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Phosphorus Dynamics: From Soil to Plant¹

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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 P is its low availability due to slow diffusion and high fixation in soils. All of this means that P can be a major limiting factor for plant growth. Applications of chemical P 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 P-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, P uptake and utilization by plants plays a vital role in the determination of final crop yield. A holistic understanding of P dynamics from soil to plant is necessary for optimizing P management and improving P-use efficiency, aiming at reducing consumption of chemical P fertilizer, maximizing exploitation of the biological potential of root/rhizosphere processes for efficient mobilization, and acquisition of soil P by plants as well as recycling P from manure and waste. Taken together, overall P dynamics in the soil-plant system is a function of the integrative effects of P transformation, availability, and utilization caused by soil, rhizosphere, and plant processes. This Update focuses on the dynamic processes determining P availability in the soil and in the rhizosphere, P mobilization, uptake, and utilization by plants. It highlights recent advances in the understanding of the P dynamics in the soil/rhizosphere-plant continuum.

P DYNAMICS IN SOIL

Soil P Transformation

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

Turner et al., 2007). Pi usually accounts for 35% to 70% of total P in soil (calculation from Harrison, 1987). Primary P minerals including apatites, strengite, and variscite are very stable, and the release of available P from these minerals by weathering is generally too slow 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 P minerals including calcium (Ca), iron (Fe), and aluminum (Al) phosphates vary in their dissolution rates, depending on size of mineral 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). The P adsorbed on various clays and Al/Fe oxides can be released by desorption reactions. All these P forms exist in complex equilibria with each other, representing from very stable, sparingly available, to plant-available P pools such as labile P and solution P (Fig. 1).

In acidic soils, P can be dominantly adsorbed by Al/Fe oxides and hydroxides, such as gibbsite, hematite, and goethite (Parfitt, 1989). P can be first adsorbed on the surface of clay minerals and Fe/Al oxides by forming various complexes. The nonprotonated and protonated bidentate surface complexes may coexist at pH 4 to 9, while protonated bidentate innersphere complex is predominant under acidic soil 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 P can be enhanced with increasing ionic strength. With further reactions, P 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, P retention is dominated by precipitation reactions (Lindsay et al., 1989), although P 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 dicalcium 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 at alkaline pH (Arai and Sparks, 2007). HAP accounts for more than 50% of total Pi in calcareous soils from long-term fertilizer experiments (H. Li, personal communication). HAP dissolution increases with decrease of soil pH (Wang and Nancollas, 2008), suggesting that

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rhizosphere acidification may be an efficient strategy to mobilize soil P from calcareous soil.

