2: Diagram illustrated soil phosphorus availability across pH ranges

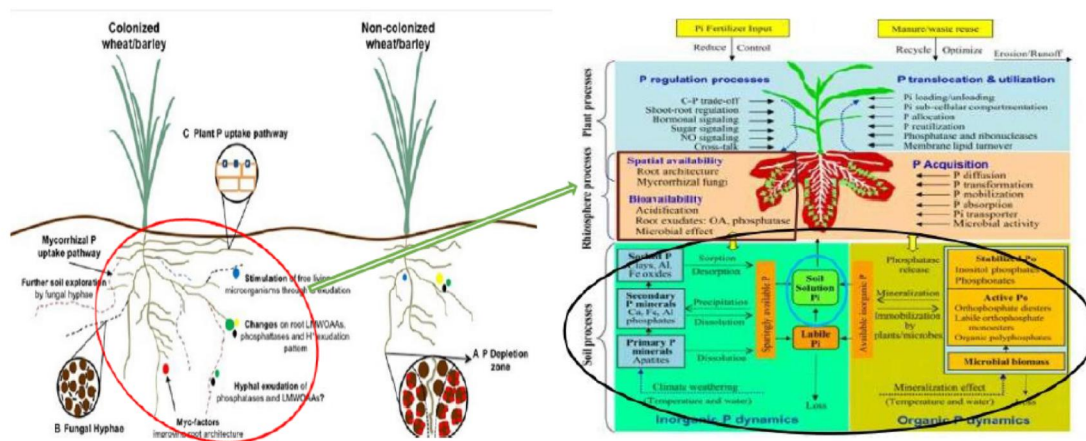


Fig. 3: Illustrates soil phosphorus dynamics in soil-Rhizosphere-plant relationships

Chemical Fertilizer Phosphorus in Soil The modern terrestrial Phosphorus cycle is dominated by agriculture and human activities Oelkers and Valsami-Jones, (2008). The concentration of available soil inorganic-phosphorus (Pi) not exceeds than 10 mM, Bielecki, (1973), which is much lower than that in plant tissues where the concentration is approximately 5 to 20 mM (Pi) Raghothama, (1999). Fertilizers-P application are needed particularly under low availability phosphorus in soils to improve growth and yield production. Available forms of phosphate fertilizers are monocalcium phosphate (MCP) and monopotassium phosphate (MPP), however MCP can significantly affect soil physicochemical characteristics. Benbi and Gilkes, (1987) application of MCP are quickly converted to phosphate, and DCP, and eventually forms a Phosphorus -saturated patch. Three different reaction zones are occurred, including direct, precipitation, and adsorption reaction zones. Direct reaction zone is very acidic (pH = 1.0–1.6), which enhancing the mobility of soil metal ions. These metal ions react with inorganic - Phosphorus causing further precipitation. However, amorphous of Fe-P and Al-P can be partly available to plants. In calcareous soil, new complexes of MCP and DCP can be formed and with time, DCP is gradually transformed into more stable forms of tri-Ca phosphates (TCP), is dominant in the outer zone due to low concentration of inorganic -P adsorption reaction by soil Moody *et al.*, (1995) Fig.(2). In contrast, the application of monopotassium phosphate has little influence on soil physical and chemical properties Lindsay *et al.*, (1962). Therefore, equivalent amount of Phosphorus

fertilizer types (MCP and DCP) to soil may be an efficient strategy for rational use of chemical phosphorus fertilizer.

2-2 Organic matter as a source of phosphorus

Prolonged of organic matter (OM) as a source of nutrients elements for enhancing soils fertility were used. With development the industries of mineral fertilizers, using of organic matter has decreased Muraishi *et al.* (2011). However, due to the growing pressures of conforming to environmental quality standards Carvajal-Muñoz and Carmona-Garcia (2012), and increasing the costs of fertilizers ANDA (2016), there is an interest for using, organic matter as a source of nutrient in agriculture soil. The quality of organic matter can vary depending on type, treatments, and its maturity (composting presses). Manure from livestock production (cow manure) contains high concentrations of available nutrients Hariadi *et al.* (2016), mainly, nitrogen, phosphorus and sulfur (S) Muraishi *et al.* (2011), however, organic matter from poultry production (chicken and turkey) which contains high concentrations of potassium and phosphorus Pinto *et al.* (2012). The process of organic composting is special technique that reduces some pathogens and enhances nutrient availability to plants. Application of limestone and gypsum through composting processes is an alternative of enrichment, for increasing nutrient availability Ramos *et al.* (2013). However, this technique needs to be more thoroughly studied because of the possible increase of Phosphorus adsorption in soil and a subsequent imbalance between the bases of Mg, Ca, K, with the formation of percolating sulfates in soil Ramos *et al.* (2013). Furthermore, farmers should pay attention to the quality and quantity of animal manure used as a source of nutrients in soil. Both quality and quantity can cause an excessive input of nutrients leading to soil as well as and groundwater contamination Min *et al.* (2012).

Organic matter applied to agricultural lands for enhancing the fertility status particularly phosphorus, is very variable and nearly 70% of total-P in manure is labile, which inorganic phosphorus were ranged between 50% to 90% (Dou *et al.*, 2000). Also contains large amounts of organic phosphorus, such as phospholipids and nucleic acids (Turner and Leytem, 2004), which can be released and increase soil the inorganic phosphorus contents through mineralization. On the other hand, small molecular of organic acids created from mineralization of humic substances from manure can increase the availability of Ca phosphate, especially for citrate, which was more efficiency (Martins *et al.*, 2008). Adsorption of phosphorus in soil can be greatly reduced through applying organic substances. The humic acids contain large numbers of negative charges, carboxyl and hydroxyl groups, which strongly compete for the adsorption sites with inorganic phosphorus. Application of organic matter can affected on the acidity of soil, furthermore increasing phosphorus availability. However, mechanisms of organic matter added encourage phosphorus alternation between inorganic and organic phosphorus in soil, further investigation still needed.

