

# Game Changer in Plant Nutrition

## Utilization of soil organic phosphorus as a strategic approach for sustainable agriculture

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### Abstract

#### Take home message

Soil organic phosphorus ( $P_{org}$ ) can significantly assist in minimizing the adverse effects of chemical phosphorus fertilizers on aquatic and marine resources. Success to achieve the desired lasting transformation is primarily reliant on the drastic reduction of wasteful applications of chemical phosphorus fertilizers, thereby paving the way for proper investment of soil  $P_{org}$  reserves. To this end, organically-bound phosphorus can be viewed as a cornerstone for the future development of agriculture. Thus, we consider it very timely to emphasize the suitability of soil  $P_{org}$  to lead the way.

**Key words:** chemical fertilizers / organic phosphorus / phosphorus acquisition / plant nutrition / soil fertility / sustainable agriculture

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### 1 Introduction

The global population is likely to grow more rapidly in the future, especially in developing regions (Fróna et al., 2019). However, most agricultural systems' crop production rate is relatively slow and not fully supportive of sustaining the massive increases in the human population. Thus, a global food crisis looms in the future if no appropriate solutions are urgently devised and implemented. Most recent studies in plant nutrition have emphasized that current fertilization approaches may not be sustainable in the future (Guignard et al., 2017). This holds especially true for phosphorus (P), a critical macronutrient that drives a wide array of functions in the plant's structural and cellular metabolism (Vance, 2011; Zhang et al., 2014). P is indispensable in many metabolic processes, such as cellular respiration, photosynthesis, and many other kinds of energetic transformation reactions. Any shortage in P availability can negatively affect plants' growth and productivity, especially legumes (Sulieman et al., 2019). Not surprisingly, substantial amounts of orthophosphate ( $P_i$ ) are required to power the  $N_2$ -fixing symbiosis through soil rhizobia (Sulieman and Tran, 2015).

Modern agricultural practices are markedly reliant on chemical-P fertilizers (Zhang et al., 2014). However, most of the P applied in fertilizers is quickly immobilized by soil particles and rendered unavailable to a wide range of plants (Shen et al., 2011; Vance, 2011). The synthesis of chemically-produced fertilizers requires substantial amounts of high-quality phosphate rock (PR), a finite non-sustainable-P resource that leads to a significant reduction in global-P reserves. Although

an intense debate has been revolved to define the actual point in time to reach what is known as "Peak P", however, the fact remains that global P mine stocks are rapidly declining and strongly exhausted (Cordell and White, 2014). Unfortunately, the overabundant load of chemical P fertilizers given to offset the soil-P limitation has negatively affected human health and created many serious environmental implications that adversely impacted our planet's water resources, e.g., eutrophication and loss of quality (López-Arredondo et al., 2014; Shepherd et al., 2016). Accordingly, it has been strongly recommended to diminish the application of PR-based fertilizers as much as possible (George et al., 2018). These implications are mostly prompted by the compelling arguments to search for alternative sustainable P resources that can help sustain plant production and tackle environmental challenges (Stutter et al., 2012; Nash et al., 2014).

Today, the global food security and the ecological challenge of over-application of synthetic-P fertilizers has been given high priority (Schoomans et al., 2015; van Dijk et al., 2016; Cooper et al., 2018; Reitzel et al., 2019). In the context of European Union environmental goals, the Association of German Agricultural Analytic and Research Institutes (VDLUFA) has recently updated its fertilizer ordinance to promote P fertilizers equitable usage [Standpoint position for P fertilization of VDLUFA (2018)]. The VDLUFA is committed to defining the principles of fertilization management at the German federal states. Using data sourced from long-term field trials on

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arable and grassland sites, it became apparent that the P-fertility class boundaries (Class A–E; Tab. 1) for soil testing must be lowered to optimize the excessive reservoir of soil-P<sub>i</sub> and to minimize the misuse of P application for best fertilization practices (VDLUFA, 2018). In 2016, the 3<sup>rd</sup> International Organic P Workshop held in the United Kingdom had thoroughly discussed this issue from different perspectives (George et al., 2018; Haygarth et al., 2018a). The meeting ended with two main recommendations that can help to improve the fertilizer P use efficiency by crop plants: (1) the current rate of water-soluble P fertilizers should be diminished to the minimum, (2) the global P dynamic system should move from a linear to a more closed cycle (George et al., 2018). This, in turn, can be exploited, for instance, by efficient utilization of residual (legacy) P stores in soil. To this end, the soil organic P (P<sub>org</sub>) pool has been nominated as a potential secondary resource that can alternatively be used for long-term sustainable production while simultaneously attaining environmental goals. This dilemma has been well-covered in many comprehensive reviews that have been recently documented (e.g., Menezes-Blackburn et al., 2018; Schneider et al., 2019).

Intriguingly, the present communication aims to discuss advances currently being made in the field of P<sub>org</sub> research. Based on previous studies, numerous kinds of plants are potentially able to use P<sub>org</sub> effectively. Organic-P utilization by plants can thus open up new avenues that might assist us to reevaluate the present concepts of plant P use efficiency. More critical attention should be given to the potential role of soil P<sub>org</sub> pool in plant-P nutrition, which remains a promising platform for further investigation.

## 2 Why is soil P<sub>org</sub> of prime importance than ever?

Research oriented to soil P<sub>org</sub> has received much less attention than inorganic mineral forms (Cade-Menun, 2017). The paucity of research is presumably attributed to the complex soil systems in which P<sub>org</sub> occurs (Richardson et al., 2009). It has been clearly demonstrated that soil P<sub>org</sub> stock is controlled by numerous key players that govern both the quantity and quality of this dynamic fraction of soil. For instance, the physical (e.g., soil texture), chemical (e.g., soil reaction, redox potential), and biological (e.g., microbial activity) states of soil can significantly control the status, turnover, and subsequently the P<sub>org</sub> utilization by plants (Bünemann and Condron, 2007; Alamgir and Marschner, 2013). Not surprisingly,

we lack information about the nature, distribution, and transformation of P<sub>org</sub> in different agroecosystems and the accessibility for future utilization by plants. Based on some estimates, organically bound P might be enough to sustain plants for hundreds of years. Accordingly, soil P<sub>org</sub> represents an important P component that can hold great promise for advancing sustainable nutrition of plants if properly invested. This will eventually contribute to attaining the environment-related sustainable development goals (Haygarth et al., 2018b; Schneider et al., 2019). As such, soil P<sub>org</sub> could have broad agronomic and environmental importance, especially in the context of climatic changes.

