

Review

# Influence and Role of Fungi, Bacteria, and Mixed Microbial Populations on Phosphorus Acquisition in Plants

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**Abstract:** Phosphorus (P) stands as a pivotal macroelement in relation to the growth of plants. It plays a significant role in physiological processes, as components of biofilms and nucleotides, and in metabolic activities within plants. The deprivation of phosphorus detrimentally impacts the growth and developmental of plants. However, the rhizosphere's beneficial fungi and bacteria augment the efficacy of phosphorus uptake, participate in the molecular regulation of phosphorus, stimulate physiological alterations in plants, and facilitate signal transmission. In order to give readers a better understanding of the effects and positive roles of soil beneficial fungi and bacteria in regulating plant phosphorus acquisition and transport, this present review introduces the role and influence of rhizosphere microorganisms (fungi and bacteria) in assisting plant phosphorus absorption, and summarizes the key phosphorus transporters found in their interaction with plants. Using mixed microbial populations as composite microbial fertilizers has a positive effect on plants under phosphorus-deficiency conditions. It will be conducive to a better understanding of the mutualistic relationship between fungi, bacteria, and plants to provide a way to reduce the application of phosphorus fertilizers efficiently, and to provide a research background for the development of microbiological fertilizers.

**Keywords:** plants; fungus; bacteria; mixed microbial populations; prospects of composite microbial fertilizers



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## 1. Introduction

Phosphorus (P), as an essential macroelement for plants, exerts profound influence on bud growth, seed germination, rhizome fortification, and seed maturation [1]. It constitutes a vital component of plasma membranes and nucleotides, governing respiration and photosynthesis while also impacting plant productivity and yield [2]. Phosphorus is mainly derived from rocks, and its availability is further affected by climatic, biological and topographic factors [3,4]. In China, the spatial distribution of soil phosphorus content exhibits wide-ranging disparities owing to climatic variations. The effective phosphorus content in soil often falls below 6 g/cm<sup>3</sup>, with plant uptake accounting for less than 1% of this fraction [5]. Considering its low mobility, phosphorus is easily fixed by soil [6]. Excessively increasing the application of phosphate fertilizers to meet the demands of plants for phosphorus [7,8] has variable repercussions on soil, vegetation, and even microorganisms [9,10].

Empirical studies have demonstrated that prolonged phosphorus fertilizer application can instigate alterations in soil phosphorus composition in acidic environments, culminating in heightened iron levels and increased iron aluminum phosphate content. In extreme cases, this leads to phosphorus leaching [11,12]. Furthermore, the excessive application of phosphate fertilizer may exert influence on the soil microorganism community structure and thus affect biodiversity [13]. The excessive utilization of phosphorus fertilizers may also result in the accentuation of heavy metal accumulation in the soil [14], thereby imposing stress on plant growth [15]. Thus, it is imperative to curtail the immoderate use of fertilizers.

Soil is teeming with an abundance of microorganisms, owing to its rich nutrient composition [16]. This diverse ecosystem harbors a multitude of microorganisms, including bacteria, fungi, actinomycetes, protozoa, and nematodes, among others. These microorganisms, each characterized by distinct traits, enact various functions within the soil, with particular emphasis on bacteria and fungi.

Microorganisms are involved in the soil phosphorus cycle and ecological balance [17]. Within the 0.5 mm radius surrounding the plant's root, known as the rhizosphere, microorganisms reside that wield significant influence over plant growth [18]. This intricate microcosm plays an indispensable role in the reproduction and growth of plants [19], while also contributing to the cycling of carbon, nitrogen, phosphorus, and sulfur in the soil [20]. Recent research has harnessed the interactions between microorganisms and plants to enhance plant growth, increase yield, improve physiological parameters, etc. [21–23]. Microorganisms also play a vital role in facilitating the uptake of both major and trace elements by plants [24], including the macroelement phosphorus. Fungi and bacteria possess different phosphate transport (PT) systems that are used for the absorption and translocation of phosphorus, encompassing phosphorus response proteins, phosphorus uptake proteins, and phosphorus transport proteins. These microorganisms exert a crucial influence on the regulation of phosphorus transport and signal transduction, notably through the direct impact of phosphate transporter family proteins such as PHT (PHT1, PHT2, PHT3, PHT4, and PHT5) and PHO1, which are associated with plant phosphorus stress [25]. Furthermore, their secretions and metabolites indirectly modulate the absorption of phosphorus by plants. By harnessing the potential of fungi and bacteria, the effective utilization of phosphorus fertilizers can be significantly enhanced, and the concurrent application of fungi and bacteria can yield even more favorable outcomes [26–28]. The combined application of various beneficial microorganisms has a more obvious absorption effect than that of single microorganisms on plant phosphorus. There is an interaction between bacteria and fungi. The division of labor and cooperation that ensue have a better effect on element absorption [29].

Therefore, elucidating the roles and mechanisms of fungi and bacteria in the absorption of plant phosphorus is instrumental in gaining a clearer understanding of the research field and molecular activities. This comprehension will facilitate the more effective identification of novel beneficial microorganisms and the advancement of microbiological fertilizers, thereby mitigating the detrimental impacts of phosphorus stress. Furthermore, it will furnish a theoretical foundation and research context for addressing the overreliance on phosphate fertilizers.

In this paper, we mainly analyze the roles of fungi in phosphorus transporters, the effects of low-phosphorus stress on plant physiological changes, the effects on plant phosphorus transport family genes, the effect of its secretions on the absorption of plant phosphorus, its regulation of phosphorus in non-mycorrhizal plants, etc. In addition, we also analyze the role of bacteria in phosphoprotein transport; the effects of bacteria on plant growth and development under phosphorus stress, or when reducing the application of phosphate fertilizer; and the effects of acid substances in bacterial secretions on soil phosphorus. Secondly, we underscore the beneficial impacts of combinations of mixed microbial populations on plants. Finally, through an analysis of the research on phosphorus in bacteria, fungi, and microbial fertilizers published in recent years, we delineate research

trends related to microorganisms, and offer recommendations and prospects for the future development of microbial fertilizers.

## 2. Mechanism of Fungal-Mediated Phosphorus Transport and Effects on Plant Growth

### 2.1. Phosphate Transporters Play a Key Role in Plant–Fungal Interactions

In recent years, there has been an increase in the number of comprehensive investigations into the molecular mechanisms governing fungal phosphorus transport. It has been revealed that the fungal phosphorus transport system plays a pivotal role in phosphorus uptake in plants, as exemplified by the involvement of Hcpt1 and Hcpt2 [30,31]. The fungal absorption of phosphate occurs via the phosphate transporter present on the external hyphae, with the acquired phosphate promptly translocated to the vacuole of arbuscular mycorrhizal fungi (AMF) [32]. *GiPT* expression is regulated in response to phosphate concentrations in the environment surrounding the extra-radical hyphae and is affected by the overall phosphate status of the mycorrhiza [33]. In the endophytic fungus *Glomus mosseae*, the expression profile of *GmosPT* was found to be affected by different phosphorus concentrations [34]. It was also found that the high-affinity phosphate transporter GigmPT in *Gigaspora margarita* is required for AMF symbiosis [35]. The RiPT7 protein, found in *Rhizophagus irregularis* (a type of arbuscular mycorrhizal fungi (AMF)), serves as an inorganic phosphate bidirectional transporter protein, ensconced within the fungal cell membrane. Furthermore, the inhibition of *RiPT7* gene expression impedes the transcriptional activities of genes associated with phosphorus response and transport. The deactivation of RiPT7 triggers the up-regulation of genes involved in polyphosphate synthesis, thereby exerting an impact on arbuscular development and phosphate homeostasis at the symbiotic interface of AMF [36].

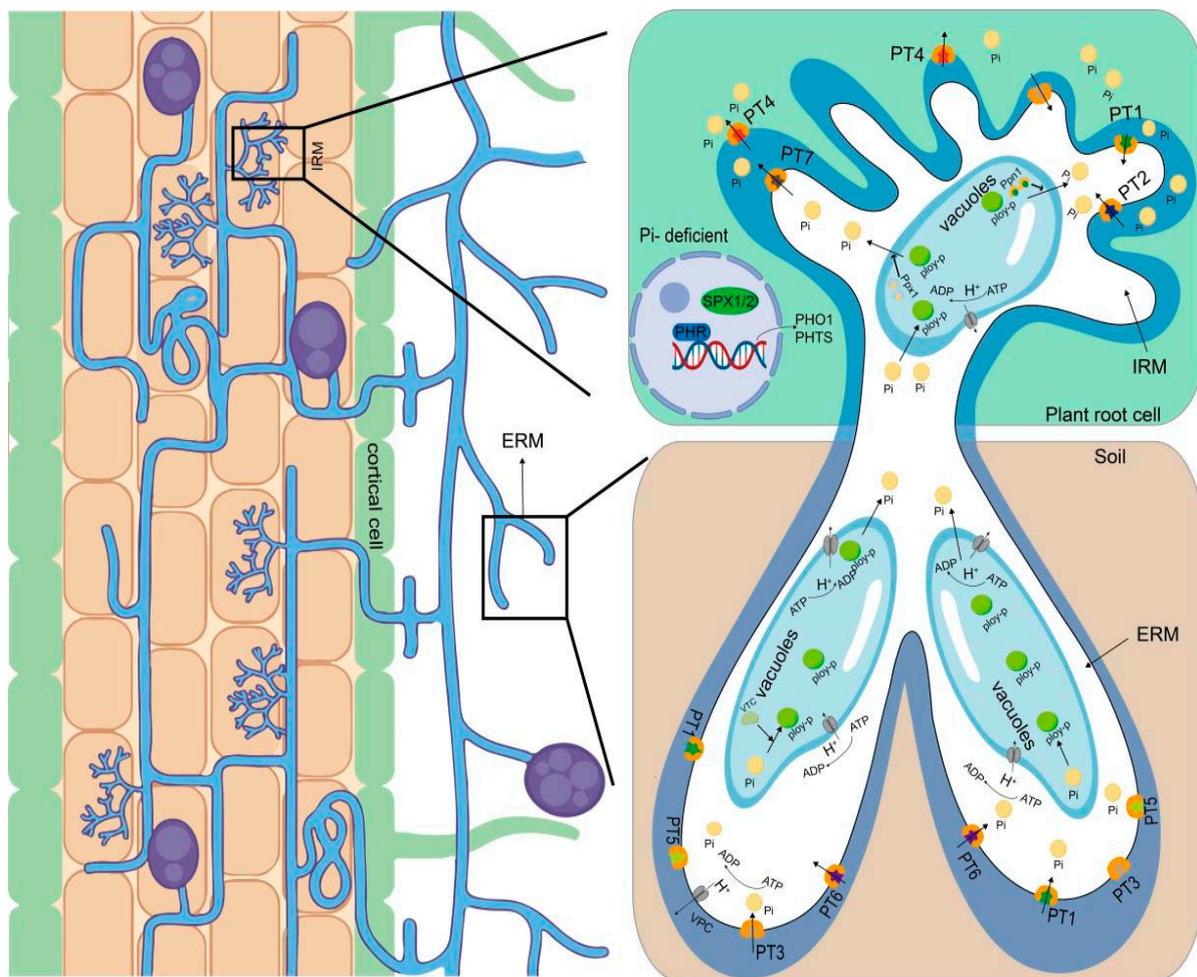
Mycorrhizal fungus symbiosis involves two main types of phosphorus transporters: mycorrhizal-inducible protein and mycorrhizal-specific protein [37], as shown in Table 1.

Notably, a significant arbuscular mycorrhiza (AM)-inducible phosphate (Pi) transporter, LjPT3, has been isolated from *Glomus mosseae*-colonized roots in *Lotus japonicus* [38]. The phosphate transporter PT4 has been separated from *Medicago truncatula* [39], an ATP-binding cassette transporter. In barley, HVPT8, an inducible phosphorus transporter, is also involved in phosphorus transport through the mycorrhizal pathway [40]. It was found that the expression of *phosphate transporter down-regulated 1 (ptd1)* in *Petunia* would seriously increase the down-regulation of inducible transporters (PhPT3, PPT4, and PPT5) in mycorrhiza [41]. There is a mycorrhizal-inducible phosphate transporter, GmPT10 (or GmPT11), in the branching domain of the peri-arbuscular membrane of soybean [42]. We summarize the phosphate transporters involved in fungal–plant symbiosis in Table 1.

Furthermore, a specific phosphate transporter, StPT4, exclusively manifests in the mycorrhizal roots of *Lycopersicon esculentum*, underscoring the intricate interplay between these fungi and their host plants [43]. Additionally, the Pi transporter ZmPT6 has been identified in *Zea mays* L., and its mutation is associated with diminished mycorrhiza formation in maize roots [44]. The mycorrhiza-inducible *PhPT3* and *PhPT5*, expressed at low levels in nonmycorrhized roots, further accentuate the significance of mycorrhizal symbiosis in facilitating phosphorus uptake [45], and the same applies to the genes linked to polyphosphate degradation in the phosphorus-responsive signaling pathway in AMF, as depicted in Figure 1. There are also specific proteins found in grapes. The high expressions of *VvPh1-1* and *VvPh1-2* promote the uptake of Pi in *Funneliformis mosseae*, thereby improving the growth of grapes [46].

Under conditions of low-phosphorus stress in rice, the transcriptional regulatory factor PHR2 emerges as the linchpin orchestrating mycorrhizal phosphate uptake. Its influence extends beyond targeted signal transduction, encompassing the modulation of mycorrhizal colonization and associated genes [47]. PHR2 exerts its regulatory effects by binding to the P1BS element in the promoter, thereby bolstering the AMF-dependent Pi uptake pathway in rice (Figure 1) [48]. Moreover, PHR can directly control gene expression in about 42% of AMF, affecting arbuscular mycorrhizal development-related genes and

phosphate transporters [49]. Notably, PHR targets can activate the elusive golden ester biosynthetic gene, which is critical to AMF metabolism and branching, as well as the actions of dual oxidases 7 and 8A (CCD7 and CCD8A). Furthermore, PHR2 can stimulate the expression of genes involved in nutritional exchange, including wrinkled 5A (*WRI5A*), *PT11*, *CERK1*, and the symbiotic receptor-like kinase (SYMRK). Intriguingly, PHR2 also plays a role in the perception of fungal signals, thereby adding another layer of complexity to its multifaceted functions [50]. The potential sugar exporter MtSWEET1b in arbuscular mycorrhizal fungi is indispensable to substance exchange in mycorrhizal fungi [51]. To facilitate enhanced phosphorus acquisition, acid enzymes play a crucial role in solubilizing inorganic phosphorus. Notably, studies have demonstrated that the introduction of fungal acid enzyme synthesis genes (*ex:: phyA*) into tobacco plants can augment soil phosphorus content, offering a promising means to curtail phosphate fertilizer application [52].



**Figure 1.** Phosphorus transport in extraradical mycelium (ERM) and intraradical mycelium (IRM) under low-phosphorus stress in arbuscular mycorrhiza. In ERM, phosphorus is transported to vacuoles through the transporters PT1, PT3 [53], PT5, and PT6 on the mycelium cell membrane. In the vacuole, inorganic Pi is polymerized into polyphosphate (polyP) [54] by the transporter chaperone (VTC) [55], and then reaches the IRM region through the hyphal channel. Within the IRM, AMF exopolyphosphatases Ppx1 and Ppn1 can precipitate polyP into inorganic Pi [56]. The transport protein PT7 on the endophyte mycelium cell is transported outside the cell membrane, and then the transport protein PT4 exports the inorganic Pi to the plant's cell. The transporters PT1, PT2, and PT7 in the cell membrane of endophytic hyphae can obtain phosphate from plant cells to provide nutrients for hyphae (Drawing tools: FigDraw 2.0).