3- Phosphorus Dynamics in the Rhizosphere

Rhizosphere is the accurate zone that interacts between plants, soils, and microorganisms. Plant roots network can greatly modify the rhizosphere environment through their various physiological activities, particularly the exudation of organic compounds such as mucilage, organic acids, phosphatases, and some specific signaling substances, which are key drivers of various rhizosphere processes Fig.(4).

Chemical and biological processes in rhizosphere not only determine mobilization and acquisition of soil nutrients as well as microbial dynamics, but also control nutrient use efficiency, and furthermore abjectly influence crop production. Hinsinger *et al.*, (2009); Richardson *et al.*, (2009); Wissuwa *et al.*, (2009); Zhang *et al.*, (2010).

Bioavailability of phosphorus can be depleted rapidly via root uptake particularly in the rhizosphere, creating in a gradient of phosphorus concentration in a radial direction away from the root surface. Phosphorus content in soil usually exceeding the plant requirements, however, low mobility of phosphorus can restrict its availability to plants. Soluble phosphorus in soil solution particularly in the rhizosphere should be replaced 20 to 50 times per day by phosphorus delivery from bulk soil to the rhizosphere to meet plant demand Marschner, (1995). Therefore, phosphorus dynamics in the rhizosphere are mainly controlled by plant root growth and function, and highly related to physical and chemical properties of soil Neumann and Römheld, (2002). Two key processes dominantly control the availability of phosphorus due to low solubility, mobility, and high fixation in soil: (a) spatial

availability and acquisition of phosphorus in terms of plant root architecture as well as mycorrhizal association, and (b) bioavailability and acquisition of phosphorus based on the rhizosphere chemical and biological processes Fig. (3).

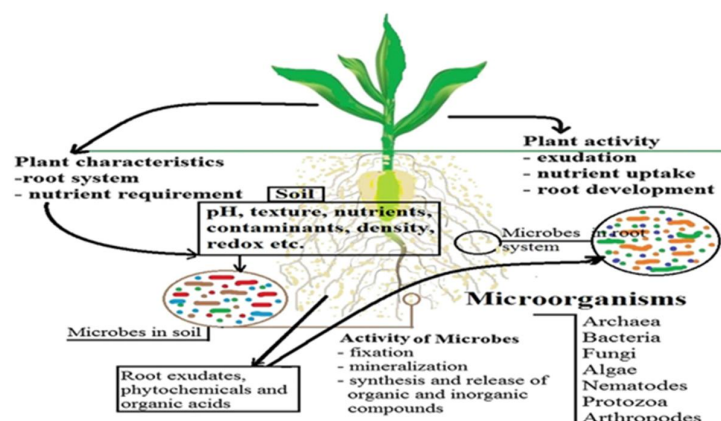


Fig. 4: Diagram illustrated chemical and biological processes in rhizosphere

3-1 Controlling of inorganic phosphate

Uptake of available inorganic phosphorus through coordinated achievement of several inorganic phosphorus transporters, which is greatly influenced by the root exploration capacity. Inorganic phosphorus uptake and scavenging capacity, which is determined mainly by the root system architecture; and integrated with microbes, such as AM fungi, that assist the plant in scavenging inorganic phosphorus from the soil Fig.(4). PAE (*Phosphorus Acquisition Efficiency*) is affected by other root traits that increase inorganic phosphorus availability in the soil solution, including the type and rate of efflux of organic acids (OAs) and phosphatases from the root.

3-1-1- Transporters of Inorganic Phosphate

Plants subjected to low inorganic phosphorus inducible high-affinity and constitutive low-affinity inorganic phosphorus uptake systems. Phosphate Transporter genes, (**Pht**) that encode inorganic phosphorus transporters have been characterized in detail in *Arabidopsis* and grouped into four families: **Pht1**, **Pht2**, **Pht3**, and **Pht4** Raghothama and Karthikeyan and Karthikeyan (2005.) Fig. (5).

Conspicuous advances has also been made for characterizing inorganic phosphorus transporters in several economically important plant species, including tomato (*Solanum lycopersicum*), potato (*Solanum tuberosum*), soybean (*Glycine max*), rice (*Oryza sativa*), barley (*Hordeum vulgare*), and maize (*Zea mays*) Ai *et al.* (2009), Fan *et al.* (2013), Glassop *et al.* (2007), Nagy, *et al.* (2005), (2007), Paszkowski *et al.* (2002), Qin *et al.* (2012), Rae *et al.* (2003), Sun *et al.* (2012), Takabatake *et al.* (1999), Versaw and Harrison (2002), Wang *et al.* (2011). Inorganic phosphorus transporters encoded by members of the Pht1 gene family, which are predominantly expressed in epidermal cells and in the outer cortex of the root, have been identified as mediators of inorganic phosphorus uptake at the root-soil interface particularly when inorganic phosphorus is limited Mudge *et al.* (2002), Sch *et al.* (2004) Fig. (5). These proteins are part of the so-called direct inorganic phosphorus uptake pathway and transport phosphorus as inorganic phosphorus anions, mainly $\text{H}_2\text{PO}_4^{-1}$ and HPO_4^{-2} , against a concentration gradient between the soil solution (which typically contains 0.1–10 μM inorganic-P) and the cytoplasm of the root epidermal cell (which typically contains 5–10 mM inorganic- P) Raghothama and (2005). Fig. (3).