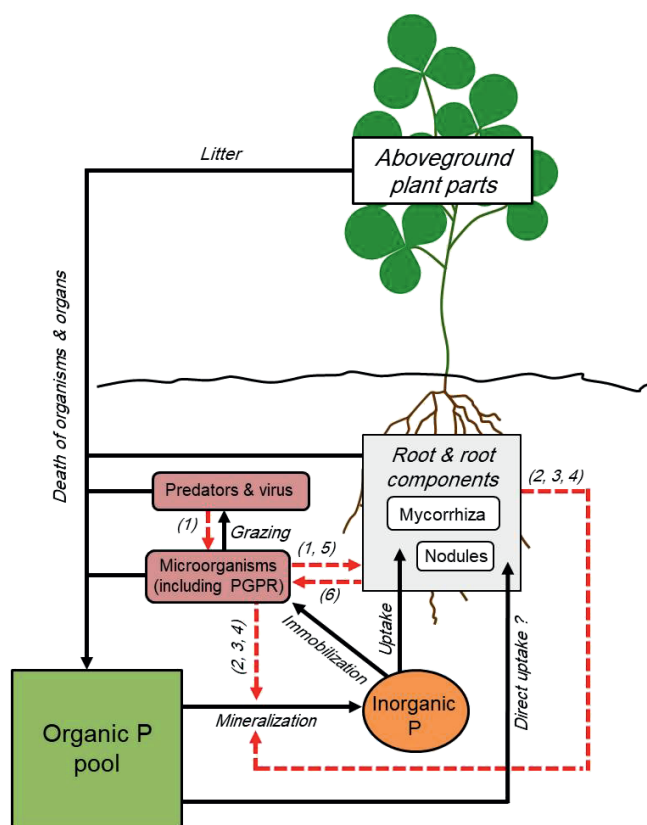
Given that soil P is predominantly accumulating in organically-bound forms, it is intuitive to see that more appreciation is dedicated to soil P<sub>org</sub> than currently being made. The amount of P<sub>org</sub> can account for more than 50% of total P quantified in the upper layers of soils (Richardson et al., 2009; Nash et al., 2014). Numerous sources, including microbial, animal, and plant tissues, can enrich this dynamic P fraction (Fig. 1). However, several other sources are potentially active but poorly characterized and remain somewhat puzzling (Richardson et al., 2011). Globally, the soil P<sub>org</sub> pool contains numerous organic substances in varying amounts. Among the notable forms are those belonging to phosphomonoesters (e.g., inositol phosphates), phosphodiesteres (e.g., nucleic acids), and organic polyphosphates (e.g., adenosine triphosphate) (Stutter et al., 2012; Nash et al., 2014). Owing to relative stability and reduced accessibility for microorganisms' degradation, it is more likely that phosphomonoesters constitute the predominant component of the soil P<sub>org</sub> pool (McLaren et al., 2015). The concentration of these organic substances can reach up to 100% of the total P measured in some soil types (Condron et al., 2005). In contrast, some other reports have argued that phosphodiesteres are more important in building up soil P<sub>org</sub> than previously thought (Schneider et al., 2019). This indicates that further research is required to elucidate these and other salient questions.

## 3 Is soil P<sub>org</sub> a reliable source for P nutrition of plants?

The debate over the applicability of soil P<sub>org</sub> as a principal source for feeding plants has been a common theme for a long time. While numerous investigations revealed that P<sub>org</sub> pools are inferior-P sources to sustain plant P requirements (Hayes et al., 2000; Richardson et al., 2005), in contrast, a

**Table 1:** P-fertility class boundaries (A–E) and updated recommendations for arable and grassland in Germany (VDLUFA, 2018).

Class of soil P values	Former recommendations		New recommendations	
	mg P 100 <sup>-1</sup>	mg P <sub>2</sub> O <sub>5</sub> 100 <sup>-1</sup>	mg P 100 <sup>-1</sup>	mg P <sub>2</sub> O <sub>5</sub> 100 <sup>-1</sup>
Very low [A]	< 2	< 5	< 1.5	< 3.4
Low [B]	2.1–4.4	6–9	1.5–3.0	3.4–6.9
Optimum [C]	4.5–9.0	10–20	3.1–6.0	7.0–13.8
High [D]	9.1–15.0	21–34	6.1–12.0	13.9–27.5
Very high [E]	> 15.0	> 34	> 12.0	> 27.5



**Figure 1:** Plant and soil-related biological processes (red-dotted arrows) that can ultimately modify the pool size of soil organic P in the rhizosphere: (1) promotion and selection of soil microbes, (2) phosphatase release, (3) pH alteration, (4) organic acid exudation, (5) rhizodeposition, (6) hormonal and signaling effects. ? = unidentified uptake system [modified from Hinsinger et al. (2015)].

range of other reports have argued that soil  $P_{org}$  substrates (i.e., phosphomonoesters and phosphodiester) can be readily utilized by plants (Tab. 2). The discrepancies in literature are probably related to the substrate complexity, plant genotypic differences, and the varying experimental conditions related to the growth media or soil characteristics. Thus, it would be not easy to arrive at a generalized conclusion based on the published reports. After having critically read the previous work, we believe that soil  $P_{org}$  can still be used as a main or complementary source for plant P nutrition. This concurs with Tarafdar and Claassen (1988), who demonstrated that many plant species (wheat, oats, barley, clover) are capable of utilizing inositol (phytin) as effectively as  $P_i$  substrate under both sterile and non-sterile conditions. A similar kind of response to phytate has been further demonstrated in other case studies (e.g., Steffens et al., 2010; Belinque et al., 2015). In the study by Steffens et al. (2010), the effect of sodium hexaphytate on a particular plant species (monocot and dicot) was evaluated using subsoils characterized by low organic matter and decreased activities of microbes. Although plants efficiently used sodium hexaphytate, the results revealed substantial differences in plants' ability to utilize  $P_{org}$ . Apart from phytate, not too much weight has been given in research to other  $P_{org}$  forms that are frequently detected at low concentrations (i.e., nucleic acids, phosphorylated sugars). Despite

this, the higher solubility and turnover of these secondary  $P_{org}$  compounds can still make them an important P source of value for plant acquisition. Thus, more credence should be given to these secondary substrates in future research.

## 4 What are the main factors that determine $P_{org}$ utilization by plants?

Factors affecting soil  $P_{org}$  availability to plants have been a subject of research for quite a long time. However, the scientific literature tells us far less than one would expect today. Unfortunately, numerous key players that potentially influence the cycling of soil  $P_{org}$  and its accessibility to plants are still missing and need to be identified. The following section is briefly summarizing the present state-of-the-art on how plant-available  $P_{org}$  is determined.

