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PLANT-MICROBE INTERACTION: MECHANISMS AND APPLICATIONS FOR IMPROVING CROP YIELD AND QUALITY

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In light of the dual challenges posed by climate change and the burgeoning global population, which are putting food security at risk, there is an urgent need to develop sustainable agricultural innovations. These innovations must be capable of increasing crop productivity and maintaining soil health, reducing our dependence on synthetic agrochemical inputs, and preserving the nutritional quality of our food crops. It is crucial to delve into the biological and physiological processes that underlie plant-microbe interactions. Such knowledge is paramount in harnessing the advantages of these interactions for sustainable agriculture. This review delves into the intricate mechanisms through which beneficial rhizosphere and soil bacteria, known as plant growth-promoting bacteria (PGPB), contribute to enhancing crop yields, bolstering stress resilience, and improving the nutritional quality of crops. We explore the vital capabilities of PGPB, encompassing nitrogen fixation, phosphorus solubilization, iron chelation through microbial siderophores, and modulation of hormonal signaling pathways. The PGPB taxa in focus include rhizobial diazotrophs (genera *Rhizobium*, *Bradyrhizobium*) and diverse heterotrophic genera (*Azotobacter, Bacillus, Pseudomonas*).

Recent studies have provided compelling evidence of the effectiveness of PGPB in biofortification interventions, which involve enriching essential micronutrients in crops through microbial enhancement of nutrient mobilization, uptake, translocation, and acquisition. Understanding the genomic and metabolic mechanisms that govern plant growth promotion, abiotic stress tolerance, pathogen inhibition, and biofortification by PGPR is pivotal. Such insights can inform endeavors to optimize, formulate, and apply tailored PGPR inoculants. Adopting a systems perspective that acknowledges the intricate interactions among plants, microbes, and soil in this context is essential. Furthermore, we

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advocate for continued research in various domains, including microbiota recruitment, PGPR screening, the cumulative effects of various approaches, developing effective delivery systems, field testing, and integrating these findings with breeding programs. Interdisciplinary collaboration among microbial ecologists, plant physiologists, crop scientists, and farmers will be instrumental in unlocking the full potential of plant-microbe associations to ensure sustainable agriculture and food crop quality. In summary, more profound insights into PGPB biology and their interactions with plants offer a promising path toward enhancing productivity and sustainability in the face of escalating demands.

Keywords: plant growth-promoting bacteria, biofortification, plant nutrition, sustainable agriculture, soil microbiome, plant-microbe interaction

INTRODUCTION

Due to the increasing demand for high-quality food and the ever-growing world population, food supply and environmental sustainability have become extremely important. Consequently, there is a pressing need for effective methods to increase crop yields and their nutritional content, maintain soil fertility, and reduce reliance on chemical fertilizers and pesticides (Garg *et al.*, 2018; Shahzad *et al*., 2021). In response to this challenge, various means, such as plant traditional breeding techniques, genetic engineering, or agronomic practices, are being developed (Sheoran *et al*., 2022). Over the past few decades, research in this field has demonstrated the potential of microorganisms, including bacteria and fungi, as valuable biological agents capable of increasing crop yields and improving nutritional quality, protecting against pathogens and abiotic stresses (Khan *et al.*, 2019). Soil and rhizosphere beneficial microorganisms *Rhizobium*, *Azotobacter*, *Bacillus*, and *Pseudomonas genera* are considered crucial players in the soil ecosystem and interact with plants in various ways (Yadav *et al*., 2020; Dhiman *et al*., 2023). Inoculation with these bacteria can also lead to reducing dependence on chemical fertilizers and pesticides (Daly *et al*., 2017). Some growth-promoting microorganisms are considered promising biofortification agents that help increase the concentration of vitamins, minerals (such as zinc, calcium, copper, magnesium, and iron) and other essential nutrients, partially, through enhanced uptake and transport to edible parts (Bouis & Welch, 2010). Greenhouse and field trials have shown success using PGPB to biofortify crops like wheat, rice, and legumes (Singh *et al*., 2022). This provides the opportunities to address micronutrient deficiencies, often referred to as 'hidden hunger,' which can result in a range of health issues and impact the overall well-being of populations, particularly in developing nations (Garg *et al*., 2018; Koç &; Karayiğit, 2022). However, the effectiveness of their application depends on different factors; further research to develop efficient microbial biofertilizers is required. In this review, we focus on the mechanisms of soil microorganisms' influence on plant mineral nutrition, growth, and development, building on our previous studies on bacterial endophytes (Makar *et al.*, 2021; Makar & Romanyuk, 2022; Kavulych *et al.*, 2023). Specifically, we focus on bacteria that produce phytohormones like auxins and cytokinins and influence plants growth and mineral concentrations through nitrogen fixation, phosphorus, and micronutrient solubilization mechanisms.