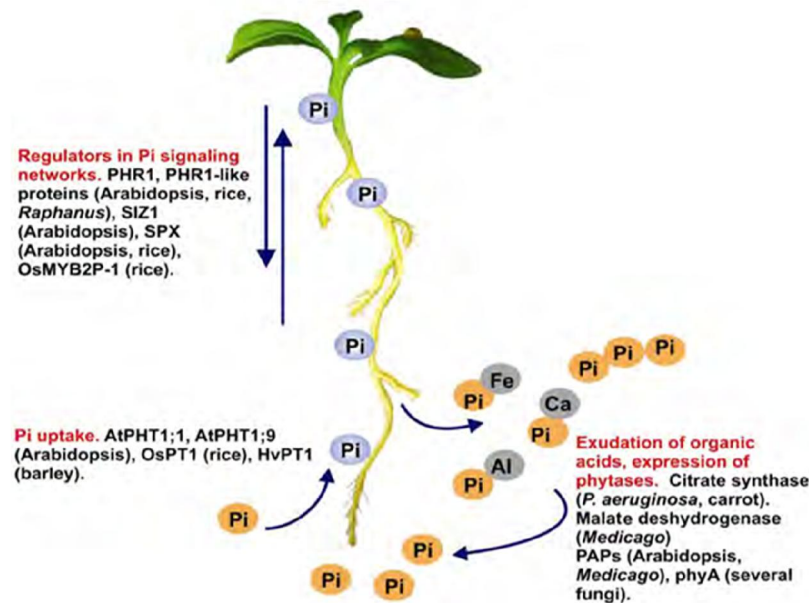


Fig. 5: Illustrates Schematic representation of the phosphorus-scavenging, uptake and assimilation processes targeted by genetic engineering strategies. Proteins involved in phosphate scavenging, transport, or regulatory mechanisms and genetically manipulated for enhancing inorganic phosphorus uptake and release from insoluble compounds.

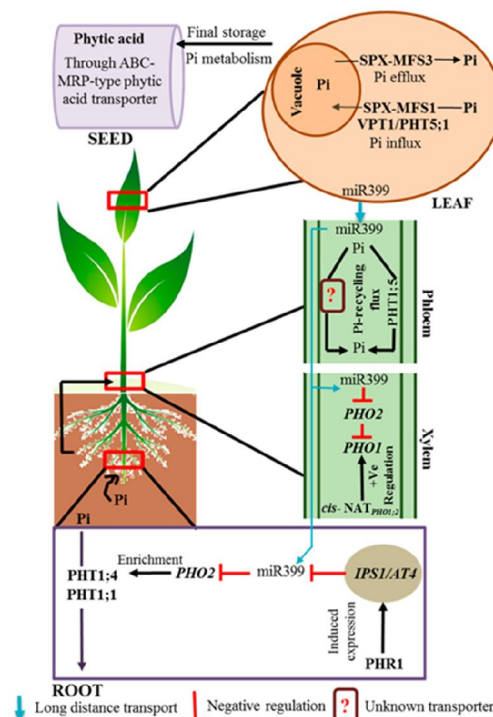


Fig. 5: PHF1 Facilitates PHT1; 2-CFP Targeting through the ER Compartment. Transient protein expression in *N.benthamiana* epidermal cells analyzed by confocal microscopy 48h. after infiltration. Transient expression of PH1; 2-CFP alone to a low (A) or High level (D) and together with YFP-PHF1 (G to L). (G to I), show localization in the ER (arrowheads indicate post-ER compartments). (J) to (L) show PHT1;2-CFP delivery to plasma at cell periphery. (M) to (O) show transient coexpression of YFP-PHF1 (J) with ER marker KDEL-DsRed (K). Bars=10mm, except in (J) to (L), where bars=50 μm

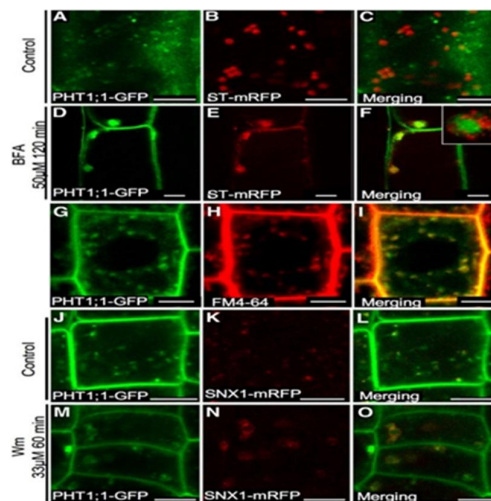


Fig. 6: Overview of phosphate (Pi) transport in Arabidopsis plants after Sudhakar Srivastava *et al.* (2018)

Sudhakar Srivastava *et al.* (2018) reported that the transport route is shown in four parts: uptake from soil to roots, transport from roots to shoots, unloading in shoots and subcellular organelles, and transport to seeds in the form of phytic acid Fig. (6). The high-affinity Pi (PHT1) family (PHT1;1 and PHT1;4) of transporters plays a major role in Pi uptake from soil to roots. The PHO1 protein increases root-Pi xylem loading, whereas PHT1;5 plays a key role in the translocation of Pi from shoots to roots, and Pi mobilization to reproductive organs. In plant cell, vacuoles act as the primary intracellular compartments for Pi storage, and SPX-MFS1 and SPX-MFS3/PHT5;1 mediate vacuolar Pi influx and efflux, respectively. Furthermore, Pi is metabolized and transported from leaves to seeds in the form of phytic acid by the ABC-MRP-type phytic acid transporter. The levels of PHT1, PHO1 and PHO2 transporters are regulated by miR399 and cis-NATPHO1;2 in xylem, and by miR399 and IPS1/AT4 in roots. ABC-MRP, ATP binding cassette-multidrug resistance-associated protein; AT4, Arabidopsis thaliana 4; IPS1, induced by phosphate starvation 1; cis-NATPHO1;2, cis-natural antisense transcript phosphate transporter 1;2; PHT, high-affinity phosphate transporter; PHR1, phosphate starvation response 1; Pi, phosphate; PHO1, phosphate transporter 1; SPX-MFS3, SYG1/PHO81/XPR1 major facilitator superfamily 3; SPX-MFS1, SPX major facilitator superfamily 1; VPT1, vacuolar phosphate transporter 1. Figure 1. Overview of phosphate (Pi) transport in Arabidopsis plants. The transport route is shown in four parts: uptake from soil to roots, transport from roots to shoots, unloading in shoots and subcellular organelles, and transport to seeds in the form of phytic acid. The high-affinity Pi (PHT1) family (PHT1; 1 and PHT1; 4) of transporters plays a major role in Pi uptake from soil to roots. The PHO1 protein increases root-Pi xylem loading, whereas PHT1;5 plays a key role in the translocation of Pi from shoots to roots, and Pi mobilization to reproductive organs. In plant cell, vacuoles act as the primary intracellular compartments for Pi storage, and SPX-MFS1 and SPX-MFS3/PHT5;1 mediate vacuolar Pi influx and efflux, respectively. Furthermore, Pi is metabolized and transported from leaves to seeds in the form of phytic acid by the ABC-MRP-type phytic acid transporter. The levels of PHT1, PHO1 and PHO2 transporters are regulated by miR399 and cis-NATPHO1; 2 in xylem and by miR399 and IPS1/AT4 in roots. ABC-MRP, ATP binding cassette-multidrug resistance-associated protein; AT4, Arabidopsis thaliana 4; IPS1, induced by phosphate starvation 1; cis-NATPHO1;2, cis-natural antisense transcript phosphate transporter 1;2; PHT, high-affinity phosphate transporter; PHR1, phosphate starvation response 1; Pi, phosphate; PHO1, phosphate transporter 1; SPX-MFS3, SYG1/PHO81/XPR1 major facilitator.

