



Phosphorus activators contribute to legacy phosphorus availability in agricultural soils: A review

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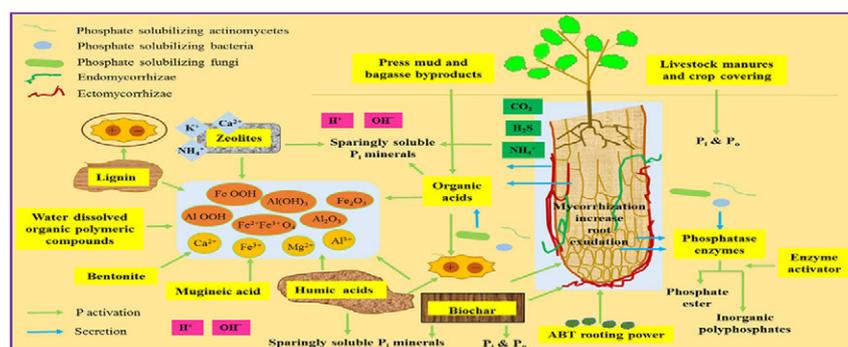
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HIGHLIGHTS

- Legacy phosphorus accumulated in soils is a large secondary global phosphorus source.
- Phosphorus activators accelerate and strengthen the phosphorus transformation process.
- Phosphorus activators can activate inorganic and organic phosphorus.
- Extensive research is needed to understand the interactions of phosphorus activators with natural soil.

GRAPHICAL ABSTRACT



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ABSTRACT

Phosphorus (P) is one of the most limiting macronutrients for crop productivity and P deficiency is a common phenomenon in agricultural soils worldwide. Despite long-term application of phosphate fertilizers to increase crop yields, P availability is often low, due to the high affinity of phosphate for the soil solid phase. It has been suggested that the accumulated (surplus) P in agricultural soils is sufficient to sustain crop yields worldwide for about 100 years. In this paper, we try to clear up the potential for making use of legacy P in soils for crop growth potentially alleviating the global P resource shortage. Specifically, we try to clear up the potential of soil “P activators” for releasing fixed P. P activators accelerate and strengthen process which transform P into bio-available forms via a range of chemical reactions and biological interactions. They include phosphate solubilizing microorganisms, phosphatase enzymes and enzyme activators, low molecular weight organic acids, humic acids, lignin, crop residues, biochar and zeolites. Although reported performance is variable, there is growing evidence that P activators can promote the release of phosphate from soil and, hence, have potential for mitigating the impending global P crisis. Further basic and applied research is required to better understand the mechanisms of interaction of P activators with natural soils and to maximize activator efficacy.

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1. Introduction

Phosphorus (P) is a major limiting nutrient for crop growth in many agroecosystems and is indispensable in several physiological and biochemical processes (Simpson et al., 2011). Consequently, the availability of P controls the growth and development of all crops (Wyngaard

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et al., 2016). Plants assimilate P (predominantly as negatively charged primary and secondary orthophosphate ions) from the soil solution. Although most soils contain considerable total P stocks, only a small fraction (<1%) of the total inorganic P (P_i) and organic P (P_o) is dissolved at any given time (Bünemann, 2015). The concentration of P in soil solution remains really low, about 0.05–0.30 $\mu\text{g P mL}^{-1}$ (Bolan, 1991). It is estimated that crop productivity is limited by P deficiency on >40% of the world's arable land (Balemi and Negisho, 2012). P limitations are also a major productivity constraint in many natural (Augustine et al., 2003) and managed (Bünemann et al., 2011) grassland systems. Although other constraints may also limit productivity, soil P often needs to be replenished repeatedly to satisfy plant demand, in part because it is quickly removed from the dissolved (plant available) form by sorption, precipitation and microbial immobilization (Roberts and Johnston, 2015) or is lost through surface runoff (in particulate and dissolved forms), subsurface flow (leaching and throughflow via the soil matrix and macropores), drain flow and even groundwater which may accelerate the eutrophication of P sensitive waters (Heathwaite and Dils, 2000; Hively et al., 2006; Holman et al., 2008; Sims et al., 1998).

Historically, chemical fertilizers, such as manufactured water-soluble phosphate have played a significant role in replenishing this P pool. However, these fertilizers are derived from mined rock-phosphate which has a finite (and rapidly diminishing) supply (Gilbert, 2009). Some studies claim that, at current rates of extraction, global commercial phosphate reserves will be depleted in 50–100 years (Abelson, 1999; Sattari et al., 2012). Opinions vary about the reliability of these data because they are principally based on second and third hand information and the figures change all the time (Gilbert, 2009). However, it is likely that remaining reserves will have increasingly lower quality and will be increasingly more costly to extract, which means that the supply of high quality phosphate fertilizer will also become progressively more restricted (Cordell et al., 2009). The rising demand for agricultural commodities in developing countries has put increasing pressure on land resources for higher yields, with associated growth in the demand for phosphate fertilizers (Weber et al., 2014). This realization (sometimes described as a “potential phosphate crisis”) is pushing global fertilizer prices up (Chowdhury et al., 2017).

The high P fixing capacity of most soils and the low P use efficiency (around 10–15%) of most crops means that surplus P input from fertilizers tends to accumulate in soils (Withers et al., 2001). This accumulation is known as “legacy P” which can be calculated as the difference between inputs (mineral P fertilizer, atmospheric deposition and weathering) and outputs (lost through surface runoff, subsurface flow, leaching, plus P in crop uptake etc.) (Havens and James, 2005; Sattari et al., 2012). In Oceania and Western Europe, for example, cumulative inputs of P fertilizer to arable land (560 and 1115 kg P ha^{-1} , respectively, for the period 1965–2007) were much greater than the cumulative uptake (100 and 350 kg P ha^{-1} , respectively) (Sattari et al., 2012). In turn, this results in changes to the concentration of P in the soil solution and its association with soil minerals and organic matter which can lead to enhanced phosphate loss (Guppy et al., 2005; Heckrath et al., 1995) and subsequent degradation of freshwater and marine resources where eutrophication can be triggered by additional P inputs (Tilman et al., 2001).

It is clear that legacy P stocks in soils have the potential to play a vital role in maintaining agricultural productivity with lower P requirements for inputs and reduced P transfers from land to water, if crops can efficiently access this P (Condrón et al., 2013). It has even been suggested that the accumulated P in agricultural soils would be sufficient to sustain maximum crop yields worldwide for about 100 years if it were available (Khan et al., 2007).

Unfortunately, most legacy P is not available for plants to absorb easily. However, it may be possible to manipulate soils to increase the availability of this P for crops. The aims of this review are to clarify our current understanding of the cycling and transformation of legacy P in agricultural soils and to present findings from the published literature

about so-called “P activators”. Furthermore, we evaluate the contribution of P activators to soil legacy P availability, assess the advantages and disadvantages of different P activator classes and summarize the key mechanisms involved.

2. The forms and mobility of soil P

More than 80% of P applied as fertilizer can become unavailable for plant uptake shortly after application via sorption, precipitation (typically by reaction with Al^{3+} and Fe^{3+} in acidic soils and Ca^{2+} in calcareous soils: Table 1) or microbial immobilization (Gustafsson et al., 2012; Roberts and Johnston, 2015; Yadav and Verma, 2012). To take full advantage of legacy P, it is necessary to understand the long-term dynamics of this P in soil (Liu et al., 2014a).

Soil P occurs in a number of different forms (organic and inorganic) which vary greatly in their bioavailability (Fig. 1). Those include constituents of rock minerals from the parent material, which are completely inaccessible, various forms of organic matter (including the constituents of humus and the cells of living organisms: Khan et al., 2014) and bio-available phosphate in solution (Dollard and Billard, 2003). The environmental behavior of P is also a function of its speciation, which is directly linked to P solubility, reactivity, and bioavailability (Liu et al., 2014b). For example, P associated with Fe (hydr) oxides (Fe-P) is sensitive to reducing conditions (Beauchemin et al., 2003). P sorbed to Al (hydr)oxides (Al-P) or calcium phosphate precipitates is likely to be more sensitive to pH changes (Yan et al., 2014), and some species of organic P tends to be more bioavailable (Li and Brett, 2013).

The total P in top soils (0–15 cm) typically ranges from 50 to 3000 mg P kg^{-1} , depending on parent material, soil texture, vegetation cover and soil management history (Sanyal and De Datta, 1991). According to Stutter et al. (2015), based on 32 soils from the United Kingdom, arable soils tend to be dominated by ortho- P_i with orthophosphate monoester species associated with strongly sorbing Al and Fe soil surfaces. Intensive grasslands tend to be dominated by orthophosphate monoesters and as grazing becomes more extensive labile orthophosphate diesters, associated with labile soil organic matter and microbial turnover, dominate. The diversity of P species in less intensively managed soils can be viewed as a positive indicator of ecosystem function and diversity.

P_i generally accounts for 60–80% of total P in agricultural soils (predominantly in minerals). The total P content is usually at least one order of magnitude larger than the amount of P that rapidly cycles through the soil-plant system and two to three orders of magnitude larger than the amount of P present as plant-available P_i in the soil solution (HPO_4^{2-} or H_2PO_4^-) (Frossard et al., 1995). The dominant form of orthophosphate ion present in the soil is pH dependent. At pH 4–5, orthophosphate usually exists as H_2PO_4^- ions but as pH increases, first HPO_4^{2-} ions and then PO_4^{3-} ions become more dominant (Yadav and Verma, 2012).

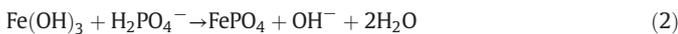
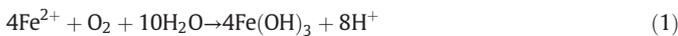
Many abiotic and biotic reactions occur in the soil P cycle (Fig. 1), some occurring within a few seconds, while others occurring slowly over several years (Bünemann and Condrón, 2007; Fardeau, 1995; Frossard et al., 2011). The initial breakdown can often be the rate-limiting step for P_o mineralization (Das et al., 2014). P availability is also greatly affected by a series of pH-dependent abiotic reactions that influence the ratio of soluble-to-insoluble P pools in the soil (DeLuca et al., 2009). These include desorption and solubilization of rapidly exchangeable P_i ; uptake of P by soil microorganisms and plants (either through their roots or through mycorrhizal hyphae); the release of P_i from the soil solid phase or from fertilizers, induced by the exudation of phosphatases and organic acids from roots or microorganisms; the release of P_i from plant residues or organic fertilizers to the soil solution; and the release of P_i from organic matter mineralization by microorganisms (Frossard et al., 2011).