### 4.1 Soil-based factors

Soil is a complex medium that strongly affects  $P_{org}$  cycling and dynamics. Despite considerable advances in the analytical platform, however, the soil remains an impenetrable “black box” that comprises a series of physicochemical and biochemical processes that are not fully understood yet (Haygarth et al., 2018a). These processes are continuously interacting to modulate the stock of  $P_{org}$  in agricultural soils. As a consequence, the organically-bound P becomes a dynamic fraction, which is difficult to predict. Despite this, there is a consensus that  $P_{org}$  substrates must be solubilized and transformed to orthophosphate before plant utilization. This is believed to be carried out by soil microorganisms that live freely in the complex plant–soil system (Richardson et al., 2005) (Fig. 1). The soil medium contains a vast number of indigenous microbes that readily hydrolyze organically-bound P through phosphatase enzymes. The distribution of phosphatases has been well characterized with the aid of soil zymography (Spohn and Kuzyakov, 2013). Numerous types of soil fungi (e.g., *Aspergillus* and *Penicillium*) and bacteria (e.g., *Actinomycetes*, *Pseudomonas*, and *Bacillus*) are well-studied and characterized (Richardson et al., 2011). Some rhizospheric microorganisms are potentially able to act as plant growth-promoting rhizobacteria (PGPR) (Hinsinger et al., 2015; Fig. 1). In addition to soluble  $P_i$ , these PGPR can provide plants with nitrogen, hormones, and iron through the strain-specific siderophores.

Factors that affect soil microorganisms are quite likely to influence their enzymatic lability. For instance, the gross mineralization of  $P_{org}$  has been identified to decrease with decreasing soil pH, while neutral pH appears to be more appropriate to a wide range of soil microorganisms (Eivazi and Tabatabai, 1977). Additional possible complications have been demonstrated upon the firm fixation of phosphatases or inositol-phosphates by soil surfaces (clay minerals) (Findenegg and Nelemans, 1993; Alamgir and Marschner, 2013; Hinsinger et al., 2015). Here, phosphodiester's sorption capacity was noted to decrease compared to that of phosphomonoesters (Condrón et al., 2005). The formation of insoluble complexes with iron and aluminum can further retard the availability of soil  $P_{org}$  for plant use. The phosphatases' activities might be

**Table 2:** Research examples of organic phosphorus ( $P_{\text{org}}$ ) substrates readily utilized by plants as phosphorus sources.

Concept	Test plant	$P_{\text{org}}$ substrate	Experimental approach	Reference
Root growth determines $P_{\text{org}}$ utilization by plants	Winter wheat	Na-hexaphytate	Contrasting genotypes in Mitscherlich pots with organic- and inorganic-P treatments	Falk et al. (2018)
Direct $P_{\text{org}}$ uptake by plant roots without external mineralization	Corn, tomato	Phytin, lecithin	Plants in nutrient solution with different $P_{\text{org}}$ substrates	Rogers et al. (1941)
	Rice, jute	Ca-glycerophosphate, lecithin, Na-phytate, inosine-5-monophosphate	Sterilization of plant roots with 0.1% $\text{HgCl}_2$ to prevent $P_i$ acquisition	Islam et al. (1979)
	<i>Arabidopsis thaliana</i>	Nucleic acids (DNA)	Plants with nuclease-resistant analog of DNA (fluorescently labeled S-DNA of 25 bp) in sterilized media	Paungfoo-Lonhienne et al. (2010)
Plants utilize $P_{\text{org}}$ with the aid of soil microorganisms	Barley	DNA, phosphatidylcholine	Plants in Dark Brown Chernozemic soil with two $P_{\text{org}}$ substrates	McKercher and Tollefson (1978)
	Oilseed rape, sunflower, soybean	Phytate, glucose phosphate (G1P)	Inoculation of plants with soil bacterial isolates ( <i>i.e.</i> , efficient phytase)	Belinque et al. (2015)
Plants acquire $P_{\text{org}}$ by root-secreted phosphatases	Summer wheat, rape, sugar beet, phacelia, maize, white lupin, Mexican sunflower, summer rye, buckwheat, pigeon pea	Na-hexaphytate	Plants on subsoil samples with low organic matter and decreased activities of microbes	Steffens et al. (2010)
	Wheat	NA <sup>a</sup>	Plants in soil extracts with deionized (2× distilled) water that simulates soil solutions	Tarafdar and Claassen (2005)
	Common bean	Phytate	Pre-screened cultivars on sand medium for phosphatase efficacy	Helal (1990)
	Maize	Phytate	Radioactive labeling ( $^{14}\text{C}/^{32}\text{P}$ -singly- or -double-labeled phytate) and radioautography of seedlings under sterile conditions	Beck et al. (1989)
	Mung bean, moth bean, cluster bean, wheat, pearl millet, sorghum, groundnut, sesame, mustard	Phytin, lecithin, glycerophosphates	Different plant species (legumes, cereals, oilseed crops) in sterile $P_i$ -deficient hydroponic system	Yadav and Tarafdar (2001)

<sup>a</sup>NA, not available.

negatively affected by the soil sorption capacity or the degradation reactions (Richardson et al., 2011). On the other hand, the preferential displacement of extractable  $P_i$  by  $P_{\text{org}}$  at the same binding sites can increase  $P_i$  availability for plant acquisition (Hübel and Beck, 1993; Condon et al., 2005). Other soil factors that control the amount of  $P_{\text{org}}$  and its turnover would need to be carefully considered. These include soil temperature, together with contents of clay, organic carbon, calcium carbonate, and extractable aluminum and iron oxides (Hayes et al., 2000; Alamgir and Marschner, 2013).

## 4.2 Plant-based factors

The contribution of plants to  $P_{\text{org}}$  availability has been acknowledged for a long time. Several physiological and biochemical traits associated with plant roots can be exploited to facilitate the mobilization of soil  $P_{\text{org}}$  at the field scale (Fig. 1). These plant-functional processes' implication is beneficial, especially in deep soil layers characterized by low-microbial activities (Adams and Pate, 1992; Steffens et al., 2010). Among the biochemical attributes, the exudation of root substances (*e.g.*, phosphatases and organic anions) has been



well-documented (Tarafdar and Claassen, 2005; Nuruzzaman et al., 2006) (Fig. 1, Tab. 2). Unlike the biochemical-transformation by acid phosphatases, the root morphological characteristics revealed a much more significant influence on  $P_{org}$  acquisition of winter wheat genotypes (Falk et al., 2018). Despite this, the biochemical and morphological modifications can vary considerably between and within plant species (Adams and Pate, 1992; Steffens et al., 2010). Admittedly, the plants' potential ability to utilize sparingly-available  $P_{org}$  sources is greatly determined by its genetic background.

