ISSN Online: 2349-7785

Phosphorus Mobilization Strategies of Grain Legumes: An Overview

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Received 24 January 2017; accepted in revised form 27 February 2017

Abstract: Phosphorus (P) is an indispensable element that may limit the agricultural production in the next millennium. Though, chemical P fertilizers are the widely used source to provide nutrition to the crop plants but depleting rock phosphate reserves, expected higher consumption, high cost of chemical P fertilizer, poor phosphorus use efficiency, adverse effect of excessive use of P fertilizer on soil health and microbial diversity, necessitate the need to adopt sustainable and environment friendly agricultural practices that maximize the crop yield by improving existing use efficiency of soil phosphorus. Organic exudates of soil microbes and roots of grain legume crops can mobilize phosphorus from unavailable soil-P pool and increase its availability for P-inefficient plant species grown in intercropping or crop rotation. Legume crops adopt different strategies such as development of cluster roots, exudation of carboxylates, protons and acid phsophatase to render the P available from inorganic and organic P sources. Thus, intercropping or crop rotation of cereal crops with such legumes that have improved mechanisms to gain access to this fixed P will contribute toward more sustainable agriculture. This review summarizes the P acquisition mechanisms adopted by specific legume crops for improving P nutrition of less P-efficient crops grown in rotation and/or intercropping as well as effect of soil properties and global warming on this trait.

Key words: Phosphorus, legumes, root exudates, mobilization.

Introduction

With ever increasing population, the projected demand for global grain production is likely to double by 2050. Increase in food grain production by two fold and its sustenance are the major challenges experienced by the agriculture scientists. Strategies to increase crop yields and improve the efficiency of nitrogen, phosphorus and water use, besides judicious application of agro-chemicals need to be adopted. Phosphorus (P), being a key nutrient, plays a significant role in crop productivity. However, its low availability due to poor fertilizer use efficiency (~ 45 %), slow diffusion and high fixation in soil [17, 25] necessitates the need to apply P in quantities in excess of the crop requirements. To meet the increasing P demands of crops, intensive P fertilization concerns about the financial burden on marginal farmer as well as its impact on environment. Moreover, the chemical P fertilizer production depends on the availability of phosphate rock, the reserves of which are finite [60] and being fast depleted with half-depletion predicted to occur between 2040 and 2060. Thus, reduction in chemical P input and improving P-use efficiency and plant P acquisition under conditions of low P availability is increasingly important.

Given the limited access of most small farmers to fertilizer P, it is desirable to identify and incorporate suitable crop species in rotations that are efficient in mobilizing P from the soil-P pool [74]. Leguminous crops are bestowed with this potential and their beneficial effect is mostly attributed to improved N status of soils through symbiotic N_2 fixation [79], enhanced P availability and to break soil-borne disease cycles [39]. The growth and P

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uptake of a subsequent crop is enhanced due to mobilization of soil P by P-efficient legume crops [43]. The present review throws light on aspects by which leguminous crops contribute to the P nutrition of less P-efficient crops grown in rotation and/ or intercropping.

Phosphorus mobilizing legume crops

The different leguminous crops with potential to mobilize P from soil-P pool include white lupin (*Lupinus albus* L.), chick pea (*Cicer arietinum*), soybean (Glycine max), mung bean (*Phaseolus vulgaris),* faba bean (*Vicia faba* L.), ground nut (*Arachis hypogea*), pigeon pea (*Cajanus cajan),* cow pea (*Vigna unguiculata*) and field pea (*Pisum sativum* L.). To cope with the scarce availability of soil inorganic P (Pi), leguminous plants have evolved various morphological, biochemical and physiological strategies to enhance Pi uptake, often termed the Pi-starvation response [100, 105]. The dominant adaptation mechanism involves the formation of proteoid roots, which at maturity combines organic-anion exudation with proton extrusion to mobilize sparingly available soil P. Legume species have high demand for calcium which leads to a net export of protons, and can acidify the rhizosphere, following N-fixation [63]. Adaptation to low P environment is also related to alteration of the citric acid cycle in the roots with subsequent adaptation of anion channels. Mobilization of P by the legume crop occurs from sparingly soil P compounds that cereals cannot use and thus contribute to the P nutrition of less P-efficient crops, grown in rotation and/or intercropping. Extra P is also likely to become available from the decomposition of the legume crop residues. With legume crop, changes in soil microbial communities occur, which may enhance soil P availability for rotational or intercrop [4]. The efficiency of P acquisition depends on plant genotype, change in expression of many genes, mycorrhizal associations, soil chemical and physical properties, and cropping system (e.g. rotation).

