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Bacillus and *Paenibacillus* as plant growth-promoting bacteria in soybean and cannabis

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Many agrochemicals designed to help plants withstand abiotic and biotic stresses can negatively impact the environment. Soil, as an essential natural resource, offers plants organic matter, nutrients, and microbial diversity to thrive in challenging environmental conditions. The soil contains plant growth-promoting bacteria that play an important role in plant/crop productivity, assisting plants through a variety of mechanisms, including nitrogen fixation, phosphate solubilization, phytohormone production, induction of resistance against a wide range of pathogens, and production of microbe-to-plant signals that regulate aspects of plant responses to stress. Plant growth-promoting bacteria such as *Bacillus* and *Paenibacillus* can contribute to sustainable agriculture by enhancing nutrient uptake, acting as biocontrol agents, and producing lytic enzymes with the potential to disrupt or destroy pathogenic organisms in important agricultural and medicinal crops including soybean and cannabis. This review explores the mechanisms of action of plant growth-promoting bacteria, focusing on *Bacillus* and *Paenibacillus* species, and their potential to enhance, optimize plant growth and promote sustainable agriculture.

KEYWORDS

***Bacillus*, cannabis, plant growth promoting bacteria (PGPB), *Paenibacillus*, plant growth, soybean**

1 Introduction

Major crop plants are challenged by biotic stressors, which include attacks from pathogens such as fungi, bacteria, and oomycetes, and/or abiotic stresses such as radiation, salinity, flooding, drought, extreme temperatures, pH, and heavy metals (Wahab et al., 2023). These stressors cause yield reductions in major crop plants throughout the world. Synthetic agrochemicals like fertilizers and pesticides used to combat the impact of stress are expensive, cause greenhouse gas emissions, leave chemical residues on food crops, and release hazardous chemicals into the environment (Mitra et al., 2021). The need for sustainable food production to sustain a growing human population calls for alternatives to agrochemicals, such as plant growth promoting bacteria (PGPB) that can be used to control biotic and mitigate abiotic stresses (De Andrade et al., 2023). PGPB have the potential to support future sustainable agricultural crop production due to their relatively low impact on native soil microorganisms, livestock, and humans, and minimal impact on soil ecology and biodiversity. Their use in integrated pest management systems has proven to be a sustainable alternative to chemical pesticides, offering a safer, eco-friendly approach to managing plant diseases (Arkhipov et al., 2024).

Plants are associated with beneficial microbial communities located on or inside tissues and are present throughout their developmental cycle. These communities include bacteria, archaea, fungi, and algae, constituting the phytomicrobiome. The portion of the soil close to the roots that is subject to nutritional interference from the roots is named rhizosphere. Plants perform photosynthesis, and depending on the plant species, they invest 10 to 40% of their photosynthetic metabolites in the rhizosphere through rhizodeposition (Vetterlein et al., 2020). Through rhizodeposition, the rhizospheric soil is fertilized and enriched with nutrients, amino acids, and organic energetic molecules such as carbohydrates. Fertilization of the rhizosphere exerts a significant influence and changes the soil microbiota near the roots (Hassan et al., 2019). Plants modulate rhizospheric microorganisms through plant physiological factors that govern plant–microorganisms interactions and by the composition of their exudates. The composition of the microorganisms in the roots is influenced by these root exudates, and the population of the root microbiome takes place in two stages. The first stage is rhizosphere colonization, accomplished by a subgroup of microorganisms from the non-rhizosphere soil and bulk soil. In the second stage, the phyllosphere and endosphere are colonized by a subset of microorganisms from the rhizosphere (Compant et al., 2021; De Andrade et al., 2023). The phytomicrobiome is comprised of the rhizome-microbiome, made up of root-associated microbes, and the phyllo-microbiome, comprised of shoot-associated microbial communities. Depending on their location on the plant surface or in internal tissues, they can also be classified as ecto-microbiome and endo-microbiome, respectively (Kumawat et al., 2023; Vimal et al., 2024). The plant and its phytomicrobiome form the holobiont; it is comprised of numerous beneficial phytomicrobiome members that bolster the plant's ability to survive in biotic and abiotic stress environments through a variety of mechanisms (Taghinasab and Jabaji, 2020; Baedke et al., 2020; Khan, 2023). *Paenibacillus triticisoli, Rhizobium* sp., *Pseudomonas* sp., *Agrobacterium tumefaciens, Azospirillum lipoferum, Azospirillum brasilense, Azoarcus* sp., and *Zoogloea* sp. are few examples of rhizospheric bacteria (Suleiman et al., 2019; Li et al., 2021; Zeng et al., 2022). *Acinetobacter, Enterobacter*, and *Pseudomonas* are the most abundant genera in the roots, stems and leaves (Dong et al., 2019; Firrincieli et al., 2020). Plant growth-promoting bacteria (PGPB) help mitigate the effects of abiotic stresses including salinity, drought, heavy metal stress and acidity which are major hurdles to agricultural production (Jain et al., 2023). Some PGPB act directly by improving the nutritional status of plants via phytonutrients such as fixed nitrogen or solubilized minerals from soil (P, K, Zn, Fe and other essential nutrients) and regulating the levels of plant phytohormone (auxins, cytokinins, gibberellins, abscisic acid and ethylene) (Odoh et al., 2020; Bhat et al., 2023). Other beneficial strains affect plant growth indirectly by suppressing phytopathogens and other deleterious microorganisms through parasitism, competing for nutrients or production of antagonistic compounds (hydrogen cyanide, siderophores, antimicrobial metabolites and antibiotics) (De Ron et al., 2024; El-Saadony et al., 2022). Certain plant growth promoting rhizobacteria produce lytic enzymes such as chitinase, glucanases, and proteases, which induce systemic resistance against foliar and root pathogens. Microbial-derived compounds can also play an important role in the mitigation of abiotic stress effects on plants (Morcillo and Manzanera, 2021), including those associated with climate change. Table 1 summarizes the mechanisms of action of various PGPB under optimal and stress conditions in various crops. This review aims to examine the mechanisms of action of plant-beneficial bacteria such as *Bacillus* and *Paenibacillus* species, their deployment for plant growth promotion, and their use to optimize plant growth in soybean, cannabis and other agricultural crops.