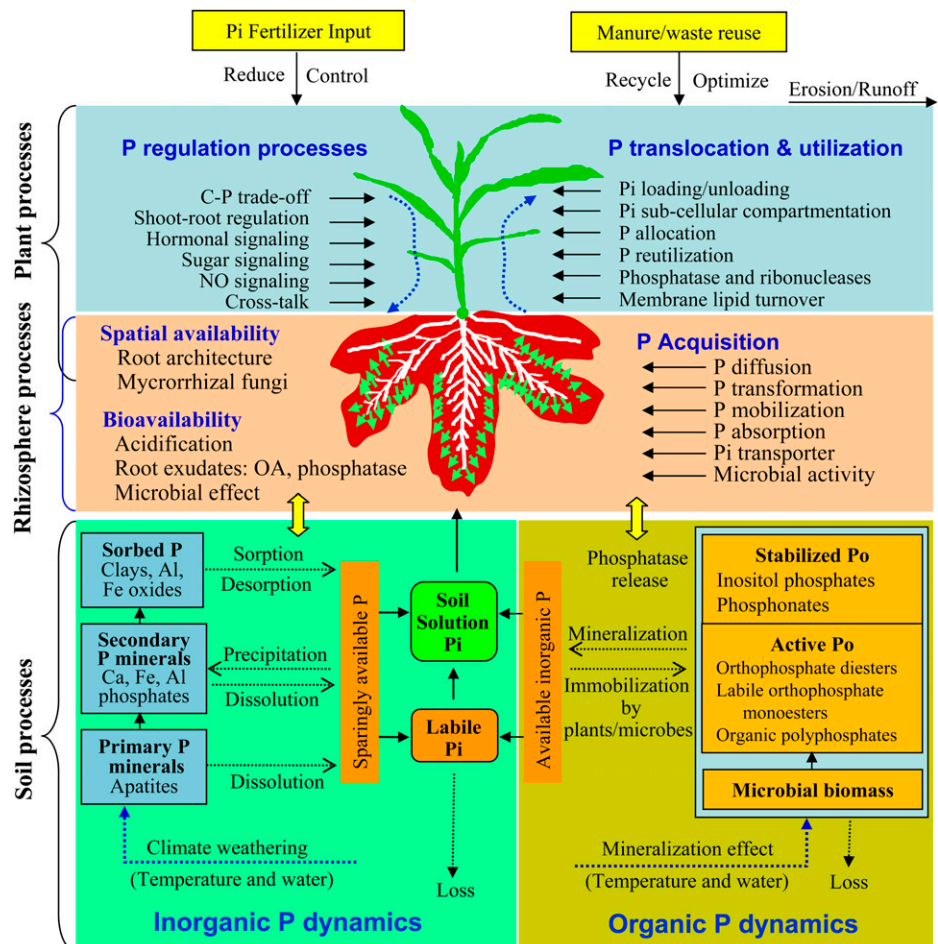
Po generally accounts for 30% to 65% of the total P in soils (Harrison, 1987). Soil Po mainly exists in stabilized forms as inositol phosphates and phosphonates, and active forms as orthophosphate diesters, labile orthophosphate monoesters, and organic polyphosphates (Turner et al., 2002; Condron et al., 2005). The Po 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 moisture, temperature, surface physical-chemical properties, and soil pH and Eh (for redox potential). Po transformation has a great influence on the overall bioavailability of P in soil (Turner et al., 2007). Therefore, the availability of soil P is extremely complex and needs to be systemically evaluated because it is highly associated with P dynamics and transformation among various P pools (Fig. 1).

Chemical Fertilizer P in Soil

The modern terrestrial P cycle is dominated by agriculture and human activities (Oelkers and Valsami-Jones, 2008). The concentration of available soil Pi seldom exceeds 10 μM (Bielecki, 1973), which is much

lower than that in plant tissues where the concentration is approximately 5 to 20 mM Pi (Raghothama, 1999). Because of the low concentration and poor mobility of plant-available P in soils, applications of chemical P fertilizers are needed to improve crop growth and yield. The major forms of phosphate fertilizers include mono-calcium phosphate (MCP) and monopotassium phosphate. Application of MCP can significantly affect soil physicochemical properties. After application to soil, MCP undergoes a wetting process, generates large amounts of protons, phosphate, and DCP, and eventually forms a P-saturated patch (Benbi and Gilkes, 1987). This Pi-saturated patch forms three different reaction zones including direct reaction, precipitation reaction, and adsorption reaction zones. The direct reaction zone is very acidic (pH = 1.0–1.6), resulting in enhanced mobilization of soil metal ions. These metal ions can also react with high concentrations of Pi in the zone thus causing further precipitation of Pi. The amorphous Fe-P and Al-P that thereby form 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 Ca phosphates (octocalcium phosphate or apatite). Because the Pi concentration is relatively low, P adsorption by soil minerals is dominant in the outer zone (Moody et al., 1995). In

Figure 1. P dynamics in the soil/rhizosphere-plant continuum. C-P, Carbon-P; NO, nitric oxide; OA, organic acids.



contrast, the application of monopotassium phosphate has little influence on soil physical and chemical properties (Lindsay et al., 1962). Therefore, matching P fertilizer types with soil physical and chemical properties may be an efficient strategy for rational use of chemical fertilizer P.