Although the majority of Pht1 transcripts have been located in root epidermal cells and root hairs, many of them have also been detected in leaves, stems, cotyledons, pollen grains, seeds, flowers, and potato tubers, suggesting their involvement not only in inorganic phosphorus uptake by roots but also in internal root-to-shoot distribution Ai, *et al.* (2009). Chiou and, Harrison (2001). Davies *et al.* (2002), Fan *et al.* (2013), Nagy *et al.* (2006). Qin *et al.* (2012). In soybean, 14 members of the Pht1 family encode high-affinity inorganic phosphorus transporters predominantly expressed in roots under low

inorganic phosphorus conditions Fan *et al.* (2013). In *Medicago truncatula*, 5 transporters encoded by Pht1 genes are inducible by low inorganic phosphorus, of which MtPT1 (*Medicago truncatula* PHOSPHATE TRANSPORTER 1) and MtPT2 play an important role in inorganic phosphorus uptake; MtPT4 plays a role in inorganic phosphorus translocation from mycorrhizal fungi into the roots Harrison *et al.* (2002), Liu *et al.* (2008). Xiao *et al.* (2006). In rice, the Pht1 gene family is composed of 13 members (OsPT1–13); 4 of www. These (OsPT2, OsPT3, OsPT6, and OsPT7) are highly expressed in inorganic phosphorus deprived roots, but several (such as OsPT6) apparently play a dual role in inorganic phosphorus uptake from the soil and inorganic phosphorus translocation inside the plant Ai, *et al.* (2009). Goff *et al.* (2002), Paszkowski *et al.* (2002). In maize, five Pht1 genes (ZmPht1;1–5) are induced by inorganic phosphorus limitation not only in roots but also in other tissues, such as young and old leaves, anthers, pollen, and seeds Nagy *et al.* (2006).

Therefore, at least some members of the Pht1 gene family play an important role in inorganic phosphorus uptake from the soil solution, particularly when this nutrient is present in limiting amounts. In contrast to Pht1 genes, members of the Pht2, Pht3, and Pht4 gene families have been associated mainly with inorganic phosphorus distribution within subcellular compartments, and their gene products are specifically located in the plastid inner membrane, mitochondrial inner membrane, and Golgi compartment, respectively Cubero *et al.* (2009), Guo *et al.* (2008). Versaw and Harrison (2002) Fig. (7).

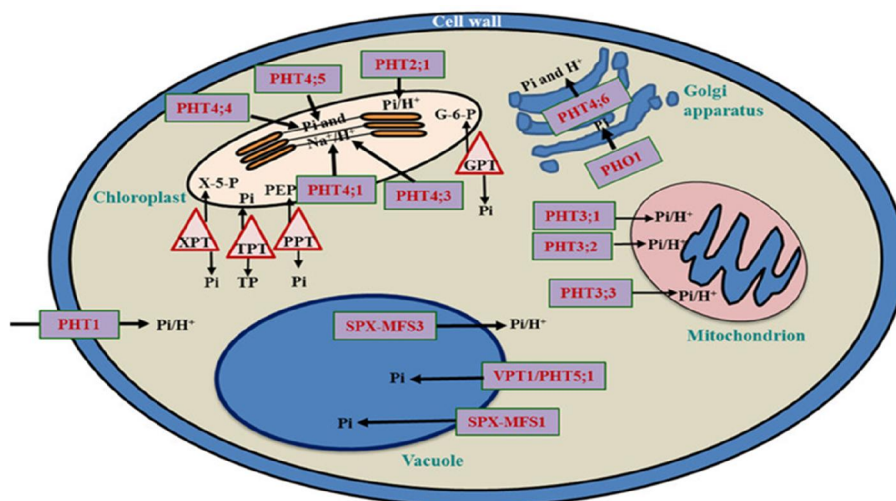


Fig. 7: Illustrates Subcellular localization of phosphate (Pi) transporters and translocators in Arabidopsis cells. PHT1, PHT2, PHT3, and SPX-MFS3 are proton-coupled Pi transporters. VPT1/PHT5; 1 and SPX-MFS1 function as Pi channels for Pi influx from the cytoplasm into the vacuoles, whereas SPX-MFS3 mediates Pi efflux from the vacuoles into cytoplasm. PHT4 proteins mediate Na⁺/H⁺-dependent Pi transport from the cytosol to the chloroplasts or Golgi. PHO1 localizes to Golgi membranes and mediates Pi transport without an H⁺ gradient across the membrane. Among the PHT2 family members, only PHT2.1 was functionally characterized as a Pi importer in the chloroplast envelope. AtPHT3 genes encode a small family of mitochondrial Pi transporters. These translocators mediate Pi transport in the exchange of various substrates. GPT, glucose 6-phosphate (G-6-P) / (Pi) trans locator; PPT, phosphoenolpyruvate (PEP)/Pi translocator; TPT, triose phosphate (TP)/Pi translocator; XPT, xylulose-5-phosphate (X-5-P)/Pi translocator. PHT, high-affinity phosphate transporter; SPX-MFS3, SYG1/PHO81/XPR1 major facilitator superfamily 3; SPX-MFS1, SPX major facilitator superfamily 1; VPT1, vacuolar phosphate transporter 1; Black arrows show the influx and efflux of Pi in the vacuole, mitochondrion, Golgi apparatus, and chloroplast through the regulation of various PHT members.