2 Workflow for isolation and identification of plant growth-promoting bacteria

Effective screening practices are essential for identifying efficient PGPB. It is therefore imperative to isolate and characterize PGPB to determine their mechanisms that confer them the ability to act as biostimulants, biofertilizers, and bioprotectants. PGPB are primarily identified based on the genomic techniques, which are essential in the deployment of these bacteria in commercial agriculture for bio-protection and yield enhancement. Several methodologies have been used to isolate PGPB. Fan et al. (2016, 2018) employ a comprehensive methodology to isolate rhizobacteria (from soil) by brushing the adhered soil from the roots, dissolving the soil in sterilized water, and diluting 10-fold before plating on different bacterial growth media. Using the sterilization method of Qin et al. (2009), endophytic bacteria can be isolated from surface-sterilized tissues of plants by grinding the tissues in a phosphate buffer solution and centrifuging. The obtained supernatant is diluted 10-fold and plated on agar to recover colonies of endophytes (Fan et al., 2023; Di et al., 2023). Figure 1 illustrates the step-by-step methodology of isolation of endophytic and rhizobacteria and highlight their important functions. Characterization and identification of PGPR has been done with PCR-based genomic fingerprinting. Williams et al. (1990) introduced the random amplified polymorphic DNA (RAPD) assay, also known as arbitrary primed PCR. The RAPD assay consists of short primers, 9 to 10 bases in length, capable of hybridizing to DNA sequences with sufficient affinity at low annealing temperatures to amplify bacterial genome regions (Boopathi and Boopathi, 2020). Whole genome techniques, such as amplified fragment length polymorphism (AFLP), have been

TABLE 1 Mechanism of action of various PGPB.

PGPR	Mode of action	Crop	Reference
Bacillus velezensis	Inhibition of motility traits of *Ralstonia solanacearum*, and damages the pathogen's cell wall through production of fengycin	Tomato	Wang et al., 2023
Paenibacillus mucilaginosus	Biofilm formation, solubilization of inorganic and organic phosphate, production of IAA	Tomato	Wang et al., 2023
Bacillus & Paenibacillus sp.	Intreases plant growth by aiding the uptake of P, N, K, Fe, and Zn	Maize	Ahmad et al., 2023
Pseudomonas fluorescens	Induces systemic resistance against sheath blight	Rice	Renganathan, 2020
Azoarcus	Nitrogen fixation	Rice	Fernández-Llamosas et al., 2020
Bacillus mucilagenosus & *Bacillus edaphicus*	Potassium solubilization	Peppery, cucumber	Ali et al., 2021
Pseudomonas putida	Antibiotic production	Bean	Abo-Elyousr et al., 2021
Paenibacillus sp.	Increases biomass, photosynthesis rate of plants, and nitrogen fixation mediated by *nifH* gene	White clover	Li et al., 2022
Rhizobia	Hydrogen cyanide production	Soybean	Zoundji et al., 2020
Rhizobia sp.	Induces stress resistance in plants	Legumes	Etesami and Adl, 2020
Pseudomonas aeruginosa	Produces toxic volatile compounds against *Fusarium oxysporum*	Egg plant	Chandra et al., 2020
Bacillus endophyticus & Pseudomonas aeruginosa	Modulates the production of IAA, SA, ABA in plants against *Spodoptera litura*	Tomato	Kousar et al., 2020
Paenibacillus polymyxa	Solublization of phosphate under varying pH, temperature, and heavy metal stress	Zea mays	Rosli et al., 2020
Bacillus & Pseudomonas sp.	Promotes plant growth, increase above ground biomass and yield, and modulate rhizosphere microbiome	Cannabis	Comeau et al., 2021
Bacillus subtilis BS-2301	Promotes plant growth and synthesizes IAA during infection with *Sclerotinia sclerotiorum*	Soybean	Ayaz et al., 2024

shown to be relatively robust and discriminatory (Louws et al., 1995; Arif et al., 2010). Restriction fragment length polymorphism (RFLP), also known as amplified ribosomal DNA restriction analysis (ARDRA) is another tool applicable to the study of microbial diversity that relies on DNA polymorphism. Rep-PCR (repetitive-sequence-based polymerase chain reaction) is one of the genomic fingerprinting techniques that is used for identification and taxonomy (Versalovic et al., 1991; Rademaker et al., 2004). PCR is used to amplify DNA sequences located between interspersed repeated sequences in prokaryotic genomes. DNA primers designed to complement naturally occurring repetitive sequences are used in Rep-PCR fingerprints, which are found in multiple copies in the genomes of many Gram-negative and Gram-positive bacteria (Lupski and Weeinstock, 1992; Fakruddin et al., 2013; Janczarek and Gałązka, 2024; Matys et al., 2024). These modern genomic techniques can help identify bacteria that can promote plant growth, leading to the deployment of beneficial microbes in sustainable agriculture production.

The culturable bacterial genera considered to be responsible for plant growth promotion include *Acinetobacter, Agrobacterium, Arthobacter, Azotobacter, Azospirillum, Burkholderia, Bradyrhizobium, Rhizobium, Frankia, Serratia, Thiobacillus, Pseudomonas*, and *Bacillus* (Pattnaik et al., 2019). Recent studies have shown that *Bacillus* and *Paenibacillus* sp. have several advantages over other PGPB strains when it comes to formulation of inoculants, long-term maintenance in rhizosphere soil, and potential in sustainable crop production (De Araújo et al., 2011; Orozco-Mosqueda et al., 2021; Saeed et al., 2021). Several species belonging to *Bacillus* and *Paenibacillus* genera are isolated from rhizosphere and plant tissues that can stimulate plant growth directly by synthesizing plant hormones or by increasing mineral nutrient uptake by fixing atmospheric nitrogen, soluble soil phosphorus, and other known mechanisms. In some species, antibiotic metabolites are produced to suppress plant pathogens, whereas other species are known to stimulate plant host defense before pathogen infection. *Paenibacillus* and *Bacillus* sp. colonize the host tissues and biofilm formation improved the bacterium's ability to act as a biocontrol agent against plant pathogens (Govindasamy et al., 2011; Khan et al., 2020; Li et al., 2022).

Through the green revolution of the 20th century, food production increased significantly; in at least some cases environmental concerns were overcome, and agriculture became more sustainable (Hyder et al., 2024). This led to innovation and the development of a "Fresh" Green Revolution, which has already gone some distance to reducing environmental impacts. One of the main inputs of the more recent bio-revolution involves utilization of