Several plant species are presumed to be relatively efficient in  $P_{org}$  utilization without assistance from soil microorganisms (Tab. 2). In particular, numerous plant species belonging to the family Fabaceae have been classified as efficient  $P_{org}$  solubilizers (Li et al., 2003; Schneider et al., 2019). For instance, legumes are more efficient than grain or oil crops in terms of extracellular acid phosphatase activity (by 72% and 22%, respectively) (Yadav and Tarafdar, 2001). Compared with non-nodulated legumes,  $N_2$ -fixing species possess a high level of functional plasticity to assist plants in facilitating  $P_{org}$  mobilization (Zogli et al., 2017). Since  $N_2$  fixation is highly expensive in terms of  $P_i$  and energy expenditure, it is likely that this group of plants can promote  $P_{org}$  bioavailability. A wide range of biochemical, physiological, and molecular mechanisms can give nodulating plants a superior dynamic capacity to utilize soil  $P_{org}$  more effectively. For example, the powerful acidification capacity and the exudation of numerous substances by nodulating roots can strongly facilitate the mineralization of soil  $P_{org}$  substances (Fig. 1). Simultaneously, most legumes have a high potential capacity to establish double symbiosis with arbuscular mycorrhizal fungi and rhizobia (Suliman and Tran, 2015). This tripartite symbiosis can provide an additional potential advantage that might assist in  $P_{org}$  mobilization. Unfortunately, it is still unclear to what extent these symbiotic associations contribute to the mobilization of sparingly-available  $P_{org}$  forms.

## 5 Are plants able to absorb P in organic forms?

It is generally admitted that plants can only utilize  $P_{org}$  substrates after soil mineralization (George et al., 2011). However, some published reports have questioned this premise, and a direct  $P_{org}$  uptake system via plant roots has been alternatively proposed (e.g., McKercher and Tollefson, 1978; Islam et al., 1979; Paungfoo-Lonhienne et al., 2010; Belinque et al., 2015) (Fig. 1). The data presented in Tab. 2 shows that plants, or at least certain species of plants, can readily absorb different types of  $P_{org}$  substrates (e.g., phytate, nucleic acids, phospholipids) without external hydrolysis. Consistent with previous observations, it was shown by Paungfoo-Lonhienne et al. (2010) that *Arabidopsis* plants were readily able to absorb intact nucleic acids (i.e., DNA) after exposure to a nuclease-resistant analog of DNA (fluorescently labeled S-DNA of 25 bp, 16.5 kDa). The uptake of DNA enhanced growth of *Arabidopsis* plants measured in terms of root hairs and root length. Likewise, plants' potential capability to absorb macromolecule compounds has been well characterized for proteins as a source of N (Paungfoo-Lonhienne et al., 2008). Although no specific  $P_{org}$  uptake system has been discovered

in plants, it was assumed that hydrolysis of organic P substances could occur in the root system's cell wall space (Richardson et al., 2009). Thus, more research is needed to confirm whether plants can absorb  $P_{org}$ , and elucidate its corresponding uptake system accordingly.

## 6 Are current analytical methodologies able to promote $P_{org}$ research?

The precise detection and accurate quantification of  $P_{org}$  compounds are among the major obstructions to soil  $P_{org}$  research (Turner et al., 2015). To meet these challenges, a much-improved analytical framework has been so far developed. This includes various wet-chemical techniques, chromatography, and recently nuclear magnetic resonance (NMR) spectroscopy (McLaren et al., 2015). Among these, solution  $^{31}P$  NMR spectroscopy is predominantly adopted and extensively used (Cade-Menun and Liu, 2014; Turner et al., 2015). In addition, other methodological approaches, such as data mining (i.e., principal component analysis), meta-analysis, and modeling, can be of great value (Nash et al., 2014; Haygarth et al., 2018a). In the process of achieving this, many soil databases can be searched to provide critical information and novel ways into  $P_{org}$  research (Cooper et al., 2018). Despite advances in the analytical techniques, most  $P_{org}$  research gets stuck in using a variety of conventional chemical extraction (Olsen, P-CAL, P-DL, Mehlich-III, Bray 1) and fractionation (i.e., Hedley) techniques (Cooper et al., 2018; George et al., 2018). Applying these traditional soil testing methods might not be adequate to assure sufficient accuracy and quality control. This can make the interpretation rather difficult and not easy to compare across trials. Several studies have criticized these classical techniques' apparent limitations, thereby reducing their trust and credibility (Steffens et al., 2010; Schick et al., 2013; Cooper et al., 2018; Gu and Margenot, 2021; Barrow et al., 2021). Thus, many published reports might be underestimated, and their recommendations might be questioned or completely rejected. There is a need for well-defined standard methods that can help to guide  $P_{org}$ 's research.

## 7 What approaches could be adopted to enhance soil $P_{org}$ cycling?

Several promising approaches and innovative techniques could enhance the cycling of soil  $P_{org}$  for plant use (Menezes-Blackburn et al., 2018). This includes a multi-pronged combination of genetically-improved plants, beneficial biota (biofertilizers), and agronomic management practices (Stutter et al., 2012). The effectiveness of genetic transformation in  $P_{org}$  utilization by crop plants is depicted in Tab. 3. For instance, the root-specific genetic modification or the induction of transgenic genotypes that overexpress phytase activity have been well-validated in *Arabidopsis* (Richardson et al., 2001a; Mudge et al., 2003), tobacco (Lung et al., 2005), potato (Zimmermann et al., 2003), and subterranean clover (Richardson et al., 2001b; George et al., 2004). To this end, many desired traits can be detected in natural soil microbes, which could ultimately assist in facilitating  $P_{org}$  mineralization. This would be much better if coupled with biofertilizers and