In Arabidopsis, the low-affinity transporter PHT2; 1, encoded by a member of the Pht2 family, is located in chloroplasts, and a pht2; 1 mutation reduces inorganic phosphorus transport into the chloroplast and decreases inorganic phosphorus allocation throughout the whole plant. However, the pht2;1 mutant is still viable, suggesting alternative mechanisms for inorganic phosphorus import into chloroplasts Versaw and Harrison (2002). Although the Pht2 family of transporter genes is also present

in *Medicago truncatula* and potato, compelling evidence of its function in these plants is still lacking. Mitochondrial inorganic-P transporter genes have also been identified in soybean, maize, and rice Takabatake *et al.* (1999); however, as is the case for chloroplast transporters, further investigation is needed to determine their physiological function and to evaluate their potential as biotechnological tools.

The concerted action of inorganic phosphorus transporters ensures inorganic phosphorus distribution to specific tissues, cells, and organelles. From an agronomic point of view, the ubiquity, diversity, and tissue distribution of inorganic-P transporters ensure that photosynthesis and respiration operate normally even under high stress conditions to sustain growth and reproduction **Fig.(7)**. Therefore, engineered alterations of the expression of different inorganic phosphorus transporters represent an opportunity to optimize uptake and proper distribution of inorganic-P within a plant to improve yield.

4- Spatial Availability and gaining Soil Phosphorus

4-1 Roots network

Plants are able to respond to phosphorus starvation by changing their root architecture, including root morphology, topology, and distribution patterns. Increases in root/ shoot ratio, root branching, root elongation, root topsoil foraging, and root hairs are commonly observed in phosphorus deficient plants, while the formation of specialized roots such as cluster roots occurs in a limited number of species Lynch and Brown, (2008); Vance, (2008). Phosphorus deficiency has been shown to reduce growth of primary roots and enhance length and density of root hairs and lateral roots in many plant species (Lo'pez- Bucio *et al.*, 2003; Desnos, (2008).

The phosphorus efficient genotypes of common bean (*Phaseolus vulgaris*) have more shallow roots in the topsoil where there are relatively high contents of P resources (Lynch and Brown, 2008). Some plant species, for example white lupin (*Lupinus albus*); can develop cluster roots with dense and determinative lateral roots, which are covered by large numbers of root hairs (Lambers *et al.*, 2006; Vance, 2008).

4-2 Regulation of Roots network.

Significant advance has been made in dissecting the mechanisms underlying changes in root system architecture in response to inorganic phosphorus deficiency, particularly in *Arabidopsis*. In wild and cultivated plants, including *Arabidopsis*, maize, rice, and tomato, inorganic phosphorus availability alters root traits by modulating the developmental programs that control lateral root primordium initiation and emergence, primary and lateral root growth, the angle of lateral root growth, and the density and elongation rate of root hairs L'opez-Bucio *et al.* (2003), (2002), P'erez-Torres *et al.* (2008), Williamson *et al.* (2001). The availability of inorganic phosphorus on root development is complex, species specific, and genotype dependent and involves crosstalk between different hormone-signaling pathways. Signaling pathways activated by auxins, ethylene, Cytokinins, gibberellins, strigolactone, jasmonic acid, nitric oxide, sugars, or the redox status of the root meristem play an important role in the root system architecture responses to low inorganic phosphorus availability Chiou and Lin (2011) , Ha and Tran (2014.). The first visible event in *Arabidopsis* plants suffering inorganic phosphorus deficiency is a strong reduction of primary root growth, which occurs rapidly after transfer to a low inorganic phosphorus medium and is followed by an arrest of cell division and loss of the quiescent center identity S'anchez-Calder *et al.* (2006),(2005), Svistoonoff *et al.* (2007) simultaneously , the formation of abundant lateral roots and root hairs expressing high levels of inorganic phosphorus transporters and phosphatases is enhanced by inorganic phosphorus limitation S'anchez-Calder *et al.* (2005), L'opez-Bucio *et al.* (2003), (2002) (2005), Nacry *et al.* (2005). P'erez-Torres *et al.* (2008) Fig. (8).

Such process occurs mainly due to changes in the acidity of rhizosphere, which influence the mobility and availability of inorganic phosphorus Geelhoed *et al.*, (1999). Plants have the ability to increase or decrease pH of rhizospheric up to 2–3 pH units, either by absorption or by release of protons in order to equilibrate cation / anion balance Hinsinger *et al.*, (2001). Gahoonia and Nielsen (1996) reported that when pH of rhizospheric was invariable, the plants (wheat and barley), displayed significant genotypic variation in terms of Phosphorus acquisition efficiency (PAE) indicating that other mechanisms should also be involved in causing variation on phosphorus acquisition. Carboxylates and the corresponding carboxylic acids, also known as *LMWOAs*, constitute the major fraction of root exudates during phosphorus deficiency Fig. (3). Usually, the most common organic acid anions found in rhizosphere are lactate, acetate, oxalate, succinate, fumarate, malate, citrate, isocitrate, and aconitate Jones, (1998). They have distinct functions on energetic cell metabolism, maintaining charge balance or osmotic potential. It has been widely suggested that *LMWOAs* can improve phosphorus availability by mobilizing sparingly available phosphorus forms in the soil solution. This occurs by chelating metals ions like Al, Fe or Ca involved in phosphorus sorption and occupying sorption sites on minerals Jones, (1998). Phosphorus mobilizing activity through *LMWOAs* is based on their variable negative charge, which would allow the complexation of metal cations and the displacement of anions from the soil matrix. The above is supported by several studies reporting an increase of organic acids exudation by roots in response to phosphorus deprivation, especially in plants from Proteacea family that possess cluster roots Jones, (1998); Vance *et al.*, (2003); Delgado *et al.*, (2013). In addition, the presence of *LMWOAs* in solution has been seen to increased phosphorus availability as compared to water treatments Gerke, (1992); Khademi *et al.*, (2009), (2010). The efficiency for mobilizing phosphorus differs across *LMWOAs* as follows: citrate > oxalate > malate > acetate. However, organic acid anion-induced phosphorus release depends on many factors, such as pH, soil mineralogy and anion concentration (>100mM for citrate, >1mM for oxalate, malate and tartrate) Bolan *et al.*, (1994); Jones and Darrah, (1994), Lan *et al.*, (1995).

