

Chapter 1

Bacillus spp.: Nature's Gift to Agriculture and Humankind



Shailesh K. Vishwakarma, Talat Ilyas, Mohammad Shahid, Deepti Malviya, Sumit Kumar, Sachidanand Singh, Parul Johri, Udai B. Singh, and Harsh V. Singh

Abstract The productivity of crops is heavily depending on microbial communities present in rhizospheric soil; within the last few decades, PGPR has emerged as significant and promising tools for the sustainable agriculture practices. PGPR related to *Bacillus* spp. as symbiotic with plant roots or free-living in rhizosphere contribute significantly to the viability, development, and yield of plants under biotic and abiotic challenges. The *Bacillus* species are rod-shaped, Gram-positive, endosporic, aerobic, or facultative anaerobic and ubiquitous in nature. Many *Bacillus* species, e.g., *B. megaterium*, *B. circulans*, *B. coagulans*, *B. subtilis*, *B. azotofixans*, *B. macerans*, *B. velezensis*, etc. are extensively researched for their PGPR actions. Enhancement of nutrient uptake (N, P, K, and other vital minerals) and regulation of plant hormones are direct actions of PGPR, while promoting plant growth by inhibiting plant pathogen and induction of ISR are indirect actions of PGPR. The genus *Bacillus* holds largest share in microbe-based agricultural and commercial products. Due to the greater efficacy of production of metabolites and spore-forming nature of *Bacillus* spp., which increases the life span of cells in commercially manufactured products, *Bacillus*-based biofertilizers are more active than *Pseudomonas*-based formulations. The *Bacillus* species are frequently regarded

S. K. Vishwakarma · T. Ilyas · M. Shahid · D. Malviya · U. B. Singh (✉) · H. V. Singh
Plant-Microbe Interaction and Rhizosphere Biology Lab, ICAR-National Bureau of
Agriculturally Important Microorganisms, Kushmaur, Maunath Bhanjan, Uttar Pradesh, India

S. Kumar
Department of Mycology and Plant Pathology, Institute of Agricultural Sciences, Banaras
Hindu University, Varanasi, Uttar Pradesh, India

Department of Plant Pathology, B.M. College of Agriculture, Khandwa, Rajmata Vijayaraje
Scindia Krishi Vishwa Vidyalyaya, Gwalior, Madhya Pradesh, India

S. Singh
Department of Biotechnology, Sankalchand Patel University, Visnagar, Gujarat, India

P. Johri
Department of Biotechnology, Dr. Ambedkar Institute of Technology for Handicapped, Kanpur,
Uttar Pradesh, India

as an ideal candidate for bioformulations because of their rapid growth, ease of handling, and better colonizing abilities. The *Bacillus*-based bioformulations for broad-spectrum application against several biotic and abiotic issues are also addressed. In this chapter we will discuss about the mechanism of *Bacillus*-mediated crop protection and their wide application. PGPR traits of *Bacillus* are discussed in terms of nutrient uptake, siderophore production, stimulation and production of phytohormone and volatile organic compounds (VOCs), antimicrobial compounds, CRY proteins, and abiotic and biotic stress tolerance. Induction of induced systemic resistance (ISR) in *Bacillus* inoculated plants and its molecular mechanism is also discussed in this chapter. *Bacillus*-mediated abiotic and biotic stress tolerance in different host, possible mechanisms, and their effects are also discussed.

Keywords *Bacillus* · PGPR · Biotic stress · Abiotic stress · Biofertilizer · Biocontrol · Secondary metabolism · Phytohormone

1.1 Introduction

The production of crops must be increased to fulfill the global need, but environmental conditions and limited mineral and water sources are making this goal harder. These difficulties will be worsened by the predicted rise in human population over the coming decades, and crops are badly impacted by climate change due to global warming. Soil and climate control the spread of various plant species, and the production of crops is heavily influenced by biotic and abiotic pressures. The anticipated crop losses for grains such as wheat and maize as a result of climate change are around 3.8–5.5% (Lobell et al. 2011; Singh et al. 2016a, 2021a, b). Among the biotic stresses, fungal diseases are major responsible factors for crop loss. More than 19,000 fungal species have been identified that infect crop plants, worldwide. Approximately 30% of crop diseases are caused by pathogenic fungus (Jain et al. 2019). Agricultural techniques must concentrate on managing soil health and crop protection alongside their natural partners, beneficial microorganisms, in order to meet this challenge. Environmental pressures are frequently applied to plants in both natural and cultivated systems. The issue of the short supply of water for agriculture is getting worse in many places of the world. Excessive use of groundwater jeopardizes future irrigation capacity. Urbanization and industrialization are disturbing important wetlands and aquatic ecosystems. Water quality problems such as salinization, nutrient overloads, and pesticide pollution are very common, worldwide (Brodt et al. 2011).

The sustainable crop production is accomplished by applying biotechnology techniques, traditional plant breeding, and agronomic practices. The conventional breeding involves choosing genotypes with the highest productive crop; genetic modification, such as gene insertions or induced mutations; and agronomic practices, such as the use of fertilizer. Because of the genetic makeup of plants and diverse environmental variables, the standard plant breeding and agronomic methods are not always effective. GM crops are commercially not so successful because of lesser