Adaptive soil-P mobilization mechanism in legumes

Legume plants enhance rhizosphere chemical processes more than cereal crops to mobilize sparingly soluble soil P by root architectural or exudation plasticity suggesting a potential benefit of crop-specific root-trait-based management to cope with variable soil P supply in sustainable grain production. Root secretions and root traits contribute to the formation of an adaptive mechanism in response to phosphorus starvation by which the plant can adjust to stress conditions.

Role of root architecture in P mobilization

Root architecture is a highly plastic trait, and varies among species. Root plasticity is strongly controlled by plant growth regulators as well as inherent genetic factors. Alteration in root architecture under low P status is associated with changes in phyto-hormone composition and their concentration, and involves expression of a number of genes. The internal balance of auxin, ethylene, and cytokinin is likely to play a role in P-deficiency induced alterations in lateral root development and architecture, root hair formation and cluster root development [127 89, 91 117, 16, 80].

Organic acid exudation

Legume plants can increase the synthesis of organic acids (OA) in roots under low P conditions. The major fraction of exuded OA includes citrate, oxalate and malate that mobilize Pi by displacing phosphate from soil matrix through ligand exchange. However, to mobilize significant quantities of P into the soil, the desired concentrations of citric acid should be > 100 µM, and oxalate, malate and tartrate > 1 mM and its effect is extremely soil-dependent [49]. Concentration of OA in the rhizosphere of non-proteoid roots is much less compared to the proteoid roots, due to lower excretion rate and the fast microbial degradation of OA. The effectiveness of carboxylates to mobilize P depends largely on carboxyl (-COOH) and hydroxyl (-OH) group. Citrate (tri-carboxylic acid) exhibits the greatest ability to desorb P, followed by oxalate (di-carboxylic acid), while malate, malonate and tartarate are moderately effective [12, 42]. Citrate is particularly effective at mobilizing P from Fe-phosphates and Al-phosphates in acid soils [12] and Ca-phosphates in calcareous soils, or from rock phosphate fertilizer [18]. Shen *et al.*[93] suggested that P is mobilized by desorbing and chelating P from Al-P and Fe-P complexes and from other non-labile pools.

Phenolics

Phenolic compounds such as piscidic acid from roots of pigeon pea (*Cajanus cajan*) [1], alfafuran from alfalfa (*Medicago sativa*) roots [65] and isoflavonoids from P-deficient cluster roots of white lupin [71] can be exuded into the rhizosphere, in response to P starvation and might act as chelators and/or reductants for increasing the release of bound Pi. Phenolics act in the same way as carboxylates [27], but may be less effective than carboxylates [73]. Release of phenolics may also serve as fungistatic [120] .

Enzyme exudation

Plants can increase the efficiency of Pi use during Pi deficiency via up-regulation of Pi starvation inducible hydrolases (non-specific phospholipases, ribo-nucleases (RNases), and acid phosphatases [9, 82] that scavenge Pi from non-essential P-esters. Phosphatases and phytases are released by plant roots into rhizosphere where they hydrolyse soil organic P (Po) pools. The abundance of acid phosphatases is more in the rhizosphere under P starvation. Organic acid secretion may increase the ability of secreted acid phosphatases to scavenge Pi from soil and localized organic-Pi-esters. Acid phosphatases may have multiple functions, such as carbon metabolism, nodule permeability for O_2 diffusion, and oxidative stress attenuation [97] .The capacity to utilize phytate P is highly limited and is detected only in the presence of phytate mineralizing microorganisms that dephosphorylate phytate P.

