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REVIEW ARTICLE

Insight into soil nitrogen and phosphorus availability and agricultural sustainability by plant growth-promoting rhizobacteria

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Abstract

Nitrogen and phosphorus are critical for the vegetation ecosystem and two of the most insufficient nutrients in the soil. In agriculture practice, many chemical fertilizers are being applied to soil to improve soil nutrients and yield. This farming procedure poses considerable environmental risks which affect agricultural sustainability. As robust soil microorganisms, plant growth-promoting rhizobacteria (PGPR) have emerged as an environmentally friendly way of maintaining and improving the soil's available nitrogen and phosphorus. As a special PGPR, rhizospheric diazotrophs can fix nitrogen in the rhizosphere and promote plant growth. However, the mechanisms and influences of rhizospheric nitrogen fixation (NF) are not well researched as symbiotic NF lacks summarizing. Phosphate-solubilizing bacteria (PSB) are important members of PGPR. They can dissolve both insoluble mineral and organic phosphate in soil and enhance the phosphorus uptake of plants. The application of PSB can significantly increase plant biomass and yield. Co-inoculating PSB with other PGPR shows better performance in plant growth promotion, and the mechanisms are more complicated. Here, we provide a comprehensive review of rhizospheric NF and phosphate solubilization by PGPR. Deeper genetic insights would provide a better understanding of the NF mechanisms of PGPR, and co-inoculation with rhizospheric diazotrophs and PSB strains would be a strategy in enhancing the sustainability of soil nutrients.

Keywords Co-inoculation · Nitrogen fixation · Plant growth-promoting bacteria · Rhizospheric diazotrophs · Soil nutrients

Introduction

Microorganisms are the key components of soil biodiversity. A unique symbiotic relationship exists between plant and soil microorganisms, including trophic interactions and spatial proximity (Berendsen et al., 2012). It is reported that grasses and crops translocate 33 and 21% of the carbon fixed by photosynthesis into the rhizosphere, respectively (Pausch and Kuzyakov 2018). For some plants, at their particular growth stage, 50% of the newly fixed carbon may be deposited into the rhizosphere (Lambers 1987). The deposited carbon is rhizodeposits consisting of several compounds, such as amino acids, peptides, proteins, enzymes, vitamins, and phytohormones (Shi et al. 2012; Ludovic et al. 2020). The rhizodeposits could be absorbed and utilized by soil microorganisms, subsequently increasing the population of bacteria and fungi and soil bioactivities in the rhizosphere (Grayston et al. 1997; Khatoon et al. 2020), which can enhance nutrient availability and pathogen resistance in the rhizosphere as positive feedback for plants (Jones and Darrah 1997). These bacteria, so-called plant growth-promoting rhizobacteria (PGPR) colonized the rhizosphere are capable of promoting plant growth and play important roles in the soil ecological environment (Lugtenberg and Kamilova 2009; Khatoon et al. 2020).

In conventional agriculture, harvest and cropping take away large amounts of nutrients from seeds and plant tissue from soil (Grand et al. 2014). To avoid yield reduction caused by the loss of soil nutrients, chemical fertilizers are widely used, which bring a large amount of available

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nutrition into the soil quickly. However, this may result in many soil problems. For instance, the extensive applications of these fertilizers destroyed the soil structure and broke the micro-ecosystem leading to the loss of soil native fertility (Singh 2018). Leaching nitrate and phosphorus into groundwater or running water into aquatic ecosystems results in eutrophication. For maintaining agricultural production, enhanced application of fertilizers has become an essential practice. Nevertheless, the cost of chemical fertilizer is increasing as the exhaustion of mineral sources, and substantial consumption of energy during production. Thus, manufacture and application of chemical fertilizer restrain the development of sustainable agriculture.

In soil, gaseous, organic, and insoluble nutrients must be fixed, mineralized, and released into the inorganic soil pool for plant accessibility (Chen et al. 2003). PGPR plays a vital role in the metabolism and circulation of soil nutrition, such as nitrogen and phosphorus (Ali et al. 2020). PGPR have the ability to improve the availability of nutrition and maintain nutrition equilibrium in soil (Vejan et al. 2016). In comparison to chemical fertilizer, the application of PGPR not only promotes plant growth and productivity but also does not elicit any environmental problems (Maksimov et al. 2011; Basu et al. 2021; Hamid et al. 2021). This review focuses on PGPR for promoting soil nutrient availabilities in terms of nitrogen and phosphorus, two of the most limited nutrients in the soil. The mechanisms and features of nutrient activation and plant growth promotion by PGPR are also discussed.

Nitrogen-fixing PGPR

Nitrogen and nitrogen fixation

Nitrogen is the most critical nutrient in the soil, giving crops a primary yield and growth response (Tomonori et al. 2002; Karceva et al. 2021). It is the most abundant natural system element, constituting approximately 78% of the atmosphere as a gaseous form (N_2). However, nitrogen is one of the most limiting nutrients for the optimal growth of plants (Kartseva et al. 2021) because plants utilize nitrogen in exclusive forms of ammonia or nitrate (more than 90%) (Barrett and Burke 2000). The transformation of atmospheric nitrogen to biologically available nitrogen is the main process for replenishing the soil nitrogen source lost during plant harvest or denitrification (Dixon and Kahn 2004). Under natural conditions, the triple-bonded N atoms comprising gaseous N_2 can be oxidized into nitric oxide (NO) or nitrogen dioxide (NO_2) with a large amount of energy provided by extreme natural phenomena—lightning subsequently falling to the ground with rain and becoming NO^{3-}. Each year, an estimated 3–10 tera-grams (Tg) of nitrogen is fixed by lightning worldwide (Fields 2004). Similar nitrogen fixation (NF) process also occurs with energy provided by volcanic activity (Martin et al. 2012).

To satisfy global agriculture's food security and development, nitrogen fertilizer has widely been applied around the globe, contributing approximately 20% of annual global NF. From the beginning, Haber–Bosch's process stimulated by lighting NF, chemical NF technology has made remarkable progress. However, the industrial processes are still carried out under high temperatures or pressure that necessitate a large amount of energy (Schroder 2014). Furthermore, excessive nitrogen fertilization upsets the balance of the nitrogen cycle in the ecosystem resulting in numerous environmental problems (Galloway et al. 2004). For instance, excess nitrogen in the soil that cannot be utilized is released into the atmosphere and increases nitrous oxide (N_2O) (Flechard et al. 2007; Wang et al. 2020b). It leaches out into the water system and creates water pollution (Kye-Han and Shibu 2005). Under natural conditions, the biological nitrogen fixation (BNF) contributes to the predominant biologically available N for terrestrial ecosystems (Vitousek et al. 2013). Reports have demonstrated that 50–70 Tg of nitrogen is fixed biologically in agricultural systems every year (Herridge et al. 2008) and 52–130 Tg for all terrestrial ecosystems (Davies-Barnard and Friedlingstein 2020). Biological nitrogen fixation plays a predominant role in global NF, representing a sustainable way to replace chemical fertilizer in modern agriculture.