Manure P in Soil

Manure can be applied to soil to increase P fertility. The total P content in manure is very variable and nearly 70% of total P in manure is labile. In manure, Pi accounts for 50% to 90% (Dou et al., 2000). Manure also contains large amounts of Po, such as phospholipids and nucleic acids (Turner and Leytem, 2004), which can be released to increase soil Pi concentrations by mineralization. Furthermore, small molecular organic acids from mineralization of humic substances in manure can dissolve Ca phosphate, and especially for citrate, it can efficiently weaken the nanoparticle stability of HAP, by controlling the free Ca availability and thereby the nucleation rate (Martins et al., 2008). P adsorption to soil particles 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 Pi. Manure can also change soil pH and thus alter soil P availability. However, mechanisms of manure-induced P transformation processes between Pi and Po in soil still need further investigation.

P DYNAMICS IN THE RHIZOSPHERE

The rhizosphere is the critical zone of interactions among plants, soils, and microorganisms. Plant roots 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. The chemical and biological processes in the rhizosphere not only determine mobilization and acquisition of soil nutrients as well as microbial dynamics, but also control nutrient-use efficiency of crops, and thus profoundly influence crop productivity (Hinsinger et al., 2009; Richardson et al., 2009; Wissuwa et al., 2009; Zhang et al., 2010).

Due to its low solubility and mobility in soil, P can be rapidly depleted in the rhizosphere by root uptake, resulting in a gradient of P concentration in a radial direction away from the root surface. In spite of total soil P content usually exceeding the plant requirements, the low mobility of soil P can restrict its availability to plants. Soluble P in the rhizosphere soil solution should be replaced 20 to 50 times per day by P delivery from bulk soil to the rhizosphere to meet plant demand (Marschner, 1995). Therefore, P dynamics in the rhizosphere are mainly controlled by plant root growth and function, and also highly related to

physical and chemical properties of soil (Neumann and Römheld, 2002). Because of the unique properties of P in soil such as low solubility, low mobility, and high fixation by the soil matrix, the availability of P to plants is dominantly controlled by two key processes (Fig. 1): (1) spatial availability and acquisition of P in terms of plant root architecture as well as mycorrhizal association, and (2) bioavailability and acquisition of P based on the rhizosphere chemical and biological processes.

Spatial Availability and Acquisition of Soil P

Root Architecture

Plants are able to respond to P 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 P-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). P 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 (López-Bucio et al., 2003; Desnos, 2008). The P-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). Therefore, root architecture plays an important role in maximizing P acquisition because root systems with higher surface area are able to explore a given volume of soil more effectively (Lynch, 1995).

Some adaptive modifications in root architecture in response to P deficiency are well documented in *Arabidopsis* (*Arabidopsis thaliana*) and in those species forming cluster roots (Lambers et al., 2006; Osmont et al., 2007; Desnos, 2008; Vance, 2008; Rouached et al., 2010). 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 (Neumann and Römheld, 2002; Nacry et al., 2005), sugar signaling (Karthikeyan et al., 2007; Vance, 2010), and nitric oxide in the case of cluster-root formation in white lupin (Wang et al., 2010).

Root proliferation is stimulated when plant roots encounter nutrient-rich patches, particularly when the patches are rich in P and/or nitrogen (Drew, 1975; Hodge, 2004). The root proliferation in P-rich topsoil layers is related to a decreased root gravitropic response under P limitation (Bonser et al., 1996), and ethylene may be involved in the regulation of these responses (Lynch and Brown, 2008). Root proliferation can be greatly stimulated in the P-enriched soil

patches. However, the mechanisms of P-dependent changes in root proliferation in response to local P supply are not fully understood. Localized application of phosphates plus ammonium significantly enhances P uptake and crop growth through stimulating root proliferation and rhizosphere acidification in a calcareous soil (Jing et al., 2010). Further studies focusing on the involvement of phytohormones and other signaling molecules in modulation of root plasticity in response to localized application of Pi are warranted.