The concentration of P in the soil solution is primarily controlled by adsorption/desorption equilibria between labile P_i in the solid phase

Table 1
Common phosphorus minerals found in acid, neutral and calcareous soils and their equilibrium dissolution reactions.
(Modified from Gustafsson et al. (2012) and Yadav and Verma (2012).)

Soil type	Minerals	Chemical formula	Equilibrium dissolution reaction
Acid soils	Strengite	$\text{FePO}_4 \cdot 2 \text{H}_2\text{O}$	$\text{FePO}_4 \cdot 2 \text{H}_2\text{O}(\text{s}) \leftrightarrow \text{Fe}^{3+} + \text{PO}_4^{3-} + 2\text{H}_2\text{O}$
	Vivianite	$\text{Fe}_3(\text{PO}_4)_2 \cdot 8\text{H}_2\text{O}$	$\text{Fe}_3(\text{PO}_4)_2 \cdot 8 \text{H}_2\text{O}(\text{s}) \leftrightarrow 3\text{Fe}^{2+} + 2\text{PO}_4^{3-} + 8\text{H}_2\text{O}$
	Variscite	$\text{AlPO}_4 \cdot 2 \text{H}_2\text{O}$	$\text{AlPO}_4 \cdot 2 \text{H}_2\text{O}(\text{s}) \leftrightarrow \text{Al}^{3+} + \text{PO}_4^{3-} + 2\text{H}_2\text{O}$
Neutral and calcareous soils	B-tricalcium phosphate	$\text{Ca}_3(\text{PO}_4)_2$	$\text{Ca}_3(\text{PO}_4)_2(\text{s}) \leftrightarrow 3\text{Ca}^{2+} + 2\text{PO}_4^{3-}$
	Dicalcium phosphate	CaHPO_4	$\text{CaHPO}_4(\text{s}) \leftrightarrow \text{Ca}^{2+} + \text{PO}_4^{3-} + \text{H}^+$
	Dicalcium phosphate dihydrate	$\text{CaHPO}_4 \cdot 2 \text{H}_2\text{O}$	$\text{CaHPO}_4 \cdot 2 \text{H}_2\text{O}(\text{s}) \leftrightarrow \text{Ca}^{2+} + \text{PO}_4^{3-} + \text{H}^+ + 2\text{H}_2\text{O}$
	Fluorapatite	$\text{Ca}_5(\text{PO}_4)_3 \text{F}$	$\text{Ca}_5(\text{PO}_4)_3 \text{F}(\text{s}) \leftrightarrow 5\text{Ca}^{2+} + 3\text{PO}_4^{3-} + \text{F}^-$
	Hydroxyapatite	$\text{Ca}_5(\text{PO}_4)_3 \text{OH}$	$\text{Ca}_5(\text{PO}_4)_3 \text{OH} \leftrightarrow 5\text{Ca}^{2+} + 3\text{PO}_4^{3-} + \text{OH}^-$
	Octacalcium phosphate	$\text{Ca}_8\text{H}_2(\text{PO}_4)_6 \cdot 5 \text{H}_2\text{O}$	$\text{Ca}_8\text{H}_2(\text{PO}_4)_6 \cdot 5 \text{H}_2\text{O} \leftrightarrow 8\text{Ca}^{2+} + 6\text{PO}_4^{3-} + 6\text{H}_2\text{O}$

(associated with positively charged minerals such as Fe and Al oxides) defined by equilibrium concentration ratios (Haynes and Mokolobate, 2001; Hinsinger, 2001). Specific adsorption (ligand exchange) occurs when P ions replace the hydroxyl groups on the surface of Al and Fe oxides and hydrous oxides (Haynes and Mokolobate, 2001). P ions can also interact chemically with minerals in combination with metals such as calcium phosphate, aluminum phosphate, iron phosphate and the reductant-soluble phosphate extractable after removal of the first three forms (Chang and Jackson, 1957). For example, oxygen (O_2) can immobilize iron through Fe(II) oxidation which precipitates as Fe(III) (hydr) oxides, resulting in the generation of H^+ and a decrease in pH (Eq. (1)) (Begg et al., 1994). This process may have some effects on the trapping of phosphate as FePO_4 (Eq. (2)) (Silva and Sampaio, 1998).



P_o may constitute 30–50% in most soils, although it can range from as low as 5% to as high as 95% (Sharpley, 1985). P_o is typically present as orthophosphate monoesters, including inositol phosphates, and as orthophosphate diesters, organic polyphosphates and phosphonates (Bünemann, 2015). P_o can be classified into four main fractions: labile, moderately labile, moderately resistant (fulvic-acid P), and highly resistant (humic-acid P) (Bowman and Cole, 1978; Randriamanantsoa et al., 2015). All fractions can be transformed into phosphate that is available to plants via microbially mediated mineralization – but at different

rates. Labile P_o is relatively easily mineralized whereas inositol phosphate (up to 50% of P_o) is considered to be stable (Dalai, 1977). The microbial biomass acts as both a source and a sink of soil P and is critical for P cycling (i.e. mineralizing P_o via enzyme-catalyzed transformations and converting P_i into their living cells during P immobilization).

Different soil P fractions can also be separated into fractions characterized operationally by the used extractants (Hedley et al., 1982): e.g. resin-P, NaHCO_3 -P, microbial-P, NaOH-P, Sonicated/NaOH-P, HCl-P and residual-P. In this kind of P fractionation, only resin-P and NaHCO_3 -P are relatively available for crops but these account for a small proportion of total P.

Both P_i and P_o are strongly bound (or fixed) to the solid phase under most soil conditions via a series of different reactions. Together with P sorption and net immobilization by the microbial biomass, this can result in low equilibrium P concentrations in the soil solution which can be manifested as P deficiency (e.g. reduced crop growth), even in moderately fertilized soils (Gerke, 2015). This can be reversed via dissolution/precipitation (mineral equilibria), sorption/desorption (interactions between P and mineral surfaces) and mineralization/immobilization (biological transformations between P_o and P_i).

3. Soil P activators and the application effect

P activators refer to a range of different methods intended to accelerate and strengthen soil P transformations to plant-available forms in the soil solution. They can be classified into three types: (1) bio-inoculants and bio-fertilizers, including phosphate solubilizing

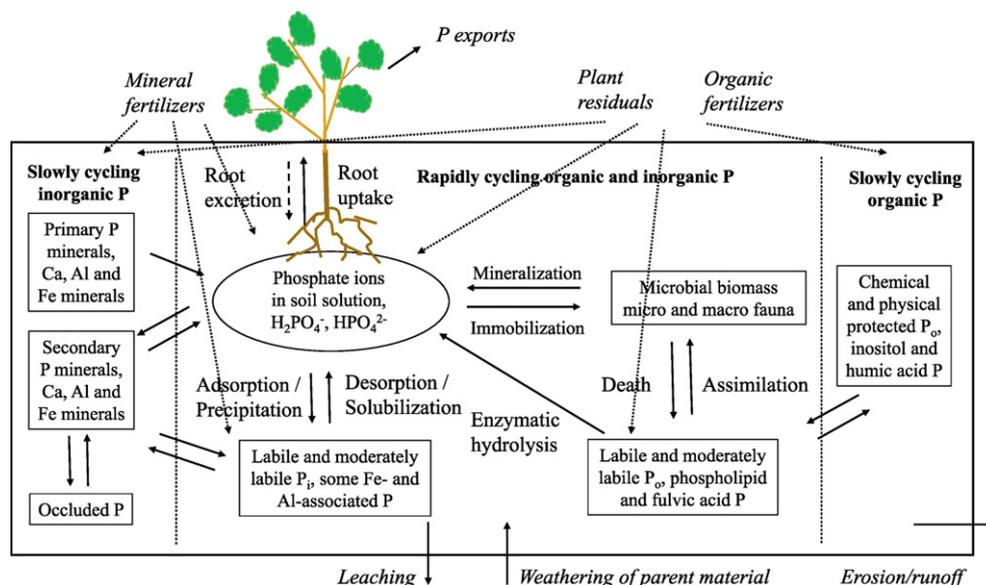


Fig. 1. The physicochemical and biological transformations of phosphorus in soil-plant and soil-solution systems (modified after Frossard et al., 2011). P_o : organic phosphorus; P_i : inorganic phosphorus. The dotted arrow indicates external phosphorus input and the solid arrow shows the internal phosphorus transformations.

microorganisms (PSMs) and phosphatase enzymes; (2) organic matter, including low molecular weight organic acids, humic acids, lignin, crop residue, manure and biochar and (3) zeolites and other materials, which have been relatively less well studied and applied.

Although activation processes are complex, several key factors have consistently been demonstrated to govern the availability of fixed P. These main factors can be broadly grouped as sorption reactions and changing the chemical and physical properties of the soil (e.g. pH, extractable Al and the net negative charge on surfaces in soil) with the net effect of increased solubility and reduced sorption of P_i in soil. It is complex to elucidate the effect of P activators based on changing of these factors. For a review of this nature, it would be useful to define a common and clearly explained set of responses to P activation. Here, we employ the P activation response based on an increase in plant-available P or on saved phosphate fertilizer inputs – focusing on experimental data (field and glasshouse) that excluded the impacts of management practices (e.g. grazing, intercropping).