Biochemical adaptations

Reorganizing cellular metabolism that conserves the limited pools of adenylates and Pi is an alternative and significant biochemical adaptation of Pi deprived plants. This is accomplished by altering the organization of glycolysis, mitochondrial respiration, and tonoplast H^+ pumps, allowing adenylate and Pi-dependent reactions to be bypassed during Pi starvation [82]. Several of these bypasses facilitate respiration and vacuolar pH maintenance during extended periods of Pi starvation by using pyrophosphate in carrying out the cellular work, while simultaneously conserving ATP and recycling Pi. Glycolytic bypass enzymes include pyrophosphate-dependent phospho-fructokinase (PFK) and phosphoenolpyruvate (PEP). The PEPc catalyzed bypass of cytosolic pyruvate kinase also results in the synthesis of OA from glycolytic metabolites which is critical for the anaplerotic replenishment of tri-carboxylic acid (TCA) cycle intermediates, as well as the root secretion of OA, a common response to Pi starvation [100].

Changes in microbial communities

Differences in amounts and composition of root exudates and rhizo-deposits may affect rhizosphere microbial communities [71]. Differences in fungal community structure in the rhizosphere of white lupin were attributed to citric acid, while differences in bacterial community structure were attributed to the presence of *cis*-aconitic, citric, and malic acids [64]. Secondary metabolites and signaling molecules exuded by roots shape microbial communities and are implicated in root-root and root-microbe communication [113]. Changes in soil chemical properties such as pH have a significant influence on the structure of soil microbial communities [88].

Re-mobilization of P within the plant

It is an important bio-chemical and physiological response to P starvation that reduces the shoot respiratory and photosynthetic metabolic reactions resulting in alteration of photosynthetic capacity, but does not restrict the supply of photosynthate from leaves to nodulated roots [125, 14]. This is an adaptive strategy for the host plant for phosphate translocation from the aerial parts to support the symbiotic N_2 fixation under P stress. In *Medicago truncatula,* nodules could maintain constant total P concentration until P concentration in the leaves is reduced to the threshold level for the organ to remain viable. Organic phosphate was of great importance for the preservation of nodule symbiotic efficiency [51].

Others

Induction of high-affinity Pi transporters in roots of P deficient plants also play a crucial role in the acquisition of limited P by some plants [72,82]. Enhanced expression of high-affinity, plasma membrane-bound Pi transporters in roots and a concomitantly increased P-uptake capacity, has been reported as a typical P-starvation response [19].

Phosphorus mobilization mechanism adopted by grain legumes

White lupin (*Lupinus albus*)

White lupin (*Lupinus albus*) responds to P deficiency stress by forming cluster roots [24] with dense and determinative lateral roots, which are covered by large numbers of root hairs [46, 103]. Cluster roots provide large surface area and their formation is accompanied by high exudation of protons, carboxylates, and acid phosphatase from such roots, that greatly enhance P acquisition from soil [105, 46, 114]. Cluster roots formed under P deficiency exude 20 to 40 times more citrate and malate than those grown under sufficient P [105]. However, in presence of adequate plant P status, cluster-root formation and the exudation of mainly citrate is suppressed and gets stimulated when the shoot P status is low [81,92]. Cluster roots may also be formed during Fe-deficiency; with even faster citrate exudation [28, 66]. Low P supply and increasing light intensity increase the production of cluster roots and citrate exudation [15]. The amount of citrate exuded may be as high that it may even lead to precipitation of Ca citrate on the root surface [18]. Excretion and concentration of citrate in white lupin root cells is dependent on the age of the cluster roots and occurs when citrate concentration reaches a critical level in the cluster root cells. Younger cluster roots appear to have maximum exudation of citrate, compared to mature ones that have decreased excretion. Accumulation of citric acid in white lupin roots occurs following an alteration of the citric-acid cycle in the roots cells [45]. Concentration and form of nitrogen and phytochrome release also affects the exudation of OA[35] that might be more related to leaf conditions rather than to amounts in the roots [76].