Biological nitrogen fixation

Biological nitrogen fixation is ubiquitous in the terrestrial and aquatic ecosystem and plays an important role in the global nitrogen cycle. This process is carried out by bacteria and archaea, which display wide biodiversity, yet, BNF has not been found in eukaryotes. Many diazotrophs are isolated and characterized in agricultural and terrestrial natural ecosystems, existing as symbiotic, associative, and free-living NF. A plethora of research focusing on symbiotic NF has offered profound insight from ecological, physiological, and molecular biological perspectives, among which legume symbiosis is the most noticeable. The *Rhizobium* infects the root of legumes and elicits the special symbiotic formation of the root, or occasionally stem, called "nodule," in which the plants provide essential nutrients for the microorganisms (Downie 2005; Heerden, et al. 2008). The symbiosis is of major ecological importance, dedicated to a dominant proportion of BNF in the agricultural system, reaching 12–25 Tg of nitrogen for crop legume x *Rhizobium* symbioses (Herridge et al. 2008). The legume-rhizobia symbionts are omnipresent in the most leguminous plant, including grain legumes, forage legumes, and leguminous trees (Liu et al. 2011; diCenzo et al. 2020). Nevertheless, the nodule structure is rarely found on the non-legume plant. Only *Parasponia* is reported to form root nodules with rhizobium (van Velzen et al. 2018). There are also two other symbiosis systems, actinorhizal (*Frankia*) symbionts (Jin et al. 2021) and cyanobacterial symbionts (Cornejo-Castillo et al. 2016), which fix nitrogen in their way. In addition, rhizospheric diazotrophs and free-living bacteria contribute to the predominant nonsymbiotic NF (Solanki et al. 2019). It is hard to distinguish between free-living NF from associative NF as the ubiquitous influences of plants. In some research, free-living and associative NF are divided into one category (Smercina et al. 2019). It is well known that symbiotic NF contributes to dominant BNF, but some strong evidence indicates the nonsymbiotic NF overweigh symbiotic NF in some biomes (Roley 2021).

Nitrogen fixation by rhizospheric diazotrophs

Rhizospheric diazotrophs are a special kind of PGPR, which have the ability of NF. In contrast to a defined host spectrum or association preference in symbiosis, rhizospheric diazotrophs display more flexible associative NF and a greater population than symbiotic NF bacteria (Sneha et al. 2021). In most ecosystems, the soil is the primary habitation for microorganisms, and the population of microorganisms in the rhizosphere is much higher than that in bulk soil, which is not under the influence of plant roots (Venturi and Keel, 2016). The microbial NF activities are always closely associated with plant roots, especially the rhizosphere (Jones et al. 2003; Nguyen et al. 2020). This closely relies on the abundant nutrients derived from root exudates (Li et al. 2021b; Hu et al. 2021). *Azospirillum* species have drawn the maximum attention as rhizospheric diazotrophs and acted as reference strains (Pathak et al. 2002; Kumar et al. 2017). Large numbers of rhizospheric diazotrophs are isolated and characterized by different plants (Table 1).

There is no clear definition between rhizospheric diazotrophs and endophytic diazotrophs. Sugarcane is supposed to be a “pioneer” plant for endophytic NF (Baldani et al. 2002). In cultivating sugarcane, endophytic diazotrophs, like *Acetobacter*, *Gluconacetobacter*, play an important role in providing nitrogen resources for plant growth (Reis and Teixeira 2015; dos Santos et al. 2017). Besides, forage grasses (Chalk et al. 2016), rice (Chaudhary et al. 2012), maize (Sheoran et al. 2021), and some other plants (Padda et al. 2019) are characterized as associated plants for endophytic diazotrophs. Although the endophytic feature has

Table 1 Species of rhizospheric diazotrophs and associated plants

Rhizospheric diazotrophs	Associated plants	References
Paenibacillus triticisoli	Wheat	(Li et al. 2021a)
Rhizobium, *Pseudomonas*, and *Agrobacterium tumefaciens*	Native plant species of Kuwait (*Rhanterium* epapposum, Farsetia *aegyptia*, *Haloxylon salicornicum*, and *Vachellia pachyceras*)	(Khalil et al. 2019)
Beijerinckia, *Azotobacter*, and *Klebsiella*	Sugarcane (*Saccharum* spp.), sweet potato (*Ipomoea batatas* L.), and paddy rice (*Oryza sativa* L.)	(Yoneyama et al. 2017)
Gluconoacetobacter diazotrophicus, *P. stutzeri*, *Klebsiella* sp. *pneumonia*, *Sinorhizobium meliloti*, *Bacillus cereus*, *Enterobacter* sp., and *Lysinibacillus* sp.	Aromatic rice (*Oryza sativa*)	(Kumar et al. 2017)
Aenibacillus, *Pseudoxanthomonas*, *Burkholderia*, and *Staphylococcus*	*Lolium perenne*	(Castellano-Hinojosa et al. 2016)
Serratia sp. and *K. pneumoniae*	Semi-arid tropical grasses	(Sarathambal et al. 2015)
Klebsiella sp., *K. pneumoniae*, *B. pumilus*, and *Acinetobacter* sp.	Maize	(Kuan 2015)
Rhodobacter and *Rhodopseudomonas*	Maize (*Zea mays*)	(Li et al. 2014)
Cellvibrio gandavensis	*Plantago winteri* and *Hordeum secalinum* (meadow plants)	(Suarez et al 2013)
Rhizobium spp., *Burkholderia, and Bradyrhizobium*	Caesalpiniaceae family (*Eperua falcata* and *Dicorynia guianensis*)	(Villadas et al. 2007)
Azospirillum lipoferum, *Azospirillum brasilense*, *Azoarcus* sp., *Pseudomonas* sp., *Zoogloea* sp.	*Leptochloa fusca* (L.) Kunth (kallar grass)	(Malik et al. 1997)
Enterobacteriaceae, *Vibrionaceae*, *Azotobacteraceae*, *Spirillaceae*, *Pseudomonadaceae*, and *Rhizobiaceae*	*Spartina alterniflora* Loisel	(Bagwell et al. 1998)
Klebsiella pneumoniae	*Poa pratensis*	(Haahtela and Kari 1986)
Azospirillum species	*Cynodon dactylon*, rice	(Khammas et al. 1989; Nur et al. 1980)

been indicated by GFP-label (Elbeltagy et al. 2001; Anand and Chanway 2013), most of the endophytic diazotrophs can be isolated from rhizosphere soil (Puri et al. 2016; Rosenblueth et al. 2018; Solanki et al. 2019). By exposing plants to ^{15} N enriched N_2, the labeled nitrogen can be fixed into rhizosphere soil (Parrotta et al. 1994; Henneron et al. 2020), demonstrating that NF occurs in the rhizosphere. Some researches reveal that the rhizospheric, endophytic, and symbiotic diazotrophs could exist in the same soil system (Solanki et al. 2019; Xie et al. 2021a, b).