3.1. Bio-inoculant and bio-fertilizer

3.1.1. Phosphate solubilizing microorganisms

Various organisms are involved in P cycling but microorganisms probably play the most important role. Much of the global cycling of insoluble organic and inorganic soil P can be attributed to bacteria and fungi. Phosphate solubilizing microorganisms are those which are capable of transforming insoluble P into soluble (plant accessible) forms. They are probably the most eco-friendly and inexpensive option for enhancing P availability for plants (Owen et al., 2015). Phosphate solubilizing bacteria (PSB: *Achromobacter*, *Aerobacter*, *Agrobacterium*, *Alcaligenes*, *Arthrobacter*, *Aspergillus*, *Azotobacter*, *Bacillus*, *Bradyrhizobium*, *Burkholderia*, *Chromobacterium*, *Enterobacter*, *Erwinia*, *Escherichia*, *Flavobacterium*, *Klebsiella*, *Micrococcus*, *Pantoea agglomerans*, *Pseudomonas*, *Rhizobium*, *Salmonella*, *Serratia*, *Thiobacillus*) and phosphate solubilizing fungi (PSF: *Alternaria*, *Arbuscular mycorrhiza*, *Aspergillus*, *Fusarium*, *Helminthosporium*, *Penicillium*, *Rhizopus*, *Sclerotium*) make up 1–50% and 0.1–0.5% respectively of the total PSMs in soil with an additional minor role played by phosphate solubilizing actinomycetes (PSA: *Streptomyces*, *Nocardia*) (Khan et al., 2007). It has long been known that there is significant variation in the ability of bacteria to solubilize P in soil. Bacteria which are known to enhance P availability include species of *Pseudomonas*, *Azotobacter*, *Burkholderia*, *Bacillus* and *Rhizobium* (Jones and Oburger, 2011). Generally, PSF produce more acids than bacteria and consequently exhibit greater P-solubilizing activity. Filamentous fungi known to be able to solubilize phosphate include the genera *Aspergillus* and *Penicillium* (Sharma et al., 2013). In recent years, the P-solubilizing ability of actinomycetes has attracted interest because this group of soil organisms are not only capable of surviving in extreme environments (e.g. drought, fire etc.) but also possess other potential features (e.g. production of antibiotics and phytohormone-like compounds etc.) that could simultaneously benefit plant growth (Hamdali et al., 2008).

The P solubilizing ability of different PSMs varies with species, strain, soil properties (inherent and seasonal) and the plant species (Table 2). A maximum increase in available P of 208% has been reported (Abdul Wahid and Mehana, 2000). However, de Freitas et al. (1997) found that application of PSB (*Bacillus sphaericus*, *B. polymyxa* and *B. thuringiensis*) significantly increased plant growth, but not P-uptake. Other studies suggest that mixtures of different PSMs may be more effective than using single organisms (Yu et al., 2011). Kim et al. (1997) reported that when vesicular-arbuscular mycorrhizae (VAM; *Enterobacter agglomerans*) and PSB (*Glomus etunicatum*) were applied together, the soil microbial colonization and phosphatase activity response was much higher than when they were used separately, suggesting a synergistic interaction, although the exact mechanisms were not fully understood. It is likely that the additional increase in P resulting from dual inoculation was due to enhanced P solubilization by PSB through the

production of organic acids, ion chelation and increasing root cell permeability, as well as supporting the establishment and function of VAM (mycorrhizal colonization alters roots physiologically as well as altering microbial populations: Suri et al., 2011).

Various “bio-fertilizers” have been developed which include bacteria (e.g. *Pseudomonas* spp., *Bacillus* spp., *Rhizobium* spp. and *Klebsiella* spp.), fungi (e.g. *Penicillium* spp., *Aspergillus* spp. and *Rhizopus* spp.) and actinomycetes (e.g. *Streptomyces* spp.). These organisms are intended to solubilize solid phosphate in soils (Mahajan and Gupta, 2009). They are cost effective, have no known environmental issues and can be used to supplement chemical fertilizers (Chesti et al., 2013). It has been estimated that inoculation with arbuscular mycorrhizal fungi (AMF) might result in a reduction of approximately 80% of the recommended phosphate fertilizer rate under certain conditions, with similar crop yields (Liu et al., 2016). The effectiveness of mycorrhizal associations on P uptake from slow-release P compounds has been elucidated in the review of Bolan, (1991). They noted that for plants the increase in P uptake associated with mycorrhizal infection was found to vary with source of P. Greatest benefit from mycorrhizal inoculation was obtained with the least soluble source of iron phosphate. Compared to normal phosphate fertilizers, dissolved P microbial mixed fertilizers appear to have a significant effect on the utilization of P – enabling a reduction in phosphate fertilizers by 25–467% (Mukherjee and Sen, 2015; Sundara et al., 2002). The effect of PSMs varies at different phases of plant growth. Sundara et al. (2002) shows that the effect of PSB fertilizer treatment on available P status varied with sugarcane growth stage. PSB fertilizers were more effective in the tilling and growth phases than during the ripening phase.

Although it is widely known that PSMs can make P available, the mechanisms underlying this phenomenon are not fully understood. The potential mechanisms are illustrated in Fig. 2 and include the microbial synthesis of a range of exudates (e.g. organic acids and H^+ , metabolites and enzymes including phosphatase) (Behera et al., 2014). The insoluble forms of P_i , such as tricalcium phosphate ($Ca_3(PO_4)_2$), aluminum phosphate ($AlPO_4$), iron phosphate ($FePO_4$), may be converted to soluble P by low molecular weight organic acids as well as facilitated by microbially released H^+ (Khan et al., 2014). Li et al. (2015) studied mechanisms for solubilizing different types of P by an efficient *Aspergillus niger* strain An2. They found An2 mainly secreted oxalic acid to solubilize Ca-P, Mg-P, Al-P and Fe-P and secreted tartaric acid to solubilize rock phosphate.

PSMs can secrete enzymes (phosphatase, phosphohydrolase, phytase, phosphonate and C-P lyase) which catalyze P_o mineralization. The most commonly secreted enzymes are phosphatase (an enzyme which eliminates P from its substrate by hydrolyzing phosphoric acid monoesters into a P ion and a molecule with a free hydroxyl group.) and phytase because of the predominant presence of their substrates in soil (Othman and Panhwar, 2014). Phosphatases or phosphohydrolases describe a broad group of enzymes that catalyze the hydrolysis of both esters and anhydrides of H_3PO_4 (Jones and Oburger, 2011). Phytase (myo-inositol hexaphosphate phosphohydrolase) can hydrolyze sodium phytate, resulting in the production of P_i (Sharma et al., 2013). Phosphonate and C-P lyase cleave the C-P of organophosphonate. Wanner (1996) found that many enzymes can function as organic phosphoester scavengers, releasing inorganic phosphates from nucleotides and sugar phosphates. PSMs can also solubilize phosphate via the production of NH_4^+ , CO_2 and H_2S , as well as releasing P during substrate degradation (Khan et al., 2010). The production of H_2S can act with ferric phosphate to yield ferrous sulphate with concomitant release of phosphate. The presence of NH_4^+ can result in pH depression via the formation of H^+ during nitrification which contributes to P solubilizing (Khan et al., 2014). Proton release also occurs from the dissociation carbonic acid (H_2CO_3) which is formed from the dissolution of CO_2 generated by biological respiration. These protons can readily solubilize Ca-apatite (Kim et al., 1997):

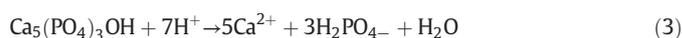


Table 2
Phosphate solubilizing microorganisms (PSMs) isolated from different soils and their effects on soil available phosphorus (AP) and the equivalent application rate of phosphate fertilizers (PF) when PSMs and phosphate solubilizing microbial mixed fertilizers (PSMF) are applied. RP: rock phosphate; PBF: phosphate solubilizing bacteria fertilizers; VAM: vesicular arbuscular mycorrhizae; PSB: phosphate solubilizing bacteria; PSF: phosphate solubilizing fungi; AMF: arbuscular mycorrhizal fungi; CGMCC: hina General Microbiological Culture Collection Center of China Administration Committee for Culture Collection of Microorganisms; NM: not mentioned.

Microorganism	Strains	Isolated area	Experiment soil	Crop	P activation response on soil	References
PSB	<i>Enterobacter agglomerans</i>	Purchased	Silt loam (pH = 5.6), Mexico	Tomato	Rhizosphere P concentration increased by 10.5–31.6%; mixed higher	(Kim et al., 1997)
	<i>Glomus etunicatum</i>					
	<i>Fusarium oxysporum</i>	Obtained from the culture collection of University of Mysore, India	Sandy loam soil (pH = 6.9), India	Tomato	AP increased by 26.7–183.3%	(Hariprasad and Niranjana, 2009)
	<i>Alternaria solani</i>	Walnut production areas from Sichuan, China	Sandy loam soil (pH = 7.1), China	Walnut	AP increased by 9.7–50.7%; mixed higher; <i>B. cereus</i> had no effect	(Yu et al., 2011)
	<i>Pseudomonas chlororaphis</i>					
	<i>Bacillus cereus</i>					
	<i>Pseudomonas fluorescens</i>	Rhizosphere of <i>Aloe barbadensis</i> from Indian	Unsterile loamy soil (pH = 7.8), India	<i>Aloe barbadensis</i>	AP increased by 230–403%	(Gupta et al., 2012)
	<i>Pseudomonas synxantha</i>					
	<i>Burkholderia gladioli</i>					
PSF	<i>Enterobacter hormaechei</i>	Sodic soil sites from Sultanpur, India	Sodic soils (pH = 9.3), India	Sweet basil (<i>O. basilicum</i>)	Residual fertility P conversion rate increased by 17.2–32.1%	(Sahay and Patra, 2014)
	<i>Serratia marcescens</i>					
PSF	<i>Ocimum basilicum</i>	Mine landfills of RP from Udaipur, India	Sandy loam soil (pH = 8.1), India	Wheat and maize	AP increased by 35.1–85.3% for wheat and 106.3–127.7% for maize	(Singh and Reddy, 2011)
	<i>Penicillium oxalicum</i>	Crops rhizospheric soil in Birbhum, West Bengal, India.	Silty clay soil (pH = 5.2), India	Maize	PF application rate reduced by 34.9–467.4%	(Mukherjee and Sen, 2015)
PSB & VAM	<i>Candida tropicalis</i>	Plant rhizospheric soils from Ismailia and South Sinai Governorates	Sandy soil (pH = 8.4), Egypt	Wheat and faba bean	AP increased by 12.1–194.2% for wheat and 15.9–208.3% for faba bean	(Abdul Wahid and Mehana, 2000)
	<i>Aspergillus niger</i>					
PSB & PSF	<i>A. fumigatus</i>	Rhizospheric soil of <i>Stevia rebaudiana</i> from Pojewa, India	Sandy loam (pH = 8.3), India	Maize-wheat Cropping	P absorption increased by 41.2–117.6% for maize and 41.05–41.8% for wheat	(Kaur and Reddy, 2015)
	<i>Penicillium pinophilum</i>					
PSB & PSF	<i>Pantoea cypripedii</i>	Purchased	Siliceous and calcareous growing media (pH = 7.8)	Cucumber	AP increased by 16.8% (Fungi T34) and 39.85 (Bacteria QST713) in siliceous soil; 6.6% (T34) and 60.7% (QST713) in calcareous soil	(García-López et al., 2016)
	<i>Bacillus subtilis</i> QST713					
PSB & AMF	<i>Trichoderma asperellum</i> T34	Andisol from Hawai'i, America	Sandy loam (pH = 5.4), Clay loam (pH = 4.9), America	<i>Leucaena leucocephala</i>	Varied from soil type; Mixed higher	(Osorio and Habte, 2015)
	<i>Mortierella</i> sp.					
PBF	<i>Claroideoglossum claroideum</i>	Rhizospheric soil of tomato, eggplant and cucumber, Iraq	Silt clay soil (pH = 8.2), Iraq	Typical torrifluent	AP increased by 24.2–138.6%	(Salih et al., 1989)
	<i>Penicillium</i> sp.					
PSMF	<i>Aspergillus foetidus</i>	Purchased	Loamy soil, (pH = 7.4), China	Soybean	AP increased by 11.8–57.1%	(Zhou et al., 2005)
	AB-233					
PSB & PSF	<i>Pseudomonas</i>	Purchased	Clay soil (pH = 8.1), China	Rape	AP increased by 1.84–15.44%; Mix PSB > mixed PSF, both higher than mixed PSB with PSF	(Li et al., 2014)
	<i>Rahnella</i>					
PSB & PSMF	<i>Aspergillus niger</i>	Depository in CGMCC	Silt clay soil (pH: NM), India	Corn	P absorption increased by 25.93–50.56% for corn and 18.58–44.09% for rice	(Ho et al., 2013)
	<i>Penicillium</i>			Rice		
PSF & PSMF	<i>Bacillus subtilis</i>					
	<i>Bacillus licheniformis</i>					
PSF & PSMF	<i>Streptomyces cellulosae</i>					
	<i>Aspergillus versicolor</i>					
PSF & PSMF	<i>Bacillus megatherium</i> var	Purchased	Clay soil (pH: NM), India	Sugarcane	PF application rate reduced by 25%	(Sundara et al., 2002)
	<i>Phosphaticum</i>					