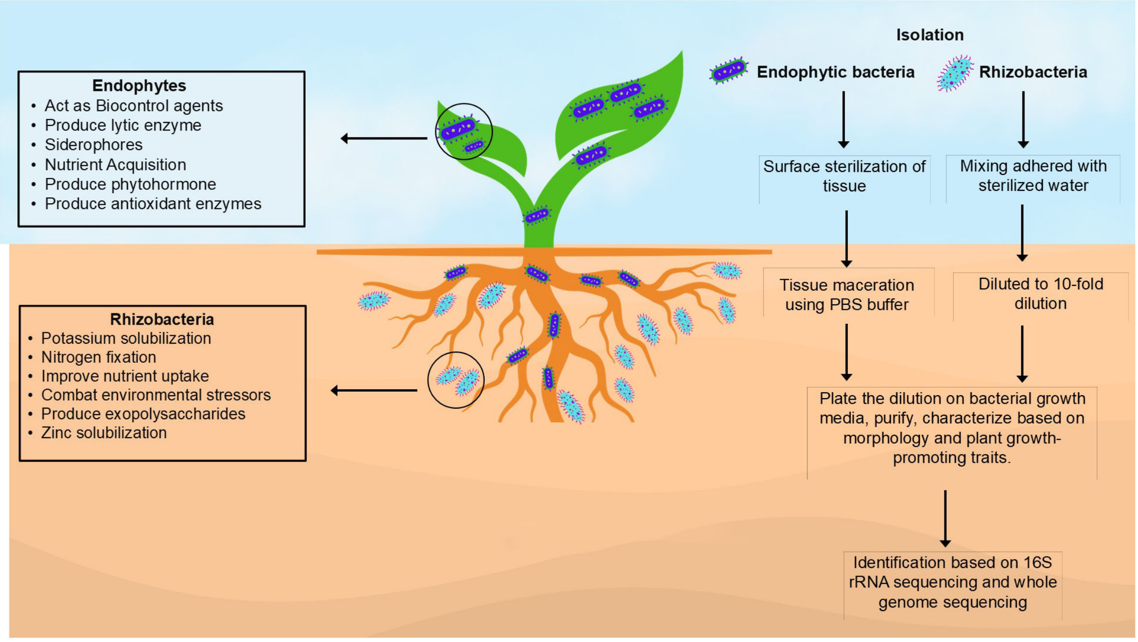

FIGURE 1
Methods for isolation and identification of PGPB.

PGPB (bio-inoculum, and bioactive compounds of inoculum) and improved crop yield through manipulation of phytomicrobiome structure (Pastor-Bueis et al., 2021; Pandey et al., 2023). As part of this review, the significant potential of the deployment of *Bacillus* and *Paenibacillus* genera is explored, highlighting the various mechanisms that have proven both genera to be effective in promoting plant growth, increasing yields, and improving stress resistance in soybean, cannabis and other crop plants.

3 *Bacillus* and *Paenibacillus*

Bacteria that are rod-shaped and can produce endospores under aerobic conditions are known as *Bacillus.* This group has been assigned as a genus because of sporulation properties and it comprises a diverse collection of species (Logan and Halket, 2011; Soares et al., 2023). Taxonomically, *Bacillus* and *Paenibacillus* fall under gram-positive, aerobic, or facultative endospore-forming bacteria but over the past decade advances in 16S rRNA oligonucleotide cataloguing and 16S rRNA sequence analysis revealed that the genus *Bacillus* is phylogenetically very heterogeneous. Consequently, there have been considerable changes in its taxonomy since the first description. The genus *Bacillus* is divided into two groups vernacularly i.e., the *B. subtilis* group and the *B. cereus* group (Claus and Fritz, 1989; Govindasamy et al., 2011). 16S rRNA studies allowed phylogenetic grouping and reclassification. Subsequently, phylogenetic analyses were carried out using other genes and proteins. Patel and Gupta (2020) conducted phylogenetic and comparative genetic sequence analyses defining the members of the *subtilis* and *cereus* clades as well as six additional genera: *Alkalihalobacillus, Cytobacillus, Neobacillus, Mesobacillus, Metabacillus*, and *Peribacillus* and proposed that new species added to the genus *Bacillus* should meet the minimum criteria of the *subtilis* or *cereus* clades and be supported by a phylogenetic tree based on 16S rRNA sequences or by concatenated protein sequences. The "*subtilis* clade", originally composed of *Bacillus subtilis, B. licheniformis, B. pumilus*, and *B. amyloliquefaciens*, has since been expanded to include several other species (Xu and Kovács, 2024). The "*cereus* clade" comprises the pathogenic species and strains of the genus, namely *B. anthracis*, causing the fatal anthrax disease; *B. cereus*, a foodborne pathogen; and *B. thuringiensis*, an entomopathogen, along with other non-pathogenic species with significant applications in agriculture and industry. There are currently 435 species and 12 subspecies of *Bacillus* in the genus (with verified publications and correct nomenclature) (Parte, 2014), and this genus is a subject to constant modifications (Blanco Crivelli et al., 2024) with advancement and refinement in instrumentation and techniques for in-depth identification.

Paenibacillus species were originally included in the genus based on morphological characteristics in common with the type species *B. subtilis*, isolated in 1872 (Zeigler, 2013). However, these characteristics are very ancient and cannot be used to group species into a single genus. Analysis of 188-unit characters suggested that *Bacillus* may be divided into several genera (Priest et al., 1988). In 1991, when 16S rRNA gene sequences were determined to do phylogenetic analyses, it was found that these sequences segregated into at least five distinct clusters, one of which was reassigned to the novel genus *Paenibacillus* in 1993 and includes the type species *Paenibacillus polymyxa* (Ash et al., 1991, 1993). The name *Paenibacillus* is derived from the Latin adverb '*paene*', meaning 'almost'—almost a *Bacillus*. Several organisms previously classified as separate *Paenibacillus* species were classified as equals shortly after their identification. Among other characteristics, a proposed amendment is described. Species of this genus can be gram-positive, gram-negative, or gram variable while sharing *Bacillus* basal characteristics (Shida et al., 1997; Grady et al., 2016). Meanwhile, novel species of *Paenibacillus* are being discovered and classified; the genus currently contains approximately 200 species (Grady et al., 2016; Lee et al., 2022). Figure 2 summarizes the various functions of *Bacillus* and *Paenibacillus* genera and their roles in plant growth promotion.

3.1 Plant growth promotion perspective of *Bacillus* and *Paenibacillus* in soybean and cannabis

Several agricultural and medicinal crops have been demonstrated to benefit from the use of *Paenbacillus* spp and *Bacillus* spp to promote plant growth and yield, including wheat, maize, soybean, sunflower, common bean, tomato, pepper, potato, cucumber, and cannabis (Aloo et al., 2019; Miljaković et al., 2020; Lyu et al., 2022). Here we focus on using *Bacillus* and *Paenibacillus* species on two important crops: soybean and cannabis. *Bacillus* sp. and *Paenibacillus* sp. stimulate the growth of these crops by increasing nutrient availability, improving soil structure, and inhibiting pathogens (our unpublished data).

3.1.1 Soybean

Soybean offers one of the most important protein sources among legume crops, and plays an important role in the human diet, food, and oil production. Approximately 80% of the soybean sown area in the world is concentrated in three countries: Brazil, the United States, and Argentina (Volkova and Smolyaninova, 2024). Canada currently ranks seventh in the world in terms of soybean production. The soybean planting area is expected to be expanded to 10 million acres (approximately 4 million hectares) by 2027 under an ambitious plan developed by Soy Canada (Soy Canada, 2023). To achieve this target the symbiotic relationship with beneficial microbes like *Bacillus*, and *Paenibacillus* can be leveraged to enhance the ability of soybean to resist abiotic and biotic stresses such as salinity, drought, and heavy metal toxicity and to enhance overall production. The genomic and metagenome analysis of the soybean endosphere reveals that the most dominant group of bacteria in its endosphere is *Streptomyces*, followed by *Chryseobacterium*, *Paenibacillus*, *Bacillus*, and *Mitsuaria.* These species play a role in a variety of biological pathways, including CMP-KDO biosynthesis II (from D-arabinose 5-phosphate), TCA cycle (plant), citrate cycle (TCA cycle), fatty acid biosynthesis, and glyoxylate and dicarboxylate metabolism (Chouhan et al., 2023). *Bacillus* and *Paenibacillus* play important roles in nitrogen fixation, priming of defense mechanisms, up- and down-regulation of various genes and proteins to make soybean resilient to various stress and improve its sustainable production for food security.

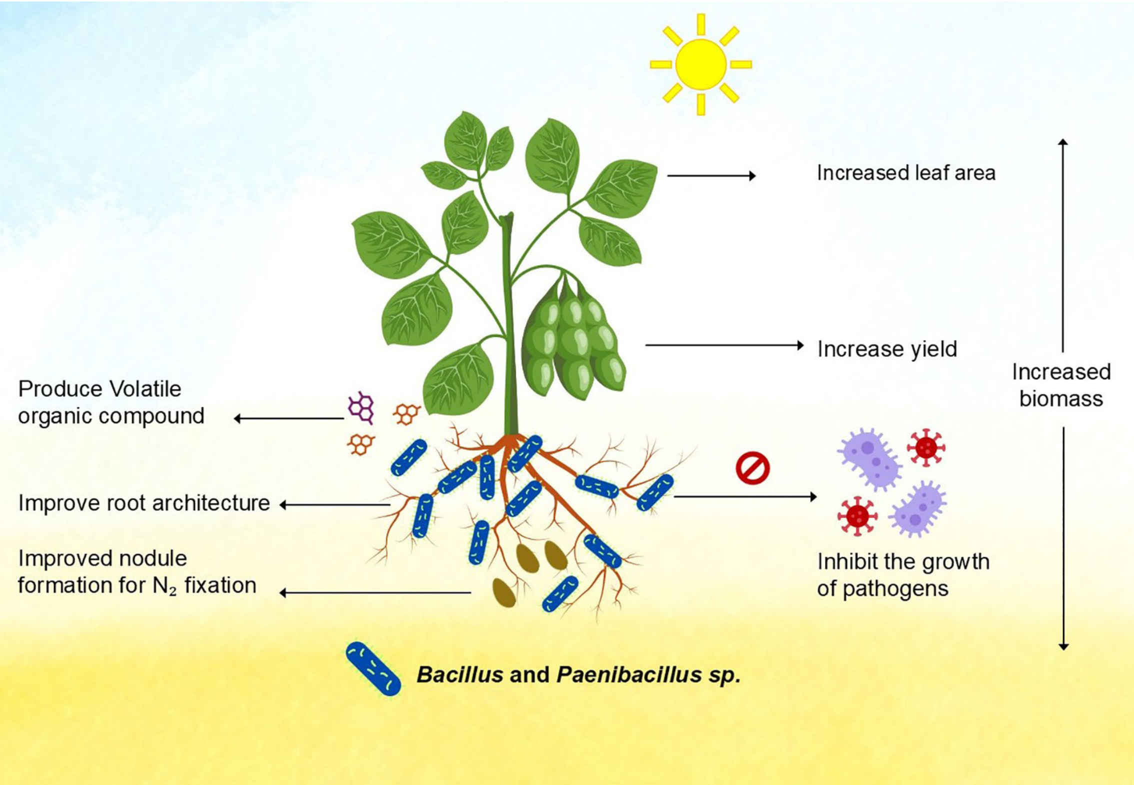

FIGURE 2
Bacillus and *Paenibacillus* promote plant growth.

Figure 2 summarizes effects of *Bacillus* and *Paenibacillus* sp. and addresses the role of these bacteria in increasing nodule formation, plant growth, biomass production and inhibiting the growth of pathogens in soybean.

3.1.1.1 Role of *Bacillus* and *Paenibacillus* in nitrogen fixation and yield improvement of soybean

Nitrogen fixation is an important ecological process in legumes, including soybean, that is facilitated by a variety of microbes, notably *Bacillus* strains. A rhizobial gene known as nodABC encodes an enzyme responsible for lipo-chitooligosaccharide synthesis, which induces symbiotic responses within the host. As a result of this process, atmospheric nitrogen (N_2) is converted into physiologically useful ammonium ions (NH^{4+}) in the Earth's nitrogen cycle (Rana et al., 2023). Some *Bacilli* produce nitrogenase, which is responsible for catalyzing nitrogen fixation into ammonia. Plants may directly absorb this ammonia, making it a key source of nitrogen for their growth and development. The ability to fix N_2 is widely dispersed among bacteria belonging to different phylogenetic groups. The nitrogenase enzyme complex is composed of two proteins: iron (Fe) and molybdenum iron (MoFe), encoded by the *nifH* and *nifDK* genes, respectively. The *nifH* gene sequence has been evolutionarily conserved and is now considered as a marker for N_2 fixation in *Bacillus* and *Paenibacillus* sp (Mehta et al., 2003; Jain et al., 2021; Li et al., 2021). Vitorino et al. (2024) reported that *Bacillus velezensis* enhances root growth and increases nodules and flowers, resulting in a positive impact on grain yield, phosphate content, and weight in soybean. *B. aerophilus* and *B. subtilis* improved soybean production, specifically seed dry weight, N uptake, and the number of soybean root nodules (Nuraini et al., 2024). *Bacillus* strains form symbiotic relationships with specific plants, known as nitrogen-fixing nodules in legumes, where they provide the host plant with a direct source of ammonia contributing to the development of plants. This mutualistic relationship also facilitates the development of sustainable agricultural practices through the reduction of nitrogenous fertilizer use (Fahde et al., 2023; Iturralde et al., 2019). *Bacillus thuringiensis* produces a peptide known as thuricin-17, which increases soybean tolerance to drought when used with *Bradyrhizobium japonicum*, modifies below-ground structures, increases root and nodule biomass, slightly increases leaf area and photosynthetic rate (Prudent et al., 2015). The *Bacillus amyloliquefaciens* EB2003A releases bioactive compounds in its growth media that enhance corn and soybean radicle length and percentage germination under optimal and NaCl-stressed growth conditions (Naamala et al., 2022).

The *Paenibacillus nif* operon consists of a cluster of genes that encode *nif*, measuring 11 kb in size and demonstrating that it is capable of fixing nitrogen (Dasgupta et al., 2021). Nitrogen fixers such as *P. azotofixans, P. macerans, P. polymyxa, P. graminis*, and *P. odorifer* contain the *nifH* gene (Prabhukarthikeyan et al., 2022). Ribeiro et al. (2024) reported insights related to alternative N_2-fixation by Fe-only nitrogenase in *P. sonchi* and also observed endospore formation during N_2-fixation in *P. durus*, coinciding with the highest levels of *nifH* transcription. Plant growth stimulation and an increase in shoot and root dry weight were observed after inoculation with *P. polymyxa-gfp* strain alone and in combination with *B. japonicum*. *In vivo* simultaneous visualization using Confocal Laser Scanning Microscopy (CLSM) demonstrated that *P. polymyxa* invades soybean roots and root nodules and improves plant growth when inoculated individually or in combination with *B. japonicum* (Annapurna et al., 2013). The *Bacillus* and *Paenibacillus* sp. provide a key mechanism of nitrogen fixation for the resilience of soybean in the face of abiotic and biotic stresses.

3.1.1.2 *Bacillus* and *Paenibacillus* sp. influence soybean plant metabolomics and proteomics profiles

Signal compounds produced by phytomicrobiome members can enhance plant growth through various mechanisms, including activation of antioxidant metabolism pathways, protein activities, induction of plant defense systems, increased photosynthesis rate, production of phytohormones and modification of plant root systems (Subramanian and Smith, 2015; Lyu et al., 2021). The plant activates the first-layer defense response, called pathogen-associated molecular patterns (PAMP)-triggered immunity (PTI) and initiates local responses where the pathogen attacks and then induces responses in the more distant uninfected plant parts; this induced systemic resistance (ISR) in plants can also be activated by non-pathogenic plant growth promoting bacteria that help in suppressing disease. It is activated through jasmonic acid/ethylene or salicylic acid (SA) signaling (Zhang et al., 2024) (Figure 3). In the host plant, ISR modulates many biochemical and cytological processes including the deposition of lignin in the cell wall, the production of phytoalexins, and the synthesis of other antimicrobial substances such as peroxidases and glucanases (Mahapatra et al., 2022). The *Bacillus* and *Paenibacillus* sp. play important roles in modulating soybean defense response. For instance, *Bacillus* and *Paenibacillus* are effective biocontrol agents and produce antimicrobial compounds such as cyclic lipopeptides that can bind membrane lipids, cause structural permeability, and damage fungal cell membranes (Yang et al., 2024; Gómez-De la Cruz et al., 2023).

Bacillus subtilis inhibits growth of *Sclerotinia sclerotiorum*, the causative agent of stem white mold disease in soybean. It causes severe oxidative stress to fungal hyphae and inhibits melanin synthesis in the sclerotia (Ayaz et al., 2024). *Bacillus velezensis* inhibits the growth of soybean root rot pathogens and reduces germination, conidia production, and mycelial growth of *F. oxysporum* resulting in hyphal malformations and effectively controlling soybean root rot (Sun et al., 2023). *Bacillus* and *Paenibacillus* species produce indole acetic acid(IAA) as secondary metabolites that aid plant growth. *B. altitudinis* TM22 produces IAA, enhances freshshoot weight, shoot length, fresh root weight, dry shoot weight, and dry root weight and upregulates the expression of growth-related genes such as those related to production of expansin (*EXP-1* and *EXP-2*), cytokinin (*CKX*), auxin (*IAA-1* and *IAA-6*), and gibberellin (*GA20OX-1* and *GA20OX-2*) (Moosa et al., 2024). *Bacillus velezensis* strain (BVPS01) was found to be more efficient at solubilizing phosphates by producing the phosphatase enzyme, as indicated by the expression of the *phoC* and *phoD* genes in soybean.

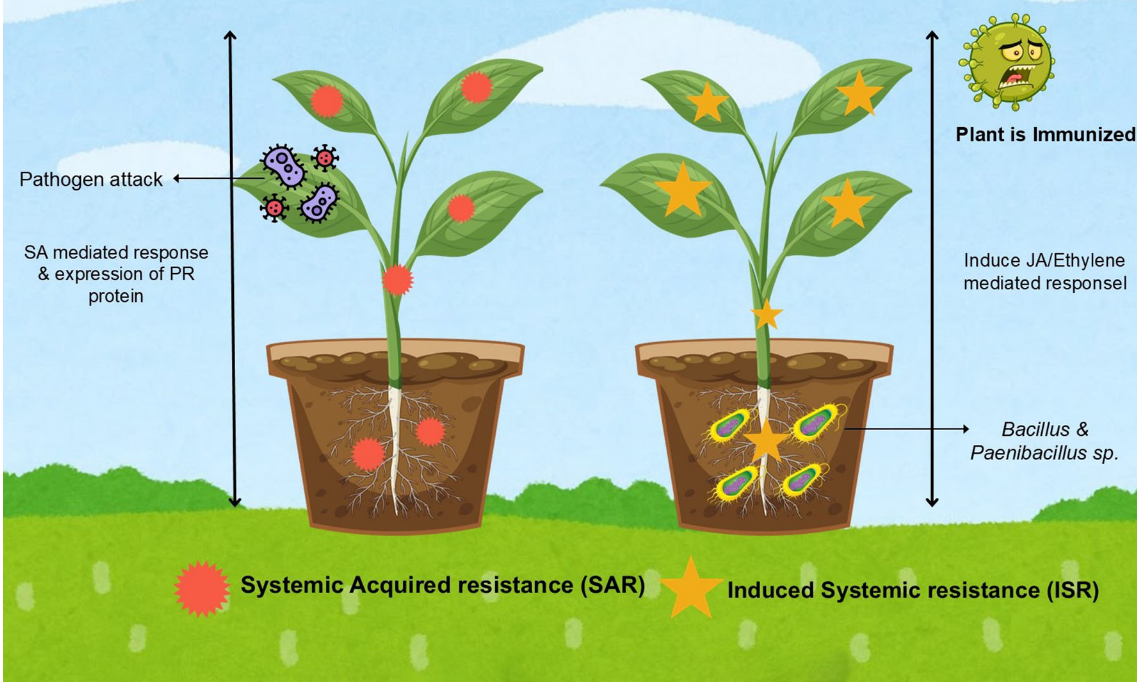

FIGURE 3
Bacillus and *Paenibacillus* as elicitors of ISR.

This bacterium has been recognized as a model plant growth-promoting bacterium for field-grown soybean owing to its excellent performance in increasing the growth of soybean and grain yield (Vitorino et al., 2024). As a result of using the signal compounds of *Brabyrhizobium japonicum* and *B. thuringiensis* in combination with optimal and NaCl-stressed seeds of soybean, Subramanian et al. (2016) identified a wide variety of proteins that are known, predicted, hypothetical, and unknown. Under both optimal and salt-stressed conditions, carbon, nitrogen, and energy metabolism pathways were affected by signals. Proteins such as phosphoenolpyruvate carboxylase, rubisco oxygenase large subunit, pyruvate kinase, and isocitrate lyase were enhanced by the signals, along with antioxidant glutathione-S transferase and other stress-related proteins that enhance tolerance or adaptation to salt stress. *Bacillus simplex* alters the soybean root metabolic profile due to the presence of soybean cyst nematodes, resulting in metabolic differences that explain the nematode resistance and *B. simplex*-treated roots contained lower levels of glucose, fructose, sucrose, and trehalose, which reduces nematodes' food sources. Moreover, treatment with *B. simplex* results in higher levels of melibiose, gluconic acid, lactic acid, phytosphingosine, and noradrenaline in soybean roots, which contributes to nematocidal activity. Oxoproline, maltose, and galactose levels are reduced following *B. simplex* treatment, thereby improving disease resistance (Kang et al., 2020). As demonstrated using scanning electron microscopy analysis, *Bacillus aryabhattai* colonizes soybean roots and its presence enhances 18 different amino acids in soybean plants. Matrix-assisted laser desorption ionization–time of flight (MALDI-TOF) mass spectrometry (MS) identified several proteins including ß conglycinin and glycinin that were traced back to their respective genes, and a significant increase in butanoic acid was observed in bacterial culture filtrates. This significant increase in butanoic acid significantly influences plant growth via chlorophyll maintenance (Mun et al., 2024).

The *P. polymyxa* CR1 is capable of priming drought tolerance in *Arabidopsis* and soybean. In addition, it induces the expression of *RD29A* and *RD29B* (memory genes), thus enhancing the plant's ability to withstand drought without reducing yield potential (Liu et al., 2020). *P. mucilaginosus* and *Bradyrhizobium japonicum* significantly alter soybean rhizobacteria compositions, increase soil-available phosphorus. The phosphatase activity significantly increases soybean biomass, nitrogen and phosphorus content in the rhizosphere (Xing et al., 2022). The influence of *Paenibacillus* on soybean plant metabolomics and proteomics profiles has not been extensively reported; and, there remains a need to investigate the actual mechanism by which these PGPB interact with soybean plants, as well as the effects of these PGPB on soybean plant transcriptomics, proteomics and metablomics.

3.1.2 Cannabis

The cultivation of cannabis has been carried out for both medicinal and industrial purposes for nearly a century, but its illegal status has resulted in limited availability of systematic studies or scientifically underpinned cultivation practices. Recent years have seen an enhanced level of research on this species allowing for knowledge databases to become more robust. Among all the cannabinoids, 9-THC (Δ9-tetrahydrocannabinol) and CBD (cannabidiol) are the major components of cannabis with pharmacological relevance.

Clinically, cannabis-derived cannabinoids have been developed and applied as treatment for chronic pain, epilepsy, multiple sclerosis, and cancer, as well as appetite stimulants and antiemetic agents in HIV/AIDS and cancer patients (Bruni et al., 2018; Cristino et al., 2020; Dhiman et al., 2024). Increasing the overall yield of these components is a necessity for the pharmaceutical industry. Abiotic and some biotic stress challenges are reported to adversely affect cannabis productivity and secondary metabolite production. The presence of PGPB, such as *Paenibacillus* and *Bacillus*, plays a significant role in improving cannabis resilience by enhancing root architecture, promoting nutrient acquisition, and reducing stress impacts (Comeau et al., 2021; author unpublished data).

3.1.2.1 *Bacillus* and *Paenibacillus* control pathogens of cannabis

Bacillus types are effective biocontrol agents and produce antimicrobial compounds such as cyclic lipopeptides that can bind membrane lipids, cause structural permeability, and damage fungal cell membranes (Yang et al., 2024). Phytomicrobiome members can inhibit the growth of pathogenic microorganisms by producing signals that are bacteriocins (small proteins/peptides such as thuricin 17), to remove competitors from niche space and promote plant growth, increasing the niche space, for this signal producing bacterium (Nazari and Smith, 2020). Bacteriocins are ribosomally synthesized peptides that inhibit the growth of microbial organisms by binding with membrane phospholipids, forming non-specific ion channels and forming pores causing cell death, and by other -cidal or -static mechanisms (Vasilchenko and Valyshev, 2019).

Bacillus sp. increases the seed germination rate of cannabis cultivars and exhibits antagonistic activities towards mycelial growth of the cannabis pathogen *F. oxysporum* (Corredor-Perilla et al., 2023). Balthazar et al. (2022) reported that *B. velezensis*, *B. subtilis* and *P. protegens* are biocontrol agents against *B. cinerea* of cannabis and exert beneficial effects through antibiosis in the phyllosphere. Afzal et al. (2015) reported that the endophytic strains of *Paenibacillus* sp. and *Pantoea vagans* successfully antagonize the pathogen *Fusarium oxysporum* in dual confrontation assays and produce fungal cell wall degrading enzymes. Cannabis accessions possess seed-inherited *P. mobilis* with the capacity to solubilize mineral phosphate and *P. polymyxa* that is antagonistic to hemp *Alternaria, Aspergillus, Fusarium, Penicillium* species affecting hemp (Dumigan and Deyholos, 2022). Clearly, the use of *Bacillus* and *Paenbacillus* sp. can help cannabis plants overcome stress challenges, allowing them to be more productive and produce higher secondary metabolite concentrations to mitigate the effects of stressful environments. Due to legal restrictions with regards to the use and research on cannabis, research data on the biocontrol mechanisms of *Bacillus* and *Paenibacillus* species against cannabis pathogens are limited.

3.1.2.2 *Bacillus* and *Paenibacillus* sp. influence cannabis plant metabolomics and proteomics profiles

There are limited studies on the use of PGPB and their effects on cannabis growth and yield. Some bacterial consortia are reported to favor plant growth development and the accumulation of secondary metabolites (i.e., CBD and THC). Jalali et al. (2019) evaluated the effect of SA and γ-aminobutyric acid (GABA) on THCAS (THC-synthase), CBDAS (CBD synthase), OLS (3,5,7-trioxododecanoyl-CoA synthase) and *PT* genes which are responsible for production of the main cannabinoids and found that SA and GABA can control the signaling cascades of genes in the cannabinoid pathway by changing their expression patterns at critical concentration. These two compounds can be considered as effective elicitors for commercial cannabinoid production. Mansouri et al. (2011) analyzed the effect of exogenous gibberellic acid (GA3) on plastidic, and cytosolic terpenoids as well as two key enzymes involved in terpenoid biosynthesis, 1-deoxy-D-xylulose-5-phosphate synthase (DXS) and 3-hydroxy-3-methylglutaryl coenzyme A reductase (HMGR). Leaves of GA3-treated plants contained increased levels of THC and CBD in comparison to control plants. It is hypothesized that exogenous PGPB can induce and will improve secondary metabolite synthesis and recovery. *Bacillus* sp. improved the cannabis yield and quality and increased the levels of cannabinoids and terpenes in *Cannabis sativa* (Lyu et al., 2023). Lyu et al. (2022) evaluated the effect of *Bacillus* sp. along with other PGPB and found that *Bacillus* sp. and *Mucilaginibacter* sp. increase flower number and axillary bud outgrowth rate. In the presence of PGPB, such as *Pseudomonas* sp. and *Bacillus* sp., trichome density was enhanced and major cannabinoid production was influenced, leading to an opportunity to reduce the use of synthetic fertilizers without compromising yield (Tanney et al., 2023).

Several studies have surveyed the diversity of bacterial and fungal endophytes in medical/recreational cannabis and hemp and have found that colonization depends on the cannabis chemovar, the plant tissue sampled, and the timing of sample collection relative to the plant growth stage. The most common bacterial genera associated with medical/recreational cannabis and hemp plants were *Pseudomonas, Staphylococcus, Bacillus, Acinetobacter, Chryseobacterium, Enterobacter*, and *Microbacterium*. *Erwinia*, and *Cedecia*. *Chryseobacterium* and *Enterobacter* were typically detected at lower frequencies (Winston et al., 2014; Scott et al., 2018; Backer et al., 2019, 2020). However, detailed knowledge is lacking because of cannabis being illegal for centuries which presented a major barrier to research. For instance, no study has investigated the interaction of *Paenibacillus* sp. and cannabis plants and how the *Paenibacillus* sp. affects the metabolic and protein profile of cannabis plants.

4 Plant growth promotion perspective of *Bacillus* and *Paenibacillus* species in other crops

4.1 *Bacillus* and *Paenibacillus* as nitrogen fixers

Species of *Bacillus* are involved in promoting plant growth and development and reducing the effects of environmental stress factors, such as prolonged drought, salinity, high temperatures, metal pollution, toxicity, and flooding (Etesami et al., 2023). Kour and Yadav (2022) reported that *B. cereus* strain BEB1, *B. cereus* strain BEB2, *B. tropicus* strain BEB3 and *B. thuringiensis* strain BEB4 showed significant growth on nitrogen-free malate media by atmospheric nitrogen fixation. Several *Bacillus* species including *B. megaterium*, *B. coagulans, B. pumilus*, *B. circulans*, *B. licheniformis*, *B. subtilis*, *B. brevis*, and *B. firmus* were found to be N_2-fixing bacteria, based on their nitrogenase activity (Kaymak et al., 2023).

The *Paenibacillus* nif operon consists of a cluster of genes that encode *nif*, measuring 11 kb in size and demonstrating that it is capable of fixing nitrogen (Dasgupta et al., 2021). Nitrogen fixers such as *Paenibacillus azotofixans, P. macerans, P. polymyxa, P. graminis*, and *P. odorifer* contain the *nifH* gene (Prabhukarthikeyan et al., 2022). Ribeiro et al. (2024) reported insights related to alternative N_2-fixation by Fe-only nitrogenase in *P. sonchi* and also observed endospore formation during N_2-fixation in *Paenibacillus durus*, coinciding with the highest levels of *nifH* transcription. NH_4^+ and nitrate (NO_3^-) uptake from soil was enhanced by inoculation with *P. beijingensis* BJ-18 especially in low soil nitrogen conditions. Enhanced gene expression and enzyme activities involved in N uptake and assimilation in plants were also reported (Li et al., 2019). The presence of *P. triticisoli* in the rhizosphere significantly increased total soil N, available P, nitrogenase activity, wheat yield, and the number of *nif* genes in the rhizosphere (Li et al., 2021).

4.2 *Bacillus* and *Paenibacillus* as biocontrol

Bacillus and *Paenibacillus* species produce broad-spectrum peptide antibiotics active against numerous pathogens and nematodes. *Bacillus velezensis* strains inhibit the growth of *B. cinerea* by producing antifungal compounds such as iturin A2, surfactin-C13 and -C15, oxydifficidin, bacillibactin, L-dihydroanticapsin in grape berries (Nifakos et al., 2021). Volatile organic compounds (VOCs) produced by one organism can travel long distances and act as biocontrol agents (Schulz-Bohm et al., 2017). One such example is that of *B. velezensis* which produces pyrazine, benzothiazole, and phenol against *B. cinerea* (Wang et al., 2022). Using scanning electron microscopy, Salvatierra-Martinez et al. (2018) reported that foliar spray of *B. amyloliquefaciens* can alter mycelial growth of *B. cinerea* in tomato leaves, while it promotes plant growth when applied through root drench by producing IAA and 2,3-butanediol. The strain *B. amyloliquefaciens* BBC047 has the ability to produce complex biofilms, improved plant resistance to pathogens and maintains an elevated population density over time on tomato leaves (Legein et al., 2020). *Bacillus* sp. are effective biocontrol agents against *Ralstonia solanacearum*, capable of significantly reducing the severity of ginger bacterial wilt and enhancing plant growth in ginger (Cui et al., 2024). The *B. velezensis* Y6 is believed to suppress potato scab caused by *Streptomyces scabies* by secreting lipopeptides (surfactin and iturin) and stimulating potato root growth by increasing the expression of genes that are involved in cell wall organization and biogenesis (Tao et al., 2023).

Paenibacillus polymyxa produces amylase, pectinase, and cellulase enzymes and inhibit the growth of the *Xanthomonas translucens* and *Fusarium graminearum* and increase grain weight, chlorophyll content, and carotenoid levels in wheat (Taheri et al., 2022). *P. chitinolyticus*, produces high levels of chitinase, and suppresses *Plasmodiphora brassicae* by targeting chitin in a critical stage of its life cycle, decreases the disease index significantly within *Brassica* species, and increases shoot dry weight (Khodashenas Rudsari et al., 2024). *P. polymyxa* PJH16 protects plants from *Fusarium* cucumber disease by forming biofilms in plant roots and resisting pathogens; this species produces a variety of hydrolases and antimicrobial lipopeptides that act on the fungal cell wall and directly inhibit the growth of pathogenic fungi. It also secretes IAA and siderophores to promote plant growth and resist pathogens (Yang et al., 2024). *P. polymyxa* produces paenibacillin which is a post-translationally modified lantibiotic, type B globular lantipeptide, that exhibits broad-spectrum antimicrobial activity against gram-positive bacteria by pore formation in the cytoplasmic membrane (Olishevska et al., 2019).

4.3 *Bacillus* and *Paenibacillus* as elicitors of induced systemic resistance

When a pathogen crosses the constitutive plant defensive barrier, the plant must defend itself by activating specific defenses, recognizing the molecular components of pathogen responses, and recognizing the molecular components of PAMPs through pattern recognition receptors (PRRs) (Rampitsch and Bykova, 2012; Tanaka and Heil, 2021). Several lines of evidence suggest that *Bacillus* species induce systemic resistance in plants in response to various biotic stresses, such as fungi, bacteria, viruses, and nematodes. *B. cereus* can trigger the JA/ET- signaling pathway and induce ISR in *Arabidopsis* plants, to act against *B. cinerea*, by reducing necrosis diameter and inhibiting leaf fungal growth (Nie et al., 2017). Figure 3 summarizes the role of pathogens in inducing SAR and the role of rhizobacteria in ISR. Root inoculation of *B. amyloliquefaciens* increases the expression of *PR1* and β-1,3-glucanase genes, through the SA-dependent pathway in the leaves of strawberries (Kamle et al., 2020). *B. velezensis* reduces disease severity by 50% in tomato leaves through the JA/ET pathway and reduces oxidative damage and callose formation (Toral et al., 2020). A significant increase in the expression of chitinase (PR-3 and PR-4), lipid transfer proteins (PR-14), peroxidase (PR-9), and lipoxygenase (LOX) was observed in vegetable crop plants after treating with *B. subtilis* (Abbas et al., 2019; Kumar et al., 2024). *B. velezensis* types are potential biocontrol agents against *B. cinerea*, releasing VOCs and increasing transcription of three *PR* genes with the ability to activate the SA-mediated defense signaling pathway (Jiang et al., 2018). In maize, *P. polymyxa* strain SF05 induces systemic resistance to maize blight by priming defense genes, producing VOCs, creating biofilms, and upregulation of ZmPR1a in the stem (Chen et al., 2022). *P. polymyxa* J2–4 exhibits excellent biocontrol efficacy against *M. incognita* in cucumber plants and active host defenses; it induces JA and SA signaling responsive gene expression and inhibits nematode development in local and systemic roots (Shi et al., 2024).