Nitrogen fixation. Nitrogen (N) is an essential macronutrient, especially for plants, as it is a component of chlorophyll, which is involved in photosynthesis (Allison *et al.*, 1997), serves as a building block for amino acids and other vital biomolecules such as adenosine triphosphate (ATP) and nucleic acids (Scheerer *et al.*, 2019). Although N is abundant in nature, mainly as gaseous atmospheric N_2, only a small portion of it can be taken by plants. Plants use the mineral ammonia or nitrate ions from fertilizers, decomposed organic material, and (or) atmospheric N_2 converted into organic compounds through natural processes such as lightning and biological nitrogen fixation (BNF) (Vance, 2001; Wagner, 2011). Prokaryotic BNF directly leads to an increased N supply to host plants. Numerous free-living soil bacteria (e.g., *Azotobacter*, *Beijerinckia,* and others), plant-associated bacteria (e.g., *Rhizobium*, *Bradyrhizobium*, *Burkholderia*, *Frankia,* and others) and cyanobacteria (Zhan & Sun, 2012) are involved in BNF. Many heterotrophic, free-living soil bacteria possess nitrogen-fixing abilities even without direct interaction with plants. These non-symbiotic nitrogen-fixing bacteria, including the genera *Beijerinckia*, *Azotobacter*, *Azospirillum*, *Herbaspirillum*, *Gluconacetobacter*, *Burkholderia*, *Clostridium*, *Methanosarcina*, and *Paenibacillus*, have been shown to have a significant impact in increasing crop growth and yield (Van Deynze *et al*., 2018; Aasfar *et al*., 2021). Similarly, symbiotic nitrogen-fixing bacteria contribute significantly to plant growth and productivity.

A recent study by Z. Pang *et al.* (2023) showed that the aboveground *Heterotis rotundifolia* root mucilage contains significant populations of nitrogen-fixing bacteria, including the genera *Klebsiella*, *Pantoea*, *Sphingobacterium*, *Herbaspirillum* and *Burkholderia*. Nitrogen isotope labeling experiments and gene expression analysis confirmed that airborne root mucilage can fix N_2 to support and promote plant growth. Alternatively, removal of surface roots negatively impacted nitrogen levels and overall plant growth. Another fascinating example is the symbiotic interaction between plants and bacteria of the genus *Frankia*. These soil actinomycetes have the unique ability to form symbiotic nitrogen-fixing nodules with 21 genera and hundreds of dicot species (Normand & Fernandez, 2019), allowing for their growth in nitrogen-poor environments (Sellstedt & Richau, 2013).

The best known root nodule bacteria belong to the families *Rhizobiaceae* (-Proteobacteria) and *Burkholderiaceae* (-Proteobacteria), which are collectively referred to as rhizobia (Lindström & Mousavi, 2020; Fahde *et al*., 2023). These bacteria form a symbiotic relationship with important legumes, including alfalfa, beans, clover, peas, lupins, peanuts, and soybeans (Graham & Vance, 2003). Rhizobia effectively colonize the root system of the host plant, and make N available to the plant (Masson-Boivin & Sachs, 2018). The increased N availability increases the photosynthetic capacity of plants, leading to growth promotion and increased seed production. A recent study showed that inoculation with *Rhizobium* strains along with the addition of phosphorus resulted in a significant increase in common bean nodulation, biomass production and overall yield. In field trials, bean yields on low fertility soils increased by an impressive 126 % (Razafintsalama *et al*., 2022). It was shown that pre-sowing inoculation of alfalfa plants with the active strains of *Sinorhizobium meliloti* led to an increased production of amino acids, in particular essential amino acids in above ground mass under optimal moisture and insufficient water supply (Kots *et al.*, 2021), showing the role of nitrogen fixers in plant biofortification.

The use of nitrogen-fixing bacteria not only promotes plant growth, but also increases stress tolerance. For example, additional application of the *Sinorhizobium meliloti* strain had a positive effect on cold tolerance of alfalfa plants (D'Amours *et al*., 2022). Inoculation of soybeans with *Bradyrhizobium japonicum* increased salt stress tolerance (Nitawaki *et al*., 2020). Additionally, BNF helps maintain soil nitrogen levels and improve soil quality.

The ability to assimilate atmospheric N_2 depends on the presence of specific enzymes that are essential for both symbiotic and non-symbiotic microorganisms.

