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Phosphate solubilizing fungi enhance insoluble phosphate dissolution via organic acid production: mechanisms and applications

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1 Introduction

Phosphorus (P) is an essential element for plant growth, which functions in photosynthesis, root development, and nucleotide incorporation (Bisson et al., 2017). However, only 0.1–0.5% of the total soil P is available for plants to absorb (Sharma et al., 2013). Generally, most P in the soil is insoluble and adsorbed, significantly affecting plant accessibility and crop yield (Tian et al., 2020). The commonly insoluble phosphates (IPs) in soils usually include ferric phosphate ($FePO_4$, Fe-P), aluminum phosphate ($AlPO_4$, Al-P), and tricalcium phosphate ($Ca_3(PO_4)_2$, Ca-P) (Tian et al., 2024). These IPs are distributed across various soil types, which limits crop yields and phosphorus use efficiency (Tian et al., 2021a).

The input of chemical phosphate fertilizer can promote plant adsorb P and increase crop yield. However, over 60% of P fertilizers rapidly react with soil metal cations (e.g., Ca^{2+}, Fe^{3+}) and become immobilized as IPs (Jayashree et al., 2011; Mahdi et al., 2020). According to the statistics, the IPs stored in soils could alleviate the expected P shortages over the next 50 years (Zhu et al., 2018). Therefore, enhancing the development and utilization of this stored P in agricultural soils is crucial for sustainable P management in the future (Tian et al., 2021b, 2024).

Phosphate-solubilizing microorganisms (PSMs) can convert IPs into plant-absorbable and utilizable P forms in soil (Gadd et al., 2014; Owen et al., 2015; Jiang et al., 2021). Using PSMs in agricultural systems is an efficient and sustainable pathway to improve plant uptake of P from soil (Sharma et al., 2013; Tian et al., 2020; Munar et al., 2023; Wu et al., 2025). The common PSMs include phosphate-solubilizing fungi (PSF), phosphate-solubilizing bacteria (PSB), and phosphate-solubilizing actinomycete (PSA). Phosphate-solubilizing fungi have greater P-dissolving capacity than bacteria and actinomycetes. In the case of PSF *Aspergillus niger*, the amount of P dissolved from Ca-P (770.5 mg/L) is approximately two times higher than the PSB *Acinetobacter spp* (Li et al., 2019). Therefore, PSF is generally considered the primary candidate for IP dissolution (Figure 1).