4.4 *Bacillus* and *Paenibacillus* produce indole acetic acid

Auxins play a role in plant gene expression, development, cell division, cell wall modification, cell elongation, fruit development, senescence, and lateral root formation. The first class of auxins identified and most abundant in nature is IAA. Plants can produce their phytohormones, but they can also use foreign sources provided by other organisms (Bertoni, 2011; Grady et al., 2016; Moreno-Serrano et al., 2024). Tran et al. (2024) reported the evaluation of a novel species of *Paenibacillus* and revealed that a strain produced phytohormones (IAA, GA3, and zeatin), biofilms, and siderophores highlighting the potential of these strains as plant growth-promoting agents for sustainable crop production. *P. polymyxa* accelerate maize, potato, cucumber, *Arabidopsis*, and tomato growth, utilize atmospheric nitrogen and insoluble phosphorus, produce IAA and degrade and use lignocellulose components (Weselowski et al., 2016). The *P. polymyxa* SK1 strain isolated from *Lilium lancifolium* produces IAA using a tryptophan-dependent pathway and was shown to promote the growth of two *Lilium* varieties (Khan et al., 2020). Sun et al. (2022) reported that *P. polymyxa* can enhance plant growth by directly secreting IAA. The authors identified the native IPyA pathway of IAA synthesis in the strain and evaluated the ability to express IAA synthetic genes using the novel and very effective promoter P04420.

4.5 *Bacillus* and *Paenibacillus* change proteomic and metabolomic responses

PGPB including *Bacillus* and *Paenibacillus* have unique methods to deal with environmental stressors and safeguard the host plant by affecting plant proteomics and metabolomics profiles. For instance, biostimulants such as lipo-chito-oligosaccharide (LCO - derived from *Bradyrhizobium japonicum*) and thuricin-17 (Th17 - derived from *Bacillus thuringiensis*) are found to alleviate drought stress by modulating drought-specific proteomics and metabolomic responses. Untargeted proteomics analysis revealed changes in the levels of drought-specific ribosomal proteins, glutathione S-transferase, proteins of late embryogenesis, vegetative storage proteins 1 and 2, thaumatin-like proteins, and proteins involved in chloroplast and carbon metabolism, all of which contribute to mitigating drought stress in *Arabidopsis thaliana*. Targeted metabolomic analysis for phytohormones revealed that LCO-treated rosettes showed decreases in total IAA, cytokinins, gibberellins, and jasmonic acid, and increased levels of ABA and SA whereas Th17-treated rosettes showed an increase in IAA and SA (Subramanian et al., 2023). *B. pumilus* and silicon (Si) increased the tolerance of *Glycyrrhiza uralensis* to drought stress by maintaining the homeostasis of reactive oxygen species (ROS), and results demonstrated that *B. pumilus* and Si enhanced the antioxidant defense system, accelerated the AsA–GSH (ascorbate (AsA)–glutathione) cycle, stimulated carotenoid metabolism, and eliminated excess ROS caused by drought. Daidzein, medicarpin, glycitin, and astragalin downstream metabolites are observed to respond differently to drought stress based on metabolomic analysis. It has been shown that 3-O-methylquercetin, a derivative of quercetin, increases in *B. pumilus* and plants treated with it, suggesting these flavonoids may play a key role in alleviating drought-induced oxidative stress (Ma et al., 2022). There are 41 proteins identified as differentially expressed in roots and shoots of Arabidopsis as a result of interaction with *P. polymyxa.* It was found that *P. polymyxa* improved plant growth by altering proteins related to defense/stress, antioxidant (GST, APX1, GPX6, PER43, CML42, and BAS1), photosynthesis, and plant hormones (auxin signaling-IAA9, HLS1, and ACT7) and tryptophan/camalexin (ASB1, GSTF6, and CYP71B15) biosynthesis-related proteins and metabolomic analyses showed that treated plants had increased levels of tryptophan, indole-3-acetonitrile (IAN), IAA, and camalexin (Kwon et al., 2016).

5 Conclusions and future prospectives

Research into the functioning of *Bacillus* and *Paenibacillus* is not only critical for advancing scientific understanding of microbial functions but it is also indispensable for real-world agricultural practices, where these bacteria can be leveraged to significantly enhance plant health and crop productivity. The *Bacillus* and *Paenibacillus* species have the potential to play a crucial role in sustainable agriculture, particularly in cases where climate change, disease, and biotic stressors are affecting our ability to feed an increasingly populous world. In addition to contributing to addressing future food security challenges, *Bacillus* and *Paenibacillus* also allow reducing the environmental impact of agricultural practices and increasing the resilience of food crop productivity against climate change. With this knowledge, it is possible to develop biotechnological products and methods for resolving plant diseases biologically, using microbes that benefit plants as bio-control, stimulate plant growth as biofertilizers, and assist with phytoremediation. To be able to implement *Bacillus* and *Paenibacillus* species practically on a wide scale, a comprehensive understanding of their mechanisms of action is imperative. Recent advances in microbial genetics have led researchers to explore ways to improve the efficiency of these bacteria as biocontrol agents, biofertilizers, and growth promoters. These species offer an opportunity to increase soybean yield and produce secondary metabolites in medicinal plants such as cannabis. PGPR strains must be evaluated concerning one another as well as with chemicals and organic supplements. The development of bioformulations and bioinoculants that can be applied to different soil types and/or foliar applications should also be a focus of future research. The mechanism of interaction between plants, *Paenibacillus*, *Bacillus* species and pathogens need to be explored using omics and imaging technology like metabolomics, proteomics and metagenomics to find out the actual mechanism of action of these bacteria in different crops including soybean and cannabis and their antagonist effect with different pathogens to implement them at a large scale.

Author contributions

HT: Conceptualization, Formal analysis, Investigation, Writing – original draft, Writing – review & editing. SS: Conceptualization, Supervision, Writing – review & editing. AG: Methodology, Writing – review & editing. DS: Conceptualization, Funding acquisition, Project administration, Resources, Supervision, Writing – review & editing.

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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.

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