Specifically, BNF is catalyzed by nitrogenase (EC 1.18.6.1), a complex enzyme composed of two components: a heterotetrameric core encoded by the genes *nifD* and *nifK*, and a dinitrogenase reductase subunit encoded by the gene *nifH* (Stacey *et al*., 1992). The *nifH* gene is the biomarker most commonly used to study BNF. The database based on the sequence of the *nifH* gene enabled the analysis of the evolution and ecology of nitrogen-fixing organisms (Gaby & Buckley, 2014). A study of the presence of the *nifH* gene in sequenced genomes and the subsequent identification of other *nif* genes in the clusters revealed the widespread distribution of nitrogen-fixing genes among soil prokaryotes (**Fig. 1**) (Pi *et al*., 2022). Such a distribution of nitrogen-fixing genes may indicate specific mutually beneficial interactions between different soil bacteria and plants and suggests the existence of many unknown PGPBs with nitrogen-fixing ability for agricultural purposes.

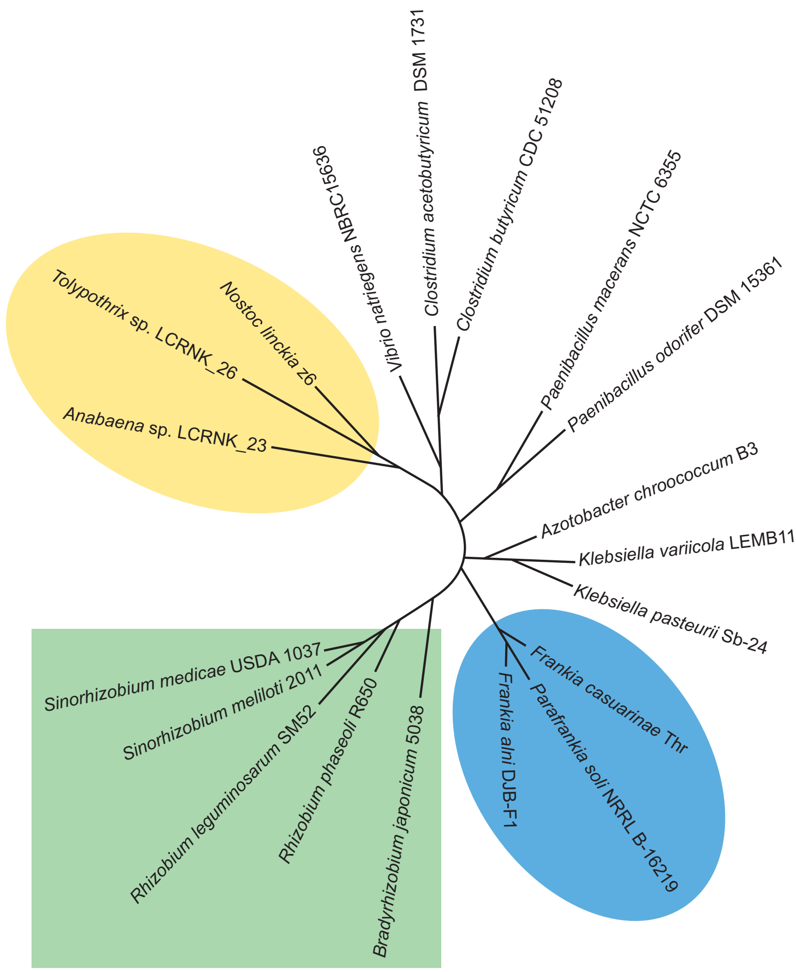

Fig. 1. Distribution of the *nifH* gene among prokaryotes. The sequences of the *nifH* were obtained from the GenBank (https://www.ncbi.nlm.nih.gov/genbank) of the National Center for Biotechnology Information. The green square is a group of nodule bacteria. The nodule bacteria form a common clade with actinomycetes, which form actinorhizal nodules (blue triangle). The yellow triangle is a clade of cyanobacteria. The rest of the bacteria are free-living nitrogen fixers

Phosphorus solubilization. Among the noteworthy properties of PGPB, a particularly important one is their capacity to transform insoluble phosphates into soluble forms. Phosphorus (P) is a vital macronutrient essential for various plant growth and developmental processes. It plays a critical role in numerous metabolic pathways and is a component of essential biological molecules such as nucleic acids, coenzymes, phosphoproteins, and phospholipids (He & Wan, 2022). Insufficient phosphorus availability in plants can have severe consequences, including retarded growth, depletion of energy reserves, and nutrient deficiencies. Ensuring an adequate supply of soil P is crucial for promoting root development, stimulating flowering and fruit formation, and enhancing overall plant immunity and yield, both in normal conditions and under biotic or abiotic stresses (Bechtaoui *et al.*, 2021).