Organic acid have a fast turnover adsorbed in acidic soils and rapidly degraded in alkaline counterparts, with half-lives of several hours Wang *et al.*, (2010). Contrasting evidence found that, despite exuding citrate, pea genotypes were not capable of mobilizing phosphorus from Al-P and Fe-P complexes Pearse *et al.*, (2007). Nevertheless, organic acid production constitutes an important carbon cost in plant metabolism, with 5–25% of total fixed carbon by photosynthesis being used to sustain exudation. However, this does not seem to significantly affect net biomass production as phosphorus deficiency which can largely reduce growth Johnson *et al.*, (1996); Keerthisinghe *et al.*, (1998). Sparingly available organic P forms represent between 30% and 90% of total phosphorus in some soils Borie *et al.*, (1989); Jones and Oburger, (2011). Substantial flows of phosphorus occur between inorganic and organic phosphorus pools in soil through immobilization and mineralization, being both processes mediated predominantly by soil microorganisms Oberson and Joner, (2005); Richardson and Simpson, (2011) Fig (3). In order to utilize source of phosphorus, organic compounds have to be mineralized; that is, organic phosphorus substrates must be hydrolyzed by enzymatic activity of phosphatases to release inorganic phosphorus. This activity seems to be more pronounced in the rhizosphere and it is associated with a depletion of soil organic phosphorus Gahoonia and Nielsen, (1992); Chen *et al.*, (2002); Spohn and Kuzyakov, (2013). Phosphatases are enzymes responsible for catalyzing the hydrolysis of phosphoric acid anhydrides and esters (Schmidt and Laskowski, 1961). The Nomenclature Committee of the International Union of Biochemistry and Molecular Biology classifies these into 5 groups: phosphomonoesterases (EC 3.1.3), phosphodiesterases (EC 3.1.4), triphosphoric monoester hydrolases (EC 3.1.5), enzymes acting on phosphoryl-containing anhydrides (EC 3.6.1) and on P–N bonds (EC 3.9) Nannipieri *et al.*, (2011). Phosphomonoesterases are the most abundant enzymes in soils and include acid and alkaline forms and phytases, among others. To date, there is no evidence that any plants produce alkaline phosphomonoesterases. There is an increasing interest on phytases because they hydrolyze inositol phosphates (isomers and lower order derivatives of inositol hexakisphosphate) which generally constitute a major component of soil total organic phosphorus. Ranging from 4 to 40% of total phosphorus in soils Borie *et al.*, (1989); Smernik and Dougherty, (2007); Turner, (2007), inositol phosphates are readily adsorbed to soil particles and can react with cations (Fe and Al in acidic soils and Ca in alkaline ones) depending on pH to form poorly soluble precipitates Shang *et al.*, (1992); Celi and Barberis, (2005). However, in most plant species phytase activity has limited capability to mineralize inositol phosphate due to its low production and exudation from roots and the poor

availability of the substrate in solution Richardson *et al.*, (2001); George *et al.*, (2007). Attempts to creating transgenic plants overexpressing phytases and/or other phosphatases have been achieved Lung *et al.*, (2005); Wasaki *et al.*, (2009) with little successes under natural soil conditions, where substrate availability is restricted Lung and Lim, (2006); Wang *et al.*, (2009). Interestingly, phosphatase activities are higher near the rhizosphere, with maximum activities found from 2 to 3.1 mm to the root surface for acid and 1.2 to 1.6 mm for alkaline phosphomonoesterases, showing a negative correlation with rhizospheric organic phosphorus content in wheat plants Nannipieri *et al.*, (2011). Phosphatase activity is regulated by other factors, such as soil mineralogy, organic matter content, phosphorus availability and bacterial communities present in the rhizosphere Joner and Jakobsen, (1995); Snajdr *et al.*, 2008; Stursova and Baldrian, (2011).

4-4 Microorganisms

Non-symbiotic soil microorganisms play a key role on organic phosphorus ecosystem dynamics Fig. (3); Harvey *et al.*, (2009); Khan *et al.*, (2010). It has been proposed that all alkaline Phosphomonoesterases found in soil have a microbial origin, mainly bacterial Tabatabai, (1994); Yadav and Tarafdar, (2003). Additionally, free-living bacteria and fungi Unno *et al.*, (2005); Richardson and Simpson, (2011) mediate the majority of inorganic phosphorus (Pi) mineralized from phytase activity. Spohn *et al.* (2013) using the ³³P isotopic approach found that the release of root exudates could be a plant strategy to increase phosphorus mineralization by enhancing microbial activity. Free-living soil microorganisms are believed to be more efficient than plants in absorbing and incorporating Phosphorus into their biomass. Therefore, microbial Phosphorus represents an important soil Sink Xu *et al.*, (2013) and a potential source of available Phosphorus for most plants as microbial Phosphorus is located in more labile intracellular compounds with a fast turnover Oberson and Joner, (2005); Bünemann *et al.*, (2013); Hinsinger *et al.*, (2015). Despite having an important role in organic Phosphorus dynamics, most research related to free-living soil microorganisms to enhance PAE (*Phosphorus Acquisition Efficiency*) has been focused on microorganisms capable of solubilizing sparingly available Phosphorus Wakelin *et al.*, (2004); Leggett *et al.*, (2007). Microorganisms can release protons, LMWOAAs, and other secondary organic metabolites that may contribute to Phosphorus solubilization from minerals Jones and Oburger, (2011). Indeed, between 1-50% of soil bacteria and about 0.5-0.1% of soil fungi can be classified as P-solubilizing microorganisms Kucey *et al.*, (1989); Gyaneshwar *et al.*, (2002). Fungal isolates (particularly the Genus *Penicillium*) stimulate the solubilizing of inorganic phosphorus in both solid and liquid media Gyaneshwar *et al.*, (2002); Leggett *et al.*, (2007); Morales *et al.*, (2011). Groups of bacteria, considers as plant growth promoting rhizobacteria (PGPR), are found in the rhizosphere and have the potential of enhancing PAE mainly through influencing nutrient availability, such as Phosphorus, or indirect through the production of phytohormones, or plant growth regulators as well Richardson *et al.*, (2009). These regulators influence root architecture and other features related to plant development such as auxin, cytokinin, ethylene, gibberellin, and abscisic acid, Peleg and Blumwald, (2011); Vacheron *et al.*, (2013). Although the benefits of using PAE that enhancing microorganisms have been evidenced in laboratory and glasshouse conditions, inconsistent results have been observed in field trials Goos *et al.*, (1994); Karamanos *et al.*, (2010), with the exception of arbuscular mycorrhizal symbiosis established with certain soil fungi.