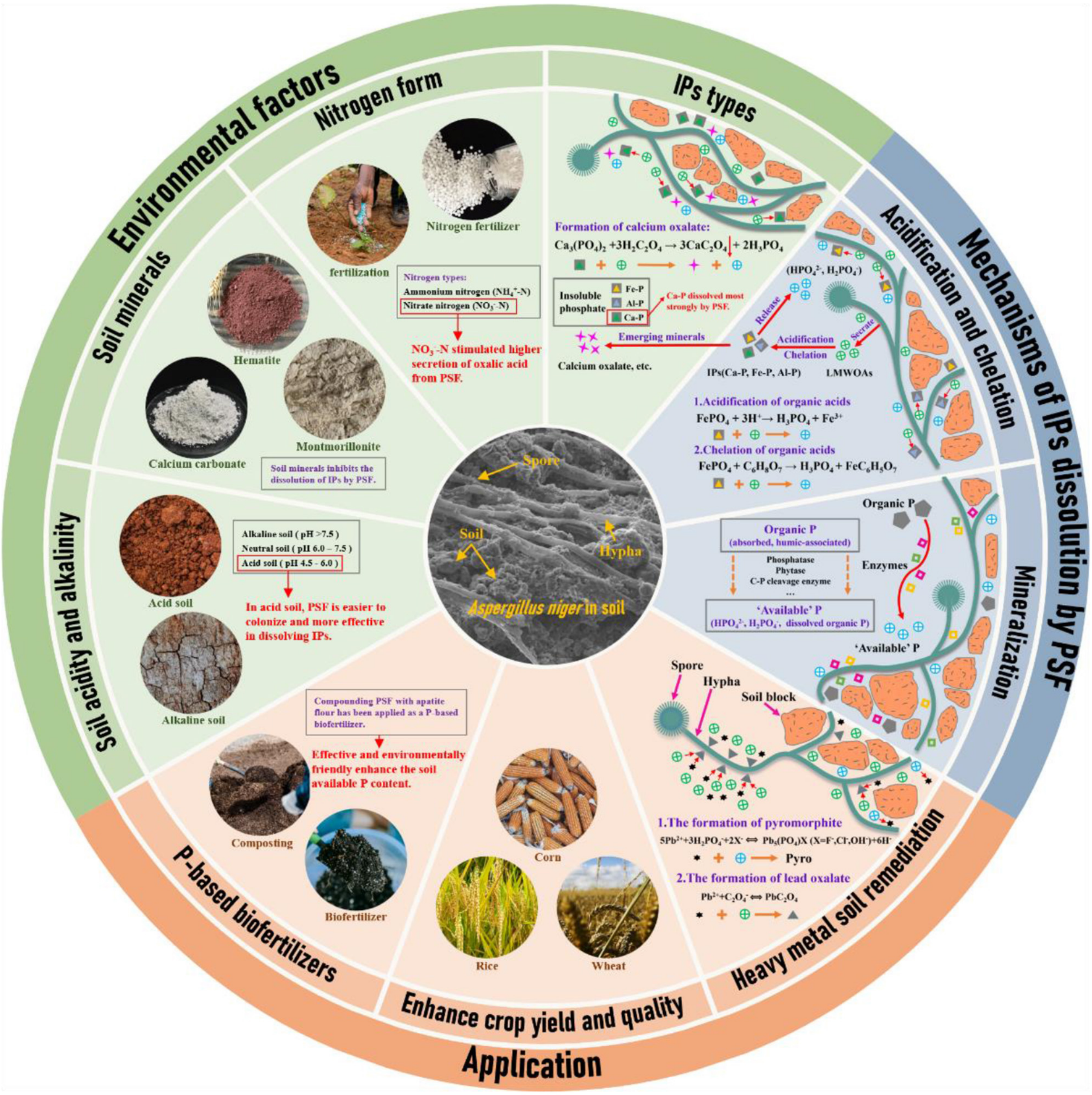

FIGURE 1
Mechanisms of phosphate-solubilizing fungi in insoluble phosphate dissolution and effects pathway in application.

PSF can secrete large amounts of organic acids, producing formic acid, oxalic acid, etc., reaching up to three times that of PSB (Li et al., 2016a). Meanwhile, PSF hyphae can directly penetrate insoluble phosphate minerals through mechanical pressure (Gadd, 2021). The highly developed hyphal network of PSF can extend several meters, significantly surpassing the range of PSB colonies (typically <1 mm; Martinez and Marschmann, 2025). In addition, PSF fungal hyphae can penetrate deep into soil aggregates, while PSB usually accumulates on pore surfaces (Tian et al., 2021b). More importantly, PSF shows significant advantages in IPs dissolution, maintaining over 90% of IPs-dissolving capacity even after 10 successive subcultures (Kucey, 1983). Meanwhile, PSF also demonstrates a higher tolerance to drought and extreme pH levels than PSB (Li et al., 2016a; Bi et al., 2022). However, PSB usually offers practical benefits in production, including faster reproduction (generation time: 30–60 min) and more excellent suitability for liquid inoculant formulation compared to PSF (Belen Lobo et al., 2019). The co-inoculation of PSB and PSF significantly enhances IPs dissolution and plant growth compared to using either microorganism alone in sterile soil (Nacoon et al., 2020). Therefore, the co-inoculation of PSF and PSB presents a more promising approach to enhance the application of PSF in IPs dissolution.

TABLE 1 Capacity of phosphate-solubilizing fungi in organic acid secretion and P release.

PSF strains	Primary organic acid types	Organic acid production	P release (mg/L)	References
Trichoderma harzianum	Glucose, citric, lactic and succinic acids	4,422.54 (mg/L)	9.31 (from RP)	Promwee et al., 2014
Trichoderma asperellum	Oxalic and citric acids	36 (mmol/L)	3.1 (from RP)	García-López et al., 2015
Aspergillus niger	Oxalic and citric acids	561.6 (mg/L)	861 (from TCP)	Tian et al., 2021b
Penicillium oxalicum	Oxalic, acetic, and lactic acids	0.143 (mmol/L)	189.1 (from TCP)	Yang et al., 2022
Penicillium sp. PSM11-5	Gluconic and citric acids	13,830 (mg/L)	300.1 (from TCP)	Chai et al., 2011
Gigaspora margarita	Citric acid	2.7 (mmol/L)	1.49 (from Fe-P)	Tawaraya et al., 2006
Penicillium chrysogenum	Oxalic acid	227.7 (mg/L)	693.6 (from TCP)	Wang et al., 2023a

IPs, insoluble phosphates; RP, rock phosphate; TCP, tricalcium phosphate.