While most soils contain more P than other elements like nitrogen or potassium, over 80% of it exists in forms that are not readily accessible for plant uptake (Xu *et al.*, 2020). Phosphate anions in the soil can readily bind to metal cations, forming insoluble inorganic salts that are unavailable to plants (Almeida *et al.*, 2019).

Soil microorganisms play a crucial role in the solubilization of P through various biological processes, including the mineralization of organic phosphorus (phytate) and the solubilization of inorganic (aluminum and iron phosphate) minerals. These processes are mainly mediated by the production of organic acids and chelating compounds by microorganisms (Tian *et al.*, 2021). Solubilization of inorganic phosphorus compounds according to S. B. Sharma *et al*. (2013) can occur via 1) the production of organic and inorganic acids that can chelate cations bound to phosphorus; 2) reduction reactions with H_2S; 3) proton release and environmental acidification. The mineralization of organic phosphorus, on the other hand, involves: 1) nonspecific acid or alkaline phosphatases which dephosphorylate organic material and release inorganic phosphate, can be acid or alkaline phosphatases; 2) phytases – break down phosphate from phytate, an organic P storage form in plants; 3) phosphonatases and C-P lyases – cleave carbon-phosphorus bonds in organophosphonates to release phosphate. In addition to chemical fertilization, microbial solubilization and P mineralization are the most important means of increasing P bioavailability for plants. The success of this process is influenced by factors such as soil pH, microbial community composition, and the availability of other nutrients.

Phosphorus-Solubilizing Microorganisms (PSMs) encompass a range of microorganisms, including bacteria, fungi, and cyanobacteria. Noteworthy bacterial genera in this context include *Azospirillum*, *Bacillus*, *Pseudomonas* (Kirui *et al*., 2022), *Streptomyces*, and *Nocardiopsis* (Boubekri *et al*., 2021). Additionally, non-mycorrhizal fungi like *Aspergillus*, *Alternaria*, *Fusarium*, and *Penicillium* (Kalayu, 2019), as well as mycorrhizal fungi like *Rhizophagus* and *Glomus* (Zhang *et al*., 2018), and cyanobacteria genera like *Anabaena* and *Westiellopsis* (Yandigeri *et al.*, 2011), and the yeast *Rhodosporidium* (Chen *et al*., 2023), are active phosphate-solubilizing representatives. The microorganisms recognized as highly efficient phosphate solubilizers include rhizobia species like *R. leguminosarum*, *R. meliloti*, *M. mediterraneum*, *Bradyrhizobium* sp., and *B. japonicum* (Fahde *et al*., 2023).

Maintaining sufficient bioavailable P levels in the soil is crucial for improving plant uptake and achieving higher yields. PSMs use various biogeochemical strategies to convert inaccessible forms of P into bioavailable forms, thereby facilitating the uptake of P from soil by plants (Silva *et al.*, 2023). The targeted isolation of phosphorus-solubilizing bacteria has led to the identification of effective growth-promoting strains. By using these strains, the root and shoot length as well as the total dry weight of maize plants (Li *et al*., 2017) were significantly increased .

Recent studies highlight the beneficial effects of some PSMs on plant growth and development, leading to increased total dry biomass. Co-inoculation of *Enterobacter cloacae*, *B. thuringiensis*, and *Pseudomonas pseudoalcaligenes* in phosphorus-deficient substrates effectively enhanced biomass and yield of potatoes (Pantigoso *et al*., 2022). Laboratory experiments with *Acinetobacter* sp. RC04 and *Sinorhizobium* sp. RC02 strains, isolated from the rhizosphere of safflower (*Carthamus tinctorius* L.), demonstrated their ability to improve seed germination and seedling growth upon co-inoculation (Zhang *et al*., 2018).

In general, the use of PSMs offers several benefits, particularly in agriculture, as it improves soil health, fertility and plant stress tolerance. In addition, the use of PSMs can also reduce the dosage of chemical phosphate fertilizers, which helps mitigate environmental impacts and increase economic yields in crop production. In some cases, excessive doses of P fertilizers caused deficiencies of micronutrients such as Zn and Fe (Xu *et al.*, 2022). At the same time, soil PSMs can both increase P availability and improve plant growth and micronutrient supply (Sharma *et al*., 2013), thereby reducing the limiting effect of P deficiency on the absorption and accumulation of target micronutrients such as zinc (Zn), copper (Cu) and magnesium (Mg). Therefore, improving P management is a priority when it comes to sustaining future food supplies and sustainably managing the environment (Beltran-Medina *et al*., 2023). In addition to providing P, microorganisms can also promote plant growth. They have direct and indirect mechanisms of action to promote plant growth, including BNF and phytohormone production. Among the PSMs, bacteria from the genera *Bacillus*, *Pseudomonas*, and *Enterobacter* were the most frequently investigated and showed the most significant potential for development as bioinoculants (Silva *et al*., 2023).