Excretion of oxalate, aconitate, α-ketoglutarate, pyruvate and fumarate from cluster roots and root tips of white lupin has also been reported in plants grown under conditions of P deficiency [24]. Release of organic anions into the rhizosphere often enhances the mobilization of sparingly soluble P in soil. Adaptive changes of root growth and architecture under P starvation are related to altered carbohydrate distribution between roots and shoots, and these changes may be caused by plant hormones [70,69], sugar signalling [44,104], and nitric oxide [117].

Biochemical niche complementarities can occur when two intercropped species tap into different pools of soil P such as inorganic and organic pools or different chemical forms of each of these pools [118]. Wheat and associated white lupin plants in mixed culture have shown to deplete water-extractable and citric-acid extractable inorganic P fractions in a low-P soil.

Chickpea (*Cicer arietinum*)

Chickpea does not form cluster roots, but has associations with mycorrhizal fungi that play an important role in P acquisition [119]. Under P deficient conditions, roots of *Cicer arietinum,* release much higher concentration of protons and carboxylates (mainly malonate) in the rhizosphere [54,72,87,108,121]. Malonate though, suggested as a selective deterrent to microorganisms, may inhibit succinate dehydrogenase, a key enzyme in the TCA-cycle [53]. Absence of malonate accumulation in the rhizosphere indicates the microbial breakdown. Though, the function of carboxylate exudation in chickpea is less clear [124] but it has been reported to provide a fitness advantage of playing a role in P acquisition. Carboxylates are released constitutively and along the entire root system [121,,122,,123] and the rate of carboxylate release into the rhizosphere [108, 121, 87] by chickpea root has a positive correlation with acid phosphatase extruded by the roots [56, 77, 78]. Higher acid phosphatase activity in the rhizosphere of *Cicer arietinum* has been reported regardless of P sources [56] while root morphological traits in *Cicer arietinum* had a minor contribution towards enhancing the P uptake under low-P environment.

A root system with mycorrhizal network has a greater effective surface area [47] due to formation of lateral roots or increased root branching [59, 84] for absorbing nutrients and exploring a greater volume of soil (100 times greater) than non-mycorrhizal roots [94]. Moreover, mycorrhizae are known to produce alkaline phosphatases, which can mobilize P from organic sources, and its low rate can have a long-term impact on mobilizing phosphate [98]. The hydrolysis of organic P (Po) by extracellular phosphatases secreted by mycorrhizae, excretion of protons, hydroxyls and organic anions [83] and modifications of the redox potential around mycelium and roots of the mycorrrhizal association might also hasten the release of P ions from soil to solution [33]. Alteration in rhizospheric pH is associated with the soil-buffering capacity, microbial activities, and plant genotypes [34,105]. These different mechanisms play a significant role, especially in response to P mobilization [48].

Soybean (*Glycine max*)

Soybean is an important food and oil seed crop. Different mechanisms are involved in the internal P-re-mobilization of soybean plant and soil P acquisition. Both young, developing and P-stressed plants usually show higher acid phosphatase activity, which ensures P supply from older tissues and re-mobilize it to the apical growing parts [20,23]. Some soybean cultivars with higher biomass production can reduce acid phosphatase activity but keep the same leaf tissue P concentration. Contrarily, other cultivars with higher biomass production can increase acid phosphatase activity, and maintain the same leaf tissue P concentration within the same maturation group. Under P starvation in monoculture, transgenic plants over express *AtPAP15* or *Gm EXPB2* that can improve the soybean growth and P efficiency by increasing acid phosphatase secretion or changing root morphological traits [116, 128]. High-molecular weight secretary proteins and low-molecular weight exudates such as carboxylates, phenols, free amino acids and sugars released from roots of soybean differentially influence genotypic P acquisition efficiency [110]. Under low P availability, efficient genotypes exude a greater quantity of organic compounds into the rhizosphere, thereby increasing the P availability to meet the crop requirement. This enables the crop to produce consistent biomass and seed yield with reduced fertilizer addition. Maintenance of growth and yield potential by mining the inherent soil P is a favourable trait in genotypes, reducing dependence on P fertilizers [110] .