**Table 3:** Approaches and technologies used to promote soil organic phosphorus ( $P_{\text{org}}$ ) cycling.

Approach/technology	Concept	$P_{\text{org}}$ substrate	Test plant	Reference
Placement (encapsulation) of phytase in the root vicinity using mesoporous silica nanoparticles materials	Phytases are stable and resistant to soil degradation	Phytate	<i>Medicago truncatula</i>	Trouillefou et al. (2015)
Intercropping of P-mobilizing and non-P-mobilizing crop species	P-mobilizing crop species (legume) improve $P_{\text{org}}$ utilization for non-P-mobilizing species (non-legume)	Phytate	Wheat/chickpea	Li et al. (2003)
Cultivation of efficient agroforestry species	Enhancement of $P_{\text{org}}$ solubilization and mineralization	NA <sup>a</sup>	Tithonia, tephrosia	George et al. (2002)
Application of phytase to the root medium of plants	Phytase increases $P_{\text{org}}$ hydrolysis	Myo-inositol hexa-phosphate (phytin)	Maize	Findenegg and Nelemans (1993)
Inoculation of plants with soil isolates/microorganisms that possess efficient phytase activity	Mineralization of complex organic substrates by phytases	Myo-inositol hexa-phosphate	Pasture legume (subterranean clover, white clover, alfalfa, burr medic) and pasture grass (wallaby grass, <i>phalaris</i> ) species	Richardson et al. (2001c)
Inoculation of plants with arbuscular mycorrhizal fungi	Mycorrhizal colonization contributes to $P_{\text{org}}$ cycling and plant $P_i$ acquisition	Phytate, RNA, lecithin	Red clover	Feng et al. (2003)
Application of bacterial grazer (nematodes) together with mycorrhiza and P-solubilizing bacteria	Interaction of bacterial grazers with mycorrhiza and phosphobacteria promotes $P_{\text{org}}$ solubilization	Phytate	Maritime pine	Irshad et al. (2012)
Biochar addition to agricultural soils	Biochar enhances $P_i$ -solubilizing bacteria	NA <sup>a</sup>	Ryegrass	Anderson et al. (2011)
	Biochar promotes soil enzymatic activities (phosphatases)	NA <sup>a</sup>	NA <sup>a</sup>	Bailey et al. (2011)
Genetic transformation of plants to overexpress extracellular phytases in root cells	Transgenic lines display better $P_i$ nutrition owing to the efficient release of extracellular root phytases	Phytate	<i>Arabidopsis</i>	Richardson et al. (2001a); Mudge et al. (2003)
			Subterranean clover	Richardson et al. (2001b); George et al. (2004)
			Potato	Zimmermann et al. (2003)
			Tobacco, <i>Arabidopsis</i>	Lung et al. (2005)

<sup>a</sup>NA, not available.

efficient crop management practices. Among these, inoculation with mycorrhizal fungi or phosphobacteria is the most prevalent one on the field scale (Cooper et al., 2018). Although added microbes can effectively enhance organically-bound P's mineralization, the native soil microbes might negatively interfere to hinder their potential contribution in  $P_{\text{org}}$  cycling. Another potential avenue to promote  $P_{\text{org}}$  utilization is, nanotechnology, which is most rapidly expanding (Liu and Lal, 2015). At present, the utilization of nanoparticles has conferred significant benefits in this regard (Trouillefou et al., 2015). On the other hand, the intercropping of P-mobilizing crop species (e.g., legumes) with non-P-mobilizing crop species (e.g., cereals) is among the agronomic practices that

could have a significant impact on  $P_{\text{org}}$  cycling in arable cropping systems (Li et al., 2014). For a more detailed review of the mechanistic approaches adopted to accelerate  $P_{\text{org}}$  cycling and bioavailability in agricultural soil, the reader is referred to Menezes-Blackburn et al. (2018).

## 8 Conclusions

$P_{\text{org}}$  is an essential component of the soil P cycle that can significantly assist in ensuring agriculture's long-term sustainability. At present, many factors influencing the cycling of  $P_{\text{org}}$  in agricultural soils are still missing. Therefore, the identifica-

tion of these factors is a crucial step in fostering the utilization of soil  $P_{org}$  by crop plants. Simultaneously, the elucidation of plants' uptake system to acquire  $P_{org}$  can provide a strong complement to these efforts. As a result, much remains to be done by the  $P_{org}$  research community that requires intensification of research. This underlines the importance of reevaluating the current P fertilizer ordinance, and new pressing strategic agendas should be prioritized in a specific time frame. Global networks among experts and research institutions must be developed and precisely coordinated to meet this challenge and leverage expertise.

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Data sharing is not applicable to this article as no new data were created or analyzed in this study.