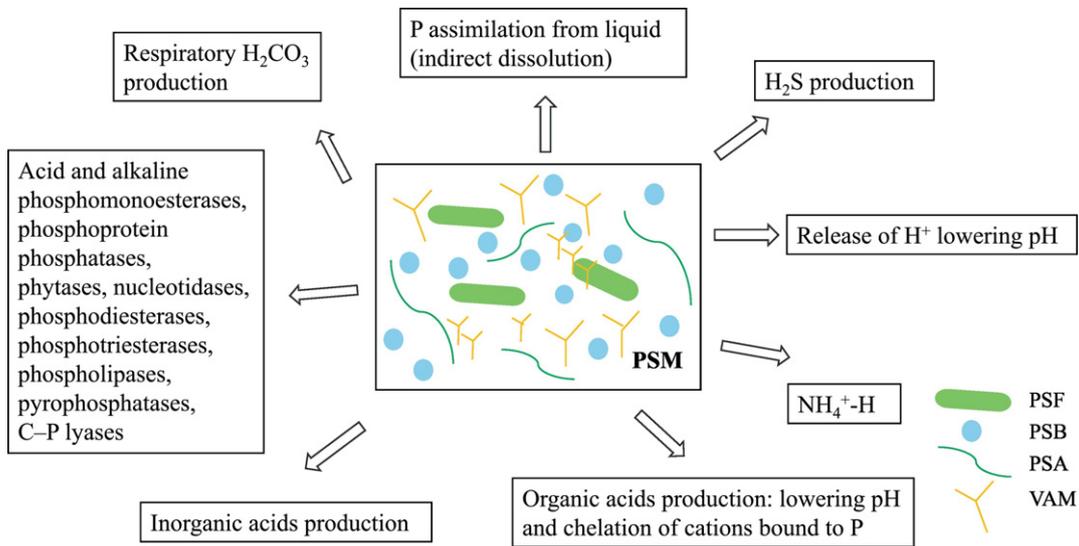


Fig. 2. Potential mechanisms for the solubilization of insoluble phosphorus by phosphate solubilizing microorganisms (PSMs). PSF: phosphate solubilizing fungi; PSB: phosphate solubilizing bacteria; PSA: phosphate solubilizing actinomycete; VAM: vesicular-arbuscular mycorrhizae (modified after Khan et al., 2010).

3.1.2. Phosphatase enzyme and enzyme activators

Phosphatase enzymes are widely distributed in natural environments and play a major role in P_o regulation (Fig. 3) by hydrolyzing ester-phosphate bonds in P_o, leading to the release of phosphate (Burns and Dick, 2002).

Phosphodiesterase and phosphomonoesterase may act sequentially in the mineralization of P_o: phosphomonoesterase can dissociate the phosphate group from phosphate monoester compounds and phosphodiesterase can hydrolyze the phosphate diester bond in nucleic acids. Lipids and nucleic acids typically make up about 7% of soil P_o (Kalsi

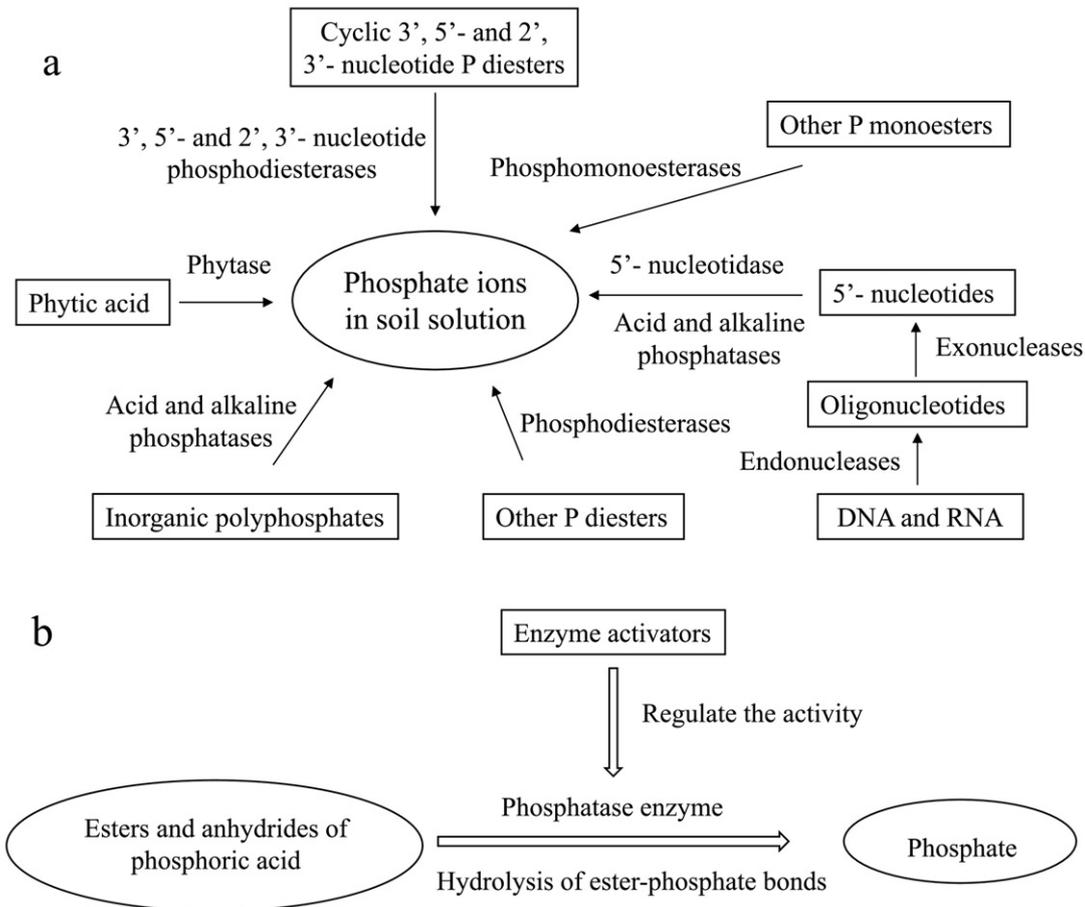


Fig. 3. (a) Phosphate regeneration through enzymatic decomposition of various phosphorus compounds in soil (modified after Burns and Dick, 2002); (b) the role of phosphatase enzymes in mineralizing organic phosphorus to phosphate and enzyme activators activating phosphatase enzymes.

Table 3

The main low molecular weight organic acids identified in agricultural soils. (Gerke, 2015; Jones, 1998; Song and Cui, 2003; Strobel, 2001; van Hees et al., 1999).

Classification	Carboxylate	Organic acid	Molecular formula	Molecular mass	Organic acid	Molecular formula	Molecular mass	
Aliphatic	Monobasic	Formic	HCOOH	46.03	Lauric	C ₁₁ H ₂₅ COOH	200.32	
		Acetic	CH ₃ COOH	60.05	Palmitic	C ₁₅ H ₃₁ COOH	256.42	
		Propionic	C ₂ H ₅ COOH	74.08	Linolenic	C ₁₇ H ₂₉ COOH	278.44	
		Butyric	C ₃ H ₇ COOH	88.11	Linoleic	C ₁₇ H ₃₃ COOH	282.47	
		Valeric	C ₄ H ₉ COOH	102.14	Oleic	C ₁₇ H ₃₃ COOH	282.47	
		Pyruvate	CH ₃ COCOOH	88.06	Arachidic	C ₁₉ H ₃₉ COOH	312.53	
		Glycolic	CH ₂ OHCOOH	76.05	Carnaubic	C ₂₃ H ₄₇ COOH	368.62	
		Lactic	CH ₃ CH(OH)COOH	90.08				
	Dicarboxylic	Oxalic	HOOCOOH	90.04	Maleic	C ₄ H ₄ O ₄	116.08	
		Malonic	HOOCCH ₂ COOH	104.06	Fumaric	C ₄ H ₄ O ₄	116.08	
		Succinic	HOOC(CH ₂) ₂ COOH	118.09	Ketoglutaric	C ₅ H ₆ O ₅	146.11	
		Tartaric	HOOC(CHOH) ₂ COOH	150.09	Aconitic	C ₆ H ₆ O ₆	174.11	
		Malic	HOOCCHOHCH ₂ COOH	134.09				
	Aromatic	Tribasic	Oxalacetic	C ₄ H ₄ O ₅	132.07	Citric	C ₆ H ₈ O ₇	192.43
			Benzoic	C ₆ H ₅ —COOH	122.12	Sinapic	C ₁₁ H ₁₂ O ₅	224.22
			Phenylacetic	C ₆ H ₅ —CH ₂ COOH	136.15	Phthalic	C ₈ H ₆ O ₄	166.13
		Monobasic	Cinnamic	C ₆ H ₅ —CH=CH—COOH	148.16	P-coumaric	C ₉ H ₈ O ₃	164.16
Ferulic			C ₁₀ H ₁₀ O ₄	194.19	Salicylic	C ₇ H ₆ O ₃	138.12	
2-Naphthoic			C ₁₁ H ₈ O ₂	172.18	Gallic	C ₇ H ₆ O ₅	170.10	
Indole-3-acetic			C ₁₀ H ₉ NO ₂	175.18	Vanillic	C ₈ H ₈ O ₄	168.15	
P-phenylcinnamic			C ₁₅ H ₁₂ O ₂	224.25	Syringic	C ₉ H ₁₀ O ₅	198.18	
P-hydroxybenzoic			C ₇ H ₆ O ₃	138.12	Shikimic	C ₇ H ₁₀ O ₅	174.16	
3-Phenylpropanoic			C ₉ H ₁₀ O ₂	150.17				
Amino acid		NH ₂ —CH(R)—COOH*						