Nature of OA exudation in soybean depends on the source of stress. As P stress specifically promotes the release of oxalate and malate whereas Al stress promotes citrate exudation. Maximum isoflavonoid exudation (daidzein) occurs in root tip [26] just before a surge of OA exudation and ATP-citrate lyase could potentially control citrate, and isoflavonoid exudation. Genistein and hydroxygenistein have been identified as the dominant isoflavonoids exuded in larger amounts from P-stressed than from P-sufficient plants and from proteoid roots than from ordinary roots [120]. Phenolic compounds could positively impact the efficiency of citrate by keeping its scavengers out of the rhizosphere. In early stages of P starvation, there is no significant alteration of the activities of phosphoenolpyruvate carboxylase (PEPC), phosphoenolpyruvate phosphatase (PEPP), malate enzyme (ME), isocitrate dehydrogenase (ICDH), malate dehydrogenase (MDH), and pyruvate kinase (PK) [19]. This activity enhancement may or may not be related to the synthesis and release of organic acids. The expression of several genes of the purple acid phosphatase GmPAP family and phytate and phosphoenol pyruvate phosphatase gets induced in soybean nodules under low-P availability [7,8,51].

Mung bean (*Vigna radiata*)

Root size and diameter are the most important morphological responses whereas carboxylate exudation and P-acquisition and P-utilization efficiency followed by rhizosphere soil pH and acid phosphatase activity are the important physiological responses for P acquisition in mung bean. Both inter and intra-species differences do exist in green gram in terms of root exudation, P uptake, and shoot and root P content. In general, green gram, has greater root exudation compared to maize. However, the amino acid content of the total root exudates in maize has been reported to be twofold compared to green gram [94].

Phosphatases and phytase secreted by plant roots and rhizospheric microbes play a significant role in P nutrition [50] . Zinc ions act as a cofactor for the phosphatase and phytase enzyme, which result in increase in enzyme acti-vity. The increase in microbial population and chlorophyll in presence of ZnO nanoparticles indi-cated that the response of mung bean is synergetic to yield of Zn and P nutrition [85]. High expression of phytase among nodule tissues for the P-deficient RIL115 has been reported and associated with an increase in phytase (33 %) and phosphatase (49 %) activities and efficiency in use of the rhizobial symbiosis (34 %). Phytase activity in nodules would contribute to the adaptation of the rhizobia-legume symbiosis to low-P environments [50].

Faba bean (*Vicia faba*)

Faba bean roots excrete protons, malate and citrate into the rhizosphere, which mobilize sparingly soluble P and contribute to increased P uptake by cereals in P-deficient calcareous soils [55]. The malate exuded by intercropped faba bean roots diffuses to the roots of intercropped cereal [52]. Faba bean even with smaller root system (due to variable P availability) has been found to exude higher content of citrate and acid phosphatase, thereby suggesting its greater capacity to mobilize P in the rhizosphere. Root interactions of neighbouring plants can be modified by increased P availability [126]. The magnitude of proton released by faba bean under P deficiency gets enhanced in presence of NH_4NO_3 as nitrogen source. Though, it may not be true for all the species of faba bean under P deficiency [29]. Use of ammonium-based fertilizers may facilitate P acquisition of legumes in non-acidic P-deficient soils.

The proton release induced by P deficiency has been found to be greater in faba bean compared to white lupin [58], as indicated by the intensive rhizosphere acidification within 30 min and more H^+ efflux on root tips of faba bean has been reported. The increased proton release by the roots of P-deficient faba bean would contribute greatly to mobilization of non-labile P in soil, especially in high-pH soils [56] and may also compensate for both excess uptake of cations [18] and a concomitant release of organic acid anions [72].

Groundnut (*Arachis hypogea*)

The ability of groundnut to take up phosphorus from soil of low P availability has been attributed to new P solubilizing mechanism known as 'contact reaction' which occurs at the interface between root surface and soil particles. However, differences in root development, excretion of root exudates capable of solubilizing Fe-P and Al-P forms in soils are less effective.