## References

- Adams, M. A., Pate, J. S. (1992): Availability of organic and inorganic forms of phosphorus to lupins (*Lupinus* spp.). *Plant Soil* 145, 107–113.
- Alamgir, M., Marschner, P. (2013): Changes in phosphorus pools in three soils upon addition of legume residues differing in carbon/phosphorus ratio. *Soil Res.* 51, 484–493.
- Anderson, C. R., Condon, L. M., Clough, T. J., Fiers, M., Stewart, A., Hill, R. A., Sherlock, R. R. (2011): Biochar induced soil microbial community change: Implications for biogeochemical cycling of carbon, nitrogen and phosphorus. *Pedobiologia* 54, 309–320.
- Bailey, V. L., Fansler, S. J., Smith, J. L., Bolton Jr., H. (2011): Reconciling apparent variability in effects of biochar amendment on soil enzyme activities by assay optimization. *Soil Biol. Biochem.* 43, 296–301.
- Barrow, N. J., Sen, A., Roy, N., Debnath, A. (2021): The soil phosphate fractionation fallacy. *Plant Soil* 459. DOI: <https://doi.org/10.1007/s11104-020-04476-6>.
- Beck, E., Fußeder, A., Kraus, M. (1989): The maize root system *in situ*: Evaluation of structure and capability of utilization of phytate and inorganic soil phosphate. *Z. Pflanzenernähr. Bodenk.* 152, 159–167.
- Belinque, H., Pucheu, N., Kerber, N., Rubio, G. (2015): Utilization of organic phosphorus sources by oilseed rape, sunflower, and soybean. *J. Plant Nutr. Soil Sci.* 178, 339–344.
- Bünemann, E. K., Condon, L. M. (2007): Phosphorus and Sulphur Cycling in Terrestrial Ecosystems, in Marschner, P., Rengel, Z. (eds.): *Nutrient Cycling in Terrestrial Ecosystems*. Springer-Verlag Berlin, Germany, pp. 65–92.
- Cade-Menun, B., Liu, C. W. (2014): Solution phosphorus-31 nuclear magnetic resonance spectroscopy of soils from 2005 to 2013: a review of sample preparation and experimental parameters. *Soil Sci. Soc. Am. J.* 78, 19–37.
- Cade-Menun, B. J. (2017): Characterizing phosphorus forms in cropland soils with solution  $^{31}P$ -NMR: past studies and future research needs. *Chem. Biol. Technol. Agric.* 4. DOI: <https://doi.org/10.1186/s40538-017-0098-4>.
- Condon, L. M., Turner, B. L., Cade-Menun, B. (2005): Chemistry and Dynamics of Soil Organic Phosphorus, in Sims, J. T., Sharp-ley, A. N. (eds.): *Phosphorus: Agriculture and the Environment*, Agronomy Monograph no. 46. ASA, CSSA, SSSA, Madison, WI, USA, pp. 87–121.
- Cooper, J., Reed, E. Y., Hörtenhuber, S., Lindenthal, T., Løes, A.-K., Mäder, P., Magid, J., Oberson, A., Kolbe, H., Möller, K. (2018): Phosphorus availability on many organically managed farms in Europe. *Nutr. Cycl. Agroecosyst.* 110, 227–239.
- Cordell, D., White, S. (2014): Life's bottleneck: sustaining the world's phosphorus for a food secure future. *Annu. Rev. Environ. Resour.* 39, 161–188.
- Eivazi, F., Tabatabai, M. A. (1977): Phosphatases in soils. *Soil Biol. Biochem.* 9, 167–172.
- Falk, J., Heßler, M., Steffens, D. (2018): Aneignungsvermögen verschiedener Winterweizen-Genotypen für organisch gebundenes Phosphat. 130. VDLUFA-Kongress "Digitalisierung in Landwirtschaft, Versuchs- und Untersuchungswesen—Anforderungen und Auswirkungen". VDLUFA-Schriftenreihe Band 75/2018. VDLUFA-Verlag, Darmstadt, Germany, pp. 95–103 (in German).
- Feng, G., Song, Y. C., Li, X. L., Christie, P. (2003): Contribution of arbuscular mycorrhizal fungi to utilization of organic sources of phosphorus by red clover in a calcareous soil. *Appl. Soil Ecol.* 22, 139–148.
- Findenegg, G. R., Nelemans, J. A. (1993): The effect of phytase on the availability of P from *myo*-inositol hexaphosphate (phytate) for maize roots. *Plant Soil* 154, 189–196.
- Fróna, D., Szenderák, J., Harangi-Rákos, M. (2019): The challenge of feeding the world. *Sustainability* 11. DOI: <https://doi.org/10.3390/su11205816>.
- George, T. S., Gregory, P. J., Robinson, J. S., Buresh, R. J. (2002): Changes in phosphorus concentrations and pH in the rhizosphere of some agroforestry and crop species. *Plant Soil* 246, 65–73.
- George, T. S., Richardson, A. E., Hadobas, P. A., Simpson, R. J. (2004): Characterization of transgenic *Trifolium subterraneum* L. which expresses *phyA* and releases extracellular phytase: growth and P nutrition in laboratory media and soil. *Plant Cell. Environ.* 27, 1351–1361.
- George, T. S., Fransson, A.-M., Hammond, J. P., White, P. J. (2011): Phosphorus Nutrition: Rhizosphere Processes, Plant Response and Adaptations, in Bünemann, E. K., Oberson, A., Frossard, E. (eds.): *Phosphorus in Action*, Soil Biology 26. Springer-Verlag Berlin, Germany, pp. 245–271.
- George, T. S., Giles, C. D., Menezes-Blackburn, D., Condon, L. M., Gama-Rodrigues, A. C., Jaisi, D., Lang, F., Neal, A. L., Stutter, M. I., Almeida, D. S., Bol, R., Cabugao, K. G., Celi, L., Cotner, J. B., Feng, G., Goll, D. S., Hallama, M., Krueger, J., Plassard, C., Rosling, A., Darch, T., Fraser, T., Giesler, R., Richardson, A. E., Tamburini, F., Shand, C. A., Lumsdon, D. G., Zhang, H., Blackwell, M. S. A., Wearing, C., Mezeli, M. M., Almås, Å. R., Audette, Y., Bertrand, I., Beyhaut, E., Boitt, G., Bradshaw, N., Brearley, C. A., Bruulsema, T. W., Ciaia, P., Cozzolino, V., Duran, P. C., Mora, M. L., de Menezes, A. B., Dodd, R. J., Dunfield, K., Engl, C., Frazão, J. J., Garland, G., González Jiménez, J. L., Graca, J., Granger, S. J., Harrison, A. F., Heuck, C., Hou, E. Q., Johnes, P. J., Kaiser, K., Kjær, H. A., Klumpp, E., Lamb, A. L., Macintosh, K. A., Mackay, E. B., McGrath, J., McIntyre, C., McLaren, T., Mészáros, E., Missong, A., Mooshammer, M., Negrón, C. P., Nelson, L. A., Pfahler, V., Poblete-Grant, P., Randall, M., Seguel, A., Seth, K., Smith, A. C., Smits, M. M., Sobarzo, J. A., Spohn, M., Tawaray, K., Tibbett, M., Voroney, P., Wallander, H., Wang, L., Wasaki, J., Haygarth, P. M. (2018): Organic phosphorus in the terrestrial environment: a perspective on the state of the art and future priorities. *Plant Soil* 427, 191–208.