* R indicates R-groups in amino acids. The R-groups give the amino acids their physical-chemical characteristics such as polarity (hydrophobic or hydrophilic) and charge (acidic or positive versus basic or negative).

et al., 2016). The influence of phytase on P_o mineralization is less well understood but is thought to be important in the mineralization of inositol P (which makes up approximately 50% of soil P_o in the form of phytin and its derivatives). Phytase can release lower forms of myo-inositol phosphates and inorganic phosphate by catalyzing the hydrolysis of phosphomonoester bonds in phytate. Xiang et al. (2005) observed that soil phosphatase activity and available P content increased significantly after applying exogenous phytase in potted *Malus hupehensis* experiments.

D-α-Glycerophosphatase is a rare phosphatase in soil which has been purified and characterized from *Bacillus licheniformis* (Skrally and Cameron, 1998). The products of the reaction catalyzed by D-α-glycerophosphatase were identified as glycerol and inorganic phosphate. In addition, a kind of inorganic phosphatase (pyrophosphate phosphohydrolase) has been identified which can hydrolyze pyrophosphate (used as a fertilizer) to P_i (Dick and Tabatabai, 1978).

It has been shown that the activities of phosphatase (like those of many hydrolases) depend on several factors including soil properties, soil organism interactions, plant cover, leachate inputs and the presence of other inhibitors and activators (Bünemann et al., 2011).

Phosphatase activity varies with pH (different phosphatases are classified as either alkaline (pH > 7) or acid (pH < 6) phosphatase). Generally, enzyme activities of soils increase with increasing soil pH with the exception of acid phosphatase which is predominant in acid soils. It is worth underlining that when the effects of soil pH on enzyme activities are studied, the concentration of organic matter should remain constant (Gianfreda and Ruggiero, 2006). For example, the significantly greater activities of alkaline phosphomonoesterase, inorganic pyrophosphatase and phosphodiesterase reported in manure-treated soils by Acosta-Martínez and Tabatabai (2000) are believed to be due to a combination of greater soil pH values and enhanced microbial activity and diversity resulting from manure input over the years. Martens et al. (1992) studied the activities of ten soil enzymes after the application of different organic amendments (poultry manure, sewage sludge, barley straw and green alfalfa) over a 31-month period. They found that the addition of amendments increased enzyme activity by an average

of 2- to 4-fold during the first year of the experiment. Similarly, phosphatase activities (acid phosphate, alkaline phosphatase, phosphodiesterase and inorganic pyrophosphatase) were significantly correlated with the organic carbon content of the 40 soil samples tested by Deng and Tabatabai (1997), confirming that organic matter plays an important role in protecting and maintaining soil enzymes in their active forms.

It is well established that phosphatase activities generally decrease with soil depth (Gianfreda and Ruggiero, 2006). Ji et al. (2014) describe a two-year field experiment on the effects of deep tillage on soil microorganisms and phosphatase activity in clay and loam soils. The data showed that tillage and soil texture had a significant influence over soil phosphatase activities and that deep tillage increased soil phosphatase activities, which was affected by soil depth. This may be because deep tillage loosens the soil and mixes organic matter into lower horizons, thereby increasing the abundance of soil microorganisms. Activities of phosphatase in clay soil were higher than those of loam by 10.9%. This may have been due to the fact that the finer particles in clay soils offer more surface area and more small pores which can trap organic matter and offer habitat for soil microorganisms (which are the source of phosphatases). Das et al. (2014) also found that soil phosphatase activity decreases with increasing depth. Soil temperature also has a significant impact on soil phosphatase activity. Higher temperatures can encourage microbial metabolism, increasing phosphatase activity and nutrient availability (Dalai, 1977). However, previous studies have also shown a significant correlation between phosphodiesterase activity and organic carbon content which complicates the explanation for this effect (i.e. the degradation of organic carbon is also correlated with temperature) (Koch et al., 2007; Štursová and Baldrian, 2011).

Some stressors such as salinity and high heavy metal concentrations may have adverse effects on the phosphatase activities. Alkaline phosphatase was observed to decline exponentially with increasing salinity and linearly with increasing sodicity by Rietz and Haynes (2003). This was ascribed to the denaturation of enzyme proteins at high salt concentrations and a decrease in microbial biomass and activity. Heavy

Table 4
The type and concentration of low molecular weight organic acids (LMWOAs) added to different types of agricultural soils and their effects on P transformation.

LMWOAs	Concentration	Soil type	Soil area	Effects	References
Citrate and Tartrate acid	0.1–0.5 mmol L ⁻¹	Black loam and gravelly clay soil	Egmont, Okaihau in New Zealand	Fe and Al sorb P; citrate (50% reduction), tartrate (20% reduction). Decrease the adsorption of P by soils: tricarboxylic acid > dicarboxylic acid > monocarboxylic acid.	(Earl et al., 1979) (Bolan et al., 1994)
Acetic, formic, lactic, citric, malic, oxalic, tartaric acid	10 mmol kg ⁻¹	Silt loam derived from volcanic ash and clay loam from loess	Patua, Italy; Tokomaru, New Zealand	No effect of acetic acid application alone on the Olsen-P. Having an effect when applied along with fertilizers P.	(Tripathi, 2005)
Acetic acid	0.2, 2 mmol kg ⁻¹	Arid soil	Rajasthan, India	Solubilizing of P; citric acid, 34.7% malic and oxalic, no significant differences.	(Wei et al., 2010)
Oxalic, citric acid	10 mmol kg ⁻¹	Plantation and natural forest soils	Subtropical and tropical areas in Australia	Malic and citric acids had no effect on Fe-Al oxide fraction, but oxalic acid significantly reduced this fraction.	(Taghipour and Jalali, 2013)
Malic acid		Vegetable, garlic, and potato land use calcareous soils	Hamedan, Iran	P _o release induced by low molecular weight organic acids is ascribed to their ability to mobilize NaHCO ₃ -P _o rather than to chelate cations (i.e., Fe ³⁺ , Al ³⁺) bound to P _o in soil.	(Wang et al., 2015)
α-naphthaleneacetic acid	10 ⁻⁴ , 10 ⁻⁵ , 10 ⁻⁶ mmol L ⁻¹	Calcareous clay soil, neutral silty clay loam, and acidic silty clay soil	Luancheng (wheat), Shenyang (corn), and Taoyuan (rice), China	The secretion of common organic acid increased by proteoid roots of white lupin.	(Gomez and Carpena, 2014)
		Nutrient solution	Spain		

metals affect enzyme activity by modifying protein conformation, due to interaction with the protein active groups and by inhibiting enzyme synthesis (Karaca et al., 2010). Kandeler et al. (2000) found that phosphatase activities decreased after 10 years of contamination with different levels of Zn, Cu, Ni, V and Cd.

Although, in principle, some P activators can strengthen (accelerate) the activity of phosphatase and, hence, activate P_o (Fig. 3b), relatively few studies have been published on this topic. An exception is the work of Fang et al. (2008) which showed that the addition of glutathione enhanced the affinity between enzymes and substrates. Ascorbic acid had a similar effect to glutathione enzyme activity. They take part in redox reactions and can combine with peroxide and free radicals to protect sulfhydryl from oxidation. As a result, proteins and enzymes containing sulfhydryl in membranes will not deactivate (Wisniewski et al., 2005). Li et al. (2014) found that soil available P content could be increased by 10–91% under the influence of glutathione in paddy soils. They also demonstrated that ascorbic acid promoted the activity of phosphomonoesterase and accelerated the mineralization of P_o. The available P content consequently increased by 2–203%.

3.2. Organic matter

Organic matter applied to soil as an amendment is also reported to increase the availability of existing soil P. A comprehensive review of the competitive sorption reactions between phosphorus and organic matter in soil is given by Guppy et al. (2005). Details of how organic matter contributes to available P in soil is reviewed further in this Section.

3.2.1. Low molecular weight organic acids

Low molecular weight organic acids are organic compounds that contain at least one carboxyl group and a molar mass < 10,000 g mol⁻¹. They are thought to activate P since plants secrete them under conditions of P deficiency and they are also derived from the decomposition of plant and animal residues (Yuan et al., 2016). The most common low molecular weight organic acids identified in soils are oxalic, malic, citric, fumaric, tartaric and succinic acids (Table 3). The most frequent agents used for mineral phosphate solubilization seem to be gluconic acid and 2-ketogluconic acid (Earl et al., 1979; Moradi et al., 2012). The concentrations of low molecular weight organic acids tend to be low in soils, ranging from 10⁻³–10⁻⁵ mol L⁻¹.

Different concentrations of low molecular weight organic acids have been added to soil in an attempt to increase P availability. Good P activation responses have been obtained using citric and oxalic acids (Table 4). Low molecular weight organic acids have also been added to soils with phosphatase enzymes in an attempt to activate P. For example, Guan et al. (2013) showed that the application of oxalic acid and phytase together significantly increased available P compared to controls. Amounts of H₂O-P, NaHCO₃-P_i, NaOH-P_i and NaOH-P_o increased by 37.8%, 21.1%, 15.5% and 24.4%, respectively, possibly as a consequence of the transformation of stable P fractions to labile fractions by phytase under the influence of exogenous oxalic acid. However, the detailed mechanisms remain speculative.