**Table 1.** Fungal phosphorus-related transporters.

Name	Species	References
Hcpt1/Hcpt2	<i>Hebeloma cylindrosporum</i>	[30]
GiPT	<i>Glomus intraradices</i>	[33]
GmosPT	<i>Glomus mosseae</i>	[34]
GigmPT	<i>Gigaspora margarita</i>	[35]
RiPT7	<i>Rhizophagus irregularis</i>	[36]
LjPT3	<i>Lotus japonicus</i>	[38]
PT4	<i>Medicago truncatula</i>	[39]
HVPT8	<i>Triticum aestivum</i>	[40]
StPT4	<i>Lycopersicon esculentum</i>	[43]
ZmPT6	<i>Zea mays</i>	[44]
PhPT3/PhPT5	<i>Solanum lycopersicum</i>	[45]
GmPT10/GmPT11	<i>Glysin max</i>	[42]
VvPht1-1/VvPht1-2	<i>Funneliformis mosseae</i>	[46]

## 2.2. Fungi Affect Plant Physiological Traits and Reduce Phosphorus Fertilizer Application

In recent years, the scientific community has dedicated significant attention to the nuanced field of AMF, recognizing their pivotal role in shaping soil ecosystems and influencing a myriad of soil ecological functions. Research findings underscore the pivotal role of AMF in facilitating plants' access to as much as 80% of inorganic phosphorus through a specialized "mycorrhizal phosphate uptake" (MPU) pathway, beside complementing the direct phosphorus uptake by the plants' own root epidermal cortical cells [57]. This symbiotic relationship not only augments nutrient absorption in plants, but also exerts profound effects on their growth and development [58–61]. The examination of the symbiotic interaction between the fungus *Botrytis cinerea goes* and the economic crop cotton has unveiled the consequential impact of *Botrytis cinerea goes* on cotton growth, fiber maturation, and yield, along with augmentations in the phosphorus contents in the roots, stems, and leaves of the plant. Notably, the fungus elicits the up-regulation of phosphorus-related genes by modulating phosphorus transporter proteins under conditions of limited phosphorus availability [62]. Furthermore, compelling evidence has demonstrated the capacity of AMF to substantially enhance cassava yield in the absence of phosphorus fertilizer, production exceeds 50% of traditional fertilizers used by farmers. Explicitly, under conditions of reduced phosphorus fertilizer application, fungal mycelium has been shown to enhance the efficiency of phosphate fertilizers [63]. Notably, a discernible correlation has been established between fungi and the quantity of phosphorus fertilizer applied [64]. In the intricate dance between plants and microorganisms, the root morphology of plants changes to meet their nutritional needs. Some studies have found that even in the absence of phosphorus fertilizers, the extent of hyphal coverage on the root surface can expand up to 30 mm, indicative of a 15-fold increase in the phosphorus absorption range facilitated by hyphal networks [65]. However, it is noteworthy that endophytic fungi do not develop a highly branched mycelial structure, and their phosphate utilization efficiency is intricately intertwined with Trp-derived metabolite pathways [66].

Inoculation with *Gigaspora margarita* in the absence of phosphorus fertilization has been found to significantly enhance mint dry matter yield and elevate the levels of nitrogen, phosphorus, and potassium therein. But, under judicious phosphorus fertilization, there is a remarkable 89% increase in the aboveground biomass and essential oil content of mint, concomitant with enhanced fungal colonization [67]. The role of fungi in diverse phosphorus fertilizer treatments has proven effective in modulating the overall nutrient status of the soil, while also exerting positive influences on rooting depth, root volume, root dry weight, and root weight density, in addition to impacting aboveground plant biometrics [68,69]. Furthermore, the involvement of fungi has been observed to stimulate lateral root development in plants under phosphorus stress [70]. It is worth noting that the uptake of phosphorus by plants is intricately linked to alterations in root morphology [71], with the root system architecture (RSA) playing a pivotal role in the acquisition of these

resources from the soil [72–74], thereby dictating a plant's capacity to access phosphate, the primary form of phosphorus uptake by plants [75].

However, the effect is related to the C3 and C4 categories of plants. Some studies suggest that C4 plants undergo stronger interactions with AMF, and this can increase leaf phosphorus content [76]. C4 plants show a more active and effective response to AMF, which may be related to the higher demand for nutrient absorption and photosynthetic rate in C4 plants [77]. In addition to being related to plant species, the symbiosis of mycorrhizal fungi is related to a potential microbial system [78], which not only results in the accumulation of macroelements, but also in the enhancement of micronutrients. The presence of mycorrhiza allows the remodeling of microbial communities in the inner layer of the root, such as *Actinomyces*. Therefore, the host also actively regulates the role of the microbial community [79].

### 2.3. Fungi Are Involved in Plant Phosphorus Signal Transduction and Hormone Synthesis

Fungi influence plant phosphorus signaling. This is foremost seen in the plant's own phosphorus transport system, and it was found that under fungal inoculation, fungi effectively activate four phosphorus transport proteins, *CoPHO1-3* in the root system of *Camellia oleifera*, as well as *CoPHO1-1*, *CoPHO1-3*, and *CoPHT1* in the leaves, thereby increasing phosphorus content in the roots [69]. The over-expression of the *pht1.8* and *pht1.6* genes in the PHT family of proteins has also been found in cereal crops (*Hordeum vulgare*, *Zea mays*) [80]. Under conditions of low-phosphorus stress, the up-regulation of three genes of SIPHT1 (*SIPT3*, *SIPT4*, and *SIPT5*) has been analyzed via the tomato transcriptome, with alterations seen in the expression of PHT family genes [81]. However, not all PHT family proteins were significantly up-regulated; *PHT1-1* was significantly up-regulated in roots after EMR formation, but *PHT1-3* and *PHT1-4* showed down-regulation in roots [82].

In addition to directly affecting plant phosphorus signal transduction, hormone synthesis is also involved in the perception and operation of phosphorus signal transduction. Hormone levels affect the absorption of phosphorus, affect the development of root structure and the production of lateral root primordium [83,84], and stimulate lateral root development [85]. Plant hormones mediate root growth in response to phosphorus stress [86]. Endophytic fungi inoculation also significantly increases the concentration of indoleacetic acid, indole butyric acid, trans-zeatin, dihydrozeatin, and isopentenyl adenine in leaves and roots, but *F. mosseae* and *S. indica* were shown to generate relatively greater effects on leaves and roots, respectively [87]. Endophytic fungi were found to be involved in the production of several phytohormones in blueberry, including jasmonic acid, indoleacetic acid, abscisic acid, gibberellin and salicylic acid, while indole-3-acetic acid amide synthetase, which encodes a key enzyme for the synthesis of IAA, was significantly up-regulated under colonization by both fungi [88].

### 2.4. Fungal Secretions Contribute to the Transport of Phosphorus

Fungal secretions also play an important role in phosphorus uptake and transport. AMF release hyphal compounds into the soil, which can coordinate the colonization of the hyphal coil by various microorganisms. The composition of the hyphal coil is closely related to the rhizosphere environment and the soil. Nutrient cycling in the hyphal coil is influenced by changes in the microbiome [89,90], and changes in microbial functions lead to changes in organic nutrient cycling, which causes the hyphal coil to become a unique and important functional area in the ecosystem [91]. Then, fungi can also secrete organic acids and acid phosphatase to dissolve the fixed phosphates in the soil, thus increasing the inorganic phosphorus in the soil, which is beneficial to the absorption and utilization of plants [92]. *Aspergillus* and *Penicillium* are typical phosphate-solubilizing fungi [93]. Even under low-phosphorus conditions, mycelium was found to secrete more phosphatase than under high-phosphorus conditions, but this was not related to the phosphorus concentration in

the plant, and was instead closely linked to the phosphorus content inside and outside the mycelium [94].

Fungi can also stimulate phosphorus-solubilizing bacteria (PSB) to produce phytic acid using the fructose secreted by mycelium as a signal, which indirectly provides a convenient medium for PSB. This improves the effectiveness of soil phosphorus by indirectly promoting its absorption by plants [95].

### 2.5. Phosphorus Transport and Uptake by Fungi Is Not limited to Mycorrhizal Plants

Previous studies on fungi have explored the relationship between symbiosis, growth promotion, and disease resistance on the basis of mycorrhizal plants, such as soybeans [96,97], wheat [98], corn [99], potatoes [100], and tomatoes [101]. At present, some correlation analyses have also been performed between non-mycorrhizal plants and fungi in relation to phosphorus absorption.

Fifteen endophytic fungi were detected in the model plant *Arabidopsis thaliana* under natural phosphorus deficiency conditions, among which fungi such as the *Pleuromycelles* were found to have positive effects on efficient phosphorus absorption and the synthesis of carbon hydrates under conditions of low-phosphorus stress [102]. In the *Microthlaspi* species of the cruciferae family, endophytic fungi are mainly saprophytic and facultative endophytic fungi, and the distribution of root microbial communities is driven by the ecological niche and environmental factors of the fungi [103]. The presence of these specific microbial communities is more adaptable to the environment of plants, and greatly improves element absorption [104,105]. In *Brassica* plants, studies have found a correlation between the types of *Brassica* plants and endophytic microbiota. The strain *Colletotrichum tofieldiae* can transfer phosphorus to the host under low-phosphorus stress, leading to phosphorus translocation, and stimulating the expression of phosphorus transport proteins PHT1.2 and PHT1.3, which colonize in the roots at high levels, thereby increasing the bud biomass of non-mycorrhizal plants (*Brassica napus* L.) and improving the phosphorus and magnesium uptake in rapeseed following inoculation in low-phosphorus environments [106]. In addition to the important role of endophytic fungi in phosphorus absorption, external hyphae can utilize external phosphorus nutrition to achieve phosphorus transfer, thereby improving the growth of non-mycorrhizal plants (spruce) and affecting the host's translocation and absorption of other elements (N, P, and Mg) [107].

## 3. Bacteria-Mediated Phosphorus Transport System and Its Effects on Plant Growth

### 3.1. Phosphate Transporters Play an Important Role in the Interaction between Bacteria and Plants

Apart from fungi, which are crucial for plant growth, the rhizosphere of plants in soil contains a high-density bacterium called Plant-Growth-Promoting Bacteria (PGPB), which stimulates plant growth and boosts crop output. They are of great significance in improving the availability of phosphorus in soil, increasing the efficiency of phosphorus absorption and utilization by plants, and promoting the cycle of phosphorus in soil. As a result, research on PGPR applications has important theoretical and practical implications for the comprehensive utilization of resources and environmental protection.

The investigation of the regulatory mechanisms and signal transduction pathways governing bacterial phosphorus transport, as well as their collaborative interactions with plants in order to enhance phosphorus uptake, has emerged as a prominent research focus in the field of microbiology. Bacteria possess a comprehensive phosphorus transport system (Pt), consisting of PstS as a substrate-binding protein, PstC and PstA as transmembrane proteins, PstB as a phosphate-specific transporter, and PhoU, which is implicated in phosphate accumulation, bacterial pathogenesis, antibiotic production, bacterial persistence, and sensitivity to various stresses [108]. However, not all bacterial strains have the PhoU, and this protein is notably absent in *Bacillus subtilis*. In addition, the Pi signal transduction network in this bacterium incorporates a positive feedback loop between the PhoP–PhoR and ResD–ResE two-component systems [109]. Furthermore, the phosphate (Pho) regulator plays a pivotal role in maintaining phosphate homeostasis [110], a process

governed by the PhoR/PhoB two-component regulatory system, in which PhoR, functioning as a membrane-signaling histidine kinase, is capable of interacting with proteins of the ABC-type phosphate-specific transport (Pst) system and PhoU, thereby exerting a crucial influence on bacterial phosphorus transport, which is vital for sustaining their metabolic activities and promoting plant growth [111]. Moreover, bacterial phosphorus transport proteins such as phoD, phoA, YP6, and phoC have been demonstrated to facilitate nutrient uptake by plants [112]. There is also a kind of symbiotic bacteria that can invade the interiors of plant tissues and lead to the local enlargement of plant roots. These are defined as *Rhizobium*, which are closely related to the absorption of nitrogen in plants, but also play an important role in the transport of phosphorus [113–115]. There is an important phosphorus transporter protein, PT7, in soybean nodules, which is located on the plasma membrane of the outer skin layer and participates in rhizosphere-to-nodule uptake and phosphorus translocation. The overexpression of this gene can effectively improve nodule development and nitrogenase activity, thereby effectively increasing soybean yield [116].

PT7 is a Pi transporter protein localized at the plasma membrane of the outer cortex and FZ of the nodules, which participates in Pi uptake from the rhizosphere to nodules and the further translocation of Pi to FZ. Most importantly, the overexpression of *GmPT7* was shown to improve nodule development and nitrogenase activity, leading to a significant increase in soybean yield in the field. There is also a nodule high-affinity phosphate (Pi) transporter gene, *GmPT5*, whose expression was found to be elevated in response to low-phosphorus levels. *GmPT5* controls Pi's movement from roots to nodules. It is critical for maintaining Pi homeostasis in nodules, and regulating soybean nodulation and growth performance [117]. Some studies have also found that vacuolar transporters (VPTs), mutants *vpt2* and *vpt3*, significantly reduce the numbers of nodules and nitrogenase activity under different phosphate conditions. *VPT2* and *VPT3* may regulate phosphorus adaptation and *Rhizobium* legume symbiosis by regulating long-distance Pi transport [118]. Additionally, in *Medicago truncatula*, the phosphate transporter gene *MtPT6* was found to be expressed in shoots, roots, and nodules, and responded to low-phosphate stress. Moreover, *MtPT6* could improve phosphate acquisition in transgenic *Arabidopsis* [119]. We summarized the phosphate transporters that play an important role in the interaction between bacteria and plants, shown in Table 2.