acceptance in public. Numerous symbiotic or free-living soil bacteria contribute significantly to the viability, development, and productivity of plants under different environmental and biotic challenges. Numerous studies have established the plant and microbe interaction that are promoting plant development and shield plants from abiotic and microbial threats. The productivity of crops heavily depends on microbial communities present in rhizospheric soil; within the last few decades, PGPR has emerged as significant and promising tools for the sustainable agriculture practices (Yadav et al. 2022a, 2023). According to the Kloepper and Schroth (1981), the term “PGPR” refers to bacteria that may colonize plant roots and stimulate plant growth. When they reintroduced microbial consortium into the soil, about 2% to 5% of rhizobacteria were showing positive impact plant development, called PGPR (Antoun and Prévost 2006). The majority of PGPR bacteria belongs to the *Bacillus*, *Acetobacter*, *Azospirillum*, *Azotobacter*, *Burkholderia*, *Klebsiella*, *Pseudomonas*, and *Serratia* genera (Glick 1995, Singh et al. 2016a, b). Many bacterial species from different genera have been characterized as PGPR, but *Bacillus* and *Pseudomonas* spp. are major contributors and have been extensively explored (Podile and Kishore 2006; Singh et al. 2016a, b). *Bacillus* spp. can produce endospores, which enable them to remain viable for a long time in unfavorable environmental circumstances. Mature endospores of *Bacillus* are resistant to heat, UV, γ -radiation, and various toxic and hydrolytic enzyme treatments (Nicholson et al. 2000). The pellets of *Bacillus subtilis* endospores can survive in free space exposed to the solar radiation (Horneck et al. 1984). Most of *Bacillus* species are rod shaped, Gram-positive, endosporic, aerobic or facultative anaerobic, and ubiquitous in nature. Members of this genus have an extensive range of physiological adaptations that allow them to survive in various types of natural habitats. They are present in all type of habitats and water bodies and can be frequently isolated from the clinical samples (Carter 1990). They also survive in extreme condition habitats such as hot springs (Panda et al. 2013), hydrothermal vents (Marteinsson et al. 1996), tidal flats (Jung et al. 2011), shallow marine water (Maugeri et al. 2001), high-salt environments (Rivadeneira et al. 1993), acidic (Mahdavi et al. 2010) and alkaline environments (Gessesse and Gashe 1997), heavy metal-contaminated sites (Egidi et al. 2016), dumping sites (Yadav et al. 2022b), and radioactive sites (Asker et al. 2007). Because of their versatile physiological ability, *Bacillus* spp. has been exploited for the production of enzymes, antibiotics, metabolites, drugs, farming, and industrial processes. *Bacillus* species are the source of two well-known antibiotics, bacitracin and polymyxin (Wu et al. 2022; Choi et al. 2009). In comparison to many other genera, the genus *Bacillus* is enormous and exhibits a high level of genetic variation. The second edition of Bergey's manual (2009) listed 141 species of *Bacillus* (Vos et al. 2009). *Bacillus* spp. can thrive in a variety of conditions, which illustrates their vast metabolic ranges and ubiquitous distribution. More than 200 *Bacillus* species have been distinguished and categorized using genomic and conventional methods combined, and their role in the environment and pathological aspect have been identified (Singh et al. 2016a, Mageshwaran et al. 2022, Shafi et al. 2023, Shahid et al. 2022a, b). *B. subtilis*, as a model organism of prokaryotes, is well explored in molecular and cell biology research area and has been frequently used as

a model organism in numerous experiments (Borriss et al. 2018; Mageshwaran et al. 2022). Many *Bacillus* species, e.g., *B. megaterium*, *B. circulans*, *B. coagulans*, *B. subtilis*, *B. azotofixans*, *B. macerans*, *B. velezensis*, etc. are extensively researched for their PGPR actions (Hashem et al. 2019; Goswami et al. 2016; Basu et al. 2021; Yadav et al. 2022a, 2023; Gupta et al. 2022). Enhancement of nutrient uptake (N, P, K, and other vital minerals) and stimulation of plant hormones are direct actions of PGPR, while promoting plant growth by inhibiting plant pathogen and induction of ISR are indirect actions of PGPR (Ahemad and Kibret 2014, Yadav et al. 2022a, 2023). The genus *Bacillus* holds largest share in microbe-based agricultural commercial products. The first *Bacillus* species-based commercialized biofertilizer was Alinit, which enhanced crop production up to 40% (Kilian et al. 2000). Kodiak (*B. subtilis* GB03), Quantum-400 (*B. subtilis* GB03), RhizoVital (*B. amyloliquefaciens* FZB42), Serenade (*B. subtilis* QST713), and YIB (*Bacillus* spp.) are some examples of *Bacillus*-based products that have been successfully commercialized (Brannen and Kenney 1997; Ngugi et al. 2005; Cawoy et al. 2011). Because of the more efficient metabolite synthesis and spore-forming nature of *Bacillus* spp., which increases the viability of cells in commercially prepared products, *Bacillus*-based biofertilizers are more efficient than *Pseudomonas*-based fertilizers (Haas and Défago 2005). The *Bacillus* species are frequently regarded as an ideal candidate for bioformulations because of their rapid growth, ease of handling, and better colonizing abilities (Dimkić et al. 2022; Malviya et al. 2020b, 2022a, b).

This chapter deals with the many PGPR candidates from *Bacillus* genera, their abilities and mechanisms to enhance plant growth, their contribution to crop protection against both abiotic and biotic stressors, and their significance in ongoing strategy for increasing yields from agriculture. The *Bacillus*-based bioformulations for broad-spectrum application against several biotic and abiotic issues are also addressed. In this chapter we will discuss about the mechanism of *Bacillus*-mediated crop protection and their wide application (Singh et al. 2021a, b, Sahu et al. 2021).

1.2 *Bacillus* spp. and Their Role as PGPR

The rhizosphere is the small region of soil where a plant's roots have a significant influence. Amino acids and sugars are excreted by the roots' system as exudates, which are a major source of energy and nutrition for microorganisms in the rhizosphere. The bacterial communities are more prevalent in the rhizosphere than any other microbial communities (Sahu et al. 2019). The research evidence indicates that Gram-positive bacteria are dominating among the microbial community in rhizospheric soil. The recent findings lend credence to this idea that *Bacillus* species are dominating populations in the chrysanthemum of barley and grass (Smalla et al. 2001). *Arabidopsis thaliana* root system can secrete up to 30% of their photosynthates via exudates that are utilized by the associated *B. subtilis* and in return provide the plant with many growth-promoting traits (Allard-Massicotte et al. 2016). The

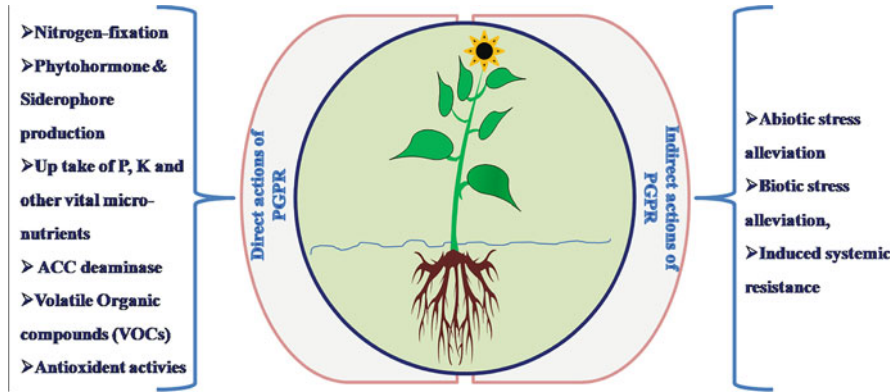


Fig. 1.1 An overview of direct and indirect PGPR actions of *Bacillus* spp.

overall actions of PGPR are depicted in Fig. 1.1, and it can be divided into two categories: (1) direct modes of action, such as stimulation of VOC and phytohormone, dropping down the level of ethylene in plant, assisting in resource acquisition (NPK and other essential minerals), N_2 -fixation, and stimulation of induced systemic resistance (ISR); (2) indirect modes of actions, such as when PGPR act like biocontrol agents reducing diseases, beneficial symbioses, or degradation of xenobiotic compounds present in contaminated soils (Jacobsen 1997; Sahu et al. 2020a, b; Singh et al. 2021a, b).

