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Original Article

Plant growth promoting bacteria drive food security

Bactérias promotoras de crescimento de plantas (BPCP) impulsionam a segurança alimentar

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Abstract

The essence of food security centers on ensuring availability and accessibility of foods in adequate amounts and quality for all populations at all times for an active and healthy life. Microorganisms are tiny bioreactors, which represent sustainable resources and promising approaches to bridging the gap between food production and consumption globally via various biotechnological applications. This review focuses on plant-growth promoting bacteria (PGPB) which exert their potential impacts on increasing soil fertility, plant growth, and productivity through a variety of processes, including direct, indirect, and synergistic mechanisms. PGPB plays a substantial role in accelerating nutrients' availability such as (N, P), producing phytohormones such as gibberellins, IAA, and bioactive compounds against biotic and abiotic stressors. Recent advances in PGPB will be addressed as a sustainable approach to satisfy global food demand.

Keywords: plant-growth promoting bacteria, plant yield, soil fertility, food security.

Resumo

A essência da segurança alimentar centra-se em garantir a disponibilidade e acessibilidade de alimentos em quantidade e qualidade adequadas para todas as populações e em todos os momentos, visando a qualidade de vida ativa e saudável. Os microrganismos são biorreatores minúsculos, que por meio de diversas aplicações biotecnológicas, representam recursos sustentáveis e possuem abordagens promissoras para preencher a lacuna entre a produção e o consumo de alimentos globalmente. Esta revisão concentra-se em bactérias promotoras de crescimento de plantas (BPCP) que exercem seus impactos potenciais no aumento da fertilidade do solo, crescimento de plantas e produtividade por intermédio de uma variedade de processos, incluindo mecanismos diretos, indiretos e sinérgicos. As BPCP desempenham um papel substancial na aceleração da disponibilidade de nutrientes como (N, P), produzindo fitormônios como giberelinas, IAA e compostos bioativos contra estressores bióticos e abióticos. Os avanços recentes das BPCP serão analisados a partir de uma abordagem sustentável para satisfazer a demanda global de alimentos.

Palavras-chave: bactérias promotoras de crescimento de plantas, produtividade de plantas, fertilidade do solo, segurança alimentar.

1. Introduction

A massive gap exists between global food production and consumption, owing in part to the world population's annual increase of about 2%. According to the Global Report on Food Crises (GRFC), approximately 193 million people are facing food insecurity and are in desperate need of emergency food supplies). Furthermore, according to FAO estimations, the world population will reach 10 billion by 2050, raising concerns about food insecurity (FAO, 2020). As a result, food demand will nearly double (FAO, 2020).

Food is a right for all, according to the United Nations Declaration of Human Rights. According to the World Bank's most recent update, food insecurity is a serious problem in many countries. Agriculture is the primary resource for food production worldwide, accounting for 98 percent of total food supply (Rao, 2013). Farmers usually use chemical fertilizers to increase soil fertility in order to increase crop yield. Nevertheless, the use of synthetic fertilizers has the potential to harm all life forms as well as the environment and economy. As a result, it is critical to improve soil fertility and plant productivity through a cost-effective, efficient, and environmentally friendly strategy in order to meet the population's food demands.

Microorganisms are tiny bioreactors that represent sustainable resources and promising approaches to bridging the global food production-consumption gap through various biotechnological applications. PGPB

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are taxonomically diverse and metabolically versatile promising groups of bacteria such as *Bacillus* (Khalifa and Almalki, 2015), *Enterobacter* (Khalifa et al., 2016; Khalifa, 2020) *Streptomyces, Sinorhizobium* (AlAli et al., 2021), *Pseudomonas* (Aldayel and Khalifa, 2021), *Delftia acidovorans* (Khalifa and Almalki 2019), *Janibacter indicus,* and *Brevibacterium casei* (Khalifa et al., 2020). The number of PGPB taxa has been steadily rising in recent years. This is due to two factors: current advances in molecular biology and bioinformatics technologies, and the isolation of PGPB from hitherto unknown places. These PGPR are classed as biofertilizers, biostimulators, biocontrol agents, and bioremediators based on their mode of action. Plant development is aided by PGPB through a variety of ways, including direct, indirect, and synergistic effects. PGPB serve important roles in increasing the availability of nutrients like (N, P, Fe) and chlorophyll formation, as well as creating phytohormones such gibberellins, IAA, and bioactive chemicals to protect plants from biotic and abiotic stresses. The wide literature on PGPB, mechanisms, impacts, and future perspectives was thoroughly reviewed due to their potential importance as drivers for food security.

2. Food Security via PGPB

Food security depends on sustainable agriculture. Agriculture produces a large portion of the world's food. However, several causes, such as soil erosion and degradation, nutrient leakage, biotic and abiotic stresses, pose serious challenges to sustainable agriculture. Degraded soils lack sufficient nutrients to support plant growth and yield. Climate change causes abiotic stressors, which limit growth. Plant yield loss is significantly influenced by phytopathogens. According to FAO statistics, nearly 38% (4,889 million ha) of the world's total land area (13,003 million ha) is agricultural land, with cropland accounting for one-third of this total. Global cropland per capita has decreased over the last five decades as a result of global population growth and cropland loss due to man-made practices. Soil is a rich source of microorganisms, which form a wide range of interconnected relationships and cross-talk with other living organisms. Plant roots come into direct contact with soil and act as anchors, absorbing water and nutrients required for normal growth. Root exudates are soluble organic substances synthesized and released by roots, including amino acids, sugars, growth factors, and enzymes. The released substances attract a diverse range of microbial cells to the plant roots, resulting in a variety of plant-microbe interactions (Gouda et al., 2018). PGPB are beneficial bacteria that colonize the root surface (rhizoplane or rhizosphere) or penetrate into root tissues (entophytic bacteria). PGPB can live on their own or form symbiotic relationships with plant roots. PGPB play an important role in soil fertility through direct, indirect, and synergistic mechanisms (Khalifa and Almalki, 2015; Khalifa et al., 2016; Khalifa et al., 2020; AlAli et al., 2021). The overall goal of PGPB is to sustain agriculture in an efficient, cost-effective, and environmentally friendly manner.

3. Diversity and Mode of Action of PGPB

PGPB diversity is crucial in sustainable agriculture because it improves plant growth and confers resistance to phytopathogens. PGPB has been extensively studied over last century, and species descriptions are largely based on phenotypic traits. Furthermore, the number of recognized validated species was small. However, thanks to modern molecular biology technological approaches such as next generation sequences, a large number of novel PGPB species have been proposed (Table.1). Another factor contributing to recent designation of PGPB is the isolation from previously unexplored ecological niches and plant hosts. Table 1 presents a summary of recently described PGPB examples and isolation sites. PGPB are diverse within Gram positive and Gram negative bacterial groups and ubiquitous in different ecological niches, as demonstrated by *Paenibacillus monticola* from High-Altitude Spruce Forests in the Qilian Mountains (Li et al., 2022a), *Streptomyces adelaidensis* root of *Callitris preissii* (Kaewkla et al., 2021), *Devosia rhizoryzae* and (Table 1). Many more PGPB are expected to emerge in the future.

PGPB sustains agriculture and drives food security by displaying various modes of action (Figure 1). PGPB are divided into four categories: biofertilizers, biostimulators, biopesticides, and bioremediators (Shah et al., 2018). Biofertilizers promote plant growth by increasing the availability of essential nutrients such as nitrogen through nitrogen fixation and phosphorous through phosphate solubilization. Nitrogen-fixing bacteria such as *Rhizobium, Azospirillum, Bacillus*, and *Pseudomonas* are examples of this category. *Bacillus* and *Pseudomonas* are instances of biostimulators, which are microorganisms capable of producing phytohormones such as indole acetic acid, cytokinins, gibberellins, and ethylene. Biopesticides are microorganisms that promote plant growth by inhibiting phytopathogenic agents through the production of bioactive compounds such as antibiotics and siderophores (Shah et al., 2018). This category includes *Bacillus megaterium* and *Psuedomonas* spp. However, many species of soil bacteria, known as PGPB, stimulate plant growth through a variety of interconnected mechanisms. Bioremediators, such as Bacillus spp., are microorganisms capable of removing or reducing environmental pollutants from soil, air, or water (Rabani et al., 2022; Thiyagarajan et al., 2020). However, a single PGP species, such as *Bacillus megaterium*, which acted as a biofertilizer, biostimulator, and biopesticide, could exhibit one or more of these actions (Khalifa and Almalki, 2015). The rhizospheric soil microbiome has a significant positive impact on crop plants (Sankaranarayanan et al., 2021; Savitha et al., 2021), plant conferring resistance against abiotic stresses (Savitha et al., 2022a), and enhancing phytoremediation (Veerapagu et al., 2022). The variability in the strategies used by PGPB to improve soil fertility and plant productivity reflects metabolic versatility and provides benefits for the environment

4. PGPB as Biofertilizers

Nitrogen is an essential nutrient for normal plant growth because it is found in amino acids, chlorophyll, nucleic acids, and crop production. The atmosphere

Table 1. Respesentatives of recently documented plant growth promoting bacterial species.

PGP species	Source	Reference
Paenibacillus monticola	High-Altitude Spruce Forests in the Qilian Mountains	Li et al., 2022b
Streptomyces adelaidensis	root of *Callitris preissii*	Kaewkla et al., 2021
Devosia rhizoryzae and Devosia oryziradicis	rhizosphere of rice plants	Chhetri et al., 2022
Metabacillus dongyingensis	Saline-Alkaline Soil	Yin et al., 2022
Rhizobium setariae	Green Foxtail, Setaria viridis	Kang and Seo, 2022
Arthrobacter wenxiniae	Rhizosphere of lily	Sun et al., 2022a
Azospirillium brasilence	Rhizosphere of *Triticum vulagre* (wheat)	Gonzalez et al., 2018
Bacillus amyloliquefaciens	Field soil, South Korea	Kazerooni et al., 2021
Bacillus halotolerans	Nodules of *P. vulgaris* L (bean)	Jiménez-Gómez et al., 2020
Bacillus megaterium	Rhizosphere of *Lactuca sativa* (Lettuce), *Camellia sinensis* (Tea) and Root-nodules of *Medicago sativa* (Alfalfa)	Khalifa and AlMalki, 2015
Bacillus subtilis	Rhizosphere of *Cucumis sativus* (Cucumber) in Bangladesh	Hashem et al., 2019
Burkholderia contaminans	A zinc and cadmium accumulator in soil of *Sedum alfredii*.	Heo et al., 2022
Pseudomonas monteilii	Rhizosphere of *Solanum lycopersicum* L. (tomato) a	Aldayel and Khalifa, 2021
Bacillus filamentosus, Janibacter indicus, and Brevibacterium casei	Rhizosphere of *Zygophyllum coccineum*	Khalifa et al., 2020
Bacillus thuringiensis	*Ephestia kuehniella*	Azizoglu, 2019
Enterobacter cloacae	Rhizosphere of *Triticum aestivum* (Wheat), Roots of *Medicago sativa* (Alfalfa) and rhizosphere of *Zea mays* (maize)	Khalifa et al., 2016
Pseudomonas alcaliphila, Pseudomonas hunanensis, Streptomyces laurentii, Sinorhizobium sp., and Bacillus safensis	Rhizosphere of the *Ocimum basilicum* (basil plant)	AlAli et al., 2021

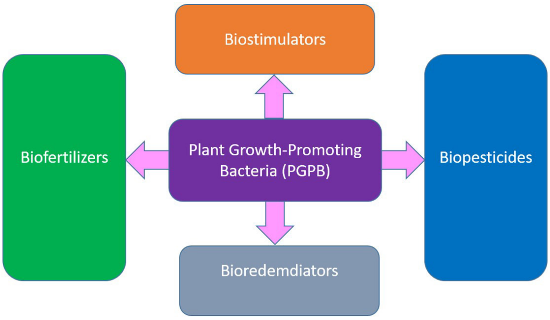

Figure 1. Mode of actions of PGPB.

contains approximately 78% nitrogen gas (N2), but it is inaccessible to plants due to a lack of the nitrogenase enzyme (Zahran et al., 2003). Nitrogen enters the ecosystem primarily through bacterial fixation by nitrogen-fixing bacteria, which can convert N2 to inorganic nitrogenous compounds, make them accessible to plants (Masson-Boivin and Sachs, 2018). In 1886, leguminous species discovered biological nitrogen fixation (BNF), which paved the way for biofertilizers. Nitrogen fixation by the legume root-nodule bacteria *Rhizobuum* is a clear example of this

There really are two types of nitrogen-fixing bacteria: symbiotic bacteria and free-living bacteria. Symbiotic bacteria form nodules mainly on legume roots. Bacteria in nodules can fix nitrogen. The well example of this type is Rhizobium sp (Kazmierczak et al., 2020). Photosynthesis provides carbohydrates to bacteria, and nitrogen fixation provides fixed nitrogen. The specificity and efficiency of this process are determined by chemical signals (flavonoids and lechtins) from plants and bacteria. Details on nodulation processes and other related issues are provided (Kazmierczak et al., 2020). The major source of nitrogen input to agricultural soils is biological nitrogen fixation. The second type is nitrogen-fixing bacteria that are free-living, such as *Gluconacetobacter diazotrophicus, Pseudomonas, and Enterobacter* (Omer, 2017). Nitrogenase is a multi-enzyme complex responsible for the conversion of molecular nitrogen to ammonia (Milton, 2022). Nitrogenase can only be found in prokaryotic organisms. Plant growth and productivity are increased when crops are inoculated with compatible bacterial strains. For example, nitrogen-fixing bacteria *Azospirillum lipoferum* and *Bacillus polymexa* are capable of enhancing maize plants by increasing available nitrogen and improving salt tolerance even under salt stress conditions. Biofertilizers have several advantages over chemical fertilizers, including their safety, sustainability, and environmentally friendly nature, as neither microbes nor toxic substances will accumulate in the food chain (Rathika et al., 2020). Besides that, unlike chemical agents, pests that are harmful to plant growth rarely develop resistance.

5. Phosphate Solubilizing Bacteria (PSB)

Phosphorus (P) is another essential macronutrient for plants. It is a structural component of several physiological processes in plants, including photosynthetic process, starch remobilization, membrane formation, and energy transfer mechanisms (Shrivastava et al., 2018). Furthermore, P is essential for seed development, root elongation, and normal crop maturity. The soil contains a lot of P, but most of it isn't bioavailable because of their high molecular weights, which limit their solubility in water.

As a result, in order for such complexes to be available to plants, they must be hydrolyzed into soluble inorganic (Numan et al., 2018). The concentration of available phosphorus in soil is typically very low, with scores as low as 1 ppm (Martínez-Gallegos et al., 2018). Chemical fertilizers use soluble inorganic phosphates that can become immobilized in the soil and thus unavailable to plants. As a result, PSB play an important role in agriculture as a method for increasing P bioavailability in plants (Martínez-Gallegos et al., 2018). PSB bacterial groups include *Pseudomonas, Bacillus, Azospirillum, Acinetobacter, Rhizobium*, and *Enterobacter*, which aid in the conversion of insoluble phosphates to soluble phosphates to improve plant phosphorous uptake (Yadav and Pandey, 2018).

The mechanisms of PSB phosphate solubilization that result in bioavailable soluble P include acidification, organic acid excretion, oxidation–reduction reactions, and the production of extracellular polymeric substances. PSB have the ability to secrete acids (e.g., citric acid) that can chelate phosphate-bound cations via carboxyl and hydroxyl groups or decrease soil pH by releasing protons (H+) that lead to the indirect solubility of P | (Yadav and Pandey, 2018). Phosphate-solubilizing bacteria have proven to be an effective solution for arid, drought-prone regions and dry land farming (Chakdar et al., 2018). Inoculating phosphate-solubilizing bacteria (PSB) with rock phosphate on maize and wheat increased crop growth, root dry biomass, and grain yield, implying that it could be used as a substitute for chemical phosphate fertilizer. In a study conducted in Saudi Arabia on the bacterium *Bacillus megaterium* isolated from root-nodules of *Medicago sativa*, the results showed that some attributes promote growth, such as indole acetic acid production and inorganic phosphate solubilization (Khalifa and Almalki, 2015). Besides that, three PSB species, *Bacillus, Azotobacter*, and *Pseudomonas*, showed a significant reduction in heavy metal uptake by corn plants due to increased P solubility and phytostabilization of heavy metals (Shahid and Khan, 2022).

6. Ammonia Production

Ammonia is a common form of nitrogen that plants can use. *Streptomyces laurentii, Sinorhizobium sp.,* and *Bacillus safensis* are among the PGPB that produce ammonia to increase nitrogen availability (AlAli et al., 2021). Bacterial ammonia production can influence plant-microbe interactions and microbial diversity by altering rhizosphere pH. (AlAli et al., 2021). Furthermore, ammonia has the potential to inhibit fungal pathogens. Bacteria that produce ammonia have inhibitory effects on *Fusarium* spp. mycelium growth (Patel et al., 2021). PGPB promote plant growth by producing ammonia, which can be used as a nitrogen source and/or an inhibitor of microbial pathogens.

7. PGPB as Biostimulators

7.1. Production of Indole Acetic Acid (IAA)

Plant growth regulators such as auxin, gibberellin, and ethylene are produced by microorganisms. Indole-3-acetic acid is an auxin (IAA). IAA is a plant hormone that increases root length, stimulates cell elongation by increasing membrane permeability and osmotic contents, and provokes flowering and fruiting (Numan et al., 2018). IAA has been shown to regulate spore germination in bacteria like *Streptomyces atroolivacezlz* (Numan et al., 2018). IAA production appears to be a common trait among rhizosphere bacteria. The PGPB metabolic processes appear to include the production of auxins. Bacillus, Pseudomonas, and other bacterial species that use tryptophan as the primary component produce IAA (Khalifa et al., 2016). *Pseudomonas* sp. role's in Canola plants, which enhanced root elongation and plant growth stimulation, result in IAA production (Duca et al., 2018). The production of IAA appears to be a common feature by which PGPB promotes plant health and yield.

7.2. Production of gibberellins

GAs are plant hormones that can boost plant growth and development, including the growth of different plant parts. More than 136 different types of GAs have been identified (Kozaki and Aoyanagi, 2022), indicating a wide range of structure and metabolic pathways. Different gibberellins have different effects on different parts of plants. Several studies, including *Streptomyces laurentii, Sinorhizobium* sp., *Bacillus safensis, and Bradyrhizobium* sp., confirmed the ability of PGPB to secrete gibberellin (Yadav and Pandey, 2018; AlAli et al., 2021). Because of their ability to produce GAs, these PGPB significantly improved the growth parameters of common bean and okra plants (AlAli et al., 2021). Because they have the Gas production trait, PGPB improve plant growth and yield.

7.3. Production of cytokinins

Cytokinins are phytohormones derived from adenine that regulate the cell cycle, cell division, and promote plant development (Numan et al., 2018). Cytokinins play important roles in plant growth by affecting cell division activity in embryos, buds, leaf expansion promotion, and senescence retardation (Shah et al., 2018). Among the bacteria that produce cytokinins are *Methylobacterium, Bacillus licheniformis, Pseudomonas fluorescens, Bradyrhizobium japonicum,* and *Pseudomonas putida* (AlAli et al., 2021; Palberg et al., 2022). A large body of evidence confirmed that cytokinin-producing bacteria benefit plants. *Bacillus* spp., for example, increased shoot and root growth in okra plants (AlAli et al., 2021). Bacteria that produce cytokinin are more likely to have multiple beneficial effects on plants.

7.4. ACC deaminase

Ethylene is a phytohormone that regulates plant growth by controlling root and shoot development, seedling emergence, fruit ripening, flower senescence, and response to abiotic and biotic stresses (Yuan et al., 2022). Recent evidence indicates that some active bacterial strains reduce ethylene by secreting the ACC deaminase enzyme (Glick, 2014). This enzyme catalyzes the conversion of ethylene in plants to -ketobutyrate and ammonia, thereby lowering ethylene levels inside plants. Studies suggested an ACC deaminase model in which bacteria associate with the surface of seeds or roots of plants, though these bacteria can also be found on leaves and within plant tissues (Glick, 2014).

Bacteria act as a sink for ACC by lowering the ethylene level in the plant. ACC deaminase is occasionally found in bacteria until it is activated. Abiotic or biotic stress causes plants to express protective/defensive genes, which causes bacteria to produce more ACC deaminase due to increased ACC flux. The ratio of ACC oxidase to ACC deaminase determines the level of ethylene in plants. As a result, in order to reduce plant ethylene levels, ACC deaminase must be activated prior to increasing the amount of ACC oxidase (Glick, 2014). Under saline conditions, ACC deaminase bacteria have been shown to promote French bean plant growth (Yavada and Pandey 2018). Recently, it was reported that ACC-deaminase producing *Bacillus filamentosus*, *Janibacter indicus,* and *Brevibacterium casei* isolated from the rhizosphere of *Zygophyllum coccineum*, Al-Ahsa, alleviated the negative effects of salinity stress on wheat. (Khalifa et al., 2020) Catalase, for example, may play an indirect role in PGP. H_2O_2 (Hydrogen peroxide) is split into H2O and O2 by catalase. H2O2 is one of the most important reactive oxygen species (ROS) in plants, attracting vital macromolecules and rendering them inactive (Zhou et al., 2006). Environmental biotic and abiotic stresses, such as pathogen attack, cause H2O2 to accumulate as a signaling molecule, causing oxidative damage. Catalase production by PGPB such as *Bacillus megaterium* and *Enterobacter cloacae* is assumed to be an indirect mechanism for enhancing plant growth (Khalifa and Almalki, 2015; Khalifa et al., 2016; Khalifa, 2020).

8. PGPB as Biocontrol Agents

8.1. Production of antibiotics

Crop disease is a major challenge for sustainable agriculture because it reduces crop yield by about one-third (Savary et al., 2019). Chemical pesticides are used, which may pose environmental and human health risks (Rathika et al., 2020). Antibiotic-producing PGPB can be used to protect agricultural crops against plant pathogens in environmentally friendly ways (Gouda et al., 2018). PGPB act as plant pathogen suppressors by secreting antagonistic agents and increasing immune responses. Antibiotics are low-molecular-weight compounds that inhibit/stop pathogen growth through a variety of mechanisms. Antibiotics attack a variety of vital cellular components such as the plasma membrane, cell wall, and ribosomes. A wide range of biological control agents have been shown to significantly inhibit plant pathogens (Table 2). *Bacillus halotolerans*, for example, had a significant antagonistic effect against *Fusarium pseudograminearum*, which causes crown rot in wheat (Li et al., 2022b). *Tylenchulus semipenetrans* was suppressed by a consortium of bioinoculants including *Bacillus subtilis, Purpureocillium lilacinum,* and *Trichoderma viride* (Nagachandrabose et al., 2022). (Table 2). The ability to produce bioactive compounds that inhibit phytopathogens appears to be shared by PGPB. These compounds protect plants by suppressing microbial pathogenic agents, which improves plant development and productivity via indirect mechanisms. As a result, PGPB may play a beneficial role by suppressing phytopathogens. Volatile organic compounds (VOCs) serve many purposes in plant growth and production, including inducing systemic disease resistance, controlling plant pathogens, and improving plant growth. The first reported VCs that induced biostimulation were 2,3-butanediol and acetoin (Jiao et al., 2021). However, over 1000 VOCs and inorganic compounds, such as NH3 and HCN, have been identified by various bacterial species (Audrain et al., 2015). Nonetheless, new VCs are on their way to providing new insights into plant-microbe interactions. Plant biostimulation via VOCs has been reported to have four distinct modes of action: 1) modulating plant photosynthesis; 2) increasing mineral uptake; alleviating biotic and abiotic stresses; and 4) modulating hormone cross-talk (Sharifi and Ryu, 2018). However, signaling pathways differ depending on the PGPB species, pathogenic agent, and plant host (Jiao et al., 2021). *Bacillus megaterium* was found to produce 2-pentylfuran, which increased the growth characteristics of *Arabidopsis thaliana. Bacillus siamensis* was recently found to synthesize ten distinct VCS, including methylbutanoic acid and 3-methylbutanoic acid, which had antibiosis against *Alternaria alternate* (Wang et al., 2022). PGPB contribute to environmentally friendly agriculture and food production by protecting crops from dangerous phytopathogens.

8.2. Siderophore production

Iron is a necessary micronutrient for many cellular processes in plants, including chlorophyll biosynthesis, respiration, and as a cofactor for many enzymes. Iron exists in soil in insoluble forms at pH (7.35–7.40) that plants cannot access. Siderophores are small organic molecules with a high affinity for iron chelation that are produced in iron-limited environments (Gouda et al., 2018). Several microorganisms, including *Enterobacter* genera, *Bacillus,* and *Pseudomonas,* can produce siderophores to increase

Table 2. Microbial control agents protecting host plants against pathogens.

Microbial control agent	Pathogenic agent	Host plant	Reference
Bacillus subtilis, Purpureocillium lilacinum, and *Trichoderma viride*	*Tylenchulus semipenetrans*	Citrus *sinensis* (citrus)	Nagachandrabose et al., 2022
1. *Trichoderma* spp	*Ceratovacuna lanigera* Zehntner	*Saccharum officinarum* (Sugarcane)	Islam et al., 2022
Trichoderma spp.	*Pratylenchus brachyurus*	*Glycine max* (soybean)	Oliveira et al., 2021
Bacillus halotolerans	*Fusarium pseudograminearum*	*Triticum aestivum* L. (wheat)	Li et al., 2022b
Erwinia persicina	*Fusarium graminearum*	*T.aestivum* L. (wheat)	Deroo et al., 2022
Brevibacillus laterosporus	Sitobion avenae (aphid)	*T. aestivum* L., (wheat)	Javed, et al., 2022
Xylaria feejeensis	*Fusarium oxysporum*	*Solanum lycopersicum* L.(Tomato)	Brooks et al., 2022
Clonostachys rosea	*Botrytis cinerea*	*S. lycopersicum* L.(Tomato)	Meng et al., 2022
Bacillus mesonae	*Ralstonia solanacearum*	*S. lycopersicum* L.(Tomato)	Yoo et al., 2022
Trichoderma, *Bacillus*, *Paenibacillus*, *Enterobacter*, *Streptomyces*, and *Pseudomonas*,	*Pseudoperonospora cubensis*	*the Cucumber*	Sun et al., 2022b
Bacillus brevis and *Paenibacillus polymyxa*	*Fusarium solani, Rhizoctonia solani, and Macrophomina phaseolina,*	*Fragaria ananassa* Duchesne (Strawberry)	Abd-El-Kareem et al., 2022
Bacillus amyloliquefaciens	Macrophomina phaseolina	*Vigna unguiculata* (Cowpea)	Rangel-Montoya et al., 2022
Achromobacter xylosoxidans	*Fusarium solani*	*Phaseolus vulgaris* L. (common bean)	Mohamadpoor et al., 2022
Trichoderma asperellum	Fusarium verticillioides	*Zea mays* (Maize)	Cuervo-Parra et al., 2022
Trichoderma asperellum	Ustilago maydis	*Z. mays* (Maize)	Cuervo-Parra et al., 2022

iron availability in the environment and uptake capacity (Gouda et al., 2018; Sultana et al., 2021). Microorganisms can synthesize siderophores similar to ferric iron by reducing ferric iron-siderophore complexes into ferrous iron in the cytosol, which becomes accessible even in the presence of other metals such as cadmium and nickel (Sultana et al., 2021). It is well-documented that siderophores could establish a stable complex with trace elements such as Cu, Zn, Ca as well as Fe. Such metals play a premium role in plant growth promotion via their involvement in enzymatic activities of the central metabolic pathways. It has been recently reported that siderophore-producing plant growth promoting vermi-bacteria were isolated from *Eisenia fetida* gastrointestinal tract. In this study, *Bacillus mycoides*, *B. aryabhattai*, *B. megaterium*, *Staphylococcushominis*, *B. subtilis*, *B. spizizenii*, *B. licheniformis*, *B. mojavensis*, *B. toyonensis*, *B. anthracis*, *B. cereus*, *B. thuringiensis*, and *B. paranthracis* were obtained (Andleeb et al., 2022). PGPB sustain plant growth by antagonistic activity against to potentially virulent rhizoplane fungal and bacterial species by depriving native microflora of iron. Therefore, siderophores play a dual action in enhancing plant growth by making iron and potentially other elements available to plants and preventing phytopathogen infection. *Pseudomonas* sp has been shown to inhibit pathogens by producing siderophore competition for iron, lytic enzymes, antibiosis, and increasing ISR (Wang et al., 2021). It was recently reported that a siderophore-like substance conferred resistance to pathogenic bacteria, *Pseudomonas syringae*, on *Arabidopsis thaliana* (Betoudji et al., 2020). Other types of siderophores are produced by non-ribosomal peptide synthetase (NRPS), which is not dependent on mRNA for biosynthesis. Siderophore-producing PGPB promote plant growth and yield by suppressing pathogens, thereby contributing to sustainable agriculture through an indirect mechanism.

9. PGPB as Bioinoculants

9.1. Increment of crop yield upon bioinoculation

Bioinoculation with an effective bacterial strain/or consortium resulted in a significant increase in the yield of many economically important crops, thereby trying to bridge the gap between food consumption and production (Table 3). As shown in Table 3, various microbial species could increase crop yield by 16% in the case of Oryza sativa (Rice) inoculated with a consortium of *Pseudomonas* sp. and *Penicillium* sp. (Fitriatin et al., 2021), 111% in the case of *Solanum lycopersicum* L. (Tomato) inoculated with a

Table 3. Percentage of yield increments, crop and microbial PGPB.

Crop	Microbial species	Increment yield (%)	Reference
Oryza sativa (Rice)	Consortium of *Pseudomonas* sp. and *Penicillium* sp.	16	Fitriatin et al., 2021
Solanum lycopersicum L. (Tomato)	Consortium of *Rahnella aquatilis* and *Acinetobacter* sp.	111	Tahiri et al., 2022
Phaseolus vulgaris (Common beans)	*R. tropici*	66	Mercante et al., 2017
Vicia faba (Faba beans)	*R. leguminosarum viciae*	81	Youseif et al., 2017
	T. asperellum	30	Doni et al., 2018
Phaseolus mungo (black gram)	*Acaulospora scrobiculata*, *Rhizophagus irregularis*	207%	Shukla et al., 2022
	Bradyrhizobium sp.1	80%	Shukla et al., 2022
	Pseudomonas	78%	Shukla et al., 2022
	Consortium of *Acaulospora scrobiculata*, *Rhizophagus irregularis*, *Bradyrhizobium* sp. 1, *Pseudomonas*	95%	Shukla et al., 2022
*Vigna radiata (*Mung bean)	Consortium of *Acaulospora scrobiculata*, *Rhizophagus irregularis*	52%	Shukla et al., 2022
	Bradyrhizobium sp. 2	47%	Shukla et al., 2022
	Pseudomonas	46%	Shukla et al., 2022
	Consortium of *Acaulospora scrobiculata*, *Rhizophagus irregularis*, *Bradyrhizobium* sp.2, *Pseudomonas*	60%	Shukla et al., 2022

consortium of *Rahnella aquat* and *Rhizophagus irregularis* (Shukla et al., 2022) compared to the untreated plants. The percentage of yield increments varied substantially depending on a variety of parameters, including PGPB strain characteristics and host range, plant variety, growing state, and soil agronomic parameters. Furthermore, *Phaseolus vulgaris* L. (Common bean) is a clearly a significant with high nutritional content that is widely consumed around the world. It has been observed that inoculating common bean with PSB increased the plant's ability to absorb P, particularly in low-fertility soils (Ramana et al., 2010). Roots of common beans have symbiotic partnerships with rhizobia that are compatible. Furthermore, symbiotic bacteria have an important role in crop development, quality, and yield in a variety of ways, including nitrogen fixation. Non-rhizobial strains, on the other hand, might colonize common bean root nodules. *Bacillus, Enterobacter, Pseudomonas,* and *Microbacterium,* for example, have been isolated from common bean nodules. A previous study conducted in Al-Ahsa found that inoculating common bean plants with *Bacillus megaterium* increased their growth (Khalifa and Almalki, 2015). PGPB has numerous advantages for crop health and yield.

9.2. Screening steps to obtain efficient bioinoculants

Developing a successful bioinoculant is a long process with numerous sequential steps. First, isolation of PGPB from various locations, particularly unexplored sites such as rhizospheric soils associated with wild desert plants, which are more likely to harbor PGPB with unique abilities (Figure 2). Wild plants are subjected to harsh conditions such as high temperatures, high salinity, and drought. Plants and the associated PGPB develop sophisticated stress response mechanisms in response, highlighting the emergence of novel metabolic pathways, products, and traits that may have greater potential biostimulating effects on plants than all previously known ones. Pure microbial strain preservation is critical for microbiology and its applications, and PGPB are no an exception. Maintenance of the purified single isolates should be carefully carried out using agar slants, glycerol stocks, freeze-drying etc. Initial in vitro screening of PGP traits by inoculation of relevant plants to save time and effort, particularly when dealing with huge numbers of bacterial isolates. Second, using phenotypic (colony characteristics such as colour, shape, elevation, margin, and cellular feature such as cell shape, cell arrangements and Gram staining reactions, and genotypic tools such 16S rRNA gene sequencing, whole genome sequencing, etc, strains with PGP traits are characterized. The chosen strains will be tested for PGP characteristics using standard laboratory tests such as phosphate solubility and bioactive compound production such as auxins, gibberellins, ammonia, antibiotics. Third, the positive biostimulatory effects of the selected strains on some

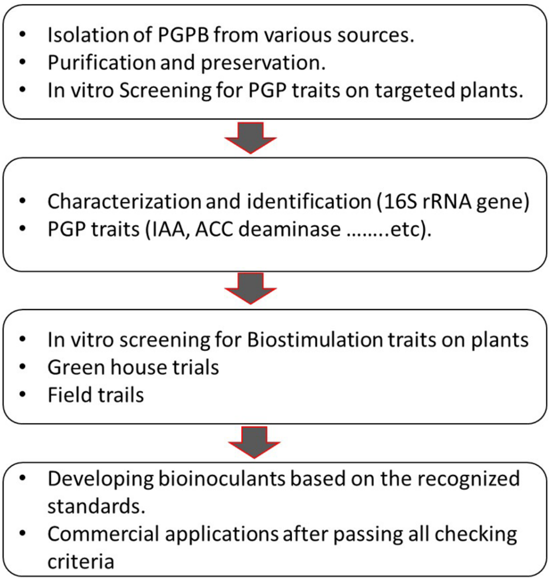

Figure 2. Screening steps to obtain efficient bioinoculants.

of the economically important plant species particulary grain legumes and crops are validated in greenhouse experiments and field trials. Fourth, after passing all of the testing criteria that ensure the biosafety, efficiency, develop bioinoculants based on recognized standards and commercial applications. Regular evaluations of efficiency, shelf life, and viability are required.

10. Conclusion

Due to the rising global food demand, PGPB is a cornerstone technique for ensuring food security through sustainable agriculture. PGPBs play a variety of roles in increasing soil fertility, plant productivity, environmental protection, and health. PGPB could act as biofertilizers, biostimulators, bioremediators and biocontrol agents. In-depth studies of the plant microbiome composition in relation to soil fertility and plant productivity should be the focus of future research. It is critical to identify the global important microbial players that have a significant impact on crop output when bioinoculants are applied. Ecological and agronomical aspects that influence microbiome modulation should be prioritized. PGP bioinoculants' prospects should also include setting acceptable criteria for quality, biosafety, efficiency, and efficacy, as well as shelf life, longevity, precipitance, and competitiveness with local microbial strains. In the future, researchers should devote more attention to understanding how PGPR causes ISR at the molecular level.

The study should also be oriented toward developing 'super bioinoculants,' which are consortia of highly active PGPB strains with exceptional abilities in increasing soil health, plant growth, and yield, in order to reduce the gap between food production and consumption and ensure food security.

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