Synthesis of siderophores. Trace elements, particularly iron (Fe), often serve as limiting factors for normal plant development due to their crucial role in enzyme function and overall plant health. The primary form of iron in soil, Fe^{3+}, is almost unavailable for plants, and its conversion to the more usable Fe^{2+} form requires significant resources and energy (Zhang *et al*., 2019). Siderophores play a crucial role in supplying Fe to plants. These are low molecular weight compounds with the ability to chelate metals. When they bind to Fe, the resulting complex interacts with receptors on the surface of plant cells, facilitating the uptake of metals (Saha *et al*., 2016). Numerous microorganisms possess the capacity to synthesize siderophores, encompassing bacterial genera such as *Bacillus*, *Pseudomonas*, *Rhodococcus*, *Micrococcus*, and *Streptomyces* (Singh *et al*., 2022), alongside various fungal genera, including *Aspergillus* and *Penicillium* (Pecoraro *et al.*, 2021). Bacteria and fungi produce siderophores from precursors such as phenolic acids, organic acids, and amino acids through nonribosomal synthesis (Khan *et al*., 2018). Depending on the ligand, there are four types of siderophores: hydroxamates, catecholates, carboxylates and mixed types. Despite their different structures, they all share a similar mechanism of Fe binding, namely the interaction of the metal with two hydroxyl groups (catecholates, carboxylates) or with a hydroxyl and a keto group (hydroxamates) (Pahari *et al*., 2017).

Siderophores are considered important components of plant growth promotion, and bacteria capable of producing these compounds have significant potential as biofertilizers. A notable example of this is the treatment of cowpea plants with siderophore-producing bacteria, which resulted in an almost three-fold increase in Fe concentration, accompanied by increased carbohydrate and protein levels (Patel *et al*., 2018). Likewise, the use of siderophore-producing strains of *Micrococcus* sp. and *Stenotrophomonas* sp. stimulated growth and facilitated Fe accumulation in maize and rapeseed plants (Ghavami *et al*., 2017). There are experimental data that some siderophore producers i.e., *Azotobacter*, *Pseudomonas*, and *Bacillus* spp. promoted plant growth and solubilized Fe and phosphate using an increased N and potassium uptake (Chaudhary *et al*., 2017). A synthetic community siderophore-producing bacteria increased soil selenium bioavailability and plant uptake (Feng *et al*., 2023). Similarly, microbial Fe biofortification based on the siderophore-producing bacteria can be a more long-term solution for wheat if compared with genetic and agronomical approaches (Ehsan *et al.*, 2022).

In addition to their role in improving Fe uptake and plant growth, siderophores find broader utility in environmental applications, especially in soil phytoremediation. Despite the established opinion, siderophores bind not only to Fe; they can transport various other metals (e.g., Zn, Mo, V, Mn) and even non-metals (e.g., B, Si). Some siderophores can also bind to heavy metals, reducing their toxicity and contributing to cellular protection against reactive oxygen species. For example, by using bioreactors with *Cupriavidus metallidurans*, heavy metal concentrations in the soil could be effectively reduced by a factor of 16. Rhizosphere actinomycetes isolated from soil contaminated with heavy metals have shown the ability to synthesize siderophores, which likely helps plants cope with heavy metal toxicity (Ostash *et al*., 2013). The siderophore-producing *Piriformospora indica* was found to increase the tolerance of alfalfa plants to cadmium (Sepehri & Khatabi, 2021). There is data that siderophores can limit the supply of heavy metals to plants: metabolic byproducts of *Streptomyces tendae* F4 limit cadmium uptake by plant organs (Kurth *et al*., 2016).

Siderophores are involved in bacterial signaling systems and may possess antibacterial properties, making siderophore-producing bacteria, especially rhizobia an instrument for the phytopathogen control (Johnstone & Nolan, 2015; Fahde *et al*., 2023).

Utilizing siderophore-producing bacteria holds significant promise in agriculture, as it can substantially enhance crop yield and, notably, the nutrient quality of plant products, especially in regions characterized by soils with limited availability of essential nutrients. Moreover, apart from their direct impact on plant mineral nutrition, these bacteria can also contribute to overall soil quality improvement, thereby promoting plant survival and growth. Employing siderophore-producing bacteria in conjunction with plants that accumulate heavy metals may offer an effective means of soil remediation for future agricultural use.

Phytohormones. In addition to their ability to improve mineral nutrition of plants, microorganisms can also directly influence growth and development of plants through the synthesis of phytohormones. Special emphasis is given to auxins, particularly indole-3-acetic acid (IAA), which is the most prevalent auxin responsible for governing a multitude of physiological processes in plants. These processes include cell division, proliferation, organogenesis, flower and fruit maturation, as well as the regulation of plant responses to light and gravity, and others (Çakmakçı *et al*., 2020). Given the essential role auxins play in regulating plant growth and development, the ability of soil microorganisms to produce auxin-like substances is considered an important indicator of the soil's growth-promoting properties. It is important to note that microorganisms have a two-fold impact on auxins. First, they produce auxins, providing an external source of these phytohormones. Second, microbes can modulate the activity of auxins by their binding to amino acids and sugars (Kochar *et al*., 2013). Studies have shown that over 80% of bacteria inhabiting the rhizosphere, such as *Azospirillum*, *Pseudomonas*, *Klebsiella*, *Rhizobium*, *Mesorhizobium*, *Bradyrhizobium*, *Paenibacillu*s, and *Bacillus*, are involved in auxin synthesis and release (Malik, 2021). The complex interaction between auxins and soil microbes highlights their combined impact on plants and emhpasises the importance of understanding these interactions to optimize agricultural practices and increase crop productivity.

Within the category of phosphate-solubilizing bacteria, there exist strains capable of producing both IAA and siderophores, both of which play pivotal roles in promoting plant mineral nutrition, growth and enhancing soil fertility (Saranaya *et al*., 2022). Thus, treatment with the IAA-producing *Bacillus* sp. doubled iron content in sorghum plants (Manasa *et al*., 2021). *Burkholderia eburnea* CS4-2 improved silicate supply in rice plants alongside IAA production (Kang *et al.*, 2017).

Another significant trait of auxin producers is their ability to increase plant tolerance to abiotic stressors. Specifically, *Bacillus amyloliquefaciens* S-134 increased drought tolerance in wheat (Raheem *et al*., 2018), while the plant growth-promoting strain *B. megaterium* NRCB001 reduced the negative effects of salinity on *Medicago sativa* (Zhu *et al*., 2020). Auxins can also increase plant immunity by activating the synthesis of antibiotics by bacteria (Matilla *et al*., 2018).

In addition to auxins, phytohormones cytokinins and gibberellins have a plant growth-promoting activity and are synthesized by soil microorganisms. Cytokinins are responsible for plant cell division, root and shoot development, chloroplast maturation, and aging. Cytokinin synthesis is intricately linked to nucleotide metabolism, and it is noteworthy that cytokinins can also originate from the degradation of RNA (Frébortová & Frébort, 2021). These phytohormones are involved in bacterial-plant interactions; in particular, they are important in nodulation (Miri *et al*., 2016). For example, *Mesorhizobium ciceri* ND-64 strain with high nitrogen-fixing activity and symbiotic efficiency is capable of synthesizing a relatively high amount of extracellular cytokinins and has a positive effect on the chickpea productivity (Lohosha *et al.*, 2023). Cytokinin-synthesizing bacteria also increase plant resistance to phytopathogenic bacteria (Großkinsky *et al*., 2016) and abiotic stresses, particularly drought (Mekureyaw *et al*., 2022).

The next classic growth-promoting phytohormones are gibberellins. This group of compounds affects many aspects of plant physiology, most notably stimulating seed germination, cell and organ elongation, organogenesis, including the formation of generative structures (Salazar-Cerezo *et al*., 2018). The synthesis of gibberellins is typical for plants, but is also common in microorganisms, and gibberellins were first described by the fungus *Gibberella fujikuroi* (Hernández-García *et al*., 2021). Bacteria that synthesize gibberellins can be exceptionally important for agriculture; in particular, the gibberellin producer *Serratia nematodiphila* PEJ1011 can increase plant tolerance to hypothermia (Kang *et al*., 2015). Gibberellin producing *B. methylotrophicus* KE2 improves plant nutrition (Radhakrishnan & Lee, 2016). In addition, gibberellins can stimulate the activity of bacteria, in particular, enhance the oxidation of nitrogen-containing compounds (Xu *et al.*, 2018).

A relatively new but promising area is the search for new compounds with phytohormonal activity. These compounds possess several advantages, including efficacy at low concentrations, bioavailability, zero-emission production; they are readily biodegradable and do not pollute the environment. These compounds include pteridic acids produced by *S. hygroscopicus* TP-A0451. They are able to stimulate additional root formation on bean hypocotyls at a concentration of 1 nM, which is several folds lower than the concentration of IAA required (Igarashi, 2004). Catellatolactams A-C produced by *Catellatospora* sp. RD067858, have antibacterial properties and stimulate root elongation and seed germination (Liu *et al*., 2022); catellatopyrroles A-B also have similar properties (Liu *et al*., 2022). Trehangelin E, produced by *Polymorphospora* sp. RD064483, has a pronounced effect on root growth and seed germination, in particular, treatment with 10 μM solution stimulates germination by 90% (Lu *et al*., 2022). Increased root growth potentially leads to an increase in the absorption area, which affects the nutrient supply. And sped up germination allows crop plants to have an advantage over weeds. However, it remains unclear what is the mechanism of action of these compounds. Further research in this area will help improve the understanding of plant-bacterial interactions.

CONCLUSIONS

The critical role of soil microorganisms in enhancing global food production and crop food cannot be understated. The utilization of beneficial microbes represents an innovative and promising strategy to substantially improve the nutritional quality of food crops in the next years. Notably, certain microorganisms can promote plant growth and development through the synthesis of key phytohormones such as auxins, cytokinins, and gibberellins. Additionally, they can enrich the micro- and macronutrient content of staple crops by facilitating the availability of essential elements including nitrogen, phosphorus, iron, and zinc. This is achieved through microbial mechanisms such as biological nitrogen fixation, phosphate solubilization, and siderophore production. **Fig. 2** provides an illustrative summary of the multifaceted mechanisms underlying the plant growth-promoting effects of soil microorganisms.

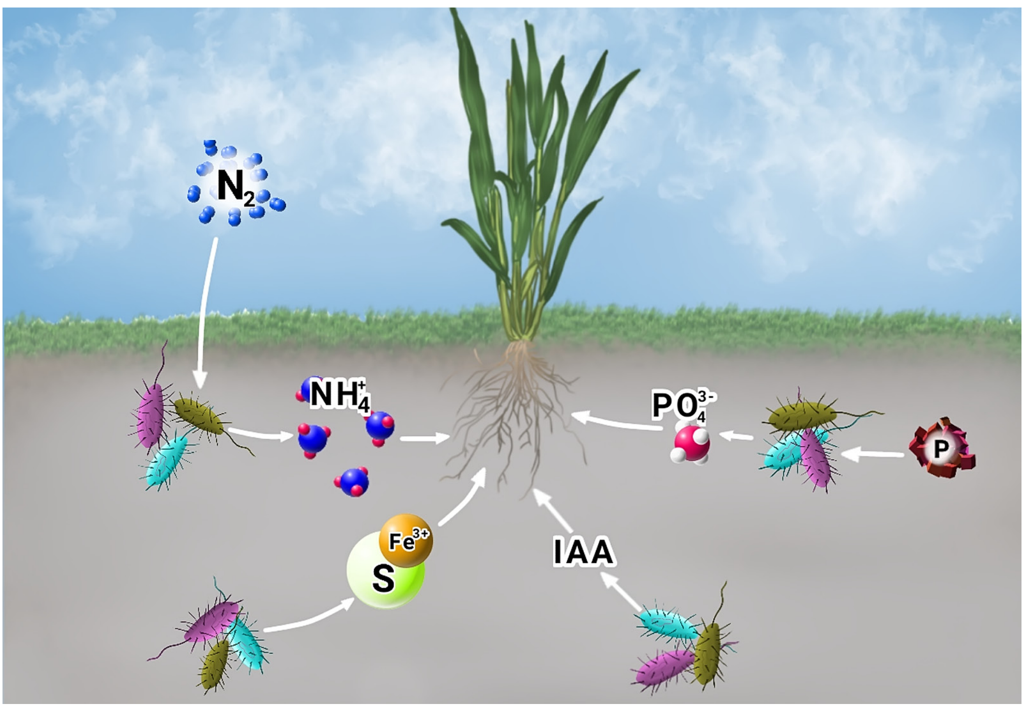

Fig. 2. Schematic illustration of the main elements of microbial impact to improve plant growth and development. Indole-3-acetic acid (IAA), siderofore (S) and inorganic salts of phosphorous (P)

The adoption of microbial biotechnologies in agriculture offers several advantages. Firstly, it can enhance crop yields and agricultural profitability by improving plant health, nutrient absorption, and resilience to stresses. The resulting boost in production levels will be key to meeting the food demands of the rising global population. Secondly, substituting synthetic chemicals with customized bioinoculants can promote sustainable farming practices that protect environmental health. This aligns with broader efforts to provide healthy, nutritious diets through safe food production. Thirdly, the selection of microorganisms and methods of their application should be tailored to address context-specific nutritional deficiencies and soil conditions. This targeted approach facilitates measurable improvements in the mineral and micronutrient composition of crops in nutrient-poor areas.

However, it is important to note that there are still challenges to be addressed before microbial solutions can be broadly implemented. The complexity of plant-microbe and microbe-microbe interactions, variability in soil properties across locations, and the need for precise management practices to ensure desirable outcomes require further investigation. Ongoing research that provides insights into these dynamics and helps refine real-world application protocols will be key to achieving the above goals. Ultimately, an integrated approach combining traditional techniques like plant breeding with modern microbial biotechnologies could provide a holistic platform to combat malnutrition and enhance global food and nutrition security.

COMPLIANCE WITH ETHICAL STANDARDS

Conflict of Interest: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

AUTHOR CONTRIBUTIONS

Conceptualization, [O.M.; N.R.]; methodology, [O.M.; Y.K.; N.R.]; validation, [N.R.; O.T.]; formal analysis, [O.M.; Y.K.; N.R.]; investigation, [O.M.; Y.K.]; resources, [O.M.; N.R.]; writing – original draft preparation, [O.M.; N.R.]; writing – review and editing, [O.M.; Y.K.; O.T.; N.R.]; visualization, [O.M.; Y.K.] supervision, [N.R.; O.T.]; project administration, [O.M.; N.R.]; funding acquisition, [O.M.; Y.K.; O.T.; N.R.]. All authors have read and agreed to the published version of the manuscript.

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РОСЛИННО-МІКРОБНІ ВЗАЄМОДІЇ: МЕХАНІЗМИ ТА ЗАСТОСУВАННЯ ДЛЯ ПІДВИЩЕННЯ УРОЖАЙНОСТІ І ЯКОСТІ СІЛЬСЬКОГОСПОДАРСЬКОЇ ПРОДУКЦІЇ

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Одночасне поєднання змін клімату і зростання світового народоселення, що загрожує продовольчій безпеці, зумовило гостру необхідність розробити сталі інноваційні підходи у рослинництві, спрямовані на підвищення продуктивності культур і збереження поживної цінності харчових продуктів. Поряд із тим необхідно зберігати здоров’я ґрунтів і зменшувати їхню залежність від синтетичних агрохімічних препаратів. Дослідження біології та фізіології рослино-мікробних взаємодій є визначальним для розуміння переваг їхнього використання у рослинництві. У наведеному огляді розглянуто механізми, за допомогою яких корисні ризосферні та ґрунтові бактерії, відомі як рістстимулювальні бактерії (PGPB), здатні підвищувати врожайність, стійкість до стресів і поживну цінність сільськогосподарських культур. Такі важливі характеристики бактерій, як їхня здатність до біологічної фіксації азоту, до перетворення неорганічного фосфату в розчинні форми, до перетворення органічних фосфатів, до синтезу сидерофорів і фітогормонів, можна розглядати як основу їхньої рістстимулювальної здатності. Продовжуючи попередні дослідження, зосереджуємо увагу на з'ясуванні механізмів взаємодії рослин і ґрунтових PGPB, їхнього впливу на мінеральне живлення, ріст і розвиток, на врожайність рослин. Увагу зосереджено на діазотрофних ризобіальних PGPB (роди *Rhizobium*, *Bradyrhizobium*) і деяких перспективних гетеротрофних бактеріях (роди *Azotobacter*, *Bacillus*, *Pseudomonas*). Наведено приклади застосування PGPB з метою біофортифікації, зокрема, підвищення вмісту заліза й інших мікроелементів унаслідок посилення мобілізації, поглинання, транслокації й акумулювання поживних речовин у органи сільськогосподарських культур. Необхідне продовження скринінгових досліджень PGPB, вивчення ефектів поєднання різних штамів для інокулювання, створення ефективних систем доставки, польових випробувань і врахування цих даних у селекційних програмах. Міждисциплінарна співпраця селекціонерів, фізіологів рослин, мікробіологів, учених-агрономів і фермерів є важливою для повноційної реалізації потенціалу рослино-мікробних взаємодій у контексті розвитку сталого сільського господарства та подолання викликів майбутнього. Поглиблення знань про біологію PGPR і їхню взаємодію з рослинами відкриває широкі перспективи у вирішенні завдань підвищення продуктивності та стабільності рослинництва в умовах зростаючого попиту.

Ключові слова: рістстимулювальні бактерії, біофортифікація, живлення рослин, сталий розвиток рослинництва, мікробіом ґрунту, рослино-мікробні взаємодії

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