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OPINION PAPER

The promotion of legume nodulation in plant-soil-microbe systems under phosphorus-limited conditions

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Abstract
Background Legume plants can establish symbiotic interactions with rhizobia to form nodules, in which atmosphere dinitrogen (N) is reduced to ammonium (NH) as a nitrogen (N) source for legume plants. This process is called biological nitrogen fixation (BNF). It is widely believed that BNF in legumes is phosphorus (P)-demanding and might be limited by P availability.
Scope Here, we first discuss the overlooked role of plant P-acquisition/−use strategies in maintaining legume nodulation and BNF, then summarize the identified genes or regulatory mechanisms supporting this. Secondly, we synthesize emerging evidences showing how microbial strategies and soil management promote legume nodulation and BNF. Finally, we propose studying legume nodulation and BNF in a plant-soil-microbe system under low-P conditions.
Conclusions Such a system perspective of plant, soil, and microbial strategies will provide valuable insights into mechanisms underlying nodulation under nutrient-limited soil conditions and how to explore belowground interactions for sustainable development in terrestrial ecosystems.

Keywords Biological nitrogen fixation · Microbial strategies · Nodulation · Phosphorus-acquisition/−use strategies · Soil management

Introduction

Nitrogen (N) is one of the macronutrients required for plant growth in natural and agricultural ecosystems. Farmers add large amounts of N fertilizer to agricultural soil, which has substantially boosted crop production and ensured food security globally. However, most of these N inputs are not taken up by crops, but leach into lakes, causing eutrophication and biodiversity loss globally (Zhang et al. 2015). In addition, the industrial production of N fertilizer in the Haber-Bosch process, which synthesizes ammonium (NH_3) from hydrogen and atmospheric dinitrogen (N_2) with the help of an iron catalyst at very high temperatures and pressures (400–500 °C, 15–20 MPa), consumes large amounts of fossil fuel and threatens environmental quality via releasing a great amount of greenhouse gases (Soloveichik 2019). In contrast, biological nitrogen fixation (BNF), which reduces N_2 to NH_3 by microorganisms, for example, in symbiosis with legume plants, is environmentally friendly

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and provides an alternative N source for green agricultural development. Meanwhile, N-fixing legumes also play essential roles in maintaining natural ecosystem services, such as enriching soil N fertility and improving soil organic matter quality (Binkley 2005; Voigtlaender et al. 2012). Therefore, it is worthwhile to study factors affecting BNF and apply them in natural and agricultural ecosystems.

Following N, phosphorus (P) is the second essential macronutrient for plant growth, but it is poorly available in natural and agricultural ecosystems (Johnston et al. 2014; Vitousek et al. 2010). It is easily absorbed by (hydr)oxides of aluminum (Al) and iron (Fe) in acid soils or precipitated as calcium (Ca)-P in calcareous soils (Hinsinger 2001). In addition, the non-renewable source of P for fertilizers, rock phosphate, is reported to disappear in the following few decades (Gilbert 2009). Therefore, P is restricting or will restrict the physiology and growth of plants in most soils. The process of BNF entails a high P cost, and low P availability might limit nodulation and productivity of the legumes (Raven 2012). However, legumes are abundant in many ecosystems with strongly weathered, P-impoverished, or low available P soils, such as the Core Cape Subregion of South Africa (Lemaire et al. 2015; Manning and Goldblatt 2012), the Brazilian Caatinga and Cerrado biomes (dos Reis Jr et al. 2010; Sprent et al. 1996), and the Southwest Australian Floristic Region (Hopper and Gioia 2004; Zemunik et al. 2015). These suggest that some native legumes might have evolved strategies to maintain nodulation and BNF under P-limiting conditions, probably because they could increase P-use efficiency by efficient plant P-acquisition/−use strategies or microbial strategies under P-limiting conditions.