PGPR are categorized into four types on the basis of their functions by Somers et al. (2004): biofertilizers (enhance the accessibility of nutrients to the plants), phytostimulants (promote growth of plant, typically by the stimulation of phytohormones), rhizoremediators (degradation of organic pollutants), and biopesticides (produce antimicrobial metabolites to control microbial diseases). In various agricultural regimes, such as permanent grassland, grassland that has been converted into cultivable land, soil DNA from these fields was analyzed by PCR and PCR-DGGE techniques; the abundance of *Bacillus*-related genera including *Paenibacillus*, *Alicyclobacillus*, *Aneurinibacillus*, *Virgibacillus*, *Salibacillus*, and *Gracilibacillus* was observed (Garbeva et al. 2003). Up to 95% Gram-positive bacteria with low G + C% from various agricultural area were inferred as *Bacillus* species: *B. mycoides*, *B. pumilus*, *B. megaterium*, *B. thuringiensis*, *B. firmus*, and *Paenibacillus*. Out of all the soil DNA samples, less than 6% of the clones associated with *Arthrobacter* species and *Frankia* were obtained (Antoun and Prévost 2006). The monitoring of temporal and geographical variety of *B. benzoevorans* and related bacilli and their abundance in the bacterial population, by applying specific PCR-primer with DGGE techniques, this species was found as cosmopolitan. Such cosmopolitan bacteria play an important role in soil ecosystems ((Tzeneva et al. 2004). In 1997, whole genome of *B. subtilis* 168 was published with 4100 protein-coding genes making up the 4.2 Mbp-long genome (Kunst et al. 1997). Many PGPR

strains of *P. polymyxa* species have been identified as having the ability to boost plant development and offer significant resistance to biotic and abiotic stress in plants (Timmusk and Wagner 1999; Singh and Wesemael 2022). However, this bacterium colonized only in root tips and form biofilm, and it was not detected in aerial tissues (Timmusk et al. 2005). Only culture-based methods of PGPR isolation may give false results because of resistant nature of endospores (Bent and Chanway 2002). The plant growth of many plants has been observed to be boosted by *Bacillus* species, and they are also highly successful as biocontrol agents in many plant microbial ailments (De Freitas et al. 1997; Kokalis–Burelle et al. 2002). The *Bacillus* consortium mediated induction of ISR against specific pathogens: *Sclerotium rolfsii* which caused southern blight of the tomato, *Colletotrichum gloeosporioides* which caused anthracnose of the long cayenne pepper, and *Cucumber mosaic virus* which caused cucumber mosaic disease were studied under greenhouse conditions. According to the findings, various PGPR mixes consistently reduced disease in all host plants. One PGPR combination, *B. amyloliquefaciens* strain IN937a + *B. pumilus* strain IN937b, substantially ($P = 0.05$) shielded plants from every pathogen evaluated in experiment (Jetiyanon et al. 2003). The antibiotic-producing strain *B. megaterium* KL39 has a broad antifungal spectrum against many pathogenic agents such as *Rhizoctonia solani*, *Pyricularia oryzae*, *Monilinia fructicola*, *Botrytis cinerea*, *Alternaria kikuchiana*, *Fusarium oxysporum*, and *F. solani*. For *Phytophthora capsici*, a MIC value of 10 g/mL was evaluated while using radioactive [³H-adenine] as the precursor; macromolecular incorporation tests with *P. capsici* revealed that the antibiotic KL39 drastically inhibits the DNA manufacture of the fungal cell (Jung and Kim 2005). *B. subtilis* isolate K18 (BS-K18) increased wilt tolerance in susceptible chickpea variety JG-62, and it also enhanced plant root and shoot development in both resistant and susceptible varieties. This putative antagonist with PGPR action may be utilized to control chickpea wilt (Suthar et al. 2017). *B. subtilis* RB14-C, a *lpa-14*-gene dependent antibiotics iturinA and surfactin producer, was found effective in reducing mortality rate of tomato seedlings caused by *Rhizoctonia solani* (Asaka and Shoda 1996). This strain is also resistant to chemical pesticide, flutolanil (Kondoh et al. 2001). Eighty-three isolates of the *Bacillus* genus from salty soils in Tunisia were evaluated for the biocontrol of dry rot of potato tubers caused by *Fusarium*; the most effective isolates were identified as *B. cereus*, *B. lentimorbus*, and *B. licheniformis*. These isolates were able to reduce the disease up to 66–89% (Sadfi et al. 2001). Their antifungal properties were linked to the ability to produce volatile compounds and a variety of complex lytic and chitinase enzymes. Increased bioavailability of nutrients, excretion of enzymes or chemical compounds to biocontrol the disease-causing agents, induction of systemic responses, enhanced secondary metabolism, and improved plant defensive responses against abiotic and biotic stresses are some main advantages of PGPR application. The PGPR traits of some *Bacillus* spp. and their effects on different host plants and mechanism are summarized in Table 1.1.

Table 1.1 Examples of *Bacillus* spp. and their PGPR action mechanisms and effects on host plant

Microorganism	PGPR activity	Reference
<i>P. polymyxa</i> P2b-2R	Enhanced seedling length and biomass atmospheric N ₂ -fixer (30%), extended trial on maize	Puri et al. (2016)
<i>G. mosseae</i> + <i>B. subtilis</i>	Synergistically enhanced growth, biomass, and yield of <i>Artemisinin annua</i> L.	Awasthi et al. (2011)
<i>Bacillus subtilis</i> B9	Promoted sugarcane growth (29.26%) and plantlets (50.78%) and increased the content of NPK in seedlings (15.49%)	Di et al. (2022)
<i>Bacillus</i> spp. (ML7, ML17, and ML46), <i>B. simplex</i> (ML12, ML25, and ML43), <i>B. megaterium</i> (ML36), <i>B. muralis</i> (ML49), <i>B. aryabhatai</i> (ML55), <i>B. pumilus</i> (ML59), <i>B. megaterium</i> (ML61), <i>B. toyonensis</i> (ML63)	Isolated from <i>M. longifolia</i> L., except ML46, all were N ₂ -fixing, all were showing different plant growth-promoting properties	Alaylar (2022)
<i>B. megaterium</i> TV-91C, <i>Pantoea agglomerans</i> RK-92, and <i>B. subtilis</i> TV-17C	GA, SA, ABA, IAA production, enhanced shoot and root fresh and dry weight, stem diameter, chlorophyll content, leaf area, and leaf number	Turan et al. (2014)
<i>Bacillus</i> sp. PM31	Exhibited P, Zn, K-solubilization ability, N ₂ -fixation, siderophore, exopolysaccharide production, and extracellular enzyme activities, can control wilt caused by <i>F. solani</i> in potato	Mehmood et al. (2023)
<i>B. amyloliquefaciens</i> subsp. plantarum UCMB5113	Enhanced cytokinin, gibberellin, and brassinolide production and increased fresh weight of shoot in <i>Arabidopsis thaliana</i>	Asari et al. (2017)
<i>Bacillus</i> sp. (12D6)	IAA and SA production, increased root length, area, and number of tips in treated maize plants	Jochum et al. (2019)
<i>B. subtilis</i> CNBG-PGPR-1	Whole genome of this strain has been sequenced (accession number CP090125). Metabolism of trp, the creation of organic acids, and sulfur metabolism and other PGPR-related genes were identified	Lu et al. (2022)
<i>Bacillus</i> sp. LC390B	Enhanced shoot and root fresh weights and chl content in leaves upon direct co-cultivation with <i>Arabidopsis</i> roots	García-Cárdenas et al. (2023)
<i>Bacillus</i> sp. IHBT-705	Whole genome and plasmid DNA were sequenced (accession numbers CP074101), exhibit promising PGP potential on rice pot trial	Ali et al. (2023)