The NF rate of diazotrophs is evaluated by acetylene reduction assay (Naqqash et al. 2020; Soper et al. 2021), which is an effective way to evaluate the NF ability of diazotrophs in in vitro conditions, usually on a combined carbon medium (CCM). However, this technique always overestimates the NF in symbiotic and free-living niches (Saiz et al. 2019). Contrary to acetylene reduction assay, ^{15} N isotope dilution and ^{15} N natural abundance techniques provide a reliable NF evaluation by diazotrophs (Puri et al. 2020). The rhizospheric diazotrophs, including *Klebsiella* sp. Br1, *Klebsiella pneumoniae* Fr1, *Bacillus pumilus* S1r1, and *Acinetobacter* sp. S3r2 are inoculated maize, and the nitrogen uptake increases in 58.6% and 69.6% in a glasshouse experiment with two harvests which is detected by using ^{15} N labeling technique (Kuan 2015). Same technique is used to evaluate the nitrogen uptake of tomato inoculated with rhizospheric diazotrophs, *Bacillus amyloliquefaciens* IN937a and *B. pumilus* T4 (Adesemoye et al. 2010).

Mechanisms of nitrogen fixation by rhizospheric diazotrophs

The mechanism of NF is not well researched in rhizospheric diazotrophs; however, they are well researched from physiological and molecular biological perspectives in symbiosis diazotrophs. Based on the research on symbiosis diazotrophs and new findings on rhizospheric diazotrophs, we will try to take deep insights into the mechanisms of NF by rhizospheric diazotrophs. Biological NF is a complicated biological process that reduces inert N_2 into ammonia. The breakdown of stable N_2 triple bonds and reconstruction is an energy-consuming process catalyzed by the nitrogenase enzyme. Nitrogenases are complex metalloenzymes widely distributed in diazotrophs (Dixon and Kahn, 2004; Bellenger et al. 2020). Mo-nitrogenase is the first nitrogenase to be found and widely distributed in symbiosis diazotrophs (Seefeldt et al. 2009). Two components constitute the Mo-nitrogenase, MoFe protein and Fe protein. The larger heterotetrameric MoFe protein consists of $\alpha_2\beta_2$ units and contains the catalytic site (FeMo-cofactor) embedded in the α subunits that account for N_2 binding and reduction. The FeMo-cofactor electron needed in the reduction is donated by the other component, Fe protein, a dimer of identical subunits bridged by a single 4Fe–4S cluster (Figure S1).

The other nitrogenases, vanadium (V) and iron-only (Fe) nitrogenases, are regarded as alternative nitrogenases found in free-living soil bacteria and cyanobacteria, respectively (Bellenger et al. 2020). They have similar structures to Mo-nitrogenase. FeV- and Fe only-cofactor are the counterparts to FeMo-cofactor in V- and Fe-nitrogenases (Benediktsson and Bjornsson 2020; Garci et al. 2020). Phylogenetic- and structure-based studies suggest that the alternative nitrogenases might be derived from Mo-nitrogenase, and environmental factors, particularly metal availability, influence this kind of evolution (Mus et al. 2018). It is also found that the V-nitrogenase activity and NF rates in rhizospheric soil increase significantly in response to vanadium addition (Bellenger et al. 2014).

Besides the structural and physiological studies, molecular biological techniques have provided genetic perspectives in understanding nitrogenases. Synthesis processing and assembly of Mo-nitrogenase involve a set of *nif* genes (Masson-Boivin et al. 2009; Kalam et al. 2020). This gene cluster presents significant diversity among different diazotrophs species, which range from 8 to 15, and the core *nif* genes at least contain the *nifHDKENB*. For alternative nitrogenases, there have been found some counterpart genes, like *vnfD*, *K*, and *vnfH* for the V-nitrogenase and *anfDK* and *anfH* for the Fe-nitrogenase (Bellenger et al. 2020). However, In *Paenibacillus* sp. WLY78, a rhizospheric bacterium from bamboo, a minimal *nif* gene cluster consisting of nine nif genes (*nifBHDKENXV* and *hesA*), is identified (Wang et al. 2013). Among the nif gene cluster, Fe protein gene *nifH* has species-conserved sequences (Singh et al. 2020) that is used to act as a target gene to detect diazotrophs or indicate the NF activity in the rhizosphere (Yu et al. 2019; Chen et al. 2019). Genetic manipulation of transferring *nif* genes to heterologous hosts is achieved on *Escherichia coli* or *Saccharomyces cerevisiae*. The genes are provided by rhizospheric bacteria *Pseudomonas stutzeri* (Yang et al. 2018), *Klebsiella oxytoca*, and *Paenibacillus polymyxa* (Li and Chen 2020). It is also found that the heterologous *nif* island affects the gene expression of the host significantly and an NtrC-dependent regulatory system is established based on *E. coli* regulation system (Dixon and Kahn 2004; Martinez-Argudo et al. 2004).

In BNF, the Mo-nitrogenase shows extreme oxygen sensitivity, conferred to the surface-exposed 4Fe–4S in Fe protein (Einsle et al. 2002). In addition, the transcriptional regulator NifA encoded by *nifA* gene is also oxygen sensitive for the cysteine-rich domain (Rutten and Poole 2019). For nodule symbiosis, the special structure, the cortical diffusion barrier, effectively reduces the oxygen concentration in the central nitrogen-fixing zone (Drevon et al. 2015). Moreover, the respiration consumption and compartmentation of the enzyme spatially also secure the process of BNF. The high concentration of leghemoglobin and high oxygen-affinity oxidase made an entire route for oxygen transport and utilization in nodules (Maier 2004; Simranjit et al. 2019). In soil, lacking protection from host plants, how the nitrogenases of rhizospheric diazotrophs (or free-living diazotrophs) work under the threat of oxygen is still not clear. Gadkari et al. (1992) declare that an aerotolerant nitrogenase has been characterized in *Streptomyces thermoautotrophicus* UBT1. The structural components of this nitrogenase have no homology to the known nitrogenases (Ribbe et al. 1997). But a latter study on *Streptomyces thermoautotrophicus* UBT1 with ^{15}N labeling and genome sequencing techniques concludes that this strain is non-diazotrophic and oxygen-tolerant nitrogenase is non-existent (MacKellar et al. 2016). Research points out that the subunits of alternative nitrogenases encoded by *vnfHDK* and *anfHDK* even show greater sensitivity to oxygen. However, an oxygen-tolerant NifA, the transcriptional activator of nif genes, has been found in rhizospheric diazotroph *Azotobacter vinelandii* (Oliveira et al. 2009). Furthermore, the oxygen concentration is lower in soil than in the air and is influenced by many parameters (Cook and Knight 2003). High moisture would cut the oxygen concentration in the soil and is beneficial for rhizospheric NF (Reed et al. 2007). The mechanisms of NF by rhizospheric diazotrophs still need further research.