PSF includes various genera such as *Penicillium*, *Aspergillus*, *Mucor*, *Trichoderma*, *Rhizopus*, *Phytophthora*, *Fusarium*, and *Saccharomyces* (Mercl et al., 2020; Zhang et al., 2020; Yang et al., 2022; Wang et al., 2023b). This diversity allows the selection of PSF strains tailored to specific environmental conditions and cropping systems (Figure 1). However, environmental factors such as soil pH, soil minerals, types of nutrients, organic fertilizer, and toxic pollutants (such as pesticides, heavy metals, and microplastics) would directly or indirectly affect the dissolution of IPs by PSF in soil (Tian et al., 2022a; Su et al., 2023; Wang et al., 2024a,b; Feng et al., 2025; Ni et al., 2025). In the case of typical PSF *Aspergillus niger*, the biomass and physiological activity were significantly higher in acidic soil than in alkaline soil (Su et al., 2023). Therefore, investigating the factors that affect the efficiency of IPs dissolution by PSF in soil is crucial for optimizing their application.

2 The secretion of dicarboxylic and tricarboxylic acids dominates the dissolution of IPs by PSF

Organic acid secretion is the primary pathway of PSF in the dissolution of IPs (Palmieri et al., 2019). On the one hand, PSF continuously releases low-molecule-weight organic acids (LMWOAs) to acidify the soil environment and significantly promote IPs dissolution (Kpomblekou-A and Tabatabai, 1994; Tian et al., 2020). On the other hand, the active functional groups of organic acids can also effectively chelate with metal cations (Ca^{2+}, Fe^{3+}, Al^{3+}, etc.), thereby promoting the release of P from Ca-P, Fe-P, and Al-P, etc. (Shen et al., 2002; Kishore et al., 2015). Moreover, the LMWOAs can also directly release orthophosphate from soil minerals and Fe/Al oxides via ligand exchange (Sharma et al., 2013; Li et al., 2021).

The LMWOAs secreted by PSF include monocarboxylic, dicarboxylic, and tricarboxylic acids (Scervino et al., 2010). The dicarboxylic and tricarboxylic acids have higher acidity constants and chelating ability for metal cations (Kpomblekou-A and Tabatabai, 1994; Patel et al., 2008). Thus, dicarboxylic acids (oxalic, malonic, fumaric, and tartaric) and tricarboxylic acids (cis-aconitic and citric) are more effective in P detoxification than monocarboxylic acids (glycolic, pyruvic, and salicylic acid) (Table 1). The tricarboxylic acid (TCA) cycle in mitochondria is the key pathway for organic acid secretion by PSF (Mäkelä et al., 2010). The activity of various enzymes in the TCA cycle determines the types and amounts of organic acids secreted by PSF. For example, Fe-P supply significantly increased the citrate synthase activity and promoted the secretion of citric acid by PSF (Tian et al., 2021a). Meanwhile, constructing *Aspergillus niger* strains with the oxaloacetate acetylhydrolase-encoding gene can increase oxalic acid production by up to 3.1 times (Xu et al., 2019). Therefore, modifying environmental factors and genetically engineering fungi to enhance organic acid production are crucial strategies for strengthening PSF efficiency in IPs dissolution.

3 Environmental factors affecting IPs dissolution by PSF in soil

3.1 Soil acidity and alkalinity

PSF dissolves IPs are generally more efficient in acidic soil than in alkaline soil. In acidic soil, the fungal abundance, microbial respiration, organic acid secretion, and phytase activity of PSF are higher than in alkaline soil (Adnan et al., 2022; Jin et al., 2022; Chandra et al., 2024). In the case of PSF, the abundance of *Aspergillus niger* in acidic red soil (pH 4.58) is approximately ten times greater than in alkaline red soil (pH 8.28) (Su et al., 2023). Generally, low soil pH values favor fungal growth, and high soil pH values promote bacterial growth (Su et al., 2023).

3.2 Soil minerals

The influence of soil minerals on the biological process of IPs dissolution by PSF is both beneficial and detrimental (Su et al., 2021). The soil mineral montmorillonite can enhance respiratory metabolism and oxalic acid secretion of PSF to improve the P-release capacity (Su et al., 2021). In contrast, other minerals (such as Calcium-bearing minerals) can also inhibit IPs dissolution by PSF via the adsorption of organic acids (do Nascimento et al., 2021; He et al., 2022). Specifically, carbonate can deplete the secreted oxalic acid to form stable calcium oxalate crystals, limiting IPs dissolution by PSF (Tian et al., 2021b). In general, soil minerals have a negative impact on the dissolution of IPs by PSF.