4-5 Mycorrhizal Association

Mycorrhizal symbioses can increase the spatial availability of phosphorus, extending the nutrient absorptive surface by formation of mycorrhizal hyphae. *Arbuscular mycorrhizal fungi* (AMF) form symbiotic associations with the roots of about 74% of angiosperms Brundrett, (2009) Fig. (11).

In the symbioses, nutrients are transferred by AMF via their extensive mycorrhizal mycelium to plants while in return the fungi receive carbon from the plant. AMF not only influence plant growth through increased uptake of nutrients but also have non-nutritional effects in terms of stabilization of soil aggregates and alleviation of plant stresses caused by biotic and abiotic factors Smith and Read, (2008).

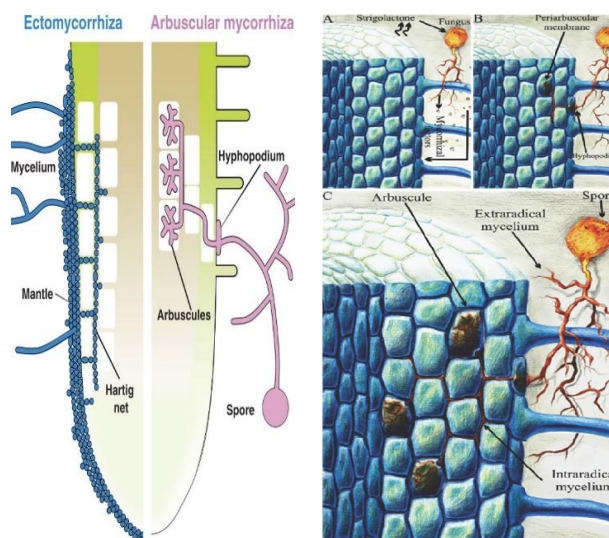


Fig. 11: Represents hypothetical root colonized by an arbuscular mycorrhizal fungus (AMF)

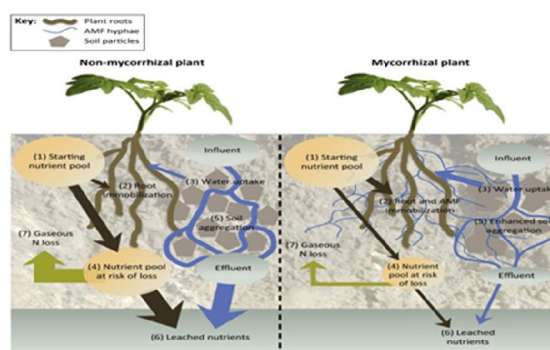


Fig. 12: Illustrates positive effects of arbuscular mycorrhizal (AM) colonization on physical, chemical, biological and nutritional status of soils.

The beneficial effects of AMF and other microorganisms on plant performance and soil health can be very important for the sustainable management of agricultural ecosystems Gianinazzi *et al.*, (2010). A primary benefit of AMF (*Arbuscular mycorrhizal fungi*) is the improved P uptake conferred on symbiotic plants. In limiting phosphorus soils, mycorrhizal plants usually grow better than non-mycorrhizal plants because of enhanced direct phosphorus uptake of plant roots via the AM pathway. However, plant growth can be suppressed even though the AM pathway contributes greatly to plant phosphorus uptake (Smith and Read, 2008). The growth inhibitions might be caused by the down regulation of the direct root phosphorus uptake pathway Grace *et al.*, (2009). Recent gene expression study Feddermann *et al.*, (2010) shows that plants induce a common set of mycorrhiza induced genes but there is also variability, indicating that there exists functional diversity in AM symbioses. The differential expression of symbiosis-associated genes among different AM associations is related to the fungal species, plant genotypes, and the environmental factors. Therefore, regulation of direct uptake pathways through epidermis and root hairs and AM pathways requires further investigation (Bucher, 2007; Smith *et al.*, 2010).

5- Maximizing phosphorus efficiency in rhizosphere

Better understanding of phosphorus dynamics in the soil rhizosphere continuously provides an important basis to optimize phosphorus management for improving phosphorus use efficiency for crop production. The effective strategies for phosphorus management may involve a series of multiple-level approaches in association with soil, rhizosphere, and plant processes. Phosphorus input into agricultural land can be optimized based on the balance of inputs/outputs of phosphorus. Soil-based phosphorus management requires for long-term management strategy to maintain the soil phosphorus available

supply at an appropriate level through monitoring soil phosphorus fertility, due to the relative stability of phosphorus within soils. Using such approach, the application of phosphorus fertilizer can be reduced by about 20% as compared to farmer practice for obtaining high yielding cereal crops. This may be of significant importance for saving phosphorus resources without sacrificing crop yields Fig. (13) though it may cause phosphorus accumulation in soil due to high threshold levels and low phosphorus use efficiency by crops.