- Gu, C., Margenot, A. J. (2021): Navigating limitations and opportunities of soil phosphorus fractionation. *Plant Soil* 459, 13–17.
- Guignard, M. S., Leitch, A. R., Acquisti, C., Eizaguirre, C., Elser, J. J., Hessen, D. O., Jeyasingh, P. D., Neiman, M., Richardson, A. E., Soltis, P. S., Soltis, D. E., Stevens, C. J., Trimmer, M., Weider, L. J., Woodward, G., Leitch, I. J. (2017): Impacts of nitrogen and phosphorus: from genomes to natural ecosystems and agriculture. *Front. Ecol. Evol.* 5. DOI: <https://doi.org/10.3389/fevo.2017.00070>.
- Hayes, J. E., Simpson, R. J., Richardson, A. E. (2000): The growth and phosphorus utilisation of plants in sterile media when supplied with inositol hexaphosphate, glucose 1-phosphate or inorganic phosphate. *Plant Soil* 220, 165–174.
- Haygarth, P. M., Harrison, A. F., Turner, B. L. (2018a): On the history and future of soil organic phosphorus research: a critique across three generations. *Eur. J. Soil Sci.* 69, 86–94.
- Haygarth, P. M., Hinsinger, P., Blackburn, D. (2018b): Organic phosphorus: potential solutions for phosphorus security. *Plant Soil* 427, 1–3.
- Helal, H. M. (1990): Varietal differences in root phosphatase activity as related to the utilization of organic phosphates. *Plant Soil* 123, 161–163.
- Hinsinger, P., Herrmann, L., Lesueur, D., Robin, A., Trap, J., Waithaisong, K., Plassard, C. (2015): Impact of roots, microorganisms and microfauna on the fate of soil phosphorus in the rhizosphere. *Annu. Plant Rev.* 48, 377–407.
- Hübel, F., Beck, E. (1993): *In-situ* determination of the P-relations around the primary root of maize with respect to inorganic and phytate-P. *Plant Soil* 157, 1–9.
- Irshad, U., Alain Brauman, A., Villenave, C., Plassard, C. (2012): Phosphorus acquisition from phytate depends on efficient bacterial grazing, irrespective of the mycorrhizal status of *Pinus pinaster*. *Plant Soil* 358, 155–168.
- Islam, A., Mandal, R., Osman, K. T. (1979): Direct absorption of organic phosphate by rice and jute plants. *Plant Soil* 53, 49–54.
- Li, L., Tang, C., Rengel, Z., Zhang, F. (2003): Chickpea facilitates phosphorus uptake by intercropped wheat from an organic phosphorus source. *Plant Soil* 248, 297–303.
- Li, L., Tilman, D., Lambers, H., Zhang, F. (2014): Plant diversity and overyielding: insights from belowground facilitation of intercropping in agriculture. *New Phytol.* 203, 63–69.
- Liu, R., Lal, R. (2015): Potentials of engineered nanoparticles as fertilizers for increasing agronomic productions. *Sci. Total Environ.* 514, 131–139.
- López-Arredondo, D. L., Leyva-González, M. A., González-Morales, S. I., López-Bucio, J., Herrera-Estrella, L. (2014): Phosphate nutrition: improving low-phosphate tolerance in crops. *Annu. Rev. Plant Biol.* 65, 95–123.
- Lung, S.-C., Chan, W.-L., Yip, W., Wang, L., Yeung, E. C., Lim, B. L. (2005): Secretion of beta-propeller phytase from tobacco and *Arabidopsis* roots enhances phosphorus utilization. *Plant Sci.* 169, 341–349.
- McKercher, R. B., Tollefson, T. S. (1978): Barley response to phosphorus from phospholipids and nucleic acids. *Can. J. Soil Sci.* 58, 103–105.
- McLaren, T. I., Smernik, R. J., McLaughlin, M. J., McBeath, T., Kirby, J. K., Simpson, R. J., Guppy, C. N., Doolette, A., Richardson, A. (2015): Complex forms of soil organic phosphorus—a major component of soil phosphorus. *Environ. Sci. Technol.* 49, 13238–13245.
- Menezes-Blackburn, D., Giles, C., Darch, T., George, T. S., Blackwell, M., Stutter, M., Shand, C., Lumsdon, D., Cooper, P., Wendler, R., Brown, L., Almeida, D. S., Wearing, C., Zhang, H., Haygarth, P. M. (2018): Opportunities for mobilizing recalcitrant phosphorus from agricultural soils: a review. *Plant Soil* 427, 5–16.
- Mudge, S. R., Smith, F. W., Richardson, A. E. (2003): Root-specific and phosphate-regulated expression of phytase under the control of a phosphate transporter promoter enables *Arabidopsis* to grow on phytate as a sole P source. *Plant Sci.* 165, 871–878.
- Nash, D. M., Haygarth, P. M., Turner, B. L., Condron, L. M., McDowell, R. W., Richardson, A. E., Watkins, M., Heaven, M. W. (2014): Using organic phosphorus to sustain pasture productivity: a perspective. *Geoderma* 221, 11–19.
- Nuruzzaman, M., Lambers, H., Bolland, M. D. A., Veneklaas, E. J. (2006): Distribution of carboxylates and acid phosphatase and depletion of different phosphorus fractions in the rhizosphere of a cereal and three grain legumes. *Plant Soil* 281, 109–120.
- Paungfoo-Lonhienne, C., Lonhienne, T. G. A., Rentsch, D., Robinson, N., Christie, M., Webb, R. I., Gamage, H. K., Carroll, B. J., Schenk, P. M., Schmidt, S. (2008): Plants can use protein as a nitrogen source without assistance from other organisms. *Proc. Natl. Acad. Sci. USA* 105, 4524–4529.
- Paungfoo-Lonhienne, C., Lonhienne, T. G. A., Mudge, S. R., Schenk, P. M., Christie, M., Carroll, B. J., Schmidt, S. (2010): DNA is taken up by root hairs and pollen, and stimulates root and pollen tube growth. *Plant Physiol.* 153, 799–805.
- Reitzel, K., Bennett, W. W., Berger, N., Brownlie, W. J., Bruun, S., Christensen, M. L., Cordell, D., van Dijk, K., Egemo, S., Eigner, H., Glud, R. N., Grönfors, O., Hermann, L., Houot, S., Hupfer, M., Jacobs, B., Korving, L., Kjærgaard, C., Liimatainen, H., Van Loosdrecht, M. C. M., Macintosh, K. A., Magid, J., Maia, F., Martin-Ortega, J., McGrath, J., Meulepas, R., Murry, M., Neset, T. S., Neumann, G., Nielsen, U. G., Nielsen, P. H., O'Flaherty, V., Qu, H., Santner, J., Seufert, V., Spears, B., Stringer, L. C., Stutter, M., Verburg, P. H., Wilfert, P., Williams, P. N., Metson, G. S. (2019): New training to meet the global phosphorus challenge. *Environ. Sci. Technol.* 53, 8479–8481.
- Richardson, A. E., Hadobas, P. A., Hayes, J. E. (2001a): Extracellular secretion of *Aspergillus* phytase from *Arabidopsis* roots enables plants to obtain phosphorus from phytate. *Plant J.* 25, 641–649.
- Richardson, A. E., Hadobas, P. A., Simpson, R. J. (2001b): Phytate as a Source of Phosphorus for the Growth of Transgenic *Trifolium subterraneum*, in Horst, W. J., Schenk, M. K., Bürkert, A., Claassen, N., Flessa, H., Frommer, W. B., Goldbach, H. E., Merbach, W., Ols, H.-W., Römhild, V., Sattelmacher, B., Schmidhalter, U., Schenk, M. K., von Wirén, N. (eds.): Progress in Plant Nutrition: Food Security and Sustainability of Agro-Ecosystems Through Basic and Applied Research. Kluwer Academic, Dordrecht, The Netherlands, pp. 560–561.
- Richardson, A. E., Hadobas, P. A., Hayes, J. E., O'Hara, C. P., Simpson, R. J. (2001c): Utilization of phosphorus by pasture plants supplied with myo-inositol hexaphosphate is enhanced by the presence of soil micro-organisms. *Plant Soil* 229, 47–56.
- Richardson, A. E., George, T. S., Hens, M., Simpson, R. J. (2005): Utilization of Soil Organic Phosphorus by Higher Plants, in Turner, B. L., Frossard, E., Baldwin, D. S. (eds.): Organic Phosphorus in the Environment. CAB International, Wallingford, UK, pp. 165–184.
- Richardson, A. E., Hocking, P. J., Simpson, R. J., George, T. S. (2009): Plant mechanisms to optimize access to soil phosphorus. *Crop Pasture Sci.* 60, 124–143.
- Richardson, A. E., Lynch, J. P., Ryan, P. R., Delhaize, E., Smith, F. A., Smith, S. E., Harvey, P. R., Ryan, M. H., Veneklaas, E. J., Lambers, H., Oberson, A., Culvenor, R. A., Simpson, R. J. (2011): Plant and microbial strategies to improve the phosphorus efficiency of agriculture. *Plant Soil* 349, 121–156.