The P-solubilizing active sites in groundnut root cell walls have been located at the root surface and could act as chelating agent with Fe (III). In early growth stages of groundnut there is high P inflow (6.8 - 10.3 $\times 10^{-14}$ mol cm^{-1} s^{-1}), which declines as the plant continues to grow with a concomitant decrease in P efficiency. Thus, P inflow differs greatly between species (0.2 and 1 μM P concentration) as well as with the stage of growth of a particular species [11]. With a 5-fold increase in the P concentration, the P inflow of groundnut in the first period increased to 1 $\times 10^{-14}$ mol cm^{-1} s^{-1} and declined later even reaching negative values between the 3rd and 4th harvest (28 and 35 days after transplanting). P uptake kinetics is not decisive for P uptake from soil. The ion absorption kinetic parameters are also influenced by several factors in addition to the arbuscular mycorrhizal fungi and especially by plant age [22, 21].

Pigeon pea (*Cajanus cajan*)

Pigeon pea can access soil P from different pools of soil due to exudation of organic anions and this ability varies with species. Exudates from pigeon pea roots contain malonate and piscidic acid and can mobilize P bound to Fe and Al [1]. P mobilizing activity of exudates increases with increasing P stress [96]. As pigeon pea plants excrete significant amount of root exudates with Fe-P solubilizing ability only after they flower. The P-solubilizing ability of root cell-walls may partially explain the high P efficiency of this species before it flowers [2]. Citric, malonic, succinic and piscidic acids have also been reported to be exuded by roots of pigeon pea [40]. Depending on the P-starvation level, plant growth stage, and genotype of pigeon pea, the secretion of piscidic acid is 5 and 100 times more than of citric acid, and the latter is most efficient in acquiring P from alfisols [40].

Cowpea (*Vigna unguiculata*)

Cowpea is a major food and fodder legume and is subjected to several constraints including P deficiency that limit its production and yields. However, the crop is well adapted to the harsh growing conditions, including low soil fertility, high temperatures, and drought [32, 101]. Genotypic variations have been observed in root traits of cowpea genotypes under P limiting conditions. Under P-limiting environments for cowpea, the size of the roots may be more important and citric acid as the only organic acid detected in measurable amounts [75]. In the root extract of cowpea plants, malonic, succinic, malic, and citric acids have been detected, but not fumaric acid. However, total content of carboxylic acid in the roots was same as that of leaves in cowpea [76]. The relative content of each organic acid in the leaves and roots was almost equal irrespective of the crop species.

Pea (*Pisum sativum*)

Citrate is the main carboxylate in the field pea (*Pisum sativum*) rhizosphere, making up 93-98 % of the total amount of carboxylates, Respiratory O_2 consumption in pea (*Pisum sativum*) roots displayed no effect of P starvation on respiration [99].

Factors affecting P mobilization

Soil texture

The root diameter of plants grown in the compacted soil is greater compared to loose soil. Thus, in a more loamy soil, rhizosphere carboxylate concentrations tend to increase with distance from the apex. Rhizosphere concentrations of carboxylates are a function of net exudation, degradation by microorganisms, and adsorption to the soil [42,90]. If exudation occurs along the entire root system at similar rates, and exudation exceeds degradation and adsorption, an increase in carboxylate concentrations with distance from the apex occurs. Similarly, carboxylate concentrations tend to be lower for the whole root system in the compacted soil.

The roots of plants grown in soil have been reported to exude only traces of malic, citric and fumaric acid whereas the roots of plants grown in sand may also exude lactic and acetic acids as the main carboxylates with traces of citric, malonic, malic, formic, fumaric, *cis*-aconitic and *trans*-aconitic acid. The predominant acid exuded was piscidic acid (a tri-carboxylic acid) but not citrate. A considerable genetic variability in organic acid exudation, especially in the presence of P has also been reported. Generally, there is less organic acid exudation by cowpea under P-deficiency conditions. A maintenance level of P is required for accelerated OA exudation.