Influential factors on nitrogen fixation of PGPR

Nitrogen fixation by PGPR is a metabolic process occurring in the rhizosphere and influenced by abiotic and biotic factors. The application of fertilizers displays significant influences on NF. High rates of nitrogen fertilization always reduce the NF activity in the rhizosphere (Yu et al. 2019; Chen et al. 2021; Volkogon et al. 2021). When co-inoculating PGPR strains *Azospirillum brasilense* with *Pseudomonas fluoresceins*, the nitrogenase activities in the rhizosphere of rice are higher with lower nitrogen applications than that with higher nitrogen applications (Zhang et al. 2021a, b). However, after 4 years of nitrogen fertilization in non-legume trees (*Eucalyptus urophylla*) plantation, the NF rates are significantly increased in rhizosphere soil but decreased in bulk soil (Zheng et al. 2016a). The rhizospheric diazotrophs contribute to balancing the nitrogen resources in the rhizosphere, and their functions are influenced by the relationship between nitrogen supply and demand locally. It is believed that even if the nitrogen availability is relatively high in the soil, the increased demand for plants, such as that in the rapid plant development stage, would also provoke the high NF rates (Smercina et al. 2019). Besides, the other pathways in the nitrogen cycle, like denitrification, also balance nitrogen in the rhizosphere (Volkogon et al. 2021).

Unlike nitrogen, phosphorus provides stimulation to BNF in the rhizosphere (Smercina et al. 2019; Wang et al. 2020a). In the forest, the phosphorus concentration is closely related NF rates in rhizosphere soil, and higher phosphorus benefits BNF (Reed et al. 2008). Moreover, combined phosphorus and nitrogen addition can still significantly increase NF rates in the rhizosphere (Zheng et al. 2016b). The inhibitory effect of nitrogen fertilization on BNF can be alleviated by phosphorus applications (Wang et al. 2018). It is demonstrated that phosphorus increases the abundance and diversity of the diazotrophic community in the soil, subsequently underlying the benefit of BNF (Reed et al. 2013; Tang et al. 2019; Wang et al. 2020a). Except for chemical fertilizers, green manure (Volkogon et al. 2021), organic manure (Shi et al. 2021), and compost (Enebe and Babalola 2021) applications show positive effects on BNF in the rhizosphere. In addition, the NF rates change with the soil moisture variation. In the wet season, the NF rates by rhizospheric diazotrophs are relatively high of 2.71 kg/ha/yr and low at 0.26 kg/ha/yr in the dry season (Reed et al. 2007).

Biotic factors also have a notable influence on BNF in the rhizosphere. Baskaran and Prabavathy (2022) investigated the diazotrophs in the rhizosphere of different mangrove plants by amplifying *nifH* genes, and the diazotroph communities are significantly different. The maize genotype also has been identified to influence the number and diversity of diazotrophs in the rhizosphere (Rodríguez-Blanco et al. 2015). A consistent result is also found in wheat species (Jain and Rennie 2011). Moreover, physiological activity also has an effect on BNF in the rhizosphere. Plant photosynthesis enhances the carbon rhizodeposition and accelerates the BNF in the rhizosphere (Henneron et al. 2020). As feedback, the improved nitrogen availability in the rhizosphere increases the nitrogen uptake by the plant and promotes photosynthesis. This interesting relationship between BNF and photosynthesis creates a plant growth-rhizodeposition-BNF cycle, underlaid by the root's exudation regulation (Wasaki and Dissanayaka 2021). As a member of the soil ecosystem, the diazotroph's metabolic activities, especially NF, are influenced by the microbial community (Hsu and Buckley 2009; Yu et al. 2019), including the nitrogen-fixers community (Zehr et al. 2003), other PGPR(Ahmad et al. 2006), and even pathogens (Knight and Langston-Unkefer 1988; Romero et al. 2003).

Plant growth promotion by rhizospheric diazotrophs

As a characteristic PGPR, rhizospheric diazotrophs show impressive ability in plant growth promotion. In agriculture practice, rhizospheric diazotrophs are applied to many crops. In a recent study, the yields of rhizospheric diazotroph *Paenibacillus triticisoli* BJ-18 inoculated wheat are increased by 8.5% to 16.9% (Li et al. 2021a). Diazotrophs *Serratia* sp. (CB2) and *K. pneumoniae* (CR3) isolated from semi-arid tropical grasses treated plots increase the grain yields of rice by 31 and 28%, respectively (Sarathambal et al. 2015). *Achromobacter* sp promoted the yield of *Vigna radiata* T44 along with other PGPR and showed good compatibility with *Bradyrhizobium* inoculation (Ahmad et al. 2006). *Azospirillum* bacteria significantly increased the dry weight of *Zea mays* and *Setaria italic* leaves as well as the total nitrogen content of these leaves (Nur et al. 1980). In addition, rhizospheric diazotrophs also display the plant growth-promotion ability to trees. With carriers of compost, *Azospirillum* increases the growth of sour orange trees (*Citrus aurantium*) (Rivera-Cruz et al. 2010).

Inoculations of rhizospheric diazotrophs combined with other microorganisms always show better plant-growth effects. Co-inoculation of rhizospheric diazotroph *Azospirillum* with symbiotic *Rhizobia* improves plant growth, crop yields, and nitrogen absorption and provides positive support to the nodulation (Vicario et al. 2015). Dually inoculated wheat plants with free-living diazotrophs and feremycorrhizal (FM) fungus *Austroboletus occidentalis* display significantly greater shoot biomass and nutrient content than the control and single inoculums (Kariman et al. 2022). Fertilization combining rhizospheric diazotroph, phosphate-solubilizing bacterium, and organic substrates yielded good plant-growth results (Rivera-Cruz et al. 2010).