Low molecular weight organic acids may activate P_i via: (1) changing soil pH which can promote the dissolution of sparingly soluble minerals containing P_i (Fox et al., 1990), including calcium phosphate, e.g., octacalcium phosphate or apatite (Andersson et al., 2015); (2) forming complexes with Fe, Al and Ca and releasing P combined with these ions (Ström et al., 2005). The release of phosphate occurs via ligand exchange between the carboxylate anion and HPO₄²⁻ or H₂PO₄⁻; (3) organic acid ions compete with P_i for the same sorption sites in soils (Lan et al., 1995). When P and organic acid anions are present in the soil solution, competition is expressed either through direct physical competition for sorption sites or through electrostatic competition.

Low molecular weight organic acids may also promote the release of P_o . Giles et al. (2014) found that the addition of organic anions from bacterial sources can improve Ca myo-inositol hexakisphosphate solubilization and, thus, P availability. Organic anion-driven solubilization of Ca myo-inositol hexakisphosphate appears complementary to hydrolysis by plant and bacterial phytases. In vitro experiments suggest that Ca myo-inositol hexakisphosphate hydrolysis is improved in the presence

of organic anions (e.g., gluconate, citrate, oxalate and acetate), due either to Ca^{2+} -mediated phytase activation or solubilization via divalent metal chelation (Patel et al., 2010). However, the exact mechanism about possible dissolution of P_o by organic acids remains unclear. It is possible that low molecular weight organic acids could influence the activity of PSMs and, hence, affect the activity of phosphatases secreted by these organisms (Turner, 2008).

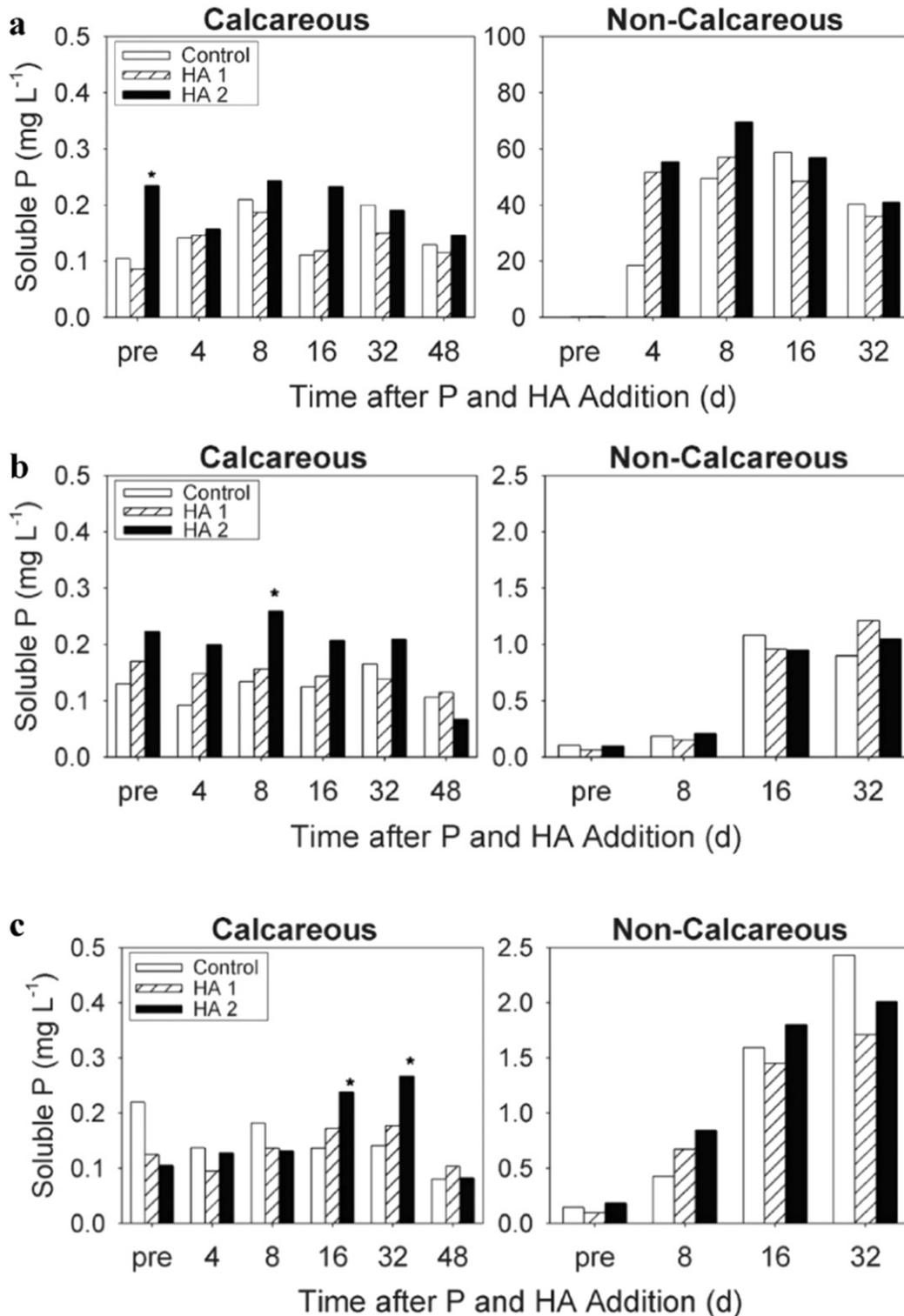


Fig. 4. (a) Water-soluble P concentrations 1.9 cm to the side of a mono-ammonium phosphate (MAP) fertilizer band, uncoated (control) or coated with a humic acid (HA) product (HA 1 or HA 2). The pre-fertilization sample (pre) was collected < 1 h prior to fertilization; (b) Water-soluble P concentrations 3.8 cm to the side of a MAP band; (c) Water-soluble P concentrations 3.8 cm below a MAP band. *Significant difference from control $p < 0.05$ (Jones et al., 2007, original images with permission from Taylor & Francis Group).

3.2.2. Humic acids and lignin

Humic acids and lignin are natural high molecular weight organic compounds derived from the decomposition of plant litter. Humic acids are composed of a range of aliphatic and aromatic structures with a variety of different functional (mainly oxygen-containing) groups. They can improve soil fertility and increase the availability of nutrient elements including P (Çimrin et al., 2010).

Humic acids can activate P via the following mechanisms: (1) Shifting soil pH; H^+ is produced during the decomposition of humic acids in soil (Hue, 1991) which can increase soluble P concentrations in calcareous soil by decreasing precipitation rates of Ca-P minerals. H^+ from humic acids can also inhibit the precipitation of hydroxyapatite, and favor the formation of dicalcium phosphate dihydrate over other, more thermodynamically stable and less soluble phosphates. The effects appear to be more effective than low molecular weight acids (Grossl and Inskeep, 1991); (2) Formation of simple organic ligands; Humic acids contain some active functional groups such as carboxyl and phenolic hydroxyl groups that can complex metal ions, especially Fe and Al (which are often associated with phosphate fixing). P availability increases when these metals are removed (Antelo et al., 2007; Gerke and Hermann, 1992). (3) Colloid interactions; Humic acids are colloidal substances and can adsorb metal and metal oxides in soil and strengthen the competitive ability of phosphate (Regelink et al., 2015). Competition between humic acids and P for sorption onto soil colloids may result in higher P dissolved concentrations.

It is worth noting that humic acids may also act as P-sorbing surfaces in some circumstances. Othieno (1973) added humic acids and P to highly weathered soils and repeatedly observed wheat yield decreases and lower tissue P concentrations, suggesting that humic acids can have a detrimental effect on P availability for plants. Further elucidation of the relationships between humic acids and P in competitive sorption processes is necessary, because both the increase and decrease of P bio-availability may occur in the presence of humic acids.

Furthermore, the addition of humic acids can also increase the distance of P movement and the concentration of extractable P in soil surrounding phosphate fertilizer placements (Du et al., 2013). A similar conclusion was reached by Jones et al. (2007). They found that soluble P concentrations were nearly identical between soils prior to fertilization (ranging from 0.1 to 0.2 mg L⁻¹). Soluble P concentrations 3.8 cm below the mono-ammonium phosphate band in the calcareous soil were significantly higher when humic acids were applied than in the control after 16 and 32 days, suggesting that humic acids may have increased P solubility and mobility. Fig. 4 demonstrates that P can move relatively far from a phosphate fertilizer band in a neutral pH, non-calcareous soil after humic acids addition (Jones et al., 2007). Soluble P concentrations were higher 3.8 cm below the band (Fig. 4c) than

3.8 cm to the side of the band (Fig. 4b), indicating that there was some downward advection of P.

Lignin is an important precursor in the formation of humic substances and can form humic acids as a result of microbial activity in soil (Bååth et al., 1995). The major chemical functional groups in lignin include hydroxyl, methoxyl, carbonyl and carboxyl groups in various amounts and proportions. Lignin can facilitate the activation of P via similar mechanisms to those described above for humic acids (Sun et al., 2011), as they share similar functional and structural properties (Tahir et al., 2011). Lignin has been reported to increase available P in calcareous, red ferrallitic (rich in iron-aluminum oxides), yellow ferrallitic (rich in ferric oxide hydrate), sandy and humid-thermo ferrallitic soils. Increases in available P of 35% in calcareous soil and 33% in red clay loam have been reported - probably from Al-P complexes (Chen et al., 2003).

Lignin can be extracted, recycled and modified from black liquor (a waste product from paper pulp manufacture), bagasse by-products (fibrous sugar cane or sorghum residues) and crop straw. The lignin content in black liquor solids (which are now regularly applied to agricultural soils) can be up to 35% (Tian et al., 2015). Dotaniya et al. (2014) reported that organic residues such as press mud and bagasse by-products could release organic acids and enhance P availability in soil. About 600 million tonnes of crop straw are produced every year in China (Zeng et al., 2007) which is often re-incorporated into soil - increasing both the lignin and organic matter contents. As a result, the content of available P, total P and the activity of phosphatase have been observed to increase (Ding et al., 2012).

3.2.3. Crop residues, manure and biochar

Like chemical phosphate fertilizer, crop residues, manure and biochar (charcoal produced from crop residues) can also act as P sources. Land application is the predominant method for disposing of agricultural residues, thereby recycling their nutrients (Fig. 5) (Dai et al., 2016). The magnitude and direction of available P change after the application of these materials to soil depends on the properties of the P source and the receiving soil environment.