Mycorrhizal Association

Mycorrhizal symbioses can increase the spatial availability of P, 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). 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 (e.g. P, zinc, and copper), but may also have nonnutritional effects in terms of stabilization of soil aggregates and alleviation of plant stresses caused by biotic and abiotic factors (Smith and Read, 2008). 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 is the improved P uptake conferred on symbiotic plants. In low-P soils mycorrhizal plants usually grow better than nonmycorrhizal plants as a consequence of enhanced direct P uptake of plant roots via the AM pathway. However, plant growth can be suppressed even though the AM pathway contributes greatly to plant P uptake (Smith and Read, 2008). The growth inhibitions might be caused by the down-regulation of the direct root P-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).

Bioavailability and Acquisition of Soil P

Root-induced chemical and biological changes in the rhizosphere play a vital role in enhancing the bioavailability of soil P (Hinsinger, 2001). These root-induced changes mainly involve proton release to acidify the rhizosphere, carboxylate exudation to mobilize sparingly available P by chelation and ligand exchange, and

secretion of phosphatases or phytases to mobilize Po by enzyme-catalyzed hydrolysis (Neumann and Römheld, 2002; Zhang et al., 2010).

Root-induced acidification can decrease rhizosphere pH by 2 to 3 units relative to the bulk soil, resulting in substantial dissolution of sparingly available soil P (Marschner, 1995). The pH change in the rhizosphere is mainly affected by cation/anion uptake ratios and nitrogen assimilation. Ammonium supply to plant roots causes rhizosphere acidification, whereas nitrate supply causes alkalization. Legumes take up excess cations over anions, resulting in proton release. P deficiency in white lupin stimulates proton release and citrate exudation by cluster roots in association with an inhibition of nitrate uptake (Neumann et al., 1999; Shen et al., 2005). The changes of rhizosphere pH are also related to soil-buffering capacity, microbial activities, and plant genotypes. Besides proton release, carboxylate exudation such as that of citrate, malate, and oxalate greatly enhances Pi acquisition through chelation as well as by ligand exchange. Organic acid excretion and function in increasing P mobilization is well documented (Raghothama, 1999; Vance et al., 2003; Hinsinger et al., 2005). However, the mechanisms of soil P mobilization by carboxylates especially the relative contributions of ligand exchange, ligand-promoted dissolution of P-bearing minerals such as Fe/Al oxides, complexation of Al, Ca, or Fe and changes in solution P speciation, and carboxylate adsorption promoting changes in surface charges on clays and Al/Fe oxides are not fully understood despite some progress on the physiological control of carboxylate synthesis and excretion. Involvement of anion channels in organic acid excretion is confirmed by the action of anion channel blockers (Neumann et al., 1999; Wang et al., 2007). It is found that the Al-activated malate transporter mediates malate exudation (Hoekenga et al., 2006) and the multidrug and toxic compound extrusion transporter mediates citrate exudation (Magalhaes et al., 2007), and both may confer Al resistance. The molecular physiological mechanisms, which underlay the survival and resistance to both P deficiency and Al toxicity shown by some plants such as white lupin (Wang et al., 2007), warrant further investigation.

Plants can secrete phosphatase to mobilize Po through enzyme-catalyzed hydrolysis. The activities of phosphatases are up-regulated under P deficiency (Vance et al., 2003; Vance, 2008). However, the efficacy of these phosphohydrolases can be greatly altered by the availability of substrate, interactions with soil microorganisms, and soil pH, depending on soil physical and chemical environments (George et al., 2005a). Therefore, there is often no significant correlation between the phosphatase activity and plant growth performance in acidic or calcareous soils (A. Richardson, personal communication). Moreover, carboxylate exudation may have strong interactions with soil, resulting in a low efficiency in P mobilization. Therefore, root-induced bioavailability and acquisition of P in association with root exudation should be systemically

evaluated in the soil/rhizosphere-plant continuum (Fig. 1).