The primary mechanism of plant growth promotion by rhizospheric diazotrophs is NF and promotes nitrogen absorption of plant, demonstrated by ^{15} N techniques (Wood et al. 2001; Bellenger et al. 2020). Apart from NF, diazotrophs synthesize and secrete plant growth promoters, such as phytohormones indole-3-acetic acid (IAA), 1-aminocyclopropane-1-carboxylate (ACC) deaminase, and siderophore (Castellano-Hinojosa et al. 2016; Liu et al. 2019). Some diazotrophs can also promote plant growth by inhibiting plant ethylene synthesis (Hafeez et al. 2008). Improving other nutrient uptake, like phosphorus, through solubilization of inorganic phosphate is another common way for diazotrophs (Dobbelaere et al. 2003).

Diazotrophs usually present indirect resistance to pathogenic microorganisms (Castellano-Hinojosa et al. 2016; X. Liu et al. 2019), which includes the synthesis of antibiotic substances, nutrient competition, or induction of plant systemic resistance to pathogens (Dobbelaere et al. 2003). Besides, rhizospheric diazotrophs can adjust the composition and function of the soil microbiome, providing a better microbial environment for the plant (Li et al. 2021a; Kariman et al. 2022), and stable colonization is also a base for their plant growth promotion (Piceno and Lovell 2000). A better understanding of the mechanism of plant growth promotion by rhizospheric diazotrophs would benefit utilization in practice and the development of biofertilizers.

Phosphate-solubilizing PGPR

Phosphorus is one of the three essential nutrients for plants, and phosphorus deficiency in soil restricts plant development in agricultural practices. Phosphorus is rich in soil and mostly exists in a precipitate form, which plants cannot absorb and utilize (Hinsinger 2001; Elser 2012). The poor availability of soil phosphorus is due to phosphate ion (P-ion) reaction with calcium, aluminum, and iron ions, which are presents in micromolar or lesser quantities in soil (Porder and Hilley 2011). To improve the soil concentration of available phosphorus, soluble phosphate fertilizer has been applied to the soil in the past decade. Besides the common disadvantages of chemical fertilizer, rapid chelation with metal ions (Ca^{2+}, Fe^{3+}, Al^{3+}) as applied to the soil makes phosphate fertilizer inefficient.

On the way to finding green environmental substitution of phosphate fertilizer, a kind of PGPR called phosphate-solubilizing bacteria (PSB) became a hot research topic. PSB could release soluble P-ion from insoluble phosphate, including mineral phosphate and insoluble organic phosphate. Up to now, the reported PSB strains consisted of *lannaesis Aerococcus*, *Alteromonas*, *Arthrobacter*, *Asaia*, *Azotobacter*, *Bacillus*, *Burkholderia*, *Chryseobacterium*, *Curtobacterium*, *Delftia*, *Enterobacter*, *Erwinia*, *Gordonia*, *Klebsiella*, *Lysinibacillus*, *Pantoea*, *Phyllobacterium*, *Pseudomonas, Rhizobium*, *Serratia*, and *Xanthomonas* (Vazquez et al. 2000; Chung et al. 2005; Pandey et al. 2006; Gulati et al. 2008; Liu et al. 2014; Bahena et al. 2016; Magallon-Servínet al. 2020; Silva et al. 2021; Özdoğan et al. 2022). According to the differences in phosphorus substrate, PSB strains are divided into mineral (inorganic) PSB and organic phosphate-solubilizing bacteria (Kuhad et al. 2011; Berde et al. 2021).

Distribution of PSB

Phosphate-solubilizing bacteria are ubiquitously present in soil and show significant rhizosphere preference that exhibited a higher population in the rhizosphere than non-rhizosphere (Reyes et al. 2006). The population and the microbial activity of PSB can be promoted by root exudates of plants (Vazquez et al. 2000). Phosphate-solubilizing bacteria and plants display an apparent relationship of reciprocal symbiosis (Berde et al. 2021). The diversity of PSB from different plant species fluctuates in a wide range and the phosphate-solubilizing (PS) activity (Amy et al. 2022). PSB strains are also found as hyphal colonizers on arbuscular mycorrhizal fungi (AMF), and the mycorrhiza influences the bacterial communities in the rhizosphere via exudation (Wang et al. 2016; Sharma et al. 2020).

In addition to the influences of plants, the soil conditions also influence the distribution of PSB. The PSB population is positively correlated with soil pH, electrical conductivity, and nitrate (Alia et al. 2013), while the abundant organic matter and high ionic content appear harmful to the colonization of PSB in soil (Srinivasan et al. 2012). Moreover, soil phosphorus status is an important factor. PSB incidence and diversity in soil with a lower level of available phosphorus are significantly higher than that in soil with a high level of available phosphorus, no matter from rhizosphere or non-rhizosphere (Mander et al. 2012). Continuous application of phosphate fertilizer could maintain a relatively higher available phosphorus level in soil, but the abundance of PSB and their phosphate solubilization ability are severely reduced, which is caused by the release of selection pressure from P-ion starvation for phosphate solubilization by PSB (Liu et al. 2014). Some research studies have shown that the PSB strains could colonize in plant root tissues or cells, but how they present their PS activity inner plant remains to be elucidated (Li et al. 2013; Oteino et al. 2015).

Mechanisms of mineral phosphate solubilization

Phosphate solubilization by PSB is a complicated process (Fig. 1). For mineral PSB, low molecular organic acid secretion is regarded as the principal mechanism of phosphate solubilization (Goldstein 1994). The organic acids are released into surroundings via the glucometabolic pathway, accompanied by the drop of pH value (Illmer and Schinner 1995). Various organic acids secreted by different PSB strains have been detected in earlier reports (Table 2). Among various acids, gluconic acid is considered the predominant organic acid in phosphate solubilization (Zeng et al. 2016; Xie et al. 2021a, b), and its function has been demonstrated through genetic manipulation (quinoprotein glucose dehydrogenase gene, *gcd*, and synthetase gene of the coenzyme pyrroloquinoline quinone, *pqq*) (Krishnaraj and Goldstein 2001; Xie et al. 2021a, b). The gcd and pqq genes are recently used to detect PSB with sequencing technologies, like metagenomics (Liang et al. 2020; Silva et al. 2021). However, few studies show that the PSB strains could still dissolve the mineral phosphate without gluconic acid. The production of succinic acid is correlated with the PS activity of *Bacillus megaterium* (Zheng et al. 2018), and oxalic and citric acids are the main organic acid exuded by *Pseudomonas* sp. (Saleemi et al. 2017). The kinds of organic acids secreted by PSB strains are correlated with the species and influenced by the unsoluble phosphorus sources (Li et al. 2019). Moreover, the nature of organic acids significantly affects the PS activity of PSB (Patel et al. 2008), and the total amount of organic acids is non-correlated with the PS activity (Zeng et al. 2017).