**Table 2.** List of phosphate transporters related to the interaction between bacteria and plants.

Name	Species	References
PstA/PstB/PstC/PstS	<i>Sinorhizobium meliloti</i>	[108]
PhoU	<i>Salmonella Typhimurium</i>	[109]
PhoR/PhoB	<i>Saccharomyces cerevisiae</i>	[111]
YP6	<i>Bacillus amyloliquefaciens</i>	[112]
PT7	<i>Glycine max</i>	[116]
GmPT5	<i>Glycine max</i>	[117]
VPT2/VPT3	<i>M. truncatula</i>	[118]
MtPT6	<i>Arabidopsis</i>	[119]

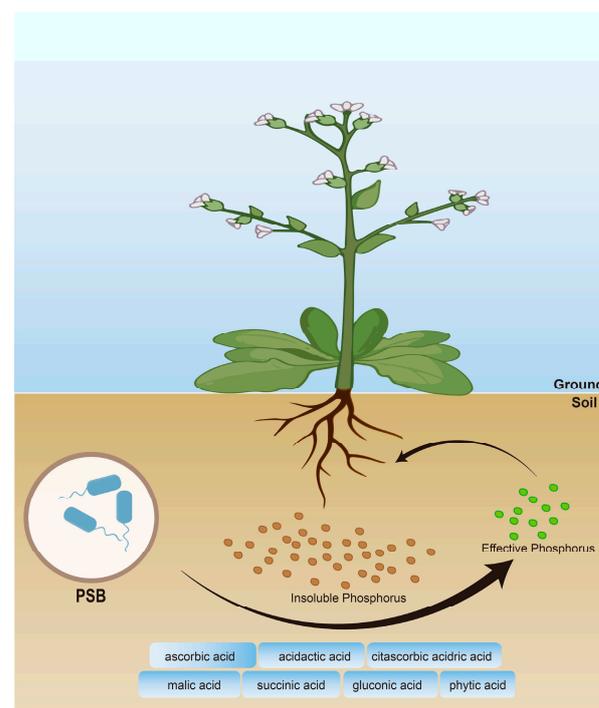
In plant phosphorus transport, PHT transporters maintain the homeostasis and transport of phosphorus in cells, as well as signal transduction [120]. Low-phosphorus stress induces phosphate starvation response 1 (PHR1) [121,122], which can directly induce the expression of *PHT1*, thereby promoting plant phosphorus acquisition [123]. The results suggest that nodule initiation and growth may both be controlled by PHR–PHT1 modules. Silencing the gene *GmPHT1;11* will reduce the numbers and sizes of nodules. The overexpression of *PHR1* affects nodulation [124]. This indicates that the growth of *Rhizobium* will also be regulated by plant genes, and the role of phosphorus for both bacteria and plants is the same. It has also been found that *GmPHR1* in soybean rhizomes is a rhizoma-specific transcription factor, different from the typical PHR1 in plants, because *GmPHR1* has a short N-terminus before its MYB-CC structural domain and is highly susceptible to being

infected by *Rhizobium*. The overexpression of the *GmPHR1* and *GmPHR16* genes affects the development of root hairs [125]. Furthermore, under conditions of Pi starvation, *GmPHR1* can bind to the promoter sequence and activate the expression of *GmPAP12* to maintain the homeostasis of P and N [126]. This is an important key to nodulation, root growth, nutrient uptake, and improved soybean yield. It also plays an important role in phosphorus uptake and the regulation of homeostasis.

### 3.2. Bacteria Convert Soil Phosphorus, Which Helps Plants to Effectively Uptake Phosphorus

Soil phosphorus is mainly composed of inorganic insoluble phosphorus. This is because the main part of soil phosphorus is tightly adsorbed in mineral particles, combined with organic matter, or precipitated as insoluble salts, and only very little phosphorus is available for plant use in soils and bedrock [127,128]. With phosphorus fertilizer inputs, soil erosion aggravates the global soil phosphorus deficiency [129–132]. While microorganisms play an important role in the solubility of insoluble phosphorus in soils, the phosphorus cycle also plays an important role, and is a potential driving factor of agricultural and environmental engineering [133].

There are a series of bacteria in the soil that have the ability to dissolve inorganic phosphates, such as dicalcium phosphate, tricalcium phosphate, and phosphate. These bacteria are considered “phosphorus-solubilizing bacteria” (PSB). While providing phosphorus to plants, they enhance the solubility of phosphorus, increase the content of inorganic phosphorus in the soil, reduce phosphorus fixation, and effectively increase phosphorus content. They include *Bacillus*, *Pseudomonas* [134], *Rhizobium* [135], and *Burkholderia* [136]. Acids are effective in dissolving insoluble chelates in the soil [137,138], and these bacteria increase phosphorus effectiveness and drive phosphorus cycling through their own secretions and metabolites [139], as shown in Figure 2.



**Figure 2.** Decomposition of insoluble phosphorus by secretion of acids. PSB dissolves soil phosphorus chelates with the secretion of various acids—lactic acid, gluconic acid, citric acid, malic acid, etc.—which facilitates the plant’s uptake and utilization of effective phosphorus.

They increase the efficiency of phosphorus utilization by secreting phytic acid, acid phosphatase [140], etc. PSB can not only promote the plant’s uptake of phosphorus, but also increase crop yield and reduce the required application of phosphorus fertilizer. An

efficient type of PSB isolated from soil strain JP233 dissolved insoluble P into soluble forms, and the molybdate reactive phosphorus (MRP) content reached 258.07 mg/L in an NBRIP medium containing 5 g/L  $\text{Ca}_3(\text{PO}_4)_2$  within 48 h [141]. Organic acids can also dissolve insoluble phosphorus compounds (calcium, iron, and aluminum phosphates) in the soil [142]. The oxalic and malic acids produced by PSB16 (*Bacillus* sp.) are capable of obtaining phosphate from phosphate rock (PR) to promote aerobic rice growth [143]. The tricarboxylic acid cycle (TCA cycle) is the main pathway leading to the production of acids, which is the core energy source and a prerequisite for the synthesis of biological compounds in living organisms [144–146]. The TCA cycle is also present in bacteria, and the acids secreted by it can efficiently dissolve insoluble phosphorus. It was found that the TCA cycle pathway-related genes of the PSB strain *Pseudomonas* W134 were up-regulated, and they produced more organic acids in the presence of different phosphorus treatments, as well as under low-phosphorus stress. A transcriptome study revealed that PSB W134's TCA cycle pathway-related genes were up-regulated, producing more organic acids, and that low-phosphorus stress resulted in significantly higher quantities of formic acid, ascorbic acid, acetic acid, citric acid, and succinic acid [147]. The researchers also identified the presence of the glucose dehydrogenase enzyme and its promoter region of *Serratia* sp. S119, a gene coding the biosynthesis pathway of gluconic acid. It is also a major member of the group that dissolves insoluble phosphorus in soil [148,149]. Some studies have also found an interaction between AFM and PSB. Under in vitro cultivation or soil conditions, arbuscular mycorrhizal hyphae transfer PSB to the vicinity of insoluble phosphorus patches. Secreting acids enhance organic phosphorus mineralization on the part of PSB. PSB move in a thick water film formed around fungal hyphae [150]. In conclusion, bacteria play an important role in helping plants to indirectly translocate phosphorus and mineralize phosphorus sources for soil phosphorus cycling and regulation, which will aid in reducing phosphorus fertilizer application, with significant prospects and implications.

### 3.3. Beneficial Bacteria Regulate Plants' Growth and Development and Reduce Phosphorus Fertilizer Application

PSB provide nutrients for plants, improve soil nutrient balance, and enhance green development. They are also considered the most environmentally friendly biotechnology that can be used to provide nutrients for plants [151]. In the 1990s, researchers discovered phosphorus-solubilizing microorganisms (PSM) and isolated some bacteria. With greater in-depth research on microorganisms, more and more studies have reported their important effects on soil phosphorus. Rafael [152] found that, under phosphate-restricted growth conditions, some bacteria replace their membrane phospholipids with phosphorus-deficient lipids. Under restricted phosphate conditions, in *Sinorhizobium melilotii*, membrane phospholipids provide a source of metabolizable inorganic phosphates that can be used to synthesize other essential phosphorus-containing biomolecules [153]. This enables it to satisfy its own phosphorus transport and plant phosphorus uptake.

Inoculating *Rhizobium* into regular soybeans was found to increase the number of pods, fresh weight, and dry weight of soybeans, and these effects have been well validated in field experiments, making a beneficial contribution to reducing fertilization and associated carbon. In [154], the combination of a phosphorus fertilizer at different gradients with PSB was more effective in promoting the tillering number and grain weight, and enhancing the yield of wheat, than using phosphorus fertilizer alone. The addition of PSB can effectively reduce the requirements for phosphorus fertilizer. Under low-phosphorus conditions, it affected the length, surface area, diameter and intracellular phosphatase activity of wheat roots, effects that are significantly correlated with better phosphorus absorption [155]. PSB can effectively increase the content of available phosphorus in soil, and promote the yield of peanut grain and the biomass of the bud [156]. PSB can provide plants with the required nutrients even at phosphorus levels ranging from 0.1 to 10  $\mu\text{m}$  [157]. On the contrary, the excessive use of phosphate fertilizer can reduce the activity of these enzymes, which can alleviate the oxidative response of plants under stress [158].

### 3.4. Colonization of Bacterial Communities in Plants Is Influenced by Phosphorus

Phosphorus not only affects plant growth, but also affects the community structure of bacteria. In the non-mycorrhizal plant *Arabidopsis thaliana* L., *Burkholderia* was specifically enriched in plant tissue under P activation, and different phosphorus concentration states affect the enrichment and colonization of the bacterial community [159]. Auxin is an important factor in phosphorus regulation [160]. PSB can also help *Solanaceae* resist pathogens after being soaked in bacterial fertilizers, such as reducing *Fusarium oxysporum* [161], *Aspergillus*, *Penicillium* [162], and *Botrytis cinerea* by 48% [163], as well as *Macropomina phaseolina* [164] and *Pseudomonas aeruginosa* [165], and this may be related to the discovery of antibiotic-resistance genes in PSB [166]. Studies have shown that under low-phosphorus stress, bacteria are more sensitive to phosphorus enrichment and recruitment than fungi [167]. Under low-phosphorus stress, the bacterial community diversity of rice (*Oryza sativa* L.) was significantly higher than that of fungi, but when the phosphorus level was sufficient, the diversity of fungi was higher than that of bacteria [168]. This shows that under different phosphorus gradients, fungi and bacteria display a clear division of labor, with their own respective dominant positions.

### 3.5. Bacterial Hormones Indirectly Affect Phosphorus Uptake by Plants

These PSB can not only dissolve phosphorus, but also produce various hormones (gibberellin [169,170], auxin [171], and cytokinin [172]) that stimulate plant growth, affect plant hormone synthesis and signal transduction, and improve crop productivity [173]. There are close links between hormone signaling and phosphorus absorption and transport [174,175]. Two bacterial strains isolated from rhizosphere (*Chryseobacterium culicis* and *Paenibacillus polymyxa*) were found to affect rhizosphere development, which appeared to be directly related to the ability of *Flavobacterium* sp. and *Chryseobacterium culicis* to produce growth hormones, while barley root sheaths inoculated with auxin-mutant strains were significantly stunted [176]. Studies have shown that the metabolic synthesis of growth hormones in plants is affected by the concentration of growth hormone in the soil, which appears to be linked to the bacterial production of the hormone [177]. There is no simple material exchange between plants and the auxin-producing bacteria. The study found that the auxin-secreting bacterium *B. velezensis* triggers an immune response in *Arabidopsis*. The auxin secreted by bacteria can reduce the amount of reactive oxygen species produced by the plant immune response. The production of reactive oxygen species in plants can induce an increase in auxin and improve root colonization [178].

## 4. Effect of a Combination of Mixed Microbial Populations on Plant Phosphorus Acquisition

### 4.1. Co-Application of Fungi and Bacteria Improves Crop Yields and Reduces Phosphorus Fertilizer

At present, research on soil microorganisms is no longer limited to the effects and impacts of single microorganisms on plants. Studies have shown that interactions between multiple strains are more beneficial to plants. There is a cooperative relationship between fungi and bacteria [179–181]. In field experiments, the effects of the interaction between AMF and PSB were significantly different compared to those derived using a single fertilizer, promoting the photosynthetic rate, leaf area, plant height, and inulin content of sunflowers. There is a significant positive correlation between the presence of PSB and the colonization of AMF [182]. Two types of microorganisms are responsible for different functions: PSB is responsible for dissolving phosphate, and AMF is responsible for transporting and helping plants absorb nutrients [183]. PSB and AMF play different roles in the intercropping of corn and soybeans. The application of arbuscular fungi and intercropping modes can effectively improve phosphorus absorption efficiency and greatly increase corn yield. However, the co-inoculation of AMF and PGPB significantly increases soil phosphorus migration [184]. The *Pseudomonas* and AMF isolated from onions significantly increase the weight of wheat grains in phosphorus-deficient soil compared to a single inoculation. Different combinations of fungi have different effects, and during the interaction, phosphorus is taken up from

the outside. AMF and endophytic bacteria not only improve the quality of fruit, but also increase the amounts of trace elements in navel oranges. The activity of soil total phosphatase is positively correlated with the amount of bacteria present, which depends upon the proportions of different strains and combinations [185].

Moreover, an exchange of elements occurs between fungi and bacteria, and AMF releases a large amount of C into the environment, triggering the growth and activity of PSB. In return, PSB enhance the mineralization of organic phosphorus and increase the phosphorus availability of AMF. When the soil's available phosphorus content is low, PSB compete with AMF for P, and this activity is not stimulated by fungi. When phosphorus is added to increase the soil's available phosphorus, PSB promote the growth of AMF hyphae, and PSB activity is stimulated by fungi [186]. In short, fungi and bacteria are beneficial for use as composite microbial fertilizers to increase agricultural production, providing a better, more sustainable approach to field management [187].

#### 4.2. Co-Application of Two or More Bacteria Is Effective for Plant Phosphorus Uptake

In addition to the significant effects of fungi and bacteria, the use of multiple bacteria also reflects their potential values. The mixed application of *Pseudomonas* and *Panococcus* can promote the leaf stem length, leaf number, stem number, and dry weight of mint. Although both chemical and organic phosphorus fertilizers can increase the photosynthesis of peppermint, the addition of biological agents not only increases the protein content, but also increases the contents of various antioxidant enzymes, such as catalase, ascorbate peroxidase, and superoxide dismutase [188]. Bacteria isolated from *Abies fabri* (Mast.), even a mixed bacterial fertilizer diluted 60 times (the basic concentration was  $3 \times 10^8$  CFU/mL), has a better effect on promoting the fresh weight and plant height of *Abies fabri* (Mast.) seedlings than a single bacterial agent. At the same time, it also increased the contents of total nitrogen, total phosphorus, and potassium in leaves, and increased the contents of acid phosphatase and urease in the soil [189]. Two types of purple nonsulfur bacteria (PNSB) from *Artemisia annua* L. [190] have been validated for use in low-acidic saline soil. They can not only dissolve insoluble phosphorus (AL-P, Ca-P) and effectively reduce salt toxicity, but they also reduce the requirements of phosphorus fertilizer application by 50% [191]. *Bacillus thuringiensis* used Ca(PO), FePO, and AlPO as the sole P resource, and this significantly increased water-soluble phosphate concentrations, which reached 555.84 mg/L. This promoted plant growth and reduced shoot Pb concentrations when the plant was grown in artificially Pb-contaminated soil [192]. Mixed bacterial fertilizers also have a significant effect on fruit. Using the mixed bacteria of *Bacillus subtilis* increased the anthocyanin content in the flesh of blood orange, improved the acidity in the juice, and enhanced the taste of the fruit, and has contributed to the growth of the agricultural economy. At the same time, it also helped farmers reduce the use of chemical fertilizers by half [193]. In addition to mixed microbial agents, the use of different composts and combinations of mixed microbial populations also improved the soil microbial community's structure, increased the phosphorus content of sugarcane buds, and increased the contents of nitrogen and potassium [194].

From the above research, we can infer the superiority of a combination of multi-microbes, implying that it is necessary to develop more combinations of mixed microbial populations. Delving into the molecular mechanisms underlying these relationships and conducting research spanning from the macrocosmic to the microcosmic will be essential. This holds great potential in relation to enhancing our understanding of the network dynamics and compositional structure, the functional expression, and other relevant facets, of these complex ecosystems.

## 5. Conclusions

Under phosphorus stress, during the symbiotic development of fungi and plants, high-efficiency phosphorus transporters such as PT1, PT3, PT8, PT5, PT6, and PT7 help plants take up phosphorus (Figure 1) and induce the phosphorus transcription factor PHR

to regulate downstream PHT family proteins. In addition, the effects of the inoculation of beneficial fungi on plant physiological traits, such as plant stem diameter, leaf and root development, and yield, under phosphorus stress have been elucidated. Furthermore, we have proposed that the inoculation of fungi can increase the absorption of phosphorus by plants, thereby reducing the amount of phosphate fertilizer required. We also discussed how the inoculation of fungi results in the stimulation of hormones and genes that regulate plant phosphorus, including PHO1 and PHT family proteins. We also found that inoculation with fungi had an effect on plant hormone synthesis, and hormones had an important connection to phosphorus transport. We also found that the organic acid and phosphatase in the secretions of fungi are beneficial to the absorption of phosphorus by plants. We also expanded our understanding of the roles and impacts of fungi on plant phosphorus uptake in relation to non-mycorrhizal plants. All of this fully illustrates the importance of beneficial fungi in plant phosphorus acquisition and the mechanisms by which they work.