All of these materials contain highly soluble P_i (e.g. orthophosphate) which can act as a primary source of nutrients. They also contain labile P_o which can be mineralized to release soluble P in the short-term. This soluble orthophosphate can also be assimilated by microorganisms and subsequently released back into soil when these organisms die and are subject to decomposition. Results from a dual-labelling experiment suggest that, on average, 16% of the P contained in surface-applied residues could be classed as labile P (Noack et al., 2014).

A review by Damon et al. (2014) concluded that several key factors govern the mineralization and availability of crop residue-derived P including the quality of the crop residues, the activity of the soil microbial biomass, and the subsequent sorption reactions of mineralized P in soil. The addition of organic residues can also alter the chemical and physical properties of the soil and, hence, affect P availability indirectly. For example, increased organic matter usually provides microbes with a more favorable habitat, enhancing P cycling via mineralization (Lone et al., 2015). However, a general finding is that the transfer of P from break crop residues incorporated into the soil is relatively low (2–20%) and is quite variable (Espinosa et al., 2017). This could be due to variable P concentrations in the crop residues, which depend on the soil P status, the physiological maturity of the residues, and on the extent of the translocation of shoot-P to the developing grain in the break crops under considerations (Thibaud et al., 1988).

Manure P is a valuable resource, comparable to inorganic fertilizer P for crop production. Compared to crop residues, manure can contain even more labile P. A large fraction of the phosphorus in manure is considered to be plant-available immediately after application. Estimated values of phosphorus availability ranged between 12% and 100% (Bahl and Toor, 2002). The total P content in manure varies depending on the animal species, age, diet and how the manure has been stored. Jia

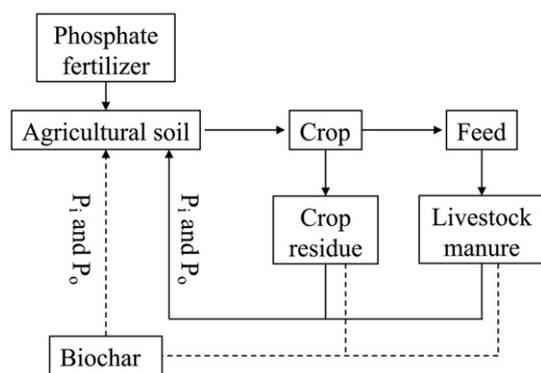


Fig. 5. Schematic illustration of the recycling of phosphorus between agricultural residues and soil, including the application of biochar. P_i is inorganic phosphorus; P_o is organic phosphorus.

et al. (2015) predicted that if manure P inputs from 2012 to 2030 were assumed to continue in soil, Olsen-P could increase to values close to or exceeding the environmentally critical value of 60 mg kg^{-1} , the tipping point above which P leaching has been shown to be significant (Heckrath et al., 1995). In addition to supplying labile P, manure can also help in mobilizing native P. This mobilization occurs by conversion of insoluble Ca, Al and Fe forms of P to soluble forms through the action of organic acids and chelates that are produced during manure decomposition of manures (El-Baruni and Olsen, 1979). Hountin et al. (2000) found that labile (resin-P₁ + NaHCO₃-P + NaOH-P) in animal manure-amended soil increased from 61% to 79% and the amounts of P generally increased in the following order: moderately labile NaOH-P₁ and NaOH-P₀ > labile P extracted by resin and NaHCO₃ > stable P. However, the potential environmental P hazard of swine manure should be considered, especially in agricultural systems in which soils receive high rates of manure application. Although P is considered immobile in agricultural soils, a decrease in the P adsorption capacity of soil following manure addition at rates greater than the nutritional requirements of plants for P may increase the potential for leaching of soluble P (Sutton et al., 1982).

The effects of biochar on P availability are variable: in some soils, biochar application has been observed to increase P availability, while in others, P availability was not affected or was observed to decrease, mainly due to increased P sorption (Chaturika et al., 2016). Biochar can induce changes in the soil ion exchange capacity. Fresh biochar in the acid pH range has a high anion exchange capacity, which can initially be in excess of the total cation exchange capacity of the biochar (DeLuca et al., 2009). It is possible that these positively charged exchange sites compete with Al and Fe oxides (e.g., gibbsite and goethite) for sorption of soluble P, similar to that observed for humic acids and fulvic acids (Hunt et al., 2007). P associated with biochar can be more labile than that associated with Al or Fe oxides. To date, however, there is noted lack of studies evaluating the effect of short-term anion exchange capacity on P cycling and availability. Biochar may also alter P availability through sorption of chelating organic molecules like phenolic acids, amino acids and complex proteins or carbohydrates (Joseph et al., 2010). Sorption of organic molecules on biochar surfaces can directly adsorb cations such as Al³⁺, Fe³⁺ and Ca²⁺, resulting in delayed P adsorption or precipitation in soil (Xu et al., 2014). A microcosm incubation study by Jin et al. (2016) suggested that soil P availability was enhanced after the addition of manure biochar (biochar from manure wastes) due to the fact that orthophosphate and pyrophosphate are the major P species in manure biochar and due to enhanced decomposition of some P_o (e.g. monoesters) by enhanced alkaline phosphomonoesterase activities. Xu et al. (2016) reported that biochar application can decrease P availability in saline sodic soil due to enhanced P sorption and precipitation.

3.3. Zeolites and other materials

Zeolites are minerals of hydrated sodium, potassium, calcium and barium aluminosilicates which are often used as cation exchangers

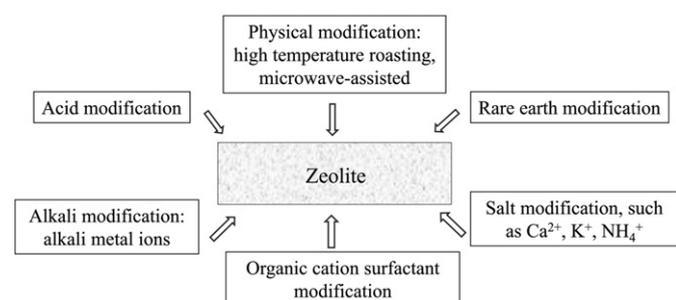


Fig. 6. Schematic summary of different approaches to modify zeolite.

(the net negative structural charge of zeolites results in the favorable ion-exchange selectivity for many cations) (Pabalan and Bertetti, 2001). They can increase soil available P concentrations and plant uptake of P. Wei et al. (2001) found that zeolite application could increase soil available P by up to 183%. Some modified zeolites can increase the available P even more (Yang et al., 2015). Fig. 6 gives a summary of several methods for the modification of natural zeolites (Dai et al., 2011) to enhance cation exchange capacity (due to the favorable ion-exchange selectivity of natural zeolites for certain cations, such as Cs⁺, Sr²⁺, and NH₄⁺) and to the pH change induced by zeolites. Acid modified zeolites can decrease the pH of soil and alkali modified zeolites can enhance cation exchange through alkali metal ions. As a result, the release of P can be enhanced (Fadaerayeni et al., 2015). Modification at high temperatures can remove organic matter in zeolite crevices and increase adsorptive capacity, thereby enhancing the capacity of zeolite to activate P (Quin et al., 1998). The combination of zeolite and NH₄⁺ can also increase the cation exchange effects of zeolite. The exchange-induced dissolution of rock phosphate proposed can be summarized for an ammonium saturated zeolite as Eq. (4):



where RP is rock phosphate (Allen et al., 1993). The zeolite/RP combination was intended to act as an exchange-fertilizer, with Ca²⁺ exchanging onto the zeolite. It is proposed that the plant uptake of NH₄⁺ or K⁺ frees exchange sites which can then be occupied by Ca²⁺, lowering the soil solution Ca²⁺ concentration and inducing further dissolution of rock phosphate (Pickering et al., 2002).

Fly ash, a coal combustion product (Parab et al., 2015) and wood ash can also be used to activate P in soil (Demeyer et al., 2001). One possible reason for the significant improvement of P availability by fly ash in acid soil was that ash addition had a liming effect which can enhance bioavailable P concentrations (Parab et al., 2015). However, fly ash may also be associated with high heavy metal loads. Compared to coal ash, reported concentrations of Mn, Zn and Cd in wood ash are higher while As, Se and Cr contents are lower (Someshwar, 1996). In addition to P, wood ash is a direct source of other major elements, notably Ca, Mg and especially K in soils. The dissolution of wood ash in soil, and the rate at which P becomes plant-available is complicated. The change in soil nutrient availability is a combination of three factors: (1) P addition from the ash; (2) shifts in pH-dependent soil chemical equilibria; (3) changes (mostly increases) in microbial activity (Demeyer et al., 2001). Furfural is an important organic compound produced from agro-industrial wastes and residues. When applied to soil, it can decrease pH and release Ca²⁺-bound phosphate (García-Domínguez et al., 2015).