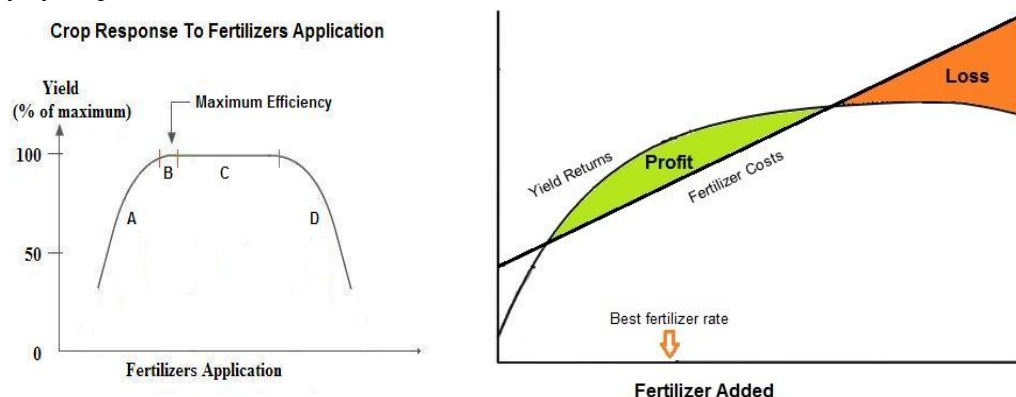


Fig. 13: Illustrates the relation between Fertilizers added and Yield production,

- (A)- Yield increases as fertilizer application rate increases
- (B)- Yield reaches a maximum.
- (C)- Addition of extra fertilizer does not increase the yield
- (D) When fertilizer application rates are too high, salinity damages and specific nutrient toxicities occur and yield declines

Rhizosphere-based phosphorus management provides an effective approach to improving phosphorus use efficiency and crop yield through exploitation of biological potential for efficient mobilization and acquisition of phosphorus by crops, and reducing the overreliance on application of chemical fertilizer phosphorus. Localized application of phosphorus plus ammonium improved maize (*Zea mays*) growth by stimulating root proliferation and rhizosphere acidification in a calcareous soil, indicating the potential for field scale modification of rhizosphere processes to improve nutrient use and crop growth Jing *et al.*, (2010). Several researches indicates that faba bean (*Vicia faba*) can acidify its rhizosphere, whereas maize does not Li *et al.*, (2007). The interaction between intercropping system (bean/maize) may enhanced phosphorus uptake by maize plants. Some soil and rhizosphere microorganisms such as AMF and plant growth promoting rhizobacteria also contribute to plant Phosphorus acquisition Richardson *et al.*, (2009). Field trials of PSM application results in increases in crop yield up to 20% Jones and Oburger, (2011), and coapplication of AMF and PSM shows synergistic effects in phosphorus acquisition Babana and Antoun, (2006). Alternatively, successful phosphorus management can be achieved by breeding crop cultivars or genotypes more efficient for phosphorus acquisition and use. Great progress has been made in traditional plant breeding programs toward selecting crop varieties for high phosphorus use efficiency. An example of efficient genotype was the wheat (*Triticum aestivum*) variety Xiaoyan54 that secreted more carboxylates (e.g. malate and citrate) into the rhizosphere than phosphorus inefficient genotypes Li *et al.*, (2005), (2006). Another promising example was soybean (*Glycine max*) 'BX10' with superior root traits that enable better adaptation to low phosphorus soils Yan *et al.*, (2006). Some important root genetic traits have been identified with potential utility in breeding phosphorus efficient crops, including root exudates, root hair traits, topsoil foraging through basal or adventitious rooting Gahoonia and Nielsen, (2004); Lynch and Brown, (2008). The ability to use insoluble phosphorus compounds in soils can be enhanced by engineering crops to exude more phytase, which results from overexpression of a fungal phytase gene George *et al.*, (2005b). The integration of genetically improved phosphorus efficient crops with advanced phosphorus management in the soil plant system is important for improving nutrient use efficiency and sustainable crop production. Cooperative work always requires between scientists from different disciplines in the crop, plant, and soil sciences. Issues involving phosphorus use in agriculture are becoming important in various fields beyond agronomy. Phosphorus management involves a series of strategies such as

increasing phosphorus uptake efficiency by plant and animal, reducing overuse of chemical fertilizer phosphorus and improving recycling efficiency of manure phosphorus. It is estimated that animal manure may substitute for 1.46 Mt phosphorus of chemical phosphorus fertilizers, and recycling manure is thus of an importance for optimizing phosphorus resource use in the future

6- Conclusion

Phosphorus fertilization is predominantly controlled by Phosphorus dynamics in the soil - plant relationships. The distribution and dynamics of Phosphorus in soil has a significant due to the variation of climatic conditions. Root distribution (*Root architecture*) throughout the soil-rhizosphere where the presence of Phosphorus fertilizer are located, plays an important part for phosphorus utilization efficiency. Moreover, root network can enhance the phosphorus mobilization particularly in the soil rhizosphere through root excretions such as carboxylates, protons, and phosphatases. The interaction between the adaptation of root morphology and physiology to low adequate of phosphorus might effectively match heterogeneous Phosphorus supply and distribution in soil. This phenomenon enhancing the bioavailability of Phosphorus in soil. Such integration of Phosphorus dynamics from soil to plant through the soil rhizosphere gradually provides a comprehensive state of available Phosphorus behavior and efficient acquisition in association with adaptation of plant approaches.

Significant progress has been made for understanding soil, rhizosphere, and plant processes associated with soil Phosphorus transformation, mobilization, acquisition, and deficiency responses, many aspects of overall Phosphorus dynamics in the soil / rhizosphere-plant are not thoroughly understood, including regulation of Phosphorus acquisition and Phosphorus starvation rescue mechanisms in plants, the complex coordination of root morphology, physiological and biochemical responses under varying Phosphorus availability, and plant sensing of heterogeneous Phosphorus supply in soil. Given the importance of Phosphorus to plants and its importance as a strategic resource, a better understanding of Phosphorus dynamics in the soil / rhizosphere plant is necessary to guide establishment of integrated Phosphorus management strategies involving manipulation of soil and rhizosphere processes, development of Phosphorus efficient crops, and improving Phosphorus recycling efficiency in the future.

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