(continued)

Table 1.1 (continued)

Microorganism	PGPR activity	Reference
<i>P. mucilaginosus</i>	K- and P-solubilizing, N ₂ -fixing, promotes soybean plant growth, increased nodulation, and changed microbial profile with more beneficial bacterial community in rhizosphere	Ma et al. (2018)

1.3 *Bacillus* spp. and N₂-Fixation

Nitrogen is a major vital element required for overall plant growth. Urea and other inorganic fertilizers have been used as a source of nitrogen on a variety of crops, worldwide. Although these nitrogen fertilizers significantly increase yields, overuse of such fertilizers poses considerable risks to the environment and public health (Ahmed et al. 2017). Reducing reliance on synthetic fertilizers is indispensable for environmentally friendly agricultural practices. The capacity to fix atmospheric nitrogen and make it accessible to host plant has been explored in microorganisms. Many *Bacillus* and *Paenibacillus* spp. such as *B. cereus*, *B. circulans*, *B. firmus*, *B. pumilus*, *B. licheniformis*, *B. megaterium*, *B. subterraneus*, *B. aquimaris*, *B. vietnamensis*, *B. aerophilus*, *Paenibacillus* sp. WLY78, and *P. mucilaginosus* are known to fix atmospheric N₂ (Ding et al. 2005; Shi et al. 2016; Ma et al. 2018; Liu et al. 2019). Enzyme nitrogenase is essential for nitrogen fixation; it is made of two protein parts: reductase and iron (Fe) protein and catalytic molybdenum iron (MoFe) protein (Owens and Tezcan 2018). For quantification of N₂ fixation, acetylene reduction assay (ARA) (Soper et al. 2021) and for the diversity of N₂-fixers and identification, *nifH* gene as genetic marker is widely accepted. The *Paenibacillus nif* operon is 11 kbp in size, and it is made up of a cluster of *nif* genes (Dasgupta et al. 2021). Fe-protein and Mo-fe-protein are encoded by the *nifH* gene and *nifDK* genes, respectively. The conserved region within the *nifH* gene has importance in the study of phylogeny and detection of molecular potential for N₂-fixation in any environment (Mehta et al. 2003). *P. azotofixans*, a diazotrophic strain, is highly effective in fixing atmospheric nitrogen, and the ability of these bacteria to fix nitrogen is unaffected by the presence of nitrate (Choo et al. 2003). Based on acetylene reduction assay (ARA), *B. circulans* and *B. polymyxa* were identified as non-symbiotic N₂-fixing in tussock-grassland soils in New Zealand (Line and Loutit 1971). Recently, *P. odorifer*, *P. graminis*, *P. peoriae*, and *P. brasiliensis* have been described as nitrogen fixers (Beneduzi et al. 2010; Li et al. 2019; Von der Weid et al. 2002). During a comprehensive study of the diversity of N₂-fixing PGPR procured from sugarcane fields, an assessment of the N₂-fixation ability of 22 isolates was done using the *nifH* gene. The most potential N₂-fixing isolates, CY5 and CA1, were identified as *B. megaterium* and *B. mycoides*, respectively. Along with the nitrogen fixation ability, these two isolates were also able to biocontrol *Sporisorium scitamineum* and *Ceratocystis paradoxa* and enhance the expression of gene related to various defense and tolerance mechanisms in

Saccharum spp. (Singh et al. 2020). An attempt was made to investigate the capability of heterotrophic *Bacillus* to fix nitrogen based on the presence of the *nifH*-gene; *B. megaterium*, *B. flexus*, and *B. circulans* were isolated from the soil samples of estuarine and coastlines in India. *B. megaterium* was the most dominant and strong N₂-fixer bacteria among all the isolates (Yousuf et al. 2017). Non-symbiotic N₂-fixing bacteria from soil of many lakes in East Java, Indonesia, were explored; isolate B2 has the most activity and was identified as *B. paramycooides*, a *B. cereus* group member (Nafisah et al. 2022). The PGPR-mediated fixation of atmospheric nitrogen and symbiotically supplying to the host plants is an important mechanism for the maintenance of nitrogen levels in agricultural lands. The biofertilizer based on *B. subtilis* successfully replaced 50% urea by lowering the nitrogen loss by 54% when applied to the fields. Additionally, this approach led to a 5.0% increase in crop output and an 11.2% improvement in nitrogen usage efficiency. The use of biofertilizer also led to an increase in bacterial communities of *Bacteroidetes* and *Chloroflexi*, which are crucial in the breakdown of soil organic matters (Sun et al. 2020).

1.4 *Bacillus* and Phosphate Solubilization

The absorption of phosphate by plant roots, which is considered to be the second most important nutrient for plants after nitrogen, is needed for optimum plant development (Bechtaoui et al. 2021). According to reports, the average amount of phosphorus (P) in soil is almost 1200 mg/kg (Tiessen 2008), but P is the least accessible to the plants in comparison to N and K, especially in low pH soils with lower organic matter and poor water-holding capacity (Yan et al. 2020). P plays an important role in the sustainability of the agricultural production system and the maintenance of soil fertility. P-based fertilizers have long been utilized successfully to replenish depleted soil phosphorus so that it is readily accessible to plants. However, the use of commercial fertilizers is a costly strategy, and since the mineral may easily be lost from the soil and subsequently mix with local streams and can pollute both terrestrial and aquatic habitats, phosphorus is frequently rendered inaccessible to plants (Adesemoye and Kloepper 2009). There are many bacteria that can mobilize insoluble forms of phosphorus, known as P-solubilizing bacteria (PSB). Many beneficial bacteria from *Bacillus* genus living in the soil as free or in association of plant roots are capable of solubilizing insoluble soil P and make it bioavailable to the host plants. Many species of *Bacillus* like *B. circulans*, *B. cereus*, *B. fusiformis*, *B. pumilus*, *B. megaterium*, *B. mycooides*, *B. coagulans*, *B. chitinolyticus*, *B. subtilis*, etc. have been reported as phosphorus solubilizers (Sharma et al. 2013). Due to their capacity to harness the precipitated phosphorus (P) in the soil, PSB has established themselves as significant biofertilizer that improve crop production and help in the nurture the soil health (Prakash and