Hassan *et al*.[30]. observed that different leguminous plants depleted the labile P pool differently and increased or decreased the less labile P pools of sandy soils in South Australia. These results suggest that it is necessary to evaluate the effect of legume growth on soil P dynamics for each leguminous species and for each soil type.

Soil moisture

Low soil moisture content, reduces the mobility of Pi in soil [101, 10] and hence tends to lower the plant's P status. A low plant P status tends to enhance exudation [57]. Thus, Pi uptake is affected much less by water shortage than expected, on the basis of the effect of soil moisture on Pi mobility in soil. Roots of many species release an array of exudates (e.g. carboxylates, phenolics, protons and other cations, phosphatases, water, mucilage), and thus enhance the availability of Pi in the rhizosphere. The nature and effectiveness of the exudates depends on species as well as environmental conditions.

Factors affecting P aquisition

Effect of elevated CO_2

Elevated CO_2 is likely to affect the transformation of P from inorganic to organic form in plant tissue, thereby mediating P use efficiency. The increase in photosynthetic rate and plant growth under elevated CO_2 is linked to the concentration of the Rubisco enzyme, because most of the carbon assimilated by autotrophic organisms is metabolized by this enzyme [3]. Elevated CO_2 increases the Rubisco concentration, and this will require more Pi being transformed into Po for the synthesis of Rubisco because Po is a major component of rRNA involved in the synthesis of the enzyme [86,109]. Thus, P-use efficiency would increase, as greater proportion of P in plant tissue is used for photosynthesis-associated metabolisms and assimilation. However, the extent that elevated CO_2 increases P desorption depends on whether elevated CO_2 stimulates the release of those carboxylates that are effective in mobilizing Pi. Elevated CO_2 alters P acquisition through changes in root morphology and increases in rooting depth. Moreover, the quantity and composition of root exudates are likely to change under elevated CO_2, due to the changes in carbon fluxes along the glycolytic pathway and the tricarboxylic acid cycle. As a consequence, these root exudates may lead to P mobilization by the chelation of P from sparingly soluble P complexes, by the alteration of the biochemical environment and by changes to microbial activity in the rhizosphere [41]. Significant volumes of root exudates have been measured following elevated CO_2 exposure [6,106]. Haase *et al.* [31] also found that the release of malate, which is the major organic acid in the exudates from *Phaseolus vulgaris*, increased by 177 % after the plants were exposed to elevated CO_2 (800 mL L^{-1}) for 18 d. The increase of these organic compounds is likely to mobilize P in the rhizosphere but to date the mobilization of P in the rhizosphere has not been assessed quantitatively.

Hydraulic distribution

Phosphorus uptake from dry shallow patches in soil is expected to increase when the soil is moistened due to hydraulic redistribution [36, 37,111]. Movement of water from moist to dry patches of soil as well as from roots in shallow layers moistened after rain to root deep in profile and horizontal movement of water via the stem depending on soil water content [38], is called hydraulic distribution [13]. Water uptake by roots requires the expression of water-channel proteins (aquaporins). These proteins are expressed in a diurnal pattern, with low expression levels at night and increasing expression early in the day [107]. As diffusion of Pi in dry soil is very slow [5, 10]. Pi uptake declines with decreasing soil moisture content [68,101,112]. Equally, when deeper soil layers contain abundant P reserves, hydraulic redistribution down the profile may enhance the uptake of Pi [67]. However, the concept of enhancing Pi availability by hydraulic redistribution has little convincing evidence to support it.

Conclusions

Though, P fertilizers will continue to play a major role in intensive agriculture, but depletion of natural resources, loss of biodiversity, and long-term un-sustainability requires alternative strategies to be investigated and implemented to provide food security and safe and healthy environment to growing population. The P accumulated due to chemical fixation of fertilizer P needs to be accessed adopting sustainable agricultural practices. Intercropping or rotation of legume-cereal crop may be more advantageous to make use of the P from soil P pool. Acidification of rhizosphere environment due to exudation of carboxylates, proton or changes in root morphological or physiological traits may help to scavange soil P and reduce the input of P based chemical fertilizers.

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