Observation in different PSB strains shows that the PS activity is negatively correlated with a change in pH value caused by organic acids (Liu et al. 2015; Zheng et al. 2018). Hydrion released from the organic acids could replace the metal ions from tricalcium phosphate, thereby releasing the soluble P-ion (Goldstein, 1994). However, PSB strain *Pseudomonas* sp. do not secrete organic acids but release hydration accompanied by respiration or NH_4^+ assimilation (Illmer and Schinner 1995), but the organic acids could chelate metal ion, consequently releasing the soluble P-ion (Ghosh et al. 2016; Sarma et al. 2016).

Besides organic acid, PSB strains could dissolve mineral phosphate in other ways. For instance, the PS activity of

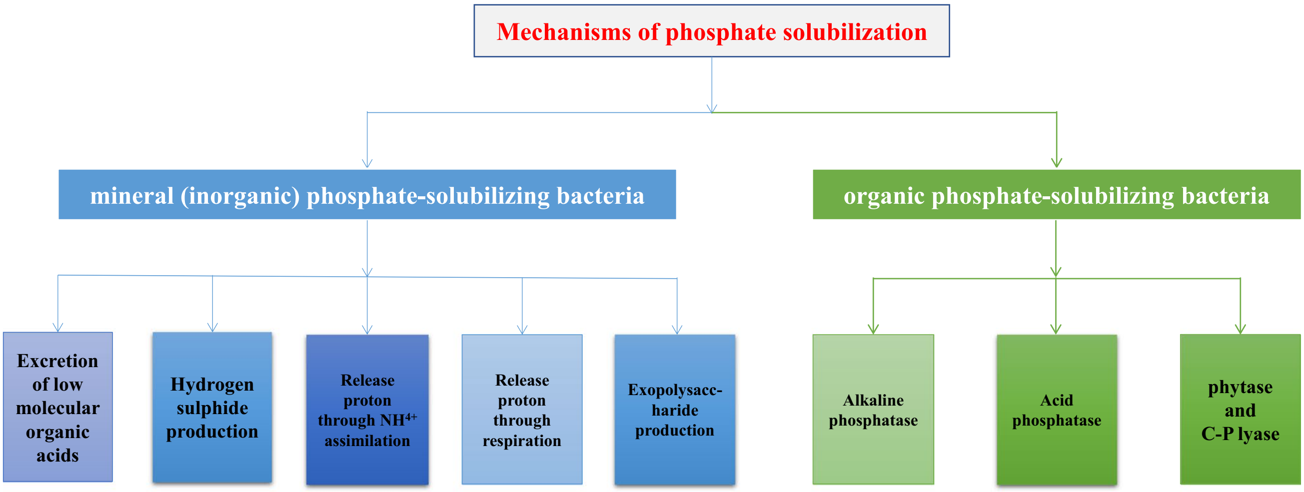

Fig. 1 Mechanisms of P-solubilization by phosphate solubilizing bacteria

Table 2 Organic acids involved in phosphate solubilization and produced by phosphate-solubilizing bacteria

Strains	Organic acids	References
Asaia lannaesis, *Pseudomonas* sp.	Gluconic and 2-ketogluconic acids	(Magallon-Servín et al. 2020)
Acinetobacter sp.	Formic and oxalic acids	(Li et al. 2019)
B. megaterium	Succinic, oxalic, and citric acids	(Zheng et al. 2018)
Pseudomonas frederiksbergensis	Gluconic, 2-ketogluconic, pyruvic, maleic, malic, lactic, malonic, acetic, methanoic, tartaric, and oxalic acids	(Zeng et al. 2017)
Brevibacillus borstelensis	Acetic, citric, formic, malic, and oxalic acids	(Yadav et al. 2015)
Enterobacter ludwigii, *Pantoea ananatis*, *Pseudomonas psychrotolerans*, *Gluconobacter frateurii*	Gluconic acid	(Han et al. 2012)
Bacillus sp.	Propionic, oxalic, succinic, and malic acids	(Panhwar et al. 2011)
Burkholderia cepacia	Gluconic acid	(Song et al. 2008)
Pseudomonas corrugata	Gluconic and 2-ketoglutaramic acids	(Trivedi and Sa 2008)
Citrobacter sp.	Gluconic and acetic acids	(Patel et al. 2008)
Enterobacter intermedium	2-ketoglutaramic acid	(Hwangbo et al. 2003)
Pseudomonas cepacia	Gluconic and 2-ketoglutaramic acids	(Bar-Yosef et al. 1999)
B. polymyxa, *B. licheniformis*, *B.* spp.	Oxalic and citric acids	(Gupta et al. 1994)

Nitrobacter and *Thiobacillus* strains accounts for hydrogen sulphide production (Shrivastava et al. 2018). *Dyella ginsengisoli* and *Microbacterium phyllosphaerae* solubilize rock phosphate through oxidation of thiosulfate to sulfuric acid (Anandham et al. 2008). Reports show that the proton involved in phosphate solubilization dissociates from acid H_2CO_3, formed from CO_2 generated from biological respiration (Hasegawa et al. 2016). Exopolysaccharides (EPS) produced by PSB greatly contribute to phosphate solubilization by holding free phosphorus and pushing homeostasis of solubilization towards phosphate dissolved (Yi et al. 2007). In conclusion, various mechanisms are involved in phosphate solubilization. It is worth noting that the PS activity of PSB is induced by low levels of P-ion and depressed by high levels of P-ion. Insufficient P-ion leads to glucose shift towards the direct oxidative pathway of glucose catabolism (Buch et al. 2008). The P-ion regulates the transcription of the *gcd* gene and triggers the secretion of gluconic acid and the gluconic acid-mediated PS ability (Zeng et al. 2016). These results suggest a genetic manipulation strategy in reducing the P-ion sensitivity of PSB by modifying the glucose oxidative pathway, which would improve the PS activity of PSB.

Mechanisms of organic phosphate solubilization

Phosphate-solubilizing bacteria solubilize phosphorus from mineral phosphate and release phosphorus from organic phosphate compounds (Ponmurugan and Gopi 2006; Jiang et al. 2021). It is well known that the organic phosphate compounds need to be degenerated by a phosphatase, phytase, or carbon-phosphorus lyase before being absorbed by the plant (Zaidi et al. 2009; Quinn et al. 2020). Phosphate-solubilizing bacteria could dissolve the organic phosphate compounds making phosphorus available for plant growth by excreting microbial phosphatases (Li et al. 2019). Ten PSB strains are isolated from soil, and their PS activity is found to be positively correlated with their activity of extracellular phosphatases (Ponmurugan and Gopi 2006). The role of phosphatases in organic phosphate solubilization has been demonstrated by molecular biological manipulation. Expression of acid phosphatase gene *phoC* from *Morganella morganii* in *E. coli* through plasmid vector can achieve acid phosphatase activity (Fraga-Vidal et al. 2007). A P-ion starvation-induced phoA gene encodes alkaline phosphatase, and expression of the gene is mediated by a phoBR operon (Agrawal and Wanner 1990). A *phn* gene from *Salmonella typhimurium* accounted for both phosphonate transport and catalysis of C–P bond cleavage (Jiang et al. 1995).