In summarizing the mechanisms of bacteria involved in plant phosphorus acquisition, we first introduced the same bacteria's own comprehensive phosphorus transport system (Pt), which is essential in helping bacteria to transport phosphorus. In addition, we found that PT7, PT2, PT3, PT6, and PT5 (Table 2) are important proteins involved in phosphorus uptake and acquisition. At the same time, we found that the inoculation of bacteria will affect the transcription factor PHR, which seems to be related to the colonization and symbiosis of bacteria in roots. Secondly, we elaborated on the transfer and dissolution roles of bacterial secretions in relation to soil phosphorus, such as phytic acid, malic acid, citric acid, and lactic acid (Figure 2). In addition, we also found that the hormones secreted by bacteria can indirectly promote the transport of phosphorus by plants, and can be utilized and transformed by plants. These include auxin and ethylene. Through the elaboration of the effects of bacterial inoculation on the plant roots' surface area, grain size, pod number, bud, tillering number, etc., we showed that beneficial bacteria can also affect plant growth and phosphorus absorption, and reduce the amount of phosphate fertilizer used. Soil phosphorus content has an important influence on the composition of the bacterial community. Under different phosphorus concentrations, the community divisions of bacteria and fungi are different, but each play an important role.

Finally, we found that using the compound microbial fertilizer as a biological fertilizer is more effective than using a single microbial inoculation. They jointly promote plant photosynthesis and yield, and stimulate soil phosphorus transfer, thereby reducing the amount of phosphorus fertilizer used. Bacteria and fungi can not only exchange elements, but also increase the availability of phosphorus in soil. Fungi can enhance the uptake of phosphorus by plants, and bacteria can also effectively increase the activity of fungi. Therefore, we analyzed the results of inoculation experiments performed on a variety of mixed microorganisms and concluded that the use of mixed microorganisms shows advantages related to the development and role of mutual relations. The two microorganisms can help plants to absorb phosphorus more efficiently.

## 6. Application Prospects of Composite Microbiological Fertilizer and Suggestions

By searching on the Web of Science (WOS) database, we found 1200 high-frequency articles with the keywords phosphorus, bacteria, fungi, growth-promoting bacteria, PGPR, and microbial inoculants, and then used the VOS viewer software (1.6.19.0) to perform a cluster analysis (Figure 3). We found that the research on phosphorus, bacterial fertilizer, biological bacteria, and growth-promoting bacteria has been popular in recent years, which has certain application and development prospects. The research on phosphorus is more focused on phosphorus fertilizers, phosphorus availability, bio-bacterial fertilizers, yield increase, phosphorus transport and absorption, gene regulation and expression, phosphorus and IAA synthesis, and the association with beneficial strains.



excessive application of chemical fertilizers, reduces carbon dioxide emissions to a certain extent, and contributes to green and sustainable development with carbohydrate-active enzymes [213].

Applying these beneficial microorganisms as biological agents to the field contributes to the concept of “green sustainable development”, and provides a feasible solution to carbon peaking and carbon neutralization. As previously suggested, the composite strain surpassed its single-strain counterpart in efficacy. The advantageous microorganisms not only enhance plant phosphorus absorption, but also confer resistance against pests and diseases. Furthermore, the developed encapsulation agents augment their effectiveness, reduce application duration, and reduce expenditure. Therefore, the cultivation of additional strain combinations and novel strains, alongside the investigation of bacterial encapsulation agents, holds great promise. Moreover, the elucidation of the mechanism by which bacteria facilitate plant growth and bolster disease resistance warrants further scrutiny. For instance, the literature is notably sparse on the subject of rhizobial phosphorus transporters. The burgeoning research interest in microbial studies, as evidenced by the aforementioned research hotspots, signifies that there remains wide scope for enhancing beneficial microorganisms.

In recent years, substantial strides have been made in the research into and development of microbial fertilizers. However, their uptake among farmers has been limited, with their usage falling well short of that of traditional fertilizers due to a lack of awareness. Addressing this disparity necessitates a two-pronged approach. Firstly, emphasizing the economic benefits of microbial fertilizers through large-scale experiments and demonstrations is imperative. Secondly, concerted efforts to underscore the ecological and societal advantages of adopting microbial fertilizers through robust policy promotions and guidance are essential. Furthermore, bolstering the fundamental theoretical research on microbial fertilizers, encompassing aspects such as microbial fertilizer mechanisms, the identification of superior microbial strains, and the development of multifunctional microbial fertilizers, is indispensable for fostering the continuous advancement of the microbial fertilizer industry and catalyzing the sustainable evolution of agriculture.

Microorganisms, though diminutive, wield considerable influence over the global market and agricultural practices, holding new economic prospects. In the context of pandemic-induced economic volatility, an unwavering commitment to scientific advancement will open new vistas in the microbial market. Embracing microbial agents as an environmentally friendly avenue is pivotal in curtailing the use of chemical fertilizers, enhancing food quality and nutritional value, rejuvenating soil health, and contributing to the nation’s sustainable development goals. This proactive approach aligns with national policies, and signifies a pivotal stride towards achieving verdant ecological progress. As the agricultural biological agent sector is still in its nascent form, there is ample potential for advancement, with the promise of transforming “clear waters and lush mountains” into tangible “gold and silver mountains”.

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## References

1. Malhotra, H.; Vandana; Sharma, S.; Pandey, R. Phosphorus Nutrition: Plant Growth in Response to Deficiency and Excess. In *Plant Nutrients and Abiotic Stress Tolerance*; Hasanuzzaman, M., Fujita, M., Oku, H., Nahar, K., Hawrylak-Nowak, B., Eds.; Springer: Singapore, 2018; pp. 171–190.
2. Chen, S.; Zhang, S.; Yan, Z.; Peng, Y.; Chen, Q. Differences in main processes to transform phosphorus influenced by ammonium nitrogen in flooded intensive agricultural and steppe soils. *Chemosphere* **2019**, *226*, 192–200. [[CrossRef](#)] [[PubMed](#)]
3. Azam, H.M.; Alam, S.T.; Hasan, M.M.; Yameogo, D.D.S.; Kannan, A.D.; Rahman, A.; Kwon, M.J. Phosphorous in the environment: Characteristics with distribution and effects, removal mechanisms, treatment technologies, and factors affecting recovery as minerals in natural and engineered systems. *Environ. Sci. Pollut. Res.* **2019**, *26*, 20183–20207. [[CrossRef](#)] [[PubMed](#)]
4. Hu, P.; Xu, J.; Wang, L.; Tang, H.; Wu, M.; Xu, P. Influence of Different Single Factors on the Spatial-Temporal Distribution Law of Phosphorus in the Generalized River. *Sustainability* **2022**, *14*, 2070. [[CrossRef](#)]
5. Zhang, C.; Tian, H.; Liu, J.; Wang, S.; Liu, M.; Pan, S.; Shi, X. Pools and distributions of soil phosphorous in China. *Glob. Biogeochem. Cycles* **2005**, *19*, B1020. [[CrossRef](#)]
6. Astiko, W.; Ernawati, N.; Silawibawa, I. Nutrient concentration of nitrogen and phosphorus on intercropping of several varieties maize and soybean in dryland North Lombok, Indonesia. *IOP Conf. Ser. Earth Environ. Sci.* **2021**, *824*, 12001. [[CrossRef](#)]
7. Nowaki, R.H.D.; Parent, S.; Cecilio Filho, A.B.; Rozane, D.E.; Meneses, N.B.; Da Silva, J.S.; Natale, W.; Parent, L.E. Phosphorus Over-Fertilization and Nutrient Misbalance of Irrigated Tomato Crops in Brazil. *Front. Plant Sci.* **2017**, *8*, 825. [[CrossRef](#)]
8. Haygarth, P.M.; Rufino, M.C. Local solutions to global phosphorus imbalances. *Nat. Food* **2021**, *2*, 459–460. [[CrossRef](#)]
9. Liu, H.; Li, S.; Qiang, R.; Lu, E.; Cuilan, L.; Zhang, J.; Gao, Q. Response of Soil Microbial Community Structure to Phosphate Fertilizer Reduction and Combinations of Microbial Fertilizer. *Front. Environ. Sci.* **2022**, *10*, 899727. [[CrossRef](#)]
10. Dinca, L.; Grenni, P.; Onet, A.; Onet, C. Fertilization and Soil Microbial Community: A Review. *Appl. Sci.* **2022**, *12*, 1198. [[CrossRef](#)]
11. Wang, X.; Xiong, J.; He, Z. Activated dolomite phosphate rock fertilizers to reduce leaching of phosphorus and trace metals as compared to superphosphate. *J. Environ. Manag.* **2019**, *255*, 109872. [[CrossRef](#)]
12. Kianpoor Kalkhajah, Y.; Huang, B.; Sørensen, H.; Holm, P.; Hansen, H. Phosphorus accumulation and leaching risk of greenhouse vegetable soils in Southeast China. *Pedosphere* **2021**, *31*, 683–693. [[CrossRef](#)]
13. Kaminsky, L.; Thompson, G.; Trexler, R.; Bell, T.; Kao-Kniffin, J. *Medicago sativa* has Reduced Biomass and Nodulation When Grown with Soil Microbiomes Conditioned to High Phosphorus Inputs. *Phytobiomes J.* **2018**, *2*, 237–248. [[CrossRef](#)]
14. Schipper, L.A.; Sparling, G.P.; Fisk, L.M.; Dodd, M.B.; Power, I.L.; Littler, R.A. Rates of accumulation of cadmium and uranium in a New Zealand hill farm soil as a result of long-term use of phosphate fertilizer. *Agric. Ecosyst. Environ.* **2011**, *144*, 95–101. [[CrossRef](#)]
15. Cheraghi, M.; Lorestani, B.; Merrikhpour, H. Investigation of the Effects of Phosphate Fertilizer Application on the Heavy Metal Content in Agricultural Soils with Different Cultivation Patterns. *Biol. Trace Elem. Res.* **2012**, *145*, 87–92. [[CrossRef](#)]
16. Coleman, D.; Wall, D. Fauna: The engine for microbial activity and transport. In *Soil Microbiology, Ecology and Biochemistry*, 3rd ed.; Academic Press: Cambridge, MA, USA, 2006; pp. 163–191. [[CrossRef](#)]
17. Sosa, O.A. Phosphorus redox reactions as pinch hitters in microbial metabolism. *Proc. Natl. Acad. Sci. USA* **2018**, *115*, 7–8. [[CrossRef](#)]
18. Pierret, A.; Doussan, C.; Capowiez, Y.; Bastardie, F.; Pagès, L. Root Functional Architecture: A Framework for Modeling the Interplay between Roots and Soil. *Vadose Zone J.* **2007**, *6*, 269–281. [[CrossRef](#)]
19. Haney, C.H.; Samuel, B.S.; Bush, J.; Ausubel, F.M. Associations with rhizosphere bacteria can confer an adaptive advantage to plants. *Nat. Plants* **2015**, *1*, 15051. [[CrossRef](#)] [[PubMed](#)]
20. Tripathi, M.; Gaur, R. 9—Bioactivity of soil microorganisms for agriculture development. In *Microbes in Land Use Change Management*; Singh, J.S., Tiwari, S., Singh, C., Singh, A.K., Eds.; Elsevier: Amsterdam, The Netherlands, 2021; pp. 197–220.
21. Choi, K.; Khan, R.; Lee, S. Dissection of plant microbiota and plant-microbiome interactions. *J. Microbiol.* **2021**, *59*, 281–291. [[CrossRef](#)] [[PubMed](#)]
22. Compant, S.; Samad, A.; Faist, H.; Sessitsch, A. A review on the plant microbiome: Ecology, functions, and emerging trends in microbial application. *J. Adv. Res.* **2019**, *19*, 29–37. [[CrossRef](#)] [[PubMed](#)]
23. Liu, H.; Brettell, L.E.; Qiu, Z.; Singh, B.K. Microbiome-Mediated Stress Resistance in Plants. *Trends Plant Sci.* **2020**, *25*, 733–743. [[CrossRef](#)] [[PubMed](#)]
24. Karimi, A.; Khodaverdiloo, H.; Sepehri, M.; Rasouli-Sadaghiani, M. Arbuscular mycorrhizal fungi and heavy metal contaminated soils. *Afr. J. Microbiol. Res.* **2011**, *5*, 1571–1576. [[CrossRef](#)]
25. Wang, D.; Lv, S.; Jiang, P.; Li, Y. Roles, Regulation, and Agricultural Application of Plant Phosphate Transporters. *Front. Plant Sci.* **2017**, *8*, 817. [[CrossRef](#)] [[PubMed](#)]
26. Huang, Y.; Dai, Z.; Lin, J.; Li, D.; Ye, H.; Dahlgren, R.A.; Xu, J. Labile carbon facilitated phosphorus solubilization as regulated by bacterial and fungal communities in *Zea mays*. *Soil Biol. Biochem.* **2021**, *163*, 108465. [[CrossRef](#)]
27. Saia, S.; Aissa, E.; Luziatelli, F.; Ruzzi, M.; Colla, G.; Ficca, A.G.; Cardarelli, M.; Roupael, Y. Growth-promoting bacteria and arbuscular mycorrhizal fungi differentially benefit tomato and corn depending upon the supplied form of phosphorus. *Mycorrhiza* **2020**, *30*, 133–147. [[CrossRef](#)] [[PubMed](#)]