Some soil and rhizosphere microorganisms except mycorrhizal fungi (for example, plant growth promoting rhizobacteria, particularly P-solubilizing bacteria [PSB] and fungi [PSF]) can also enhance plant P acquisition by directly increasing solubilization of P to plants, or by indirect hormone-induced stimulation of plant growth (Richardson et al., 2009). P-solubilizing microorganisms (PSM; PSB plus PSF) account for approximately 1% to 50% in P solubilization potential (Chen et al., 2006). The PSB or PSF may mobilize soil P by the acidification of soil, the release of enzymes (such as phosphatases and phytases), or the production of carboxylates such as gluconate, citrate, and oxalate (Jones and Oburger, 2011).

P UPTAKE AND UTILIZATION BY PLANTS

Plant roots absorb P as either of H_2PO_4^- or HPO_4^{2-} . Because the concentrations of these ions in soils are in the micromolar range, high-affinity active transport systems are required for Pi uptake against a steep chemical potential gradient across the plasma membrane of root epidermal and cortical cells. This process is mediated by high-affinity Pi/ H^+ symporters that belong to the *PHT1* gene family. Disruption of *PHT1* gene expression results in a significant decrease of P acquisition by roots (Shin et al., 2004; Ai et al., 2009). In addition, some members of this family are expressed specifically and/or up-regulated in roots colonized by mycorrhizal fungi, indicating their function in transport of Pi via a mycorrhizal-dependent pathway (Bucher, 2007). Most of the Pi taken up by roots is loaded into the xylem and subsequently translocated into shoots. Two rice (*Oryza sativa*) phosphate transporters OsPht1;2 and OsPht1;6 with different kinetic properties are involved in Pi translocation from roots to shoots (Ai et al., 2009). The putative regulators PHO1 and PHO1;H1 containing the SPX (for SYG/PHO81/XPR1) tripartite domain also contribute to Pi translocation through loading Pi to the xylem (Hamburger et al., 2002; Stefanovic et al., 2007).

Within plant cells, P is a major component of nucleic acids, membrane lipids, and phosphorylated intermediates of energy metabolism. Thus, the cellular Pi homeostasis is essential for physiological and biochemical processes. Under P deficiency, plants can develop adaptive responses not only to facilitate efficient Pi acquisition and translocation, but also to utilize efficiently stored P by adjusting Pi recycling internally, limiting P consumption, and reallocating P from old tissues to young and/or actively growing tissues. Although 85% to 95% of the cellular P is present in the vacuole, ^{31}P -NMR studies reveal that the Pi efflux from the vacuole is insufficient to compensate for a rapid decrease of the cytosolic Pi concentration during P starvation (Pratt et al., 2009). By contrast, a phosphate transporter PHT4;6 is located in the Golgi membrane, probably transporting

Pi out of the Golgi luminal space for the recycling of the Pi released from glycosylation (Cubero et al., 2009). Another phosphate transporter PHT2;1 is present in the chloroplast, and can affect allocation of Pi within the plant (Versaw and Harrison, 2002). Releasing Pi from organic sources, such as phosphomonoesters and nucleic acids, is also an important step for internal P-recycling processes. Phosphatases are needed to release Pi from phosphomonoesters, and a dual-targeted purple acid phosphatase isozyme AtPAP26 (intracellular and secreted APase) is essential for efficient acclimation of Arabidopsis to P deprivation (Hurley et al., 2010). Ribonucleases are responsible for P mobilization from RNA, and two genes (*AtRNS1* and *AtRNS2*) are up-regulated by P starvation (Bariola et al., 1999). These phosphatase and ribonuclease genes are also induced by leaf senescence, further supporting their important role in the P remobilization process (Gepstein et al., 2003).

To limit P consumption, membrane lipid composition can be altered to some extent through a decrease of phospholipids and an increase of non-P lipids under P limitation (Essigmann et al., 1998). Degradation of phospholipids into Pi and diacylglycerol is mediated by phospholipases C and D, which are essential for lipid turnover in plants acclimating to P deficiency (Li et al., 2006). Diacylglycerol is subsequently converted into galactolipids or sulfolipids by two enzymes SQD1 and SQD2 to functionally substitute for phospholipids (Yu et al., 2002). In addition, plants can also use the alternative cellular respiratory pathways bypassing the adenylate and Pi reaction for reduction of P demand under P starvation (Theodorou and Plaxton, 1993).