Besides phosphatases, organic PSB *Klebsiella variicola* displays phytase activity (Kusale et al. 2021a). Rhizospheric bacteria *Rahnella aquatilis* and *Pseudomonas fluorescens* dissolve phytate and improve the available phosphate by excreting phytase, eventually promoting plant growth (Li et al. 2013). Studies show a synergistic effect between organic PSB strain and AMF that *Pseudomonas alcaligenes* and *Rhizophagus irregularis* achieve mineralization of phytate and phosphorus transferred to plant issues synergistically (Artursson et al. 2006; Zhang et al. 2014). Phytase gene *phyL* has been cloned from *Bacillus subtilis* and *Bacillus licheniformis*, and over-expressed in a *B. subtilis* recombinant constructed by a phage vector (Tye et al. 2002).

Plant growth promotion by PSB

Phosphate-solubilizing bacteria are important PGPR members, and their plant growth-promoting ability to crops is tested in both pot and field conditions. Inoculation of PSB strains *Pantoea cypripedii* (PSB-3) and *Pseudomonas plecoglossicida* significantly increases shoot height, shoot and root dry biomass, and grain yield in maize and wheat crops (Kaur and Reddy 2015). Rice (*Oryza sativa* L.) inoculated PSB strains *B. licheniformis*, *Pantoea dispersa*, and *Staphylococcus* sp. are promoted in shoot length, dry weight, and yield (Rawat et al. 2021). The plant growth-promotion effects of PSB have also been demonstrated on *Arabidopsis thaliana* (Xie et al. 2021a, b), chickpea (Alemneh et al. 2021), maize (Gong et al. 2022), peanuts (Wang et al. 2021), tomato (Sharma et al. 2020), and sorghum (Benbrik et al. 2020). Similarly, PSB inoculations with *R. aquatilis* increase the grain yield, biological yield, and a total number of rice stems in field trials (Bakhshandeh et al. 2015). In addition, to improve crops' growth and yield, PSB strains also show their plant growth-promoting ability to non-crop plants. The growth of elm (*Ulmus chenmoui*) increases as inoculated with four indigenous PSB (Song et al. 2021). PSB strain *R. aquatilis* and *P. fluorescens* promote poplar and Masson pine (Li et al. 2013). PSB strains also exhibit plant growth-promoting ability on an apple tree (Mehta et al. 2013), Lycopodiaceae plant (Ghosh et al. 2016), and tea tree (Gong et al. 2022).

Some researches reveal that the over-dose application of chemical fertilizers significantly reduces the plant growth promotion by PSB (Bakhshandeh et al. 2015; Rawat et al. 2021). On the other hand, the application of PSB as a biofertilizer can reduce the use of chemical fertilizers and provide an economic strategy for agricultural production (Bargaz et al. 2021). On the contrary to chemical fertilizers, application accompanied with unsoluble phosphorus resources can support the performance of PSB as a biofertilizer. Application of PSB *Pseudomonas* combined with tricalcium phosphate can significantly improve the biomass parameters and grain yield of rainfed wheat compared to single inoculations (Shirmohammadi et al. 2020). Similar results are obtained when the application of PSB is combined with rock phosphate (Costa et al. 2015) or lecithin (Panda et al. 2021). In addition, co-inoculation of PSB with biochar (Jabborova et al. 2020) or compost (Wickramatilake et al. 2011) shows a better promotion of plant growth, which would be caused by the improvement of bacterial survival and population in the rhizosphere.

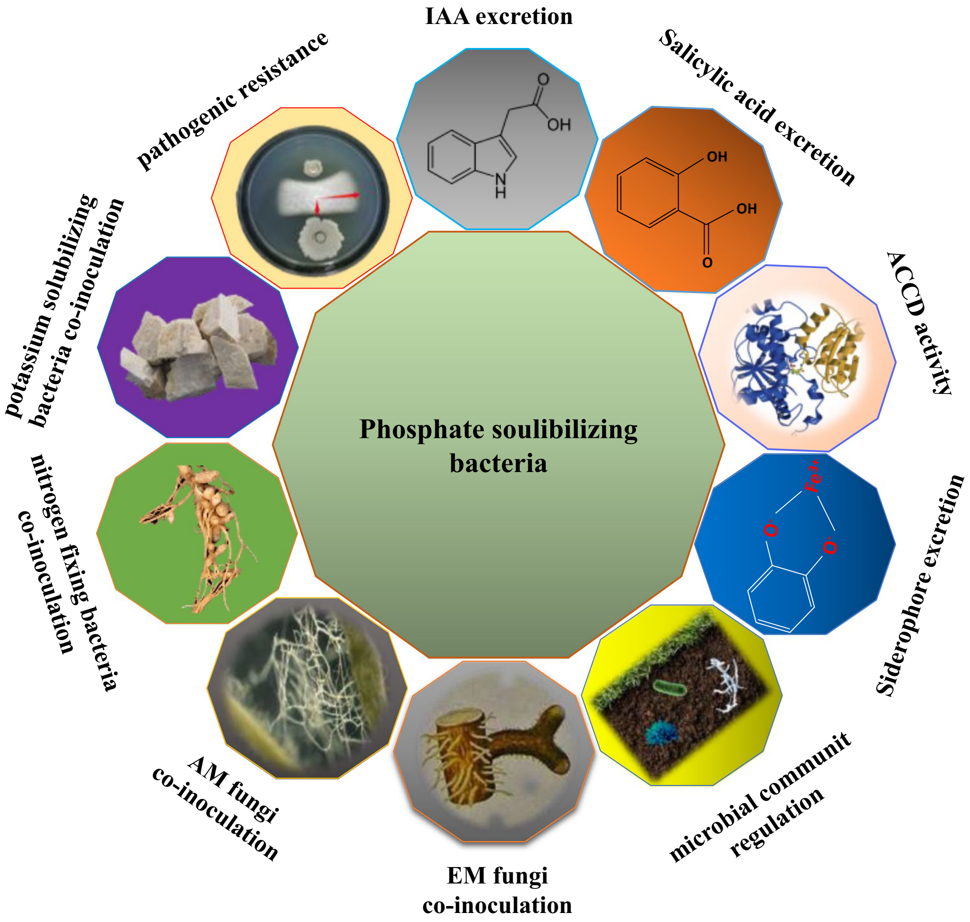

Fig. 2 Mechanism of plant growth promotion by phosphate solubilizing bacteria

Facilitating soil phosphorus availability and promoting phosphorus uptake are regarded as the primary mechanisms of plant growth promotion by PSB (Shirmohammadi et al. 2020) (Fig. 2). Inoculating PSB strains into rice increased 110.37% of the plant phosphorus uptake (Rawat et al. 2021). Improvement of plant phosphorus uptake by PSB is also in other research (Panda et al. 2021; Kaur and Reddy 2015).

In addition, PSB can excrete other nutrients to benefit plant growth. PSB strains *Pandoraea* sp. and *Leifsonia shinshuensis* isolated from winter pea and faba bean rhizosphere can produce phytohormones IAA (Kaur and Reddy 2015). Phosphate-solubilizing *Acinetobacter* sp. secretes IAA and ammonia and increases plant chlorophyll content (Xie et al. 2021a, b). *Burkholderia* sp. shows ACC deaminase production ability (Alemneh et al. 2021). Phosphate-solubilizing bacteria *Pseudomonas* sp., *Sphingobacterium suaedae*, *Bacillus pimilus*, and *Bacillus cereus* produce indole acetic acid, siderophores, hydrogen cyanide (Benbrik et al. 2020). Investigation of PSB strains from the rhizosphere of apple trees shows that the IAA, siderophores, and hydrocyanic acid production is increased by 24.2%, 25.7%, and 19.4%, respectively (Mehta et al. 2013). It is also reported that PSB strains provide various amino acids, amino acid derivatives, and other plant growth-regulating molecules (Shen et al. 2021).

Besides improving nutrition supplements, PSB strains play roles in the rhizosphere microbial community. Inoculation of PSB strain influences the microbial community of indigenous soil bacteria and changes the diversity of soil microorganism, which help in selecting potentially beneficial microorganisms for the plants (Liu et al. 2020; Song et al. 2021). Part of PSB strains possesses soil pathogenic resistance ability, including bacteriostasis ability (Zhang et al. 2021a, b) and antifungal activity (Ghosh et al. 2016; Muhammad et al. 2017). An antifungal volatile dimethyl disulfide is identified from *Serratia marcescens*, and it can inhibit the germination of *Aspergillus flavus* (Gong et al. 2022).

Phosphate-solubilizing bacteria also show other beneficial characteristics for plant growth. Studies have reported that inoculation with PSB strains improved plant performance under drought stress (Shirmohammadi et al. 2020) and salt stress (Kusale et al. 2021b). The mechanisms of increasing the plant tolerance to abiotic stresses by PGPR are complicated, mainly accounting for improving the root architecture and plant health status (Khan et al. 2021). It is reported that a higher population of PSB increases the available phosphorus in the soil and thereby improves the plant's capability to cope with the impacts of drought-flood abrupt alternation, an extreme climate event (Bi et al. 2020). A study displays that PSB significantly upregulates the plant translocation factors of cuprum, improving phytoremediation efficiency in *Wedelia trilobata* (Lin et al. 2018). PSB-assisted phytoremediation presents a bright prospect in dealing with soil heavy metal pollution (Ahemad 2015). Recent research shows that PSB is important in enhancing phosphorus cycling in soil following soil restoration (Liang et al. 2020). PSB strains also display the ability to reuse phosphate sludge as supplementary in the application (Benbrik et al. 2020). This research reveals the potential of PSB in environmental protection.

Co-inoculation of PSB with other PGPR

Co-inoculation of PSB strains with other plant-friendly microorganisms usually achieves good efficiency. Compared to all other treatments, co-inoculation treatment of PGPR and PSB performs better in promoting crop growth and controlling disease (Saleemi et al. 2017). Synergistic cooperation between AMF and PSB strains presents a more beneficial effect on phosphorus uptake, plant growth, and production (Sharma et al. 2020; Cozzolino et al. 2021). In AMF-PSB synergistic activities, PSB positively affects AMF spore density and colonization rate to the host plant (Nacoon et al. 2021). Co-inoculation with ectomycorrhizal (EM) fungus, *Pisolithus* sp. on *Pinus halepensis* (Allepo pine) seedlings distinctly increases the counts of PSB *P. fluorescens* in the rhizosphere and subsequently improves the plant growth together with the EM fungus (Ouahmane et al. 2009). Co-inoculation with nitrogen-fixing *Azospirillum* sp. and *Azotobacter* sp, PS *Phosphobacteria* sp. significantly increases the plant growth and grain yield of wheat compared to single inoculation or control (Vafa et al. 2021). Similar formula application of nitrogen-fixing bacteria and PSB increases plant growth and yield of rice (Ikhwani et al. 2022). Co-inoculation with diazotrophic bacterium and PSB results in a synergistic improvement in both NF and phosphate solubilization (Li et al. 2020). Phosphate-solubilizing strain *B. megaterium* is inoculated into pepper and cucumber rhizosphere, combining with potassium-solubilizing bacteria *Bacillus mucilaginosus* resulting in consistently higher P and K availability in soil. The greater N, P, and K uptakes are observed in shoot and root than in single inoculation and control (Han et al. 2006). Co-inoculation of PGPR strains with multiple plant growth-promoting traits would significantly promote the ecosystem function in the rhizosphere (Singh et al. 2015), which would bring more benefits to the rhizosphere.

Conclusion and future perspectives

Soil sustainability refers to the sustainable development of agriculture, and the development and utilization of biofertilizer are irresistible in the future. As two of the most important nutrients, nitrogen and phosphorus, the revolution in their application can make prodigious changes in agriculture and great progress in environmental protection. PGPR has several advances in plant growth promotion compared with other microorganisms, such as wide distribution in soil, easy isolation and cultivation, a wide range of host spectrum, and less association preference. A better understanding of the rhizospheric diazotrophs and PSB would help their biofertilizers' development and utilization. The rhizospheric microbial diversity delivered by bacterial co-inoculation with the complementary relationship will improve plant growth by affecting ecosystem functioning. Rhizospheric diazotrophs and PSB can promote plant growth individually or co-inoculation with other PGPR. In soil, phosphorus benefits BNF, and nitrogen is also suitable for phosphate solubilization by PSB. Plants are inoculated with a combination of rhizospheric diazotrophs and PSB, forming a complementarity degree, which would provide better microbial service to the plant. Therefore, the compatibility of certain rhizospheric diazotrophs and PSB strains and co-inoculation applications still needs specific studies and details of the soil condition.

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