28. Tang, M.; Zhu, Q.; Zhang, F.; Zhang, W.; Yuan, J.; Sun, K.; Xu, F.; Dai, C. Enhanced nitrogen and phosphorus activation with an optimized bacterial community by endophytic fungus *Phomopsis liquidambari* in paddy soil. *Microbiol. Res.* **2019**, *221*, 50–59. [[CrossRef](#)] [[PubMed](#)]
29. Liu, J.; Hu, J.; Cheng, Z.; Li, M.; Liu, Z.; Wang, J.; Lin, X. Can phosphorus (P)-releasing bacteria and earthworm (*Eisenia fetida* L.) co-enhance soil P mobilization and mycorrhizal P uptake by maize (*Zea mays* L.)? *J. Soil Sediments* **2021**, *21*, 842–852. [[CrossRef](#)]
30. Tatry, M.; El Kassis, E.; Lambilliotte, R.; Corratgé, C.; Van Aarle, I.; Amenc, L.K.; Alary, R.; Zimmermann, S.; Sentenac, H.; Plassard, C. Two differentially regulated phosphate transporters from the symbiotic fungus *Hebeloma cylindrosporum* and phosphorus acquisition by ectomycorrhizal *Pinus pinaster*. *Plant J.* **2009**, *57*, 1092–1102. [[CrossRef](#)] [[PubMed](#)]
31. Shi, J.; Wang, X.; Wang, E. Mycorrhizal Symbiosis in Plant Growth and Stress Adaptation: From Genes to Ecosystems. *Annu. Rev. Plant Biol.* **2023**, *74*, 569–607. [[CrossRef](#)]
32. Hijikata, N.; Murase, M.; Tani, C.; Ohtomo, R.; Osaki, M.; Ezawa, T. Polyphosphate has a central role in the rapid and massive accumulation of phosphorus in extraradical mycelium of an arbuscular mycorrhizal fungus. *New Phytol.* **2010**, *186*, 285–289. [[CrossRef](#)]
33. Maldonado-Mendoza, I.E.; Dewbre, G.R.; Harrison, M.J. A Phosphate Transporter Gene from the Extra-Radical Mycelium of an Arbuscular Mycorrhizal Fungus *Glomus intraradices* Is Regulated in Response to Phosphate in the Environment. *Mol. Plant-Microbe Interact.* **2001**, *14*, 1140–1148. [[CrossRef](#)]
34. Benedetto, A.; Magurno, F.; Bonfante, P.; Lanfranco, L. Expression profiles of a phosphate transporter gene (GmosPT) from the endomycorrhizal fungus *Glomus mosseae*. *Mycorrhiza* **2005**, *15*, 620–627. [[CrossRef](#)] [[PubMed](#)]
35. Xie, X.; Lin, H.; Peng, X.; Xu, C.; Sun, Z.; Jiang, K.; Huang, A.; Wu, X.; Tang, N.; Salvioli, A.; et al. Arbuscular Mycorrhizal Symbiosis Requires a Phosphate Transceptor in the *Gigaspora margarita* Fungal Symbiont. *Mol. Plant* **2016**, *9*, 1583–1608. [[CrossRef](#)] [[PubMed](#)]
36. Xie, X.; Lai, W.; Che, X.; Wang, S.; Ren, Y.; Hu, W.; Chen, H.; Tang, M. A SPX domain-containing phosphate transporter from *Rhizophagus irregularis* handles phosphate homeostasis at symbiotic interface of arbuscular mycorrhizas. *New Phytol.* **2022**, *234*, 650–671. [[CrossRef](#)] [[PubMed](#)]
37. Xie, X.; Huang, W.; Liu, F.; Tang, N.; Liu, Y.; Lin, H.; Zhao, B. Functional analysis of the novel mycorrhiza-specific phosphate transporter AsPT1 and PHT1 family from *Astragalus sinicus* during the arbuscular mycorrhizal symbiosis. *New Phytol.* **2013**, *198*, 836–852. [[CrossRef](#)]
38. Maeda, D.; Ashida, K.; Iguchi, K.; Chechetka, S.A.; Hijikata, A.; Okusako, Y.; Deguchi, Y.; Izui, K.; Hata, S. Knockdown of an Arbuscular Mycorrhiza-inducible Phosphate Transporter Gene of *Lotus japonicus* Suppresses Mutualistic Symbiosis. *Plant Cell Physiol.* **2006**, *47*, 807–817. [[CrossRef](#)]
39. Harrison, M.J.; Dewbre, G.R.; Liu, J. A Phosphate Transporter from *Medicago truncatula* Involved in the Acquisition of Phosphate Released by Arbuscular Mycorrhizal Fungi. *Plant Cell* **2002**, *14*, 2413–2429. [[CrossRef](#)]
40. Grace, E.J.; Cotsaftis, O.; Tester, M.; Smith, F.A.; Smith, S.E. Arbuscular mycorrhizal inhibition of growth in barley cannot be attributed to extent of colonization, fungal phosphorus uptake or effects on expression of plant phosphate transporter genes. *New Phytol.* **2009**, *181*, 938–949. [[CrossRef](#)]
41. Wegmüller, S.; Svistoonoff, S.; Reinhardt, D.; Stuurman, J.; Amrhein, N.; Bucher, M. A transgenic dTph1 insertional mutagenesis system for forward genetics in mycorrhizal phosphate transport of *Petunia*. *Plant J.* **2008**, *54*, 1115–1127. [[CrossRef](#)]
42. Tamura, Y.; Kobae, Y.; Mizuno, T.; Hata, S. Identification and Expression Analysis of Arbuscular Mycorrhiza-Inducible Phosphate Transporter Genes of Soybean. *Biosci. Biotechnol. Biochem. Biotechnol. Biochem.* **2012**, *76*, 309–313. [[CrossRef](#)]
43. Nagy, R.; Karandashov, V.; Chague, V.; Kalinkevich, K.; Tamasloukht, M.; Xu, G.; Jakobsen, I.; Levy, A.A.; Amrhein, N.; Bucher, M. The characterization of novel mycorrhiza-specific phosphate transporters from *Lycopersicon esculentum* and *Solanum tuberosum* uncovers functional redundancy in symbiotic phosphate transport in solanaceous species. *Plant J.* **2005**, *42*, 236–250. [[CrossRef](#)]
44. Willmann, M.; Zellerhoff, N.; Buer, B.; Polatajko, A.; Nagy, R.; Koebke, E.; Jansa, J.; Flisch, R.; Bucher, M. Mycorrhizal phosphate uptake pathway in maize: Vital for growth and cob development on nutrient poor agricultural and greenhouse soils. *Front. Plant Sci.* **2013**, *4*, 533. [[CrossRef](#)]
45. Molinero-Rosales, N.; Martín-Rodríguez, J.Á.; Ho-Plágaro, T.; García-Garrido, J.M. Identification and expression analysis of the arbuscular mycorrhiza-inducible Rieske non-heme oxygenase Ptc52 gene from tomato. *J. Plant Physiol.* **2019**, *237*, 95–103. [[CrossRef](#)]
46. Valat, L.; Deglène-Benbrahim, L.; Kendel, M.; Hussenet, R.; Le Jeune, C.; Schellenbaum, P.; Maillot, P. Transcriptional induction of two phosphate transporter 1 genes and enhanced root branching in grape plants inoculated with *Funneliformis mosseae*. *Mycorrhiza* **2018**, *28*, 179–185. [[CrossRef](#)]
47. Das, D.; Paries, M.; Hobecker, K.; Gigl, M.; Dawid, C.; Lam, H.; Zhang, J.; Chen, M.; Gutjahr, C. PHOSPHATE STARVATION RESPONSE transcription factors enable arbuscular mycorrhiza symbiosis. *Nat. Commun.* **2022**, *13*, 477. [[CrossRef](#)] [[PubMed](#)]
48. Chen, A.; Gu, M.; Sun, S.; Zhu, L.; Hong, S.; Xu, G. Identification of two conserved cis-acting elements, MYCS and P1BS, involved in the regulation of mycorrhiza-activated phosphate transporters in eudicot species. *New Phytol.* **2011**, *189*, 1157–1169. [[CrossRef](#)] [[PubMed](#)]
49. Wang, P.; Limpens, E.; Yao, R. Orchestrating plant direct and indirect phosphate uptake pathways. *Trends Plant Sci.* **2022**, *27*, 319–321. [[CrossRef](#)] [[PubMed](#)]

50. Zhao, B.; Jia, X.; Yu, N.; Murray, J.D.; Yi, K.; Wang, E. Microbe-dependent and independent nitrogen and phosphate acquisition and regulation in plants. *New Phytol.* **2023**. [[CrossRef](#)] [[PubMed](#)]
51. Zhang, Q.; Wang, S.; Xie, Q.; Xia, Y.; Lu, L.; Wang, M.; Wang, G.; Long, S.; Cai, Y.; Xu, L.; et al. Control of arbuscule development by a transcriptional negative feedback loop in *Medicago*. *Nat. Commun.* **2023**, *14*, 5743. [[CrossRef](#)] [[PubMed](#)]
52. George, T.S.; Simpson, R.J.; Hadobas, P.A.; Richardson, A.E. Expression of a fungal phytase gene in *Nicotiana tabacum* improves phosphorus nutrition of plants grown in amended soils. *Plant Biotechnol. J.* **2005**, *3*, 129–140. [[CrossRef](#)]
53. Giovannini, L.; Sbrana, C.; Giovannetti, M.; Avio, L.; Lanubile, A.; Marocco, A.; Turrini, A. Diverse mycorrhizal maize inbred lines differentially modulate mycelial traits and the expression of plant and fungal phosphate transporters. *Sci. Rep.* **2022**, *12*, 21279. [[CrossRef](#)]
54. Kikuchi, Y.; Hijikata, N.; Yokoyama, K.; Ohtomo, R.; Handa, Y.; Kawaguchi, M.; Saito, K.; Ezawa, T. Polyphosphate accumulation is driven by transcriptome alterations that lead to near-synchronous and near-equivalent uptake of inorganic cations in an arbuscular mycorrhizal fungus. *New Phytol.* **2014**, *204*, 638–649. [[CrossRef](#)]
55. Uetake, Y.; Kojima, T.; Ezawa, T.; Saito, M. Extensive tubular vacuole system in an arbuscular mycorrhizal fungus, *Gigaspora margarita*. *New Phytol.* **2002**, *154*, 761–768. [[CrossRef](#)]
56. Andreeva, N.; Ledova, L.; Ryazanova, L.; Tomashevsky, A.; Kulakovskaya, T.; Eldarov, M. *Ppn2* endopolyphosphatase overexpressed in *Saccharomyces cerevisiae*: Comparison with *Ppn1*, *Ppx1*, and *Ddp1* polyphosphatases. *Biochimie* **2019**, *163*, 101–107. [[CrossRef](#)]
57. Wipf, D.; Krajinski, F.; van Tuinen, D.; Recorbet, G.; Courty, P. Trading on the arbuscular mycorrhiza market: From arbuscules to common mycorrhizal networks. *New Phytol.* **2019**, *223*, 1127–1142. [[CrossRef](#)] [[PubMed](#)]
58. Dąbrowska, G.; Garstecka, Z.; Trejgell, A.; Dąbrowski, H.; Konieczna, W.; Szyg-Borowska, I. The Impact of Forest Fungi on Promoting Growth and Development of *Brassica napus* L. *Agronomy* **2021**, *11*, 2475. [[CrossRef](#)]
59. Begum, N.; Qin, C.; Ahanger, M.; Raza, S.; Khan, M.; Ashraf, M.; Ahmed, N.; Zhang, L. Role of Arbuscular Mycorrhizal Fungi in Plant Growth Regulation: Implications in Abiotic Stress Tolerance. *Front. Plant Sci.* **2019**, *10*, 1068. [[CrossRef](#)] [[PubMed](#)]
60. Rigobelo, E.; Baron Cozentino, N. Endophytic fungi: A tool for plant growth promotion and sustainable agriculture. *Mycology* **2021**, *13*, 39–55. [[CrossRef](#)]
61. Silva, J.; Montaldo, Y.; Almeida, A.; Dalbon, V.; Acevedo, J.; Santos, T.M.; Lima, G.S.D. Rhizospheric Fungi to Plant Growth Promotion: A Review. *J. Agric. Stud.* **2021**, *9*, 411. [[CrossRef](#)]
62. Gao, X.; Guo, H.; Zhang, Q.; Guo, H.; Zhang, L.; Zhang, C.; Gou, Z.; Liu, Y.; Wei, J.; Chen, A.; et al. Arbuscular mycorrhizal fungi (AMF) enhanced the growth, yield, fiber quality and phosphorus regulation in upland cotton (*Gossypium hirsutum* L.). *Sci. Rep.* **2020**, *10*, 2084. [[CrossRef](#)]
63. Ceballos, I.; Ruiz, M.; Fernández, C.; Peña, R.; Rodríguez, A.; Sanders, I.R. The In Vitro Mass-Produced Model Mycorrhizal Fungus, *Rhizophagus irregularis*, Significantly Increases Yields of the Globally Important Food Security Crop Cassava. *PLoS ONE* **2013**, *8*, e70633. [[CrossRef](#)] [[PubMed](#)]
64. El-Sherbeny, T.M.S.; Mousa, A.M.; El-Sayed, E.R. Use of mycorrhizal fungi and phosphorus fertilization to improve the yield of onion (*Allium cepa* L.) plant. *Saudi J. Biol. Sci.* **2022**, *29*, 331–338. [[CrossRef](#)]
65. Mai, W.; Xue, X.; Feng, G.; Yang, R.; Tian, C. Arbuscular mycorrhizal fungi—15-Fold enlargement of the soil volume of cotton roots for phosphorus uptake in intensive planting conditions. *Eur. J. Soil Biol.* **2019**, *90*, 31–35. [[CrossRef](#)]
66. Hiruma, K.; Kobae, Y.; Toju, H. Beneficial associations between Brassicaceae plants and fungal endophytes under nutrient-limiting conditions: Evolutionary origins and host–symbiont molecular mechanisms. *Curr. Opin. Plant Biol.* **2018**, *44*, 145–154. [[CrossRef](#)]
67. Merlin, E.; Melato, E.; Lourenço, E.L.B.; Jacomassi, E.; Junior, A.G.; Da Cruz, R.M.S.; Otênio, J.K.; Da Silva, C.; Alberton, O. Inoculation of arbuscular mycorrhizal fungi and phosphorus addition increase coarse mint (*Plectranthus amboinicus* Lour.) plant growth and essential oil content. *Rhizosphere* **2020**, *15*, 100217. [[CrossRef](#)]
68. Yadav, A.; Suri, V.K.; Kumar, A.; Choudhary, A.K. Effect of AM fungi and phosphorus fertilization on P-use efficiency, nutrient acquisition and root morphology in pea (*Pisum sativum* L.) in an acid Alfisol. *J. Plant Nutr.* **2018**, *41*, 689–701. [[CrossRef](#)]
69. Cao, M.; Liu, R.; Xiao, Z.; Hashem, A.; Abd Allah, E.F.; Alsayed, M.F.; Harsonowati, W.; Wu, Q. Symbiotic Fungi Alter the Acquisition of Phosphorus in *Camellia oleifera* through Regulating Root Architecture, Plant Phosphate Transporter Gene Expressions and Soil Phosphatase Activities. *J. Fungi* **2022**, *8*, 800. [[CrossRef](#)] [[PubMed](#)]
70. Chen, W.; Li, J.; Zhu, H.; Xu, P.; Chen, J.; Yao, Q. The differential and interactive effects of arbuscular mycorrhizal fungus and phosphorus on the lateral root formation in *Poncirus trifoliata* (L.). *Sci. Hortic.-Amst.* **2017**, *217*, 258–265. [[CrossRef](#)]
71. Yuan, Z.Y.; Chen, H.Y.H.; Reich, P.B. Global-scale latitudinal patterns of plant fine-root nitrogen and phosphorus. *Nat. Commun.* **2011**, *2*, 344. [[CrossRef](#)] [[PubMed](#)]
72. Kirchgesser, J.; Hazarika, M.; Bachmann-Pfabe, S.; Dehmer, K.J.; Kavka, M.; Uptmoor, R. Phenotypic variation of root-system architecture under high P and low P conditions in potato (*Solanum tuberosum* L.). *BMC Plant Biol.* **2023**, *23*, 68. [[CrossRef](#)]
73. Liu, C.; Yan, H.; Wang, W.; Han, R.; Li, Z.; Lin, X.; Wang, D. Layered application of phosphate fertilizer increased winter wheat yield by promoting root proliferation and phosphorus accumulation. *Soil Tillage Res.* **2023**, *225*, 105546. [[CrossRef](#)]
74. Pongrac, P.; Castillo-Michel, H.; Reyes-Herrera, J.; Hancock, R.D.; Fischer, S.; Kelemen, M.; Thompson, J.A.; Wright, G.; Likar, M.; Broadley, M.R.; et al. Effect of phosphorus supply on root traits of two *Brassica oleracea* L. genotypes. *BMC Plant Biol.* **2020**, *20*, 368. [[CrossRef](#)] [[PubMed](#)]
75. Liu, D. Root developmental responses to phosphorus nutrition. *J. Integr. Plant Biol.* **2021**, *63*, 1065–1090. [[CrossRef](#)] [[PubMed](#)]