- Rogers, H. T., Pearson, R. W., Pierre, W. H. (1941): Absorption of organic phosphorus by corn and tomato plants and the mineralizing action of exo-enzyme systems of growing roots. *Soil Sci. Soc. Am. J.* 5, 285–291.
- Schick, J., Kratz, S., Rückamp, D., Shwiekh, R., Haneklaus, S., Schnug, E. (2013): Comparison and inter-calibration of different soil P tests used in the Baltic Sea countries. Baltic Manure Knowledge Report. JKI, Quedlinburg, Germany.
- Schneider, K. D., Thiessen Martens, J. R., Zvomuya, F., Reid, D. K., Fraser, T. D., Lynch, D. H., O'Halloran, I. P., Wilson, H. F. (2019): Options for improved phosphorus cycling and use in agriculture at the field and regional scales. *J. Environ. Qual.* 48, 1247–1264.
- Schoomans, O. F., Bouraoui, F., Kabbe, C., Oenema, O., van Dijk, K. C. (2015): Phosphorus management in Europe in a changing world. *AMBIO* 44, 180–192.
- Shen, J., Yuan, L., Zhang, J., Li, H., Bai, Z., Chen, X., Zhang, W., Zhang, F. (2011): Phosphorus dynamics: from soil to plant. *Plant Physiol.* 156, 997–1005.
- Shepherd, J. G., Kleemann, R., Bahri-Esfahani, J., Hudek, L., Suriyagoda, L., Vandamme, E., van Dijk, K. C. (2016): The future of phosphorus in our hands. *Nutr. Cycl. Agroecosyst.* 104, 281–287.
- Spohn, M., Kuzyakov, Y. (2013): Distribution of microbial- and root-derived phosphatase activities in the rhizosphere depending on P availability and C allocation—Coupling soil zymography with  $^{14}\text{C}$  imaging. *Soil Biol. Biochem.* 67, 106–113.
- Steffens, D., Leppin, T., Luschin-Ebengreuth, N., Yang, Z. M., Schubert, S. (2010): Organic soil phosphorus considerably contributes to plant nutrition but is neglected by routine soil-testing methods. *J. Plant Nutr. Soil Sci.* 173, 765–771.
- Stutter, M. I., Shand, C. A., George, T. S., Blackwell, M. S. A., Bol, R., MacKay, R. L., Richardson, A. E., Condon, L. M., Turner, B. L., Haygarth, P. M. (2012): Recovering phosphorus from soil: a root solution? *Environ. Sci. Technol.* 46, 1977–1978.
- Suliman, S., Tran, L. S. (2015): Phosphorus homeostasis in legume nodules as an adaptive strategy to phosphorus deficiency. *Plant Sci.* 239, 36–43.
- Suliman, S., Kusano, M., Ha, C. V., Watanabe, Y., Abdalla, M. A., Abdelrahman, M., Kobayashi, M., Saito, K., Mühlhling, K. H., Tran, L. S. (2019): Divergent metabolic adjustments in nodules are indispensable for efficient  $\text{N}_2$  fixation of soybean under phosphate stress. *Plant Sci.* 289. DOI: <https://doi.org/10.1016/j.plantsci.2019.110249>.
- Tarafdar, J. C., Claassen, N. (1988): Organic phosphorus compounds as a phosphorus source for higher plants through the activity of phosphatases produced by plant roots and microorganisms. *Biol. Fertil. Soils* 5, 308–312.
- Tarafdar, J. C., Claassen, N. (2005): Preferential utilization of organic and inorganic sources of phosphorus by wheat plant. *Plant Soil* 275, 285–293.
- Trouillefou, C. M., Le Cadre, E., Cacciaguerra, T., Cunin, F., Plassard, C., Belamie, E. (2015): Protected activity of a phytase immobilized in mesoporous silica with benefits to plant phosphorus nutrition. *J. Sol-Gel Sci. Technol.* 74, 55–65.
- Turner, B. L., Cheesman, A. W., Condon, L. M., Reitzel, K., Richardson, A. E. (2015): Introduction to the special issue: Developments in soil organic phosphorus cycling in natural and agricultural ecosystems. *Geoderma* 257, 1–3.
- Vance, C. P. (2011): Phosphorus as a Critical Macronutrient, in Hawkesford, M. J., Barraclough, P. (eds.): *The Molecular and Physiological Basis of Nutrient Use Efficiency in Crops*. John Wiley & Sons, Inc., West Sussex, UK, pp. 229–264.
- van Dijk, K. C., Lesschen, J. P., Oenema, O. (2016): Phosphorus flows and balances of the European Union Member States. *Sci. Total Environ.* 542, 1078–1093.
- VDLUFA (2018): *Phosphordüngung nach Bodenuntersuchung und Pflanzenbedarf*. Standpunkt des VDLUFA. VDLUFA-Verlag, Darmstadt, Germany (in German).
- Yadav, R. S., Tarafdar, J. C. (2001): Influence of organic and inorganic phosphorus supply on the maximum secretion of acid phosphatase by plants. *Biol. Fertil. Soils* 34, 140–143.
- Zhang, Z., Liao, H., Lucas, W. J. (2014): Molecular mechanisms underlying phosphate sensing, signaling, and adaptation in plants. *J. Integr. Plant Biol.* 56, 192–220.
- Zimmermann, P., Zardi, G., Lehmann, M., Zeder, C., Amrhein, N., Frossard, E., Bucher, M. (2003): Engineering the root–soil interface via targeted expression of a synthetic phytase gene in trichoblasts. *Plant Biotechnol. J.* 1, 353–360.
- Zogli, P., Pingault, L., Libault, M. (2017): Physiological and Molecular Mechanisms and Adaptation Strategies in Soybean (*Glycine max*) under Phosphate Deficiency, in Suliman, S., Tran, L. S. (eds.): *Legume Nitrogen Fixation in Soils with Low Phosphorus Availability*. Springer International Publishing AG, Cham, Switzerland, pp. 219–242.