3.3 NO_3^--N and NH_4^+-N

Nitrogen can significantly affect the phosphate-solubilizing capacity of PSF. Typically, the supply of NO_3^--N is more efficient than NH_4^+-N in IPs dissolution by PSF. Nitrogen forms can significantly affect the secretion of organic acids by PSF. For example, PSF *Aspergillus niger* predominantly secrete citric and malic acids in the supply of NH_4^+-N, while it primarily secrete oxalic acid under NO_3^--N conditions (Gadd et al., 2014). NO_3^--N stimulates the secretion of oxalic acid by *Aspergillus niger* primarily through the upregulation of the oxaloacetate acetylhydrolase (OAH) gene (Kobayashi et al., 2014). Oxalic acid is the primary organic acid that functions in IPs dissolution by PSF due to the high acidity constant (Feng et al., 2022). Consequently, the form of nitrogen can modulate the activity of enzymes involved in the TCA cycle of PSF, thereby impacting their IPs dissolution capacity.

3.4 IPs types

The different phosphates can affect the types and amounts of organic acids secreted by PSF (Tian et al., 2021a). Compared with Fe-P and Al-P, PSF is more effective in promoting P release from Ca-P (Tian et al., 2021a). On the one hand, Ca-P promotes PSF to secrete more oxalic acid compared with Fe-P (Wang et al., 2023a). On the other hand, oxalic acid secreted by PSF can combine with Ca^{2+} to form relatively stable calcium oxalate crystals, which can promote the release of P from Ca-P (Tian et al., 2021a; Wang et al., 2022). Therefore, Ca-based phosphate fertilizer shows excellent potential in producing " phosphate-based biofertilizer ".

4 Application of PSF in soil P cycle, crop yield, and heavy metal remediation

PSF can significantly increase soil P effectiveness and plant P uptake (Ahmad et al., 2013; Fiuza et al., 2022). For instance, *Trichoderma harzianum* inoculation can increase wheat biomass and plant P content and improve crop yield (Akbar et al., 2023). The combination of native arbuscular mycorrhizal fungi (AMF) and PSF (*Aspergillus niger* and *Penicillium brevis*) can significantly enhance soil available P, stimulate phosphatase activity in the coffee rhizosphere and promote coffee growth (Rojas et al., 2019). More importantly, multiple field experiments demonstrated that the application of " phosphate-based biofertilizer " (PSF and apatite) can significantly improve soil P utilization and enhance crop quality and yield (da Silva et al., 2017; Arias et al., 2023; Wang et al., 2023b). Compared with chemical phosphate fertilizers, inoculating with PSF can increase approximately 30% P uptake efficiency and approximately 16% yield of eggplant (Yin et al., 2021). Meanwhile, the absorption efficiency of soybeans for phosphate rock powder also improved by 56.1% after *Trichoderma* inoculation (Bononi et al., 2020). Even in barren desert soils, adding silicon (Si) can enhance the phosphate solubilization of fungi by 50%, providing a promising solution to P deficiency in desert soils (Ameen et al., 2019).

The combination of PSF and apatite also shows excellent potential in the remediation of heavy metal-contaminated soil (Tian et al., 2018, 2022b). Oxalic acid secreted by PSF can also react with heavy metal cations (e.g., Pb^{2+}) to form insoluble oxalate minerals, e.g., lead oxalate (Li et al., 2016b; Tian et al., 2023). The combination of *Penicillium oxalicum* and tricalcium phosphate not only increases soil available P but also reduces the environmental exposure toxicity of soil Pb (Hao et al., 2022).

5 Potential pathways to enhance the insoluble phosphate solubilization and application of PSF

PSFs can secrete large amounts of organic acids to promote P release from IPs in soil. The critical enhancements that improve the dissolution of IPs by PSF are fungal bioactivity and organic acid secretion capacity. However, the application of PSF in agricultural production also faces several limitations, including inconsistent performance and poor environmental adaptability. Hence, improving the IPs dissolution by PSF remains a considerable challenge in the future. Firstly, screening and cultivating more efficient and adaptable PSF and using genetic engineering to improve existing strains is necessary. Secondly, modifying environmental factors like soil pH and organic matter content to create more favorable conditions for the PSF. Thirdly, developing multifunctional composite biofertilizer products of PSF. Lastly, conducting long-term field experiments to accumulate application data of PSF under different soil types and climatic conditions. Overall, improving the practical application effect of PSF in agricultural production requires further attention in the future.

Author contributions

YM: Formal analysis, Software, Writing – original draft, Writing – review & editing. SC: Data curation, Writing – original draft. SL: Data curation, Writing – original draft. LG: Data curation, Writing – original draft. CZ: Writing – original draft, Writing – review & editing. XY: Conceptualization, Writing – original draft, Writing – review & editing. DT: Conceptualization, Writing – original draft, Writing – review & editing.

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