76. Frew, A. Arbuscular mycorrhizal fungal diversity increases growth and phosphorus uptake in C3 and C4 crop plants. *Soil Biol. Biochem.* **2019**, *135*, 248–250. [[CrossRef](#)]
77. Hoeksema, J.D.; Chaudhary, V.B.; Gehring, C.A.; Johnson, N.C.; Karst, J.; Koide, R.T.; Pringle, A.; Zabinski, C.; Bever, J.D.; Moore, J.C.; et al. A meta-analysis of context-dependency in plant response to inoculation with mycorrhizal fungi. *Ecol. Lett.* **2010**, *13*, 394–407. [[CrossRef](#)] [[PubMed](#)]
78. Wang, G.; Jin, Z.; George, T.S.; Feng, G.; Zhang, L. Arbuscular mycorrhizal fungi enhance plant phosphorus uptake through stimulating hyphosphere soil microbiome functional profiles for phosphorus turnover. *New Phytol.* **2023**, *238*, 2578–2593. [[CrossRef](#)] [[PubMed](#)]
79. Lagunas, B.; Richards, L.; Sergaki, C.; Burgess, J.; Pardal, A.J.; Hussain, R.M.F.; Richmond, B.L.; Baxter, L.; Roy, P.; Pakidi, A.; et al. Rhizobial nitrogen fixation efficiency shapes endosphere bacterial communities and *Medicago truncatula* host growth. *Microbiome* **2023**, *11*, 146. [[CrossRef](#)] [[PubMed](#)]
80. Glassop, D.; Smith, S.E.; Smith, F.W. Cereal phosphate transporters associated with the mycorrhizal pathway of phosphate uptake into roots. *Planta* **2005**, *222*, 688–698. [[CrossRef](#)] [[PubMed](#)]
81. Rui, W.; Ma, J.; Wei, N.; Zhu, X.; Li, Z. Genome-Wide Analysis of the PHT Gene Family and Its Response to Mycorrhizal Symbiosis in Tomatoes under Phosphate Starvation Conditions. *Int. J. Mol. Sci.* **2023**, *24*, 10246. [[CrossRef](#)]
82. Binbin, C.; Vancov, T.; Si, H.; Yang, W.; Tong, K.; Chen, W.; Fang, Y. Isolation and Characterization of Endomycorrhizal Fungi Associated with Growth Promotion of Blueberry Plants. *J. Fungi* **2021**, *7*, 584. [[CrossRef](#)]
83. Javed, S.; Chai, X.; Wang, X.; Xu, S. The phytohormones underlying the plant lateral root development in fluctuated soil environments. *Plant Soil* **2023**, 1–14. [[CrossRef](#)]
84. Du, Y.; Scheres, B. Lateral root formation and the multiple roles of auxin. *J. Exp. Bot.* **2017**, *69*, 155–167. [[CrossRef](#)]
85. Ivanchenko, M.G.; Muday, G.K.; Dubrovsky, J.G. Ethylene–auxin interactions regulate lateral root initiation and emergence in *Arabidopsis thaliana*. *Plant J.* **2008**, *55*, 335–347. [[CrossRef](#)]
86. Sun, L.; Tian, J.; Zhang, H.; Liao, H. Phytohormone regulation of root growth triggered by P deficiency or Al toxicity. *J. Exp. Bot.* **2016**, *67*, 3655–3664. [[CrossRef](#)]
87. Liu, R.; Yang, L.; Zou, Y.; Wu, Q. Root-associated endophytic fungi modulate endogenous auxin and cytokinin levels to improve plant biomass and root morphology of trifoliolate orange. *Hortic. Plant J.* **2023**, *9*, 463–472. [[CrossRef](#)]
88. Wu, F.; Li, Y.; Tian, W.; Sun, Y.; Chen, F.; Zhang, Y.; Zhai, Y.; Zhang, J.; Su, H.; Wang, L. A novel dark septate fungal endophyte positively affected blueberry growth and changed the expression of plant genes involved in phytohormone and flavonoid biosynthesis. *Tree Physiol.* **2020**, *40*, 1080–1094. [[CrossRef](#)]
89. Saha, A.; Mandal, P.; Dasgupta, S.; Saha, D. Influence of culture media and environmental factors on mycelial growth and sporulation of *Lasiodiplodia theobromae* (Pat.) Griffon and Maubl. *J. Environ. Biol./Acad. Environ. Biol. India* **2008**, *29*, 407–410. [[CrossRef](#)]
90. Cunguo, W.; Zong, S.; Li, M. The Contrasting Responses of Mycorrhizal Fungal Mycelium Associated with Woody Plants to Multiple Environmental Factors. *Forests* **2019**, *10*, 973. [[CrossRef](#)]
91. Zhang, L.; Zhou, J.; George, T.S.; Limpens, E.; Feng, G. Arbuscular mycorrhizal fungi conducting the hyphosphere bacterial orchestra. *Trends Plant Sci.* **2022**, *27*, 402–411. [[CrossRef](#)] [[PubMed](#)]
92. Liu, Y.; Zhang, G.; Luo, X.; Hou, E.; Zheng, M.; Zhang, L.; He, X.; Shen, W.; Wen, D. Mycorrhizal fungi and phosphatase involvement in rhizosphere phosphorus transformations improves plant nutrition during subtropical forest succession. *Soil Biol. Biochem.* **2021**, *153*, 108099. [[CrossRef](#)]
93. Khan, M.R.; Khan, S.M. Effects of root-dip treatment with certain phosphate solubilizing microorganisms on the fusarial wilt of tomato. *Bioresour. Technol.* **2002**, *85*, 213–215. [[CrossRef](#)] [[PubMed](#)]
94. Sato, T.; Hachiya, S.; Inamura, N.; Ezawa, T.; Cheng, W.; Tawarayama, K. Secretion of acid phosphatase from extraradical hyphae of the arbuscular mycorrhizal fungus *Rhizophagus clarus* is regulated in response to phosphate availability. *Mycorrhiza* **2019**, *29*, 599–605. [[CrossRef](#)]
95. Zhang, L.; Feng, G.; Declerck, S. Signal beyond nutrient, fructose, exuded by an arbuscular mycorrhizal fungus triggers phytate mineralization by a phosphate solubilizing bacterium. *ISME J.* **2018**, *12*, 2339–2351. [[CrossRef](#)] [[PubMed](#)]
96. Liu, Z.; Kong, X.; Long, Y.; Liu, S.; Zhang, H.; Jia, J.; Cui, W.; Zhang, Z.; Song, X.; Qiu, L.; et al. Integrated single-nucleus and spatial transcriptomics captures transitional states in soybean nodule maturation. *Nat. Plants* **2023**, *9*, 515–524. [[CrossRef](#)] [[PubMed](#)]
97. Yu, H.; Xiao, A.; Wu, J.; Li, H.; Duan, Y.; Chen, Q.; Zhu, H.; Cao, Y. GmNAC039 and GmNAC018 activate the expression of cysteine protease genes to promote soybean nodule senescence. *Plant Cell* **2023**, *35*, 2929–2951. [[CrossRef](#)] [[PubMed](#)]
98. Li, J.; Liu, R.; Zhang, C.; Yang, J.; Lyu, L.; Shi, Z.; Man, Y.B.; Wu, F. Selenium uptake and accumulation in winter wheat as affected by level of phosphate application and arbuscular mycorrhizal fungi. *J. Hazard. Mater.* **2022**, *433*, 128762. [[CrossRef](#)]
99. Zhang, F.; Hou, Y.; Zed, R.; Mauchline, T.H.; Shen, J.; Zhang, F.; Jin, K. Root exudation of organic acid anions and recruitment of beneficial actinobacteria facilitate phosphorus uptake by maize in compacted silt loam soil. *Soil Biol. Biochem.* **2023**, *184*, 109074. [[CrossRef](#)]
100. Zhou, X.; Zhang, J.; Khashi U Rahman, M.; Gao, D.; Wei, Z.; Wu, F.; Dini-Andreote, F. Interspecific plant interaction via root exudates structures the disease suppressiveness of rhizosphere microbiomes. *Mol. Plant* **2023**, *16*, 849–864. [[CrossRef](#)]

101. Ho-Plágaro, T.; Morcillo, R.J.L.; Tamayo-Navarrete, M.I.; Huertas, R.; Molinero-Rosales, N.; López-Ráez, J.A.; Macho, A.P.; García-Garrido, J.M. DLK2 regulates arbuscule hyphal branching during arbuscular mycorrhizal symbiosis. *New Phytol.* **2021**, *229*, 548–562. [[CrossRef](#)]
102. Almario, J.; Jeena, G.; Wunder, J.; Langen, G.; Zuccaro, A.; Coupland, G.; Bucher, M. Root-associated fungal microbiota of nonmycorrhizal *Arabidopsis thaliana* and its contribution to plant phosphorus nutrition. *Proc. Natl. Acad. Sci. USA* **2017**, *114*, E9403–E9412. [[CrossRef](#)]
103. Glynou, K.; Nam, B.; Thines, M.; Maciá-Vicente, J.G. Facultative root-colonizing fungi dominate endophytic assemblages in roots of nonmycorrhizal *Microthlaspi* species. *New Phytol.* **2018**, *217*, 1190–1202. [[CrossRef](#)]
104. Bai, B.; Liu, W.; Qiu, X.; Zhang, J.; Zhang, J.; Bai, Y. The root microbiome: Community assembly and its contributions to plant fitness. *J. Integr. Plant Biol.* **2022**, *64*, 230–243. [[CrossRef](#)] [[PubMed](#)]
105. Mahala, D.M.; Maheshwari, H.S.; Yadav, R.K.; Prabina, B.J.; Bharti, A.; Reddy, K.K.; Kumawat, C.; Ramesh, A. Microbial Transformation of Nutrients in Soil: An Overview. In *Rhizosphere Microbes: Soil and Plant Functions*; Sharma, S.K., Singh, U.B., Sahu, P.K., Singh, H.V., Sharma, P.K., Eds.; Springer: Singapore, 2020; pp. 175–211.
106. Kariman, K.; Scanlan, C.; Boitt, G.; Rengel, Z. Ferromycorrhizal symbiosis confers growth and nutritional benefits to mycorrhizal and non-mycorrhizal crops. *Soil Biol. Biochem.* **2020**, *151*, 108060. [[CrossRef](#)]
107. Jentschke, G.; Brandes, B.; Kuhn, A.J.; Schröder, W.H.; Godbold, D.L. Interdependence of phosphorus, nitrogen, potassium and magnesium translocation by the ectomycorrhizal fungus *Paxillus involutus*. *New Phytol.* **2001**, *149*, 327–337. [[CrossRef](#)]
108. DiCenzo, G.C.; Sharthiya, H.; Nanda, A.; Zamani, M.; Finan, T.M. PhoU Allows Rapid Adaptation to High Phosphate Concentrations by Modulating PstSCAB Transport Rate in *Sinorhizobium meliloti*. *J. Bacteriol.* **2017**, *199*, 10–1128. [[CrossRef](#)] [[PubMed](#)]
109. Robichon, D.; Arnaud, M.; Gardan, R.; Pragai, Z.; O'Reilly, M.; Rapoport, G.; Débarbouillé, M. Expression of a New Operon from *Bacillus subtilis*, ykzB-ykoL, under the Control of the TnrA and PhoP-PhoR Global Regulators. *J. Bacteriol.* **2000**, *182*, 1226–1231. [[CrossRef](#)]
110. Santos-Beneit, F. The Pho regulon: A huge regulatory network in bacteria. *Front. Microbiol.* **2015**, *6*, 402. [[CrossRef](#)] [[PubMed](#)]
111. Lamarche, M.G.; Wanner, B.L.; Crépin, S.; Harel, J. The phosphate regulon and bacterial virulence: A regulatory network connecting phosphate homeostasis and pathogenesis. *FEMS Microbiol. Rev.* **2008**, *32*, 461–473. [[CrossRef](#)]
112. Siles, J.; Starke, R.; Martinovic, T.; Fernandes, M.; Orgiazzi, A.; Bastida, F. Distribution of phosphorus cycling genes across land uses and microbial taxonomic groups based on metagenome and genome mining. *Soil Biol. Biochem.* **2022**, *174*, 108826. [[CrossRef](#)]
113. Ma, Y.; Chen, R. Nitrogen and Phosphorus Signaling and Transport During Legume–Rhizobium Symbiosis. *Front. Plant Sci.* **2021**, *12*, 683601. [[CrossRef](#)]
114. Qin, L.; Jiang, H.; Tian, J.; Zhao, J.; Liao, H. Rhizobia enhance acquisition of phosphorus from different sources by soybean plants. *Plant Soil* **2011**, *349*, 25–36. [[CrossRef](#)]
115. Buernor, A.; Kabiru, M.; Bechtaoui, N.; Jibrin, J.M.; Asante, M.; Bouraqqadi, A.; Dahhani, S.; Ouhdouch, Y.; Hafidi, M.; Jemo, M. Grain Legume Yield Responses to Rhizobia Inoculants and Phosphorus Supplementation Under Ghana Soils: A Meta-Synthesis. *Front. Plant Sci.* **2022**, *13*, 877433. [[CrossRef](#)] [[PubMed](#)]
116. Chen, L.; Qin, L.; Zhou, L.; Li, X.; Chen, Z.; Sun, L.; Wang, W.; Lin, Z.; Zhao, J.; Yamaji, N.; et al. A nodule-localized phosphate transporter GmPT7 plays an important role in enhancing symbiotic N<sub>2</sub> fixation and yield in soybean. *New Phytol.* **2019**, *221*, 2013–2025. [[CrossRef](#)]
117. Qin, L.; Zhao, J.; Tian, J.; Chen, L.; Sun, Z.; Guo, Y.; Lu, X.; Gu, M.; Xu, G.; Liao, H. The High-Affinity Phosphate Transporter GmPT5 Regulates Phosphate Transport to Nodules and Nodulation in Soybean. *Plant Physiol.* **2012**, *159*, 1634–1643. [[CrossRef](#)]
118. Liu, J.; Yang, R.; Yan, J.; Li, C.; Lin, X.; Lin, L.; Cao, Y.; Xu, T.; Li, J.; Yuan, Y.; et al. VPT-like genes modulate *Rhizobium*–legume symbiosis and phosphorus adaptation. *Plant J.* **2023**, *116*, 112–127. [[CrossRef](#)]
119. Cao, Y.; Liu, J.; Li, Y.; Zhang, J.; Li, S.; An, Y.; Hu, T.; Yang, P. Functional Analysis of the Phosphate Transporter Gene *MtPT6* From *Medicago truncatula*. *Front. Plant Sci.* **2021**, *11*, 620377. [[CrossRef](#)] [[PubMed](#)]
120. Nussaume, L.; Kanno, S.; Javot, H.; Marin, E.; Pochon, N.; Ayadi Robert, A.; Nakanishi, T.; Thibaud, M. Phosphate Import in Plants: Focus on the PHT1 Transporters. *Front. Plant Sci.* **2011**, *2*, 83. [[CrossRef](#)] [[PubMed](#)]
121. Puga, M.I.; Rojas-Triana, M.; de Lorenzo, L.; Leyva, A.; Rubio, V.; Paz-Ares, J. Novel signals in the regulation of Pi starvation responses in plants: Facts and promises. *Curr. Opin. Plant Biol.* **2017**, *39*, 40–49. [[CrossRef](#)]
122. Barragán-Rosillo, A.C.; Peralta-Alvarez, C.A.; Ojeda-Rivera, J.O.; Arzate-Mejía, R.G.; Recillas-Targa, F.; Herrera-Estrella, L. Genome accessibility dynamics in response to phosphate limitation is controlled by the PHR1 family of transcription factors in *Arabidopsis*. *Proc. Natl. Acad. Sci. USA* **2021**, *118*, e2107558118. [[CrossRef](#)]
123. Bari, R.; Datt Pant, B.; Stitt, M.; Scheible, W. PHO2, MicroRNA399, and PHR1 Define a Phosphate-Signaling Pathway in Plants. *Plant Physiol.* **2006**, *141*, 988–999. [[CrossRef](#)]
124. Lu, M.; Cheng, Z.; Zhang, X.; Huang, P.; Fan, C.; Yu, G.; Chen, F.; Xu, K.; Chen, Q.; Miao, Y.; et al. Spatial Divergence of PHR-PHT1 Modules Maintains Phosphorus Homeostasis in Soybean Nodules. *Plant Physiol.* **2020**, *184*, 236–250. [[CrossRef](#)]
125. Li, Y.; Ma, W.; Zhang, K.; Wang, X.; Liu, R.; Tian, Y.; Ma, N.; Zhao, Q.; Xu, R.; Zhong, Y.; et al. Overexpression of *GmPHR1* Promotes Soybean Yield through Global Regulation of Nutrient Acquisition and Root Development. *Int. J. Mol. Sci.* **2022**, *23*, 15274. [[CrossRef](#)] [[PubMed](#)]
126. Wang, Y.; Yang, Z.; Youbin, K.; Li, X.; Li, W.; Du, H.; Zhang, C. GmPAP12 Is Required for Nodule Development and Nitrogen Fixation Under Phosphorus Starvation in Soybean. *Front. Plant Sci.* **2020**, *11*, 450. [[CrossRef](#)] [[PubMed](#)]

127. Smil, V. PHOSPHORUS IN THE ENVIRONMENT: Natural Flows and Human Interferences. *Annu. Rev. Energy Environ.* **2000**, *25*, 53–88. [[CrossRef](#)]
128. Riskin, S.H.; Porder, S.; Neill, C.; Figueira, A.M.E.S.; Tubbesing, C.; Mahowald, N. The fate of phosphorus fertilizer in Amazon soya bean fields. *Philos. Trans. R. Soc. B Biol. Sci.* **2013**, *368*, 20120154. [[CrossRef](#)]
129. Alewell, C.; Ringeval, B.; Ballabio, C.; Robinson, D.A.; Panagos, P.; Borrelli, P. Global phosphorus shortage will be aggravated by soil erosion. *Nat. Commun.* **2020**, *11*, 4546. [[CrossRef](#)]
130. Yu, Y.; Du, C. Leaching of phosphorus from phosphate tailings and extraction of calcium phosphates: Toward comprehensive utilization of tailing resources. *J. Environ. Manag.* **2023**, *347*, 119159. [[CrossRef](#)]
131. Wei, Z.; Zuo, H.; Li, J.; Ding, G.; Zhan, Y.; Zhang, L.; Wu, W.; Su, L.; Wei, Y. Insight into the mechanisms of insoluble phosphate transformation driven by the interactions of compound microbes during composting. *Environ. Sci. Pollut. Res.* **2021**, *28*, 32844–32855. [[CrossRef](#)]
132. Kalayu, G.; Clay, D. Phosphate Solubilizing Microorganisms: Promising Approach as Biofertilizers. *Int. J. Agron.* **2019**, *2019*, 4917256. [[CrossRef](#)]
133. Wang, C.; Pan, G.; Lu, X.; Qi, W. Phosphorus solubilizing microorganisms: Potential promoters of agricultural and environmental engineering. *Front. Bioeng. Biotechnol.* **2023**, *11*, 1181078. [[CrossRef](#)]
134. Sun, B.; Jing, R.; Wang, Z.; Tian, L.; Mao, F.; Liu, Y. Diversity and community structure of endophytic *Bacillus* with antagonistic and antioxidant activity in the fruits of Xisha Wild Noni (*Morinda citrifolia* L.). *Microb. Pathog.* **2021**, *158*, 105065. [[CrossRef](#)] [[PubMed](#)]
135. Wolde-meskel, E.; van Heerwaarden, J.; Abdulkadir, B.; Kassa, S.; Aliyi, I.; Degefu, T.; Wakweya, K.; Kanampiu, F.; Giller, K.E. Additive yield response of chickpea (*Cicer arietinum* L.) to *Rhizobium* inoculation and phosphorus fertilizer across smallholder farms in Ethiopia. *Agric. Ecosyst. Environ.* **2018**, *261*, 144–152. [[CrossRef](#)]
136. Rodríguez, H.; Fraga, R. Phosphate solubilizing bacteria and their role in plant growth promotion. *Biotechnol. Adv.* **1999**, *17*, 319–339. [[CrossRef](#)]
137. Yang, F.; Zhang, S.; Song, J.; Du, Q.; Li, G.; Tarakina, N.V.; Antonietti, M. Synthetic Humic Acids Solubilize Otherwise Insoluble Phosphates to Improve Soil Fertility. *Angew. Chem. Int. Ed.* **2019**, *58*, 18813–18816. [[CrossRef](#)]
138. Hu, H.; Tang, C.; Rengel, Z. Influence of phenolic acids on phosphorus mobilisation in acidic and calcareous soils. *Plant Soil* **2005**, *268*, 173–180. [[CrossRef](#)]
139. Li, Y.; Wang, J.; He, L.; Xu, X.; Wang, J.; Ren, C.; Guo, Y.; Zhao, F. Different mechanisms driving increasing abundance of microbial phosphorus cycling gene groups along an elevational gradient. *iScience* **2022**, *25*, 105170. [[CrossRef](#)]
140. Tian, Y.; Shi, C.; Malo, C.U.; Kwatcho Kengdo, S.; Heinzle, J.; Inselsbacher, E.; Ottner, F.; Borcken, W.; Michel, K.; Schindlbacher, A.; et al. Long-term soil warming decreases microbial phosphorus utilization by increasing abiotic phosphorus sorption and phosphorus losses. *Nat. Commun.* **2023**, *14*, 864. [[CrossRef](#)]
141. Yu, H.; Wu, X.; Zhang, G.; Zhou, F.; Harvey, P.; Wang, L.; Fan, S.; Xie, X.; Li, F.; Zhou, H.; et al. Identification of the Phosphorus-Solubilizing Bacteria Strain JP233 and Its Effects on Soil Phosphorus Leaching Loss and Crop Growth. *Front. Microbiol.* **2022**, *13*, 892533. [[CrossRef](#)] [[PubMed](#)]
142. Bolan, N.S.; Naidu, R.; Mahimairaja, S.; Baskaran, S. Influence of low-molecular-weight organic acids on the solubilization of phosphates. *Biol. Fert. Soils* **1994**, *18*, 311–319. [[CrossRef](#)]
143. Panhwar, Q.A.; Jusop, S.; Naher, U.A.; Othman, R.; Razi, M.I.; Andrade, P.; Zhou, D. Application of Potential Phosphate-Solubilizing Bacteria and Organic Acids on Phosphate Solubilization from Phosphate Rock in Aerobic Rice. *Sci. World J.* **2013**, *2013*, 272409. [[CrossRef](#)] [[PubMed](#)]
144. Kwong, W.K.; Zheng, H.; Moran, N.A. Convergent evolution of a modified, acetate-driven TCA cycle in bacteria. *Nat. Microbiol.* **2017**, *2*, 17067. [[CrossRef](#)] [[PubMed](#)]
145. Wang, L.; Qu, F.; Zhu, Z.; Zhao, Y.; Chen, X.; Shi, M.; Wei, Z. The important role of tricarboxylic acid cycle metabolism pathways and core bacterial communities in carbon sequestration during chicken manure composting. *Waste Manag.* **2022**, *150*, 20–29. [[CrossRef](#)] [[PubMed](#)]
146. Liu, Y.; Qu, J.; Zhang, L.; Xu, X.; Wei, G.; Zhao, Z.; Ren, M.; Cao, M. Identification and characterization of the TCA cycle genes in maize. *BMC Plant Biol.* **2019**, *19*, 592. [[CrossRef](#)]
147. Wang, S.; Li, Y.; Zhang, J.; Wang, X.; Hong, J.; Qiu, C.; Meng, H. Transcriptome Profiling Analysis of Phosphate-Solubilizing Mechanism of *Pseudomonas* Strain W134. *Microorganisms* **2022**, *10*, 1998. [[CrossRef](#)]
148. Ludueña, L.; Anzuay, S.; Angelini, J.; McIntosh, M.; Becker, A.; Rupp, O.; Goesmann, A.; Blom, J.; Fabra, A.; Taurian, T. Strain *Serratia* sp. S119: A potential biofertilizer for peanut and maize and a model bacterium to study phosphate solubilization mechanisms. *Appl. Soil Ecol.* **2018**, *126*, 107–112. [[CrossRef](#)]
149. Wang, L.; Zhou, F.; Zhou, J.; Harvey, P.; Yu, H.; Zhang, G.; Zhang, X. Genomic Analysis of *Pseudomonas asiatica* JP233: An Efficient Phosphate-Solubilizing Bacterium. *Genes* **2022**, *13*, 2290. [[CrossRef](#)]
150. Jiang, F.; Zhang, L.; Zhou, J.; George, T.S.; Feng, G. Arbuscular mycorrhizal fungi enhance mineralisation of organic phosphorus by carrying bacteria along their extraradical hyphae. *New Phytol.* **2021**, *230*, 304–315. [[CrossRef](#)] [[PubMed](#)]
151. Sharma, S.B.; Sayyed, R.Z.; Trivedi, M.H.; Gobi, T.A. Phosphate solubilizing microbes: Sustainable approach for managing phosphorus deficiency in agricultural soils. *SpringerPlus* **2013**, *2*, 587. [[CrossRef](#)]

152. Leite, R.D.A.; Martins, L.C.; Ferreira, L.V.D.S.; Barbosa, E.S.; Alves, B.J.R.; Zilli, J.E.; Araújo, A.P.; Jesus, E.D.C. Co-inoculation of *Rhizobium* and *Bradyrhizobium* promotes growth and yield of common beans. *Appl. Soil Ecol.* **2022**, *172*, 104356. [[CrossRef](#)]
153. Zavaleta-Pastor, M.; Sohlenkamp, C.; Gao, J.; Guan, Z.; Zaheer, R.; Finan, T.M.; Raetz, C.R.H.; López-Lara, I.M.; Geiger, O. *Sinorhizobium meliloti* phospholipase C required for lipid remodeling during phosphorus limitation. *Proc. Natl. Acad. Sci. USA* **2010**, *107*, 302–307. [[CrossRef](#)]
154. Alam, F.; Khan, A.; Fahad, S.; Nawaz, S.; Ahmed, N.; Arif Ali, M.; Adnan, M.; Dawar, K.; Saud, S.; Hassan, S.; et al. Phosphate solubilizing bacteria optimize wheat yield in mineral phosphorus applied alkaline soil. *J. Saudi Soc. Agric. Sci.* **2022**, *21*, 339–348. [[CrossRef](#)]
155. Elhaissofi, W.; Ghoulam, C.; Barakat, A.; Zeroual, Y.; Bargaz, A. Phosphate bacterial solubilization: A key rhizosphere driving force enabling higher P use efficiency and crop productivity. *J. Adv. Res.* **2022**, *38*, 13–28. [[CrossRef](#)]
156. Pradhan, M.; Sahoo, R.; Pradhan, C.; Tuteja, N.; Mohanty, S. Contribution of native phosphorous-solubilizing bacteria of acid soils on phosphorous acquisition in peanut (*Arachis hypogaea* L.). *Protoplasma* **2017**, *254*, 2225–2236. [[CrossRef](#)]
157. Six, J. Plant nutrition for sustainable development and global health. *Plant Soil* **2011**, *339*, 1–2. [[CrossRef](#)]
158. Sharma, P.; Tripathi, S.; Sirohi, R.; Kim, S.H.; Ngo, H.H.; Pandey, A. Uptake and mobilization of heavy metals through phytoremediation process from native plants species growing on complex pollutants: Antioxidant enzymes and photosynthetic pigments response. *Environ. Technol. Innov.* **2021**, *23*, 101629. [[CrossRef](#)]
159. Finkel, O.M.; Salas-González, I.; Castrillo, G.; Spaepen, S.; Law, T.F.; Teixeira, P.J.P.L.; Jones, C.D.; Dangl, J.L. The effects of soil phosphorus content on plant microbiota are driven by the plant phosphate starvation response. *PLoS Biol.* **2019**, *17*, e3000534. [[CrossRef](#)] [[PubMed](#)]
160. Wang, Z.; Wang, Y.; Du, Q.; Yan, P.; Yu, B.; Li, W.; Zou, C. The auxin signaling pathway contributes to phosphorus-mediated zinc homeostasis in maize. *BMC Plant Biol.* **2023**, *23*, 20. [[CrossRef](#)]
161. Palmieri, D.; Vitale, S.; Lima, G.; Di Pietro, A.; Turrà, D. A bacterial endophyte exploits chemotropism of a fungal pathogen for plant colonization. *Nat. Commun.* **2020**, *11*, 5264. [[CrossRef](#)] [[PubMed](#)]
162. Wei, M.; Zhang, M.; Huang, G.; Yuan, Y.; Fu, C.; Yu, L. Coculture with two *Bacillus velezensis* strains enhances the growth of *Anoectochilus* plants via promoting nutrient assimilation and regulating rhizosphere microbial community. *Ind. Crop. Prod.* **2020**, *154*, 112697. [[CrossRef](#)]
163. Berlanga-Clavero, M.V.; Molina-Santiago, C.; Caraballo-Rodríguez, A.M.; Petras, D.; Díaz-Martínez, L.; Pérez-García, A.; de Vicente, A.; Carrión, V.J.; Dorresteijn, P.C.; Romero, D. *Bacillus subtilis* biofilm matrix components target seed oil bodies to promote growth and anti-fungal resistance in melon. *Nat. Microbiol.* **2022**, *7*, 1001–1015. [[CrossRef](#)] [[PubMed](#)]
164. Baptista, J.P.; Teixeira, G.M.; de Jesus, M.L.A.; Bertê, R.; Higashi, A.; Mosela, M.; Da Silva, D.V.; de Oliveira, J.P.; Sanches, D.S.; Brancher, J.D.; et al. Antifungal activity and genomic characterization of the biocontrol agent *Bacillus velezensis* CMRP 4489. *Sci. Rep.* **2022**, *12*, 17401. [[CrossRef](#)]
165. Liotti, R.G.; Da Silva Figueiredo, M.I.; Da Silva, G.F.; de Mendonça, E.A.F.; Soares, M.A. Diversity of cultivable bacterial endophytes in *Paullinia cupana* and their potential for plant growth promotion and phytopathogen control. *Microbiol. Res.* **2018**, *207*, 8–18. [[CrossRef](#)]
166. Shen, Y.; Korkor, N.L.; Xiao, R.; Pu, Q.; Hu, M.; Zhang, S.; Kong, D.; Zeng, G.; Hu, X. Antagonistic activity of combined bacteria strains against southern blight pathogen of *Dendrobium officinale*. *Biol. Control* **2020**, *151*, 104291. [[CrossRef](#)]
167. Chen, Y.; Yin, S.; Shao, Y.; Zhang, K. Soil bacteria are more sensitive than fungi in response to nitrogen and phosphorus enrichment. *Front. Microbiol.* **2022**, *13*, 999385. [[CrossRef](#)]
168. Ruibo Sun, W.Z.Y.L. Changes in phosphorus mobilization and community assembly of bacterial and fungal communities in rice rhizosphere under phosphate deficiency. *Front. Microbiol.* **2022**, *13*, 953340. [[CrossRef](#)]
169. Kang, S.; Radhakrishnan, R.; Khan, A.L.; Kim, M.; Park, J.; Kim, B.; Shin, D.; Lee, I. Gibberellin secreting rhizobacterium, *Pseudomonas putida* H-2-3 modulates the hormonal and stress physiology of soybean to improve the plant growth under saline and drought conditions. *Plant Physiol. Biochem.* **2014**, *84*, 115–124. [[CrossRef](#)]
170. Dao, G.; Wang, S.; Wang, X.; Chen, Z.; Wu, Y.; Wu, G.; Lu, Y.; Liu, S.; Hu, H. Enhanced *Scenedesmus* sp. growth in response to gibberellin secretion by symbiotic bacteria. *Sci. Total Environ.* **2020**, *740*, 140099. [[CrossRef](#)]
171. Hu, L.; Li, D.; Sun, K.; Cao, W.; Fu, W.; Zhang, W.; Dai, C. Mutualistic fungus *Phomopsis liquidambari* increases root aerenchyma formation through auxin-mediated ethylene accumulation in rice (*Oryza sativa* L.). *Plant Physiol. Biochem.* **2018**, *130*, 367–376. [[CrossRef](#)] [[PubMed](#)]
172. Cosme, M.; Wurst, S. Interactions between arbuscular mycorrhizal fungi, rhizobacteria, soil phosphorus and plant cytokinin deficiency change the root morphology, yield and quality of tobacco. *Soil Biol. Biochem.* **2013**, *57*, 436–443. [[CrossRef](#)]
173. Rawat, P.; Das, S.; Shankhdhar, D.; Shankhdhar, S.C. Phosphate-Solubilizing Microorganisms: Mechanism and Their Role in Phosphate Solubilization and Uptake. *J. Soil Sci. Plant Nutr.* **2021**, *21*, 49–68. [[CrossRef](#)]
174. Spring, A.; Rowan, K.S. Phosphorous Metabolism and Auxin Action. *Nature* **1966**, *210*, 1166–1167. [[CrossRef](#)]
175. Huang, J.; Wu, Q.; Jing, H.K.; Shen, R.F.; Zhu, X.F. Auxin facilitates cell wall phosphorus reutilization in a nitric oxide-ethylene dependent manner in phosphorus deficient rice (*Oryza sativa* L.). *Plant Sci.* **2022**, *322*, 111371. [[CrossRef](#)]
176. Xu, F.; Liao, H.; Yang, J.; Zhang, Y.; Yu, P.; Cao, Y.; Fang, J.; Chen, S.; Li, L.; Sun, L.; et al. Auxin-producing bacteria promote barley rhizosheath formation. *Nat. Commun.* **2023**, *14*, 5800. [[CrossRef](#)]