Arora 2019). According to Sundara et al. (2002), PSB can lower the dependency on synthetic P by 25%. Better results can be achieved when PSB are inoculated as a consortium with other PGPR or arbuscular mycorrhizal fungi (AMF); its effect can rise up to 50% (Khan et al. 2009). The P solubilization mechanism of PSB is mediated by their capacity to release organic acids, i.e., gluconic and keto-gluconic acids, through their hydroxyl and carboxyl groups; their ability to chelate the cations bound to phosphate, siderophore, protons, hydroxyl ions, and CO₂; as well as their ability to release extracellular enzymes and degrade substrate (Alori et al. 2017; Richardson and Simpson 2011; Heidari et al. 2020). The phosphate availability was found highest at an acidic pH (5.5) and poorest at a near-neutral pH in the crops *Brassica campestris*, *Medicago sativa*, and *Oryza sativa* (Barrow et al. 2020). Using chicken bones, fish bones, and ash as substrates, three PSB strains, *B. megaterium* PCM 1855, *B. cereus* PCM 1948, and *B. subtilis* PCM 1938, were tested to examine their ability to liberate phosphorus from unavailable structures. All the isolates were producing organic acid such as gluconic, lactic, acetic, succinic, and propionic, and maximum concentration of P was recovered from the fish bone as substrate inoculated with *B. megaterium*; however, this strain was not producing propionic acid (Saeid et al. 2018). PSB solubilize the mineral P by lowering the pH of micro-environments and make it available for plant uptake (Riaz et al. 2021). Isolate GQYP101, procured from the rhizospheric soil of *Lycium barbarum* L., was showing potential as a PSB. A pot trial with maize was conducted to assess the PGPR capabilities of the PSB, and whole genome sequencing was done to investigate the possible mechanism. This strain, identified as *B. altitudinis*, GQYP101 proved capable to boost the fresh weight and maximum leaf area and increased stem diameter and nitrogen (100%) and phosphorus (47.9%) levels of aerial portion in maize seedlings (Zhao et al. 2022). Alkaliphilic bacterial strain, isolated from mangrove ecosystem, *B. marisflavi*, was capable of tri-calcium phosphate solubilization by producing alkaline phosphatase (Prabhu et al. 2018). In addition to having a strong capacity to dissolve insoluble inorganic phosphates, a PGPR strain of *B. firmus* NCIM-2636 was inoculated in the fields of the Jaya and IR-8 varieties of rice (*Oryza sativa* L.) in Nagaland, India. For 2 years, the rice fields were supplied with single super phosphate (SSP) and Mussoorie rock phosphate (RP) as fertilizers. The findings from experiments indeed show that the bacteria generated the desired effect more strongly when implemented in combination with RP than with SSP (Datta et al. 1982). PGPR strain CB7, isolated from apple root soil, was identified as *B. circulans* in Himachal Pradesh, India. This isolate showed traits of P-solubilization, siderophore and auxin production, ACC-deaminase and nitrogenase activity, and antagonistic effects against *Dematophora necatrix* (Mehta et al. 2015). P-solubilizing *Bacillus* represents an economic and ecological and sustainable strategy to improve crop production. Therefore, more research is necessary to study potent biofertilizers and plant growth-stimulating properties at the field trial.

1.5 *Bacillus* and Potassium Uptake and Translocation

Potassium (K) is important for plant physiology, cellular development, water movement, transfer of nutrients and metabolites, and responses to stresses (Sardans and Peñuelas 2021). Although K is the most prevalent inorganic cation, only 1–2% of it can be utilized by plants; the rest of it is bonded with different minerals and is therefore inaccessible to plants. K supplied as fertilizers change the physiochemical and biological characteristics of the lands in addition to increasing crop yield. Consequently, consistent application of artificial fertilizers results in a decrease of organic matter in the soil and an overall decrease in agricultural soil health. Chemical fertilizers used in excess make the soil more hard, reduce soil fertility, pollute ecosystems, and deplete essential nutrients of soils (Pahalvi et al. 2021). Bacteria that can increase bioavailability of K by releasing the K from complex minerals and convert it to soluble forms for plant uptake are called K-solubilizing bacteria (KSB). Many *Bacillus* spp. such *B. aryabhatai*, *B. mucilaginosus*, *B. edaphicus*, *B. circulans*, *B. cereus*, *B. subtilis*, *B. coagulans*, *B. amyloliquefaciens*, *B. megaterium*, and *Paenibacillus* spp. have the capacity to solubilize K minerals (Yadav and Sidhu 2016; Etesami et al. 2017). KSBs solubilize K minerals in their surrounding micro-environment by altering the pH and chelation of the cations bound to K. KSB change pH by releasing the organic acids including citric, tartaric, and oxalic acids and proton pump mechanism. KSBs release K-rich minerals and other nutrients from nonsoluble mineral deposits in the soil and help in K-uptake and improve plant health (Sharma et al. 2016). *B. mucilaginosus* has the ability to dissolve silicate mineral in culture solutions, and the rates of dissolution considerably depend on the silicate mineral type. *B. mucilaginosus* produced extracellular polysaccharides that allowed it to form bacterial-mineral complexes. These bacterial-mineral complexes show different micro-environmental physicochemical characteristics in comparison to their surroundings in terms of pH value, viscosity, and organic acid concentrations. These bacterial-mineral complexes were dissolved and later transformed into secondary silicate minerals by the combined action of H⁺ ion exchange and acetate (Mo and Lian 2011). The potassium content was raised in cotton and rape plants growing in soils treated with insoluble potassium and inoculated with strain NBT by 30% and 26%, respectively. Additionally, higher N and P levels of above-ground plant components were a result of bacterial inoculation. This bacterial strain was able to colonize and grow in the cotton and rape rhizospheric soil (Sheng 2005). *Bacillus subtilis* has KtrAB, KtrCD, and KimA transporter for K uptake. KtrAB and KimA are high-affinity transporters that permit fast development at micromolar K concentrations, but KtrCD is a low-affinity transporter that is crucial for potassium absorption in a broad range of environmental circumstances (Gundlach et al. 2017). In China, *B. aryabhatai* SK1-7 strain was tested for K-solubilizing ability and applied it to *Populus alba* L. By converting insoluble potassium in the soil into usable potassium, strain SK1-7 can boost plant K concentration and plant growth (Chen et al. 2020). The tomato crop was inoculated with *B. megaterium* and *P. mucilaginosus* with biochar for 2 years in a greenhouse.