Different P-acquisition or -use strategies and biological nitrogen fixation

For most crop legumes, low-P conditions may curtail BNF directly by impairing nodule formation and activity; or indirectly, by restricting the growth and photosynthesis of host plants (Sulieman and Tran 2015). Low P availability may limit nitrogenase activity by restricting ATP production in nodules and ribosomal RNA turnover required to replace damaged nitrogenase enzymes, or by impairing signal transduction, membrane biosynthesis, or activation of enzymes involved in nodule development and function (Graham and Vance 2000; Raven 2012). Low P availability may also restrict photosynthesis and plant growth, or negatively affect carbon flow to nodules and down-regulate BNF (Almeida et al. 2000; Schulze 2004). However, this negative effect of low P availability would not apply to BNF in legumes with efficient P-acquisition strategies or those adapted to soils with low P availability (Fig. 1a). For example, exuded phosphatases enhance the capacity of legumes to acquire soil P and contribute to their abundance in tropical forests and other low-P ecosystems (Houlton et al. 2008; Nasto et al. 2014; Olde Venterink 2011; Png et al. 2017). Arbuscular mycorrhizal fungi (AMF) also improve P acquisition, and then stimulate BNF and photosynthesis under low-P conditions (Bournaud et al. 2018; Bulgarelli et al. 2017; Nasto et al. 2014; Püschel et al. 2017). Carboxylates also enhance the capacity of white lupin (*Lupinus albus*) and chickpea (*Cicer arietinum*) to acquire soil P and maintain a stable P concentration in nodules and BNF under low-P conditions; nodules tend to be located in the cluster-root zones of white lupin where carboxylates are released (Nasr Esfahani et al. 2016; Schulze et al. 2006; Wang et al. 2019). Other studies reported that legume crops could acclimate to low-P stress by increasing root nodule phytase and phosphatase activities (Araújo et al. 2008). Some legumes may use more than one P-acquisition strategy, for example, *Kennedia*, which is native to the south-western Australian kwongan, release carboxylates and form AMF under P-limited conditions (Adams et al. 2002; Ryan et al. 2012). Therefore, the contribution of efficient P-acquisition strategies in maintaining nodulation and BNF warrants further investigation.

Efficient P-use strategies would allow legumes to maintain a stable P concentration in nodules and BNF (Fig. 1a). For example, chickpea tends to reallocate P from leaves and roots to nodules under low-P conditions (Nasr Esfahani et al. 2016). In a hydroponic experiment, *Acacia mangium* was also shown to preferentially allocate P to nodules and enhance P use efficiency to maintain BNF under P-limited conditions (Ribet and Drevon 1996). To use P efficiently, some plants also replace phospholipids with sulfolipids and galactolipids under low-P conditions (Andersson et al. 2003; Hammond et al. 2011). Genes involved in galactolipid synthesis are induced in P-deficient root nodules of common bean

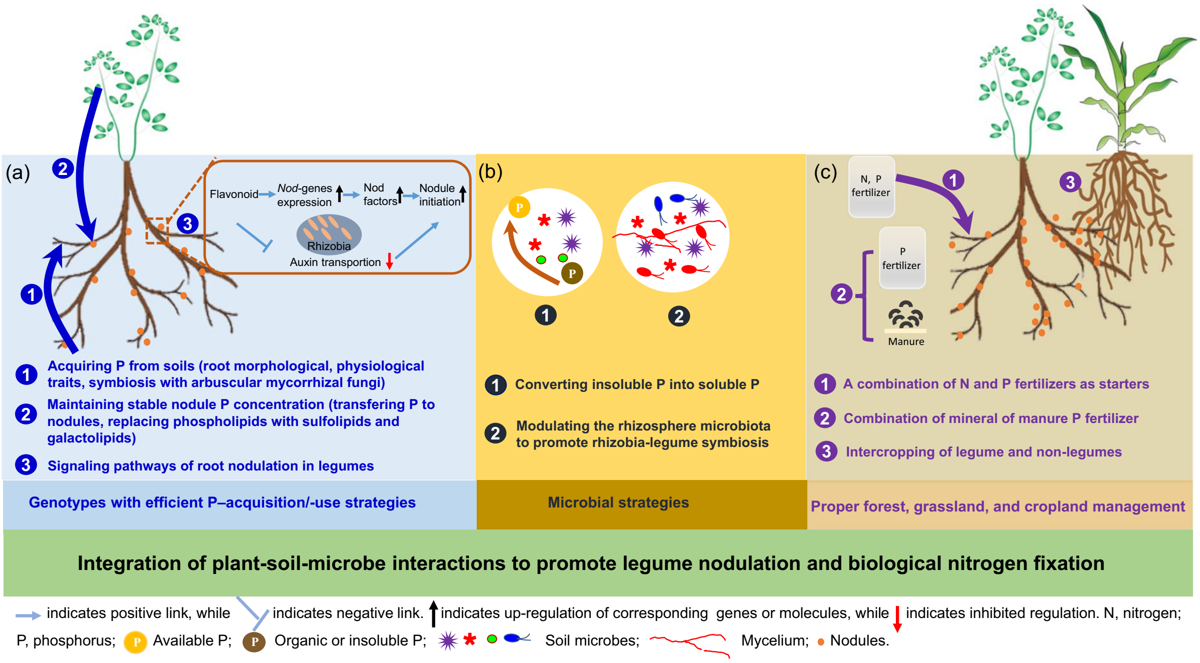

Fig. 1 Schematic diagrams of integrating plant phosphorus (P)-acquisition/−use strategies, microbial strategies, and forest, grassland, and cropland management to enhance biological nitrogen fixation (BNF) in legumes under P-limited conditions. Detailed information on efficient plant or microbial strategies in P acquisition or utilization could be found in these reviews (Castagno et al. 2021; Lambers 2022; Lambers et al. 2015; Pang et al. 2018; Richardson and Simpson 2011)

(*Phaseolus vulgaris*), suggesting that replacing phospholipids with galactolipids or sulfolipids helps maintain a stable P concentration in nodules and BNF (Hernández et al. 2009). This indicates that legume nodules express very flexible mechanisms for P recycling and internal P conservation. Efficient P-use strategies contribute to the functioning of BNF and should be considered in studies of BNF.

Efficient P-acquisition or -use strategies may maintain BNF differently (Fig. 1a). For example, flavonoids produced under P-limited conditions may induce nodule initiation by affecting auxin metabolism (Hassan and Mathesius 2012; Wasson et al. 2006) or activating the expression of nod-genes in legume hosts (Cooper 2007; Hassan and Mathesius 2012; Zhang et al. 2009) (Fig. 1a). In addition, carboxylates are generally considered the major energy sources for the respiration of bacteroids in nodules and serve as the predominant carbon skeletons for NH_4^+ assimilation in nodules (Rosendahl et al. 1990; Valentine et al. 2017). This suggests that efficient P-acquisition and -use strategies are essential for BNF, and more studies on their potential roles in BNF may enhance our understanding of functioning in natural and agroecosystems.

Molecular mechanisms involved in nodulation under P deficiency

Pi transporters and their regulators in P acquisition and transport in legumes and nodules

Plants acquire P from the soil via inorganic P (Pi) transporters located in the plasma membrane (PM) of roots cells, and most Pi transporters belong to the PHOSPHATE TRANSPORTER 1 (PHT1) family (Wang et al. 2021b). There are two pathways describing Pi entry into nodules, namely a direct uptake by the nodule and an indirect pathway involving Pi transfer from host plant roots to the nodule (Al-Niemi et al. 1998). Studies on soybean (*Glycine max*) showed that a nodule-localized PHT1 gene *GmPT7* is responsible for direct Pi entry into the nodules (Chen et al. 2019), and another PHT1 gene *GmPT5* functions in transporting Pi from the host roots to nodules, especially under P-limited conditions (Qin et al. 2012), thus enhancing BNF and production. PHOSPHATE1(PHO1)-type Pi transporters were described in multiple plant species and play important roles in allocating Pi between different plant tissues or organs. For example, *Arabidopsis thaliana* PHO1 functions in the loading of Pi into the xylem and transfer of Pi to the shoot (Hamburger et al. 2002). Recently, two closely related members of the *Medicago truncatula* PHO1 family, namely *MtPHO1.1* and *MtPHO1.2*, were identified in nodules and shown to transport Pi from infected nodule cells to bacteroids (Müller 2021; Nguyen et al. 2021). All of this suggests that Pi transporters play important roles in BNF by maintaining P concentrations in plants, nodules, or bacteroids.

PHOSPHATE STARVATION RESPONSE1 (PHR1), a constitutively expressed MYB-domain transcription factor, induces the expression of PHT1 under P deficiency.This PHR1-PHT1 module plays important role in maintaining stable Pi concentrations in different organs (Guo et al. 2015; Nilsson et al. 2007). PHR-PHT1 modules also maintain a stable P concentration in soybean nodules (Lu et al. 2020). *GmPHR1/4* proteins directly bind to P1BS elements on *GmPHT1;1/4/11* promoters and subsequently regulate their expression. In N_2-fixing regions, *GmPHR1* not only enhances *GmPHT1;1* expression, but also represses *GmPHT1;11* in non-N_2-fixing regions, both *GmPHR1* and *GmPHR4* enhance the expression of *GmPHT1;1* and *GmPHT1;4*, and repress the expression of *GmPHT1;11* (Lu et al. 2020). *GmPHR25* is also induced by Pi starvation which in turn increases the transcripts of 11 out of 14 high-affinity Pi transporters as well as other five Pi starvation-responsive genes in soybean hairy roots, indicating that *GmPHR25* is also a vital regulator in maintaining a stable Pi concentration in soybean (Xue et al. 2017). This suggests the complexity and tight control of PHR-PHT1 modules in maintaining P concentration in nodules.

The microRNA399 (miR399), which belongs to the most ancient and highly conserved microRNA families in monocots and dicots, is a vital regulator of P uptake and transport in plant (Cuperus et al. 2011). The miR399 downregulates its target gene PHOSPHATE 2 (*PHO2*), a ubiquitin conjugating E2 enzyme which results in repression of Pi transporters and then Pi uptake and transport in *A. thaliana*, maize (*Zea mays*), and rice (*Oryza sativa*) (Bari et al. 2006; Du et al. 2018; Wu et al. 2013). Induction of miR399 in nodules also enhances BNF and soybean growth, possibly via improving Pi uptake to achieve a better Pi-N balance in the nodules (Fan et al. 2021; Xu et al. 2013), suggesting that miR399 plays similar roles in non-legumes and legumes. Further research showed that Pi deficiency-dependent induction of miR399 is significantly suppressed in a phosphate-starvation responsive1 (*phr1*) loss-of-function *Arabidopsis* mutant (Bari et al. 2006), indicating that miR399 is the target gene of *PHR1*. Similarly, rice *OsPHR2* enhances the accumulation of OsmiR399 and subsequently suppresses the expression of *OsPHO2*. Mutation of *OsPHO2* increases the expression of several *PHT* genes (e.g., *OsPT1, OsPT2, OsPT4, and OsPT18*), which results in an increase of Pi uptake in the roots and transport from roots to shoot under low-P conditions (Hu et al. 2011). These findings suggest that PHR1, miR399, and PHO2 define a conserved signaling pathway that responds to Pi deficiency in plants (Bari et al. 2006).

As mentioned above, *PHRs* activate the expression of several phosphate-starvation-induced genes (including PHTs) by binding to the P1BS element under low-P conditions to improve Pi uptake and transport (Guo et al. 2015; Nilsson et al. 2007). However, proteins containing the SYG1/PHO81/XPR1 (SPX) work as phosphate sensors and negatively regulate the binding affinity of PHRs to P1BS element through protein-protein interaction in *Arabidopsis* and rice under P-limited conditions (Puga et al. 2014; Wang et al. 2014; Zhong et al. 2018). Further studies showed that proteins containing the SPX-domain also play important roles in regulating Pi uptake and transport in the legumes (Yao et al. 2014a; Yao et al. 2014b). Proteins containing the SPX-domain suppress OsPHR2-mediated induction of symbiosis-related genes via the P1BS element and inhibit mycorrhizal colonization. In contrast, plants overexpressing *OsPHR2* show increased mycorrhizal colonization (Das et al. 2022; Shi et al. 2021). All of this indicates that PHR-SPX modules are not only involved in direct P uptake and transport pathways in plants, but also in indirect P uptake pathways (mycorrhizal symbiosis) under P deficiency.

Taken together, Pi transporters and their vital regulators, including PHR1, miR399, and proteins containing SPX domains, play essential roles in maintaining stable P concentration in nodules mainly via maintaining overall plant P uptake. However, it should be borne in mind that this may only function with a combination of P-mining strategies under P deficiency, for example, the hydrolyzation of organic P by phosphatases or other enzymes. This is because under low-P conditions, soil characteristics and root morphology, rather than the kinetic properties of the P-uptake system, dominate the rate of plant P acquisition (Lambers 2022). There are also some other genes involved in adjusting root architecture to take up P. For example, *GmPTF1* regulates the expression of *GmEXPB2* via binding the E-box motif in its promoter region which adjusts root architecture and increases the P-acquisition efficiency (Li et al. 2015; Yang et al. 2021a). All of this suggests that all the genes or regulatory mechanisms involved in increasing whole-plant P acquisition (architectural, morphological, or physiological strategies) and transport between different organs might be involved in maintaining nodular P concentration, nodulation, and BNF.

Genes involved in P utilization in nodulation

Normal nodulation and BNF can be sustained in white lupin after 21 days of P withdrawal and in *M. truncatula* on day five after P withdrawal (Cabeza et al. 2014; Schulze et al. 2006), suggesting that P can be translocated preferentially to nodules to maintain BNF. Among all the genes related to maintaining stable nodular P concentrations, those encoding acid phosphatases (APases) have been studied most, as APases hydrolyze organic P (Po) to Pi and increase whole plant Pi uptake under low P supply. Purple acid phosphatases (PAPs), a distinct group of APases, are predominantly studied for their roles in Pi uptake and translocation in plants. For example, overexpression of *OsPAP26* in rice increases Po utilization; it also remobilizes P from senescing to growing leaves (Gao et al. 2017). Several PAPs are upregulated in nodules or other organs under low-P conditions, indicating that they might be involved in P acquisition and assimilation, and possibly BNF (Li et al. 2012). Indeed, overexpression of *GmPAP12* increases APase activity of nodules and promotes P utilization in soybean nodules, thus resulting in enhanced nodulation and BNF (Wang et al. 2020). Overexpression of intracellular PAP, *GmPAP21*, also significantly enhances both acid phosphatase activity and growth of hairy roots under P-limited conditions without inoculation, although overexpression of *GmPAP21* resulted in lower soluble P concentration than that in the control line, suggesting it enhanced internal P utilization. However, it significantly inhibited nodule growth after inoculation (Li et al. 2017). In addition, overexpression of a PAP gene from *Astragalus sinicus*, *AsPDD1*, inhibits nodulation through hydrolysis of ADP and ATP (Wang et al. 2015). This indicates that PAPs may also play a role in nodule formation and BNF beyond P utilization. The expression of phosphoenol pyruvate phosphatase (PEPase) and fructose-1,6-bisphosphatase (FPBase) in common bean also correlated well with P-use efficiency in nodules (Bargaz et al. 2012; Lazali et al. 2016), suggesting there exist other pathways for nodules to acclimate to P depletion.

Other plant strategies of legume nodules to acclimate to P deficiency

Phosphate-starvation responsive *GmSPX5* interacts with *GmNF-YC4* to activate *GmASL6* expression and promotes BNF, suggesting that nodules may acclimate to P starvation through mediating asparagine metabolic process (Zhuang et al. 2021). In addition, soybean genotypes enhance transcription of β-expansin gene INCREASING NODULE SIZE 1 (*GmINS1*) and *GmEXPB2* develop more and larger nodules under P-limited conditions. Further experiments showed that overexpression of *GmINS1* and *GmEXPB2* promotes nodule enlargement (Li et al. 2015; Yang et al. 2021b). This suggests that soybean expansion members (i.e., *GmEXPB2* and *GmINS1*) acclimate to P-limited conditions by contributing to nodule development and growth. In addition, expression of *GmEXPB2* increases P-acquisition efficiency via adjusting root architecture, suggesting that these genes have multiple functions in acclimating to P deficiency. All of this indicates that in addition to maintaining stable P concentration through increasing P uptake from soil or translocation from other organs, legumes also use other strategies to acclimate to low-P conditions.

Microbial strategies in maintaining nodulation

Except for the AMF that forms a symbiosis with plants and transfers P mobilized by bacteria to the host plant, there are other microbes, which are endowed with P-solubilizing activity and are called P-solubilizing microorganisms (Fig. 1b). These P-solubilizing microorganisms may convert insoluble P to soluble P by various mechanisms such as acidification, chelation, exchange reactions, and phosphatase enzymes (Bargaz et al. 2018; Jones and Oburger 2011; Richardson and Simpson 2011; Zaidi et al. 2017). Like plant P-acquisition strategies, of all the mechanisms of P-solubilizing microorganisms, the release of carboxylates and their functions in converting insoluble P to soluble P is considered a principal strategy in acquiring P from the soil (Bargaz et al. 2018; Zaidi et al. 2017). Thus, increased whole-plant P acquisition may maintain a stable P concentration in nodules and ensure nodulation and BNF in legumes. For example, compared with single inoculation with *Bradyrhizobium*, co-inoculation with P-solubilizing *Pseudomonas* strains significantly increases nodule numbers, and dry weight of soybean in pot and field experiments (Afzal et al. 2010; Rosas et al. 2006). Phosphate-solubilizing *Pseudomonas* sp. FM7d also increases the symbiotic properties of the alfalfa plants (Guiñazú et al. 2010). These P-solubilizing microorganisms and other plant-growth-promoting bacteria may also enhance nodulation, BNF, and yield by producing plant-growth-promoting enzymes, phytohormones, antifungal compounds, toxin-resistance compounds, and other high-value bioactive molecules, which play vital roles in whole-plant growth, like deleterious microbe inhibition, disease suppression (Bargaz et al. 2018; Naik et al. 2008; Rosier et al. 2018). All of this suggests that plant-growth-promoting bacteria, including P-solubilizing microorganisms, also promote the growth of legumes by other mechanisms.

Integration of nodulation in a plant-soil-microbe system

Plant are hosts to various microbes in their natural environments, trading or competing for carbon and nutrients with microbes, thus affecting microbial communities; microbes may also affect plant health and growth via their metabolites. As mentioned above, both efficient plant and microbial P-acquisition/−use strategies contribute to nodulation and BNF, and there are many studies summarizing efficient plant or microbial strategies in the P acquisition or utilization (Castagno et al. 2021; Lambers 2022; Pang et al. 2018). However, few studies focused on promoting nodulation and BNF via a combination of efficient plant P-acquisition/utilization and microbial strategies under P-limited conditions. Recent studies show that one of the main P-acquisition strategies, i.e., AMF, may modulate the rhizosphere microbiota to promote nodulation of *M. truncatula* and other legumes (Wang et al. 2021a) (Fig. 1b). Extraradical hyphae produced by AMF also facilitated translocation of rhizobia from non-legume to legume plant, which stimulated nodulation in the host legume (de Novais et al. 2020) (Fig. 1b). In addition, the release of flavonoids by non-legumes, another P-acquisition strategy, also acts as a signal to enhance nodulation and BNF in neighboring legumes (Li et al. 2016) (Fig. 1c). This suggests that plants may regulate nodulation and BNF via efficient plant-microbe or microbe-microbe interactions. The release of carboxylates, one of the main P-acquisition strategies, could enhance soil organic matter decomposition and thus making P and other nutrients available to plants (Clarholm et al. 2015; Ding et al. 2021; Keiluweit et al. 2015). This may shift the microbial composition (Ding et al. 2021; Marschner et al. 2002; Sasse et al. 2018). Will this shift in microbial composition promote nodulation and BNF in legumes under low-P conditions? *NRT1.1B*, a rice nitrate transporter and sensor, is associated with the recruitment of a large proportion of bacteria with N metabolism functions which contribute to the N-use efficiency (Zhang et al. 2019). How about those legumes with efficient P uptake and transport genes or regulatory mechanisms? Will the change of these genes or regulatory mechanisms recruit P-solubilizing bacteria or rhizobia in legumes? How about other P-acquisition/−use strategies? There are too many questions that still need an answer. Therefore, we propose to consider these questions from a system perspective, namely integrating P-acquisition/−use and microbial strategies in the study of nodulation and BNF under P-limited conditions (Fig. 1).

Except for plant and microbial strategies, soil management is also important in improving plant P uptake and nodulation (Bi et al. 2020; Jing et al. 2010; Li et al. 2016). For example, a combination of mineral P and manure increased *phoD* gene abundance and P availability in paddy soil, and the reduced P input enriched the abundance of *Bradyrhizobium* and *Methylobacterium* (Bi et al. 2020), suggesting its potential role in promoting inoculation and BNF. In the intercropping system, faba bean (*Vicia faba*) root exudates (citrate and phosphatase) promoted root growth and P uptake of maize via increasing soil P availability, while maize root exudates promoted flavonoid synthesis in faba bean, which triggered the expression of Nod factor and increased nodulation and BNF in faba bean. This indicates facilitative root–root interactions in promoting P uptake and the nodulation (Li et al. 2016; Zhang et al. 2016). In addition, a localized application of P combined with ammonium significantly enhanced maize growth and nutrient use at the early stages by stimulating root proliferation and rhizosphere acidification, suggesting that modifying rhizosphere processes in the field may be an effective management strategy for improving nutrient use efficiency and plant growth (Jing et al. 2010). All of this emphasizes the importance of soil management in P uptake and inoculation, and they should also be considered to maximize plant and soil microbial strategies in promoting P uptake and nodulation in this whole system (Fig. 1).

Recently, two new concepts, “Rhizobiont” and “Holo-omics” were conceived (Shen et al. 2021; Xu et al. 2021). In Rhizobiont, plants, roots, rhizosphere, hyphosphere, and their associated microbes were integrated to unravel underlying mechanisms of plant-microbe and microbe-microbe interactions that drive high nutrient-use efficiency (Shen et al. 2021). We might adapt this theory to uncover the mechanisms of plant-microbe and microbe-microbe interactions that drive BNF under low-P conditions. Specifically, we need to choose legume genotypes with efficient P-acquisition/−use strategies, add microbes that could enhance P solubilization or plant growth, and adopt soil management to maximize plant or microbial effect (Fig. 1). We need to design experiments that consider and trace the carbon and nutrients exchanged in the plant, soil, and microbial parts, and analyze signaling and metabolic interactions in plant-soil, plant-microbe, and soil-microbe surfaces from a system perspective. The theory of “Holo-omics”, which incorporates data from transcriptomics, metabolomics, epigenomics, and proteomics from both plant and microbes (Xu et al. 2021), might be the key to opening the window of plant-soil-microbial interactions. A case study using holo-omics to investigate the interaction between drought stress and the development of the sorghum microbiome is well demonstrated by Xu et al. (2018). Detailed careful considerations and challenges while adopting this method could be found in the review written by Xu et al. (2021).

Concluding remarks

Nitrogen and P are two macronutrients that are needed in large amounts by plants in terrestrial natural and agricultural ecosystems; both play vital roles in photosynthesis, respiration, productivity, and terrestrial plant diversity (Lambers and Oliveira 2019; Oldroyd and Leyser 2020). Therefore, a large amount of N and P fertilizers are used in intensive agriculture. This is valuable in promoting agricultural productivity, but causes environmental problems, like eutrophication. In addition, phosphate rock is finite, and the world may run out of it in the future (Fixen and Johnston 2012; Gilbert 2009; Johnston et al. 2014). To mitigate these problems and maintain plant productivity, we need to search for sustainable natural and agricultural ecosystems. Efficient plant P-acquisition/−use strategies, microbial strategies, and sustainable forest, grassland, and cropland management are effective in promoting P-use efficiency and nodulation, and integration of these strategies might maximize their functions in N and P uptake and assist the development of sustainability in natural and agricultural ecosystems.

Many studies are focusing on exploring genes or regulatory mechanisms involved in P acquisition and its effect on BNF; however, the effect of the investigation of genes related to P-use efficiency and its effect on BNF, and their related metabolites involved in attracting P-solubilizing bacteria or regulating microbial composition that is beneficial for inoculation are rarely studied. Further studies of these aspects will advance our knowledge of the essential genetic and molecular components required for the promotion of P uptake/use and nodulation, enhance our understanding of plant-microbe and microbe-microbe interactions, and provide potential tools to boost P and N uptake in legumes. As a vital component of plant-soil-microbe systems, soil management should also be carefully studied and adopted in the whole system. Overall, underpinning genes and regulatory mechanism of legume P uptake and nodulation from a system perspective will probably provide new insights to increase plant productivity and nutrient-use efficiency via optimizing plant, soil, and microbe combinations.

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Declarations

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