177. Jiang, Y.; Wu, Y.; Hu, N.; Li, H.; Jiao, J. Interactions of bacterial-feeding nematodes and indole-3-acetic acid (IAA)-producing bacteria promotes growth of *Arabidopsis thaliana* by regulating soil auxin status. *Appl. Soil Ecol.* **2020**, *147*, 103447. [[CrossRef](#)]
178. Tzipilevich, E.; Russ, D.; Dangl, J.L.; Benfey, P.N. Plant immune system activation is necessary for efficient root colonization by auxin-secreting beneficial bacteria. *Cell Host Microbe* **2021**, *29*, 1507–1520. [[CrossRef](#)]
179. Arnold, A.E. Bacterial–fungal interactions: Bacteria take up residence in the house that Fungi built. *Curr. Biol.* **2022**, *32*, R327–R328. [[CrossRef](#)]
180. Baudy, P.; Zubrod, J.P.; Korschak, M.; Kolbenshlag, S.; Pollitt, A.; Baschien, C.; Schulz, R.; Bundschuh, M. Fungal–fungal and fungal–bacterial interactions in aquatic decomposer communities: Bacteria promote fungal diversity. *Ecology* **2021**, *102*, e3471. [[CrossRef](#)] [[PubMed](#)]
181. Robinson, A.J.; House, G.L.; Morales, D.P.; Kelliher, J.M.; Gallegos-Graves, L.V.; LeBrun, E.S.; Davenport, K.W.; Palmieri, F.; Lohberger, A.; Bregnard, D.; et al. Widespread bacterial diversity within the bacteriome of fungi. *Commun. Biol.* **2021**, *4*, 1168. [[CrossRef](#)] [[PubMed](#)]
182. Nacoon, S.; Jogloy, S.; Riddech, N.; Mongkolthananuk, W.; Ekprasert, J.; Cooper, J.; Boonlue, S. Combination of arbuscular mycorrhizal fungi and phosphate solubilizing bacteria on growth and production of *Helianthus tuberosus* under field condition. *Sci. Rep.* **2021**, *11*, 6501. [[CrossRef](#)] [[PubMed](#)]
183. Nacoon, S.; Jogloy, S.; Riddech, N.; Mongkolthananuk, W.; Kuyper, T.W.; Boonlue, S. Interaction between Phosphate Solubilizing Bacteria and Arbuscular Mycorrhizal Fungi on Growth Promotion and Tuber Inulin Content of *Helianthus tuberosus* L. *Sci. Rep.* **2020**, *10*, 4916. [[CrossRef](#)] [[PubMed](#)]
184. Song, C.; Sarpong, C.K.; Zhang, X.; Wang, W.; Wang, L.; Gan, Y.; Yong, T.; Chang, X.; Wang, Y.; Yang, W. Mycorrhizosphere bacteria and plant–plant interactions facilitate maize P acquisition in an intercropping system. *J. Clean. Prod.* **2021**, *314*, 127993. [[CrossRef](#)]
185. Cheng, X.; Xie, M.; Li, Y.; Liu, B.; Liu, C.; Wu, Q.; Kuča, K. Effects of field inoculation with arbuscular mycorrhizal fungi and endophytic fungi on fruit quality and soil properties of Newhall navel orange. *Appl. Soil Ecol.* **2022**, *170*, 104308. [[CrossRef](#)]
186. Zhang, L.; Xu, M.; Liu, Y.; Zhang, F.; Hodge, A.; Feng, G. Carbon and phosphorus exchange may enable cooperation between an arbuscular mycorrhizal fungus and a phosphate-solubilizing bacterium. *New Phytol.* **2016**, *210*, 1022–1032. [[CrossRef](#)]
187. Godara, M.; Saxena, J.; Chandra, S.; Nain, L. Synergistic effect of phosphate solubilizing rhizobacteria and arbuscular mycorrhiza on growth and yield of wheat plants. *J. Soil Sci. Plant Nutr.* **2013**, *13*, 511–525. [[CrossRef](#)]
188. Gupta, P.; Kumar, V.; Usmani, Z.; Rani, R.; Chandra, A.; Gupta, V.K. A comparative evaluation towards the potential of *Klebsiella* sp. and *Enterobacter* sp. in plant growth promotion, oxidative stress tolerance and chromium uptake in *Helianthus annuus* (L.). *J. Hazard. Mater.* **2019**, *377*, 391–398. [[CrossRef](#)] [[PubMed](#)]
189. Chen, J.; Zhao, G.; Wei, Y.; Dong, Y.; Hou, L.; Jiao, R. Isolation and screening of multifunctional phosphate solubilizing bacteria and its growth-promoting effect on Chinese fir seedlings. *Sci. Rep.* **2021**, *11*, 9081. [[CrossRef](#)] [[PubMed](#)]
190. George, D.M.; Vincent, A.S.; Mackey, H.R. An overview of anoxygenic phototrophic bacteria and their applications in environmental biotechnology for sustainable Resource recovery. *Biotechnol. Rep.* **2020**, *28*, e563. [[CrossRef](#)] [[PubMed](#)]
191. Khuong, N.Q.; Huu, T.N.; Thuc, L.V.; Thu, L.T.M.; Xuan, D.T.; Quang, L.T.; Nhan, T.C.; Tran, H.N.; Tien, P.D.; Xuan, L.N.T.; et al. Two strains of *Luteovulum sphaeroides* (purple nonsulfur bacteria) promote rice cultivation in saline soils by increasing available phosphorus. *Rhizosphere* **2021**, *20*, 100456. [[CrossRef](#)]
192. Liu, X.; Chen, C.; Wang, J.; Zou, S.; Long, X. Phosphorus solubilizing bacteria *Bacillus thuringiensis* and *Pantoea ananatis* simultaneously promote soil inorganic phosphate dissolution and soil Pb immobilization. *Rhizosphere* **2021**, *20*, 100448. [[CrossRef](#)]
193. Qiu, F.; Liu, W.; Chen, L.; Wang, Y.; Ma, Y.; Lyu, Q.; Yi, S.; Xie, R.; Zheng, Y. *Bacillus subtilis* biofertilizer application reduces chemical fertilization and improves fruit quality in fertiligated Tarocco blood orange groves. *Sci. Hortic.-Amst.* **2021**, *281*, 110004. [[CrossRef](#)]
194. Estrada-Bonilla, G.A.; Durrer, A.; Cardoso, E.J.B.N. Use of compost and phosphate-solubilizing bacteria affect sugarcane mineral nutrition, phosphorus availability, and the soil bacterial community. *Appl. Soil Ecol.* **2021**, *157*, 103760. [[CrossRef](#)]
195. Vidal, A.; Klöffel, T.; Guigue, J.; Angst, G.; Steffens, M.; Hoeschen, C.; Mueller, C.W. Visualizing the transfer of organic matter from decaying plant residues to soil mineral surfaces controlled by microorganisms. *Soil Biol. Biochem.* **2021**, *160*, 108347. [[CrossRef](#)]
196. Mendes, R.; Garbeva, P.; Raaijmakers, J. The rhizosphere microbiome: Significance of plant beneficial, plant pathogenic, and human pathogenic microorganisms. *FEMS Microbiol. Rev.* **2013**, *37*, 634–663. [[CrossRef](#)] [[PubMed](#)]
197. Gonzalez, M.; Ocampo Alvarez, H.; Santacruz-Ruvalcaba, F.; Sánchez-Hernández, C.; Casarrubias-Castillo, K.; Becerril, A.; Castañeda-Nava, J.; Hernández-Herrera, R. Physiological, Ecological, and Biochemical Implications in Tomato Plants of Two Plant Biostimulants: Arbuscular Mycorrhizal Fungi and Seaweed Extract. *Front. Plant Sci.* **2020**, *11*, 999. [[CrossRef](#)] [[PubMed](#)]
198. Ahmad, V.; Muhammad Zafar Iqbal, A.N.; Haseeb, M.; Khan, M.S. Antimicrobial potential of bacteriocin producing *Lysinibacillus jx416856* against foodborne bacterial and fungal pathogens, isolated from fruits and vegetable waste. *Anaerobe* **2014**, *27*, 87–95. [[CrossRef](#)] [[PubMed](#)]
199. Shaheen, H.A.; Issa, M.Y. In vitro and in vivo activity of *Peganum harmala* L. alkaloids against phytopathogenic bacteria. *Sci. Hortic.-Amst.* **2020**, *264*, 108940. [[CrossRef](#)]
200. Ghosh, S.K.; Bera, T.; Chakrabarty, A.M. Microbial siderophore—A boon to agricultural sciences. *Biol. Control* **2020**, *144*, 104214. [[CrossRef](#)]

201. Rodríguez Chávez, J.L.; Juárez-Campusano, Y.; Delgado, G.; Pacheco Aguilar, J.R. Identification of lipopeptides from *Bacillus* strain Q11 with ability to inhibit the germination of *Penicillium expansum*, the etiological agent of postharvest blue mold disease. *Postharvest Biol. Technol.* **2019**, *155*, 72–79. [[CrossRef](#)]
202. Kutschera, A.; Dawid, C.; Gisch, N.; Schmid, C.; Raasch, L.; Gerster, T.; Schäffer, M.; Smakowska-Luzan, E.; Belkhadir, Y.; Vlot, A.C.; et al. Bacterial medium-chain 3-hydroxy fatty acid metabolites trigger immunity in *Arabidopsis* plants. *Science* **2019**, *364*, 178–181. [[CrossRef](#)]
203. Sehrawat, A.; Sindhu, S.; Glick, B. Hydrogen cyanide production by soil bacteria: Biological control of pests and promotion of plant growth in sustainable agriculture. *Pedosphere* **2022**, *32*, 15–38. [[CrossRef](#)]
204. Dakora, F.D.; Phillips, D.A. Root exudates as mediators of mineral acquisition in low-nutrient environments. *Plant Soil* **2002**, *245*, 35–47. [[CrossRef](#)]
205. Harbort, C.J.; Hashimoto, M.; Inoue, H.; Niu, Y.; Guan, R.; Rombolà, A.D.; Kopriva, S.; Voges, M.J.E.E.; Sattely, E.S.; Garrido-Oter, R.; et al. Root-Secreted Coumarins and the Microbiota Interact to Improve Iron Nutrition in *Arabidopsis*. *Cell Host Microbe* **2020**, *28*, 825–837. [[CrossRef](#)]
206. Zhang, X.; Khadka, P.; Puchalski, P.; Leehan, J.D.; Rossi, F.R.; Okumoto, S.; Pilot, G.; Danna, C.H. MAMP-elicited changes in amino acid transport activity contribute to restricting bacterial growth. *Plant Physiol.* **2022**, *189*, 2315–2331. [[CrossRef](#)]
207. Czaban, W.; Rasmussen, J.; Laursen, B.B.; Vidkjær, N.H.; Sapkota, R.; Nicolaisen, M.; Fomsgaard, I.S. Multiple effects of secondary metabolites on amino acid cycling in white clover rhizosphere. *Soil Biol. Biochem.* **2018**, *123*, 54–63. [[CrossRef](#)]
208. Palacios, O.A.; Bashan, Y.; De-Bashan, L.E. Proven and potential involvement of vitamins in interactions of plants with plant growth-promoting bacteria—An overview. *Biol. Fert Soils* **2014**, *50*, 415–432. [[CrossRef](#)]
209. Klee, H.J.; Hayford, M.B.; Kretzmer, K.A.; Barry, G.F.; Kishore, G.M. Control of ethylene synthesis by expression of a bacterial enzyme in transgenic tomato plants. *Plant Cell* **1991**, *3*, 1187–1193. [[CrossRef](#)] [[PubMed](#)]
210. Singh, S.; Kumar, V.; Datta, S.; Singh, S.; Dhanjal, D.S.; Dhaka, V.; Sharma, K.; Singh, J. Chapter 12—Commercial production and formulation of microbial biocontrol agents. In *Food Security and Plant Disease Management*; Kumar, A., Droby, S., Eds.; Woodhead Publishing: Sawston, UK, 2021; pp. 241–256.
211. Liu, C.; Wu, J.; Chang, J. Diffusion characteristics and controlled release of bacterial fertilizers from modified calcium alginate capsules. *Bioresour. Technol.* **2008**, *99*, 1904–1910. [[CrossRef](#)] [[PubMed](#)]
212. Wu, C. Controlled release evaluation of bacterial fertilizer using polymer composites as matrix. *J. Control. Release* **2008**, *132*, 42–48. [[CrossRef](#)] [[PubMed](#)]
213. Trivedi, P.; Leach, J.E.; Tringe, S.G.; Sa, T.; Singh, B.K. Plant–microbiome interactions: From community assembly to plant health. *Nat. Rev. Microbiol.* **2020**, *18*, 607–621. [[CrossRef](#)] [[PubMed](#)]

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