Taken together, plants have developed a series of adaptive responses to take up and utilize P efficiently, including morphological, physiological, and biochemical responses (Fig. 1). This complex network is required to control Pi nutrition in plants either locally or systemically. The molecular mechanisms defining the phosphate signaling pathway have been presented in several reviews published recently (Doerner, 2008; Lin et al., 2009; Rouached et al., 2010). Indeed, many key players within the network, such as transcriptional factors (PHR1), microRNA (miR399), and ubiquitin E2 conjugase (PHO2), are able to regulate *PHT*, *PHO1*, *APase*, and *RNS* genes at different regulatory levels. In addition, the sugar-signaling and hormonal networks are also involved in the Pi response (Hammond and White, 2008; Vance, 2010).

STRATEGIES FOR IMPROVING P EFFICIENCY IN THE SOIL/RHIZOSPHERE-PLANT CONTINUUM

Better understanding of P dynamics in the soil/rhizosphere-plant continuum provides an important basis for optimizing P management to improve P-use efficiency in crop production. The effective strategies for P management may involve a series of multiple-

level approaches in association with soil, rhizosphere, and plant processes. P input into farmland can be optimized based on the balance of inputs/outputs of P. Soil-based P management requires a long-term management strategy to maintain the soil-available P supply at an appropriate level through monitoring soil P fertility because of the relative stability of P within soils. By using this approach, the P fertilizer application can be generally reduced by 20% compared to farmer practice for the high-yielding cereal crops in the North China Plain (Zhang et al., 2010). This may be of significant importance for saving P resources without sacrificing crop yields (Fig. 2) though it may cause P accumulation in soil due to high threshold levels and low P-use efficiency by crops.

Rhizosphere-based P management provides an effective approach to improving P-use efficiency and crop yield through exploitation of biological potential for efficient mobilization and acquisition of P by crops, and reducing the overreliance on application of chemical fertilizer P (Fig. 2). Localized application of P 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). Another study indicates that faba bean (*Vicia faba*) can acidify its rhizosphere, whereas maize does not (Li et al., 2007). The enhanced P uptake and maize yields in the faba bean/maize intercropping system are mainly attributed to the rhizosphere interactions between the two plant species. Some soil and rhizosphere microorganisms such as AMF and plant growth promoting rhizobacteria also contribute to plant P acquisition (Richardson et al., 2009). Field trials of PSM application results in increases in crop yield by 0% to 20% (Jones and Oburger, 2011), and coapplication of AMF and PSM shows synergistic effects in P acquisition (Babana and Antoun, 2006).

Alternatively, successful P management can be achieved by breeding crop cultivars or genotypes more efficient for P acquisition and use. Great progress has been made in traditional plant breeding programs in China toward selecting crop varieties for high P-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 P-inefficient genotypes (Li et al., 1995). Another promising example was soybean (*Glycine max*) 'BX10' with superior root traits that enable better adaptation to low-P soils (Yan et al., 2006). Some important root genetic traits have been identified with potential utility in breeding P-efficient crops, including root exudates, root hair traits, topsoil foraging through basal, or adventitious rooting (Gahoonia and Nielsen, 2004; Lynch and Brown, 2008). In addition, the ability to use insoluble P 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

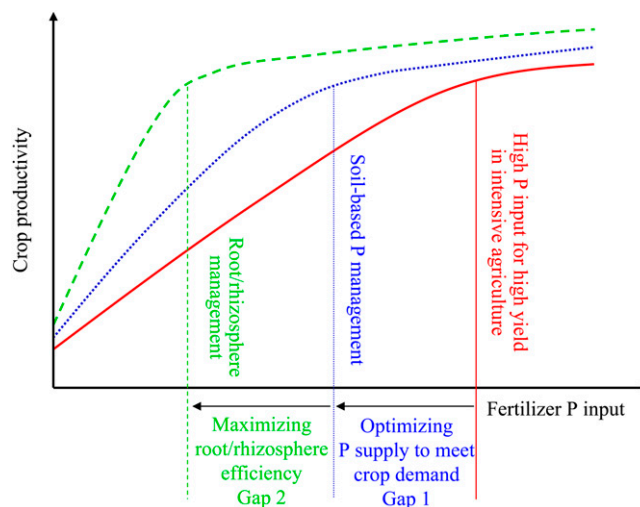


Figure 2. Conceptual model of root/rhizosphere and soil-based nutrient managements for improving P-use efficiency and crop productivity in intensive agriculture. Gap 1 for saving P input can be achieved by soil-based nutrient management for optimizing P supply to meet crop demand. Gap 2 can be realized by root/rhizosphere management for improving P-use efficiency and crop production through exploitation of root/rhizosphere efficiency and further saving P resource input. The red line (solid curve) represents crop productivity response to high-P input under intensive agriculture. The blue line (dotted curve) represents crop productivity response to P input under soil-based P management. The green line (dashed curve) represents crop productivity response to P input under root/rhizosphere management.

improved P-efficient crops with advanced P management in the soil-plant system is important for improving nutrient-use efficiency and sustainable crop production. This approach requires cooperative work between scientists from different disciplines in the crop, plant, and soil sciences.

Issues involving P use in agriculture are becoming important in various fields beyond agronomy. In the past two decades, the amount of P cycling in intensive agriculture has been significantly changed. For example, in China, the amount of P fertilizer (P) applied to farmland has increased dramatically from 1.18 Mt P in 1985 to 4.80 Mt P in 2005, and meanwhile the amount of P entering animal-production systems from crop-production systems in the form of phytate feed has increased by 3.7-fold from 0.31 to 1.44 Mt P. However, the proportion of animal manure P returned to the field decreased from 78% to 41%, resulting in 1.57 Mt P released into the environment. This is clearly a waste of P resources as well as an environmental risk. The holistic P management involves a series of strategies such as increasing P uptake efficiency by plant and animal, reducing overuse of chemical fertilizer P, and improving recycling efficiency of manure P. It is suggested that employing the integrated approach of P management may reduce chemical P fertilizer by 0.51 Mt P and animal manure discharge by 0.48 Mt P in China. It is estimated that animal manure may substi-

tute for 1.46 Mt P of chemical P fertilizers, and recycling manure is thus of huge importance for optimizing P-resource use in the future (F. Wang, personal communication).

CONCLUSION

The P nutrition of plants is predominantly controlled by P dynamics in the soil/rhizosphere-plant continuum. The distribution and dynamics of P in soil has a significant spatio-temporal variation. Root architecture that distributes more roots to the place where P resources are located plays an important role in efficiently exploiting these P resources. Furthermore, root architecture can exhibit functional coordination with root exudation of carboxylates, protons, and phosphatases in P mobilization and acquisition. The coordination of plant adaptations in root morphology and root physiology to P-limiting environments may effectively match heterogeneous P supply and distribution in soil, resulting in increased spatial availability and bioavailability of soil P. The integration of P dynamics from soil to plant via the rhizosphere provides a comprehensive picture of available P behavior and efficient acquisition in association with plant adaptive strategies (Fig. 1). In the past two decades, significant progress has been made in understanding soil, rhizosphere, and plant processes associated with soil P transformation, P mobilization and acquisition, and P-deficiency responses. However, many aspects of overall P dynamics in the soil/rhizosphere-plant continuum are not thoroughly understood, including regulation of P acquisition and P-starvation rescue mechanisms in plants, the complex coordination of root morphology, physiological and biochemical responses under varying P availability, and plant sensing of heterogeneous P supply in soil. Given the importance of P to plants and its importance as a strategic resource, a better understanding of P dynamics in the soil/rhizosphere-plant continuum is necessary to guide establishment of integrated P-management strategies involving manipulation of soil and rhizosphere processes, development of P-efficient crops, and improving P-recycling efficiency in the future (Fig. 2).

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