Other P activators include water-dissolved organic polymeric compounds, bentonite, mugineic acid and ABT rooting powder (ABT has the ability to promote rooting and to increase the survival rate of plants under abiotic stress). Polyvinyl alcohol, polyacrylamide and polyethylene glycol have been shown to increase P sorption and pH in red ferralitic soils (rich in ferric oxide hydrate). Polyvinyl alcohol is a polymer containing hydroxyl groups, which has low permeability and high water adsorption capability (Chai et al., 2012). Polyacrylamide is a polymer of acrylamide which is soluble in polar solvents and nontoxic in nature. Polyethylene glycol has special solubility and chain-folding properties. Phosphate is released as a consequence of the protonation of hydroxyl and amide groups in these water-dissolved organic polymers and their interaction with Al³⁺ and Fe³⁺ phosphate (Hua et al., 2005). Bentonite can also increase P_i in soil (principally Ca₂-P followed by Ca₈-P, Al-P and Fe-P) (Liu and Sun, 2004). Mugineic acid has a high affinity for Fe and can activate Fe-P (Zhang et al., 1989). ABT rooting powder is an efficient plant growth promoter developed by the Chinese Academy of Forestry, which can promote root P absorption and plant growth. The active components of ABT rooting powder include indole-3-butyric acid and indole-3-acetic acid, which are regulators of plant

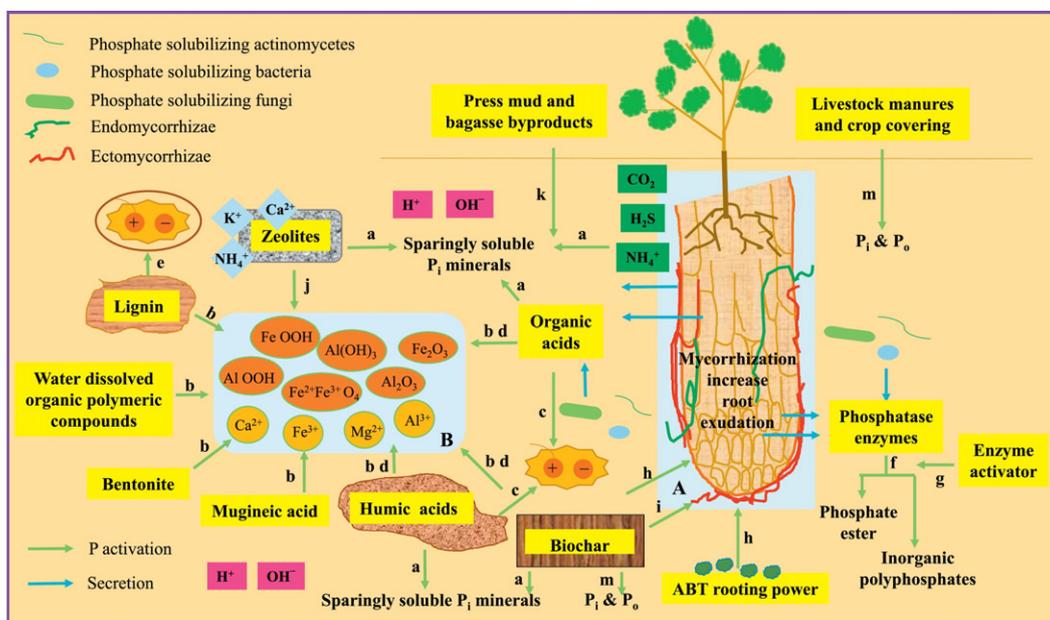


Fig. 7. Illustration of different mechanisms involved in the solubilization and mineralization of insoluble P by P activators in soils. (A) Enlarged drawing of root; (B) Metal ions and metal oxides which easily form P-O-M compounds in soil. (a) Effect of soil pH on sparingly soluble P₁ (inorganic phosphorus) minerals; (b) formation of complexes with (B) to release phosphate; (c) competition for sorption sites with phosphate in soil; (d) adsorption of metal and metal oxides to release phosphate; (e) sheltering sorption sites in soil; (f) hydrolysis of P₀ (organic phosphorus) and P_i; (g) strengthening of phosphatase enzyme activity; (h) promotion of root growth; (i) biochar increasing mycorrhizal-plant associations; (j) exchange-induced dissolution; (k) production of organic acids by microbial processes; (m) P₀ & P_i retention and release. ABT rooting powder: have the ability to promote rooting and to increase the survival rate of plants under abiotic stress.

growth (Zhang et al., 2010). Liu et al. (2002) found that the phosphate fertilizer utilization ratio of wheat increased by 12% when ABT rooting powder was used.

4. Discussion

4.1. Practical applications

A variety of different soil P activators have been reported to activate legacy P over the last few decades. These include PSMs, phosphatase enzymes, enzyme activators, low molecular weight organic acids, humic acids, lignin, crop residues, manure, biochar, zeolites, fly and wood

ash, water-dissolved organic polymers, bentonite, mugineic acid and ABT rooting powder.

Each P activator can act in one or more ways to promote the solubilization of insoluble P_i and/or the mineralization of P₀. The range of mechanisms is illustrated in Fig. 7. The most common activation pathways are: (1) Dissolution. P activators change the chemical structure of the sorbing components – principally via metal complexation and removal; (2) Competitive inhibition of P sorption. P activators compete with phosphate for sorption sites or compete with metal oxides for exchange sites in soil; (3) Organic ligands. Functional groups such as carboxyl and phenolic hydroxyl can complex metal ions and release P bound to these cations; (4) enzymolysis. P activators catalyze the hydrolysis of ester-phosphate bonds, leading to the release of phosphate;

Table 5

Summary of the advantages and disadvantages of the P activators described in this review. P_i: inorganic P, P₀: organic P.

P activators	Advantages	Disadvantages
Phosphate solubilizing microorganisms	Economically feasible; Activate both P ₀ and P _i ; High activation effect	Complex screening and domesticating process; Easily affected by environment; Time consuming; Potential invasions
Phosphatase enzyme and enzyme activators	Mineralize complex P ₀ compounds	High specificity; Easy to be inactive
Low molecular weight organic acid	Fast responding speed; High activation effect; Amend soil salinization	Cause soil acidification
Humic acid and lignin	Increase soil organic matter; Improve soil conditions	May sorb phosphate itself
Crop residue and manure	Biodegradable, abundant resources found in nature; Low processing costs; Release both P _i and P ₀ ; Secondary nutrient supply	Bring soil pests; Contain microbial populations; Easily lost in runoff
Biochar	Improve soil conditions; Release P _i and P ₀ ; Good for microorganisms	Preparation process is complex; Mixed reports on activation effect
Zeolites and others	Reuse and recycle waste resources	Seldom used in soil; Non-indigenous in soil; May bring heavy metal to soil

(5) P release. Bio-resource P activators contain both P_i and P_o which can be released into the soil.

Each type of P activator has its own specific advantages and disadvantages (Table 5), so activator selection should be tailored to the specific context in which the activator is to be used. Key factors to be considered include: (1) Specific optimum conditions, including soil physico-chemical properties. This is particularly the case for PSMs; (2) the nature of the legacy P pool targeted (P_i or P_o or both); (3) the cost and access to the P activators under consideration; (4) the influence of the P activator on crops, the prevailing microbial community and soil physical and chemical characteristics.

All types of bio-resource P activator, such as crop residues, manure and biochar, have both primary and secondary P supply functions. They can be usefully separated according to their form and principal mode of action: i.e. direct inorganic nutrient supply for direct uptake and the input of organic nutrients which are subsequently mineralized. They may also contain microbial populations (e.g. rhizobacteria) which can affect secondary nutrient (P) supply and other plant growth promotion functions. P-solubilization in the field tends to be much more difficult to demonstrate than solubilization of P in the laboratory. Crops respond differently to P activator amendments and are dependent on several factors such as soil temperature, moisture content, pH, salinity, organic matter content, microorganisms, the rhizosphere effect and soil fauna. The effects of these factors on the role of P activators need to be studied more extensively at the field scale before P activators can be used reliably.

4.2. Environmental considerations

Making full use of legacy P in soil is an environmentally desirable and economically feasible strategy for improving crop production, particularly in P-deficient soils. Agricultural P loss is a global concern due to the effects of P in receiving water bodies (eutrophication). By reducing the need for P fertilizer addition and enabling crops to efficiently access legacy P, the transfer of P from land to water can be reduced. There is now increasing evidence that P availability can be controlled by P activators. However, increasing P availability using P activators in soil can also increase the risk of P losses to surface and ground waters via dissolved and colloid-facilitated transport (Hens and Merckx, 2001).

Some P activators can contain potential toxicants, such as heavy metals (As, Cr, Zn, Cd). For example, ashes originating from co-firing of bark or wood with tyres can contain high levels of Zn (1%) (Someswar, 1996). Such sources should be avoided (or at least rates should be controlled) in order to avoid contamination of both soil and receiving water bodies after P activator addition.

Although generally regarded as environmentally-friendly, P activators such as PSMs may also have some negative impacts such as triggering plant diseases or problems for native organisms (i.e. they can potentially act as biological invasions in soil: Amsellem et al., 2017). That said, they may also act to curb invasions of other invasive species (i.e. they can act as a biological control) (Santini et al., 2013).

4.3. Future research directions

Despite the fact that P activators have been shown to increase available P, precise mechanisms remain uncertain in most cases and additional insight is required. For example, further elucidation of the relationships between organic P activators and P in competitive sorption processes is necessary. Similarly, the available literature regarding the effects of biochar on P availability is inconsistent and mechanistic understanding of biochar-P interactions remains poor. Moreover, the response of plants to soil P activators in the field is often difficult to predict. Future research is, therefore, required to identify underlying biochemical and physical processes, which alter the bioavailability of legacy soil P.

Application of single activators may be insufficient to activate the broad range of P forms typically present in soil and the use of several activators together may produce better results. For instance, some studies have reported that the addition of citric acid and phosphatase together can be beneficial, although the exact mechanism by which additional P is released in this case is uncertain. Further research is required to uncover the mechanisms underpinning the compound effects of different P activators used in concert. Specifically, long-term field experiments should be conducted to address the interactions of P activators with natural soil and their impacts on crop yield.

Even though, various amendments have been reported for managing legacy P in different soils, some of these can be costly and or practically difficult to implement. Although P-solubilizing microorganisms have yet to fulfill their promise as commercial bio-inoculants, scientists need to address certain issues, like how to improve the efficacy of bio-fertilizers, what the optimal delivery system should be, how to stabilize these microbes in soil systems, and how nutritional and root exudation aspects can be controlled in order to get maximum benefits from PSM application. Finally, research is also required to discover and enable efficient, feasible, cheap and environmentally-friendly solutions for improving access to legacy P stocks in soil.

5. Conclusion

P is a major macronutrient needed for plant growth and development. It has been historically oversupplied as phosphate fertilizers in many agricultural systems to increase crop yields. However, there are a number of adverse environmental impacts associated with the use of inorganic P fertilizers. These include increasing risk of P loss from soils with elevated P concentrations (so-called legacy P), which may lead to eutrophication in water bodies receiving phosphate in agricultural runoff (diffuse-source pollution), and the depletion of finite resources of high grade phosphate rocks with associated price increases in the context of ever-increasing global demands for food and bioenergy. A more sustainable approach to managing P availability in agriculture is, therefore, required.

Legacy P that has accumulated in soils represents a significant potential secondary P source that could substitute (at least in part) manufactured fertilizers, if ways can be found for unlocking it (P activation). A number of P activators have been proposed which have been reviewed here. However, soil P cycling is extremely complex and varies with soil morphogenesis, mineralogy, organic matter content, pH, water relations, etc. Taking full advantage of legacy P, therefore, remains a significant challenge. Complicating influences include tillage, residue management and fertilization practices, as well as the effects of interactions between soil microbes, soil structure and organic matter on operational soil P fractions.

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