The findings showed that adding 75 L/ha of microbial inoculants to greenhouse, tomato yield increased by 23.41% and concentrations of soluble sugar and vitamin C by 13.62% and 14.41%, respectively (Yang et al. 2023b). To grow sudangrass, mica waste was added to two different types of alfisols, and *B. mucilaginosus* was utilized as a biofertilizer. Dry biomass yield, absorption, and percent K-recoveries were found higher in bacteria-treated trial in comparison to the untreated control. *B. mucilaginosus* mediated a higher degree of mica solubilization in soils which was confirmed by X-ray diffraction analysis (Basak and Biswas 2009). When tea plants were cultivated on mica waste and a KSB *B. pseudomycolides* was inoculated, similar findings were obtained. Soil treated with mica waste and bacteria had increased potassium availability, which led to improved potassium absorption in tea plants (Pramanik et al. 2019). The K-solubilizing bacteria as biofertilizer are gaining popularity as a key component of global food security and integrated nutrient management solutions (INM) (Shrivastava et al. 2016).

1.6 *Bacillus* and Zinc Uptake

Zinc (Zn) is a crucial co-factor for many enzymes and DNA-binding Zn-finger proteins in animal and microorganisms. Additionally, Zn is essential for metabolism, mitosis, growth, and mitochondrial function (Frassinetti et al. 2006). Zn can be found in all kinds of enzymes and is the second most prevalent transition metal for living things (Keith et al. 2000). As per World Health Organization (WHO) reports, 4–73% of global population is facing scarcity of zinc, which impacts 31% of people globally. The top ten main risk factors for illness in developing nations are associated with zinc deficiency. The lack of micronutrients like zinc poses a serious threat to sustainability of global health. Almost 50% of soils is deficit of zinc that affects majority of agricultural production. Up to 95% of the population of Gram-positive bacteria in plant rhizosphere is composed by *Bacillus* spp. One of the most extensively researched bacterial species, *Bacillus*, has the capacity to dissolve zinc minerals (Masood et al. 2022). Numerous processes, including chelation, pH alteration, and proton extrusion, have been described in bacteria that aid in the solubilization of zinc (Yadav et al. 2022a, 2023). The sequestration of cations in bacterial cell and release of organic acids such as gluconic acid, butyric acid, lactic acid, and oxalic acid and decrease the pH in rhizospheric region enhance the bioavailability of Zn to the plant roots (Mumtaz et al. 2019). Agricultural productivity and environmental sustainability goals might benefit from the possible contribution of *Bacillus* genera in Zn solubilization. In a study with isolates *B. aryabhatai* and *B. subtilis*, maximum solubilization of zinc was obtained with *B. aryabhatai*. These isolates were suggested as prospective bio-inoculants for the biofortification of maize to help solve the issues of Zn malnutrition because of their capacity to stimulate growth (Mumtaz et al. 2017). Isolate CDK25, isolated from cow dung, was identified as *B. megaterium* through the 16S rRNA gene sequencing. The pot trial of *Capsicum annuum* L., inoculated with CDK25, enhanced growth parameters and increased

zinc content in fruit (0.25 mg/100 g) (Bhatt and Maheshwari 2020). Bacterial isolates BT3 and CT8, isolated from the rhizospheric soil of chickpea from different parts of Indo-Gangetic Plains (IGP), India, were identified as *B. altitudinis*. Chickpea growth measures were enhanced by the inoculation BT3 and CT8, and the plant's intake of zinc increased by 3.9–6.0%. For increasing zinc intake and chickpea development, BT3 and CT8 have the outstanding ability to solubilization of insoluble Zn compounds such oxides, phosphates, and carbonates of Zn (Kushwaha et al. 2021; Yadav et al. 2022a, 2023).

1.7 *Bacillus* and Siderophore Production

Small iron-chelating molecules known as siderophores have a strong affinity for metal ions. The structure of siderophores exhibits a broad range of variation. A short polypeptide chain with different coordinating iron-ligating groups makes up the majority of several siderophores (Ahmed and Holmström 2014). The *Bacillus* species generate a vast range of siderophores that are important to their survival, including bacillibactin, pyoverdine, pyochelin, schizokinen, and petrobactin (Crosa and Walsh 2002; Khan et al. 2016). Bacterial siderophores are divided into four main classes based on their structural characteristics, kinds of ligands, and iron-coordinating functional groups: carboxylate, hydroxamates, phenol catecholates, and pyoverdines (Chimiak et al. 1984). Many species of *Bacillus*, i.e., *B. anthracis*, *B. thuringiensis*, *B. cereus*, *B. velezensis*, *B. atrophaeus*, *B. mojavensis*, *B. licheniformis*, *B. pumilus*, *B. halodenitrificans*, and *B. subtilis*, are known as prolific producer of siderophores (Ramadoss et al. 2013; Goswami et al. 2014; Khan et al. 2016). In agriculture, siderophore and its derivatives are widely used to improve soil fertility, biofortification of nutrients, and biocontrol fungi pathogens (Crowley 2006). Siderophore is also used for mitigating environmental metal pollution, particularly from soil and water (Ali and Vidhale 2013). *B. subtilis* LSBS2, procured from sesame plant rhizosphere in Tamil Nadu, India, was producing catecholate siderophore bacillibactin (296 mg/L). This isolate promoted plant growth and increased oil content in sesame plants (Nithyapriya et al. 2021). *B. megaterium* and *B. subtilis* were found capable of siderophore production under alkaline condition. A higher iron-chelating siderophore was obtained by *B. megaterium* (pH 9.0,) followed by *B. subtilis* and *A. vinelandii* (Ferreira et al. 2019). Siderophores bind iron and make it less available to competing microbes and help in biocontrol of plant pathogens (Kesaulya et al. 2018). Hydroxamate siderophores producing strain *Bacillus* sp. PZ-1 potential enhanced the phytoextraction of Pb from soil when inoculated with *Brassica juncea* (Yu et al. 2017). Siderophore also forms complexes with many other vital metal ions, i.e., Mo, Mn, Co, and Ni, and make them available to the host.

1.8 Stimulation/Production of Phytohormone

PGPR found in the rhizosphere secrete the hormones auxin (IAA), gibberellin (GA), cytokinin (CK), ethylene (ET), and abscisic acid (ABA) for manipulating the balance of plant hormones, which in turn controls root/shoot growth and development as well as the plant response to stress (Sgroy et al. 2009; Antar et al. 2021). Many members of *Bacillus* and *Paenibacillus* such as *B. velezensis*, *B. subtilis*, *B. megaterium*, *B. aquimaris*, *B. licheniformis*, *B. amyloliquefaciens*, and *P. polymyxa* are known as potent phytohormone producer (Lim and Kim 2009). Indole-3-acetic acid (IAA) is a powerful signaling necessary for interactions between plants and microbes and has direct effects on plant development (Matsuda et al. 2018). Bacterial auxins alter the auxin pool to either a suboptimal or optimal level which enhances plant root development, particularly the formation of secondary roots, and increases root surface area, thus enhancing plant nutrition and leading to improved plant growth and productivity. *B. amyloliquefaciens* FZB42 can synthesize auxin through a trp-dependent pathway, and plant growth promotion was found functionally correlated in *Lemna* (duckweed). IAA secretion increased five times when 5 mM tryptophan was added in the medium (Idris et al. 2007). Higher auxin-producing *B. cereus* (So3II) (35.8 mg/mL) and *B. subtilis* (Mt3b) (36.6 mg/mL) were isolated from the rhizospheric soils of *S. nigrum* and *M. tricuspidatum*. Both strains were able to produce auxin without adding any substrate as a precursor. Both isolates were also producing siderophore and ACC deaminase (Wagi and Ahmed 2019). Through the transcriptome analysis of *B. amyloliquefaciens* SQR9 and *B. subtilis* 168, six genes were identified for IAA biosynthesis. *IPyA* pathway for IAA biosynthesis, consisting of *patB*, *yclC*, and *dhaS* genes, was confirmed through homologous and heterologous expression in both strains (Shao et al. 2015). *B. licheniformis* MML2501 can produce IAA (23 µg/mL) under optimized conditions such as pH 7.0, temperature 35 °C, and tryptophan conc. 16 mM. However, this strain failed to solubilize phosphate, but it was having a positive effect on seed germination and growth parameters when inoculated in groundnut pot trials (Prashanth and Mathivanan 2010). The mass production of IAA with cost-effective medium was done with *B. circulans* E9 (Sarmiento-López et al. 2022). A significant amount of ABA, IAA, CKs, and GAs was observed in a culture growth medium of *B. aryabhatai* strain SRB02. Plants treated with SRB02 were substantially less prone to heat stress than untreated plants. High levels of IAA, JA, GA12, GA4, and GA7, were detected in SRB02-treated plants (Park et al. 2017). Phytohormone producer *B. megaterium* was used in study to confirm the role of cytokinin-receptor CRE1, AHK2 and AHK3, and RPN12 in growth of *A. thaliana* and *P. vulgaris*. Plants with triple knockouts for ctk receptor CRE1-12/AHK2-2/AHK3-3 were found insensitive to bacterial inoculation in terms of growth promotion and root developmental responses, while *B. megaterium* was exhibited in AHK2 single and double mutation in combinations with RPN12. These findings indicate that ctk receptors function as a complementary in *B. megaterium*-mediated plant growth (Ortiz-Castro et al. 2008).

1.9 *Bacillus* and Antimicrobial Metabolites

Bacteria have biosynthetic gene clusters (BGCs) to produce different types of secondary metabolites, i.e., polyketides, terpenes, siderophores, and ribosomal and non-ribosomal synthesized peptides (Harwood et al. 2018). *B. thuringiensis*, *B. cereus*, *B. velezensis*, and *B. licheniformis* belonging to the genus *Bacillus*, especially *B. subtilis* and *B. amyloliquefaciens*, are extensively studied for their antimicrobial properties and their use as biocontrol agents against multiple soil-borne or postharvest plant pathogens. Many commercial biocontrol products based on *Bacillus* spp. have been commercialized successfully (Table 1.2). About 4–5% genome of *B. subtilis* is devoted to antibiotic production (Stein 2005). Many PGPR candidates of *Bacillus* genus have been exploited as microbial biopesticides (Kiesewalter et al. 2021). Approximately, 50% of commercially available bacterial biocontrol agents are *Bacillus*-based products (Arguelles-Arias et al. 2009). Antimicrobial compounds erucamide, behenic acid, palmitic acid, phenylacetic acid, and β -sitosterol were recovered, extracted, and purified from *B. megaterium* and tested against *A. tumefaciens* (T-37), *E. carotovora* (EC-1), and *R. solanacearum* (RS-2). Among all five compounds, phenylacetic acid was found most effective against all tested plant pathogens (Xie et al. 2021). Macrolactin A, 7-O-malonyl macrolactin AB, and surfactin B-producing *B. amyloliquefaciens* HR62 was applied on tomato with a biofertilizer, BIO62, against *R. solanacearum*. This combination successfully inhibits the growth of *R. solanacearum*, thereby decreasing disease incidence to 65% (Huang et al. 2014). *B. amyloliquefaciens* strain FZB42 can inhibit fire blight in orchard trees caused by *Erwinia amylovora*, by producing antibacterial polyketide difficidin and dipeptide bacilysin (Chen et al. 2009). Organic solvent-based crude extract of *B. velezensis* DTU001 strain can inhibit the growth of plant pathogenic fungi, *A. uvarum*, *P. ulaiense*, and *P. expansum*. The main bioactive lipopeptides were characterized as iturins, fengycins, and surfactins. Secondary metabolites, non-ribosomal production of antimicrobial chemicals, and siderophores account for 15.4% of the whole genome of DTU001 (Devi et al. 2019, Malviya et al. 2020a, b, 2022a, b). *B. subtilis* 22 and *Trichoderma atroviride* SG3403 used together shown improved antifungal activity against *Fusarium graminearum*. The lack of antimicrobial activity of the fungus SG3403 as a single culture shows that interactions between the two microorganisms in a coculture setting may result in the development of certain antifungal compounds. LC–MS analysis revealed eight specific compounds including mevastatin and koniginin which were present only in co-culture (Li et al. 2020).

Table 1.2 Some examples of commercial biocontrol products based on *Bacillus* spp. and their applications

Product name	Manufacturing company	strain	Application
Serenade [®] , Rhapsody [®] , Sonata [®]	AgraQuest, Inc., California, USA	<i>Bacillus subtilis</i> strain QST716; QST 713 and <i>B. pumilus</i> strain QST 2808	Biological control agent, micro- bial fungicide
Companion [®] liquid biologi- cal fungicide	Growth Products USA;	<i>B. subtilis</i> GB03, megaterium	Biocontrol of <i>Rhizoctonia</i> , <i>Pythium</i> , <i>Fusarium</i> , and <i>Phytophthora</i> in greenhouse and nursery
HiStick <i>N/T</i>	Becker Under- wood Inc., MicroBio Group, Ltd., USA	<i>B. subtilis</i> MBI600	<i>Fusarium</i> , <i>Rhizoctonia</i> , <i>Asper- gillus</i> control in soybean, alfalfa, dry/snap beans, peanuts
Kodiak	Gustafson, Inc., USA	<i>B. subtilis</i> GB03	<i>Rhizoctonia solani</i> , <i>Fusarium</i> spp., <i>Alternaria</i> spp., and <i>Asper- gillus</i> spp. that attack in roots cotton, legumes
YieldShield	Gustafson, Inc., USA	<i>B. pumilus</i> GB34	Soilborne fungal pathogens causing root disease in soybean
RhizoVital 42 liquid	ABiTEP GmbH	<i>B. amyloliquefaciens</i> FZB42	Protection against various soil- borne diseases and generally strengthens plants' vitality and yield
Larva termi- nator [®] Bacto Treat [®]	R.B. Herbal Agro, India	<i>B. thuringiensis</i> subsp. kurstaki	Diamondback moth control in cabbage
Crymax, Deliver	Certis Biologicals, USA	<i>B. thuringiensis</i>	It has the ability to manage cer- tain worm and worm species, caterpillars, and diamondback in vegetables, fruits, and ornamen- tal plants
Stargus [®] biofungicide	Pro Farm, Califor- nia, United States	<i>B. amyloliquefaciens</i> F727	Control downy mildew, botrytis, and other fungal and bacterial diseases in commercial crops
CEASE [®]	BioWorks, New York	<i>B. subtilis</i> strain QST 713	Broad spectrum of fungal and bacterial diseases
Quartzo [®] bionematicide Presence [®] bionematicide Zironar TM biofungicide	FMC Philadelphia, United States	<i>B. subtilis</i> <i>B. licheniformis</i>	Control of fungus and nematodes in soybean and corn

1.10 *Bacillus* and Volatile Organic Compounds (VOCs)

Microbial volatile organic compounds (MVOCs) are a group of chemicals produced by fungal and bacterial metabolic reactions. Bacterial VOCs occur in a variety of chemical forms, such as ketones, alcohols, terpenoids, sulfur compounds, alkenes, etc. Some chemicals are shared by the entire group of microorganisms, while others are exclusive to distinct strains. A single bacterium can produce up to 100 distinct VOCs (Sidorova et al. 2021). VOCs are important for intra- and interspecific communication between bacteria and hosts. Plants synthesize VOCs in order to protect themselves from herbivores and diseases, communicate with other plants, or feed microbes. Microorganisms release VOCs to communicate, attack, or defend themselves. Due to their capacity to either trigger the plant defenses mechanisms, limit the expansion of plant diseases, or encourage plant growth and development, microbial VOCs (MVOCs) play significant role in to plant's health status (Poveda 2021). *Bacillus* spp. are considered as factories of plant protective VOCs and have various roles in plant protection against bacterial and fungal diseases, induction of ISR, and plant growths (Poulaki and Tjamos 2023). Several *Bacillus* spp. particularly *B. amyloliquefaciens*, *B. velezensis*, *B. subtilis*, and *B. altitudinis* are most explored for their VOC-producing abilities (Grahovac et al. 2023). A number of VOC compounds such as 2-decanone, benzothiazole, phenol (4-chloro-3-methyl) 2,3,5-trimethylpyrazine, 2-nonanone, 2-dodecanone, styrene, 1-tetradecene (Yuan et al. 2012; Guevara-Avendaño et al. 2019; Gao et al. 2017; Insam and Seewald 2010) have been isolated from different *Bacillus* spp. and found effective against many plant pathogens. VOCs produced by *B. subtilis* AP-3 have positive effects on plant biomass of shoot and roots of soyabean by 88% and 18%, respectively, compared to the untreated control. The root architecture of soybeans exposed to VOCs was found altered with increased length, diameter, surface area, and numbers (Bavaresco et al. 2020). VOCs produced by *B. amyloliquefaciens* CPA-8 strain were showing promising results in sweet cherry fruit against postharvest pathogens *Monilinia laxa*, *M. fructicola*, and *Botrytis cinerea*. The VOCs were identified as 1,3-pentadiene, acetoin (3-hydroxy-2-butanone), and thiophene by solid-phase micro-extraction (SPME)-gas chromatography. The mycelial development of all target pathogens could be suppressed by all identified VOCs; however, thiophene was the most potent VOC, displaying more than 82% reduction of mycelial growth (Gotor-Vila et al. 2017). VOCs can modify the plant hormone levels by directly acting on related genes. In response to *B. subtilis* SYST2 VOCs albuterol and 1,3-propanediol, tomato plants displayed differential expression of genes involved in the production or metabolism of IAA (*SlIAA1* and *SlIAA3*), GAs (*GA20ox-1*), Cks (*SICKX1*), expansin (*Exp2*, *Exp9*, *Exp18*), and ET (*ACO1*) in plants. VOCs produced by *B. methylotrophicus* BCN2 and *B. thuringiensis* BCN10 can suppress the growth of postharvest pathogens *F. oxysporum*, *Botryosphaeria* sp., *T. atroviride*, *C. gloeosporioides*, and *P. expansum* (He et al. 2020).

1.11 *Bacillus Thuringiensis* (Bt) and CRY Proteins

B. thuringiensis (Bt), *B. popilliae*, and *B. sphaericus* are well known for their insecticidal properties. However, Bt is most studied and commercialized as biopesticide because it is safe for humans and has a broad-spectrum insecticidal nature (Ibrahim et al. 2010). Bt-based biopesticides are considered as the safest and most environment-friendly insecticides (Caballero et al. 2020). Bt produces crystal (Cry) and cytolytic (Cyt) proteins in the sporulation phase and Vip and Sip proteins in the vegetative growth phase (Gonzalez-Vazquez et al. 2021). The cry protein consists of proteins called δ -endotoxin. Cry proteins create pores and disrupt the gut epithelial membranes of juvenile insects (Latham et al. 2017). These proteins are toxic against a wide range of insect orders such as Coleoptera, Lepidoptera, Diptera, Hemiptera, and Hymenoptera, nematodes, and human cancer cells (Palma et al. 2014). The Cry protein family is categorized into at least 50 subgroups with more than 200 members (Bravo et al. 2007). Biopesticide manufactured from *B. thuringiensis* (Bt) contributes to over three quarters of the 3 billion dollar global market. Cry proteins were obtained by transgenic expression of the Bt gene in *E. coli* BL21, and their toxicity was evaluated against *H. armigera* larvae. On behalf of LD50 and ID50, Cry1Ab, Cry1Ac, and Cry2Aa, Cry proteins were found most toxic (Li and Bouwer 2012). A patent (No. 336230) was granted on “a process for the mass production of *Bacillus thuringiensis* (Bt) biocide using millet grain based agro-medium” invented by ICAR-VPKAS, Almora, India. This cold-tolerant strain *Bacillus thuringiensis* subsp. *galleriae/colmeri* (MTCC 8997) was isolated from North-Western Himalaya, India, and exhibited tendency of producing larger quantity of highly insecticidal cry proteins against many plant-harming insect (Kant and Shahid 2022).

1.12 *Bacillus*-Mediated Abiotic Stress Tolerance in Plants

Drought or excessive water condition, low or high temperature, unusual pH, salinity, metal pollution, and UV radiation all work against the growth and development of plants, limiting their ability to flourish and lowering agricultural productivity (He et al. 2018). PGPR-mediated physiochemical changes in plants that help in the alleviation of abiotic stress are called “induced systemic tolerance” (IST) (Yang et al. 2009). Low crop yield due to drought conditions is a cumulative result of diminished stomatal function, decreased transpiration and photosynthesis rates, and early crop maturity. PGPR can alter the root structure, phytohormone pool, osmolyte deposits, antioxidant enzymatic activity, and expression of defense-associated genes (Seleiman et al. 2021). Alleviation of drought stress in *A. thaliana* with the inoculation of PGPR *P. polymyxa* was confirmed by Timmusk and Wagner (1999). This strain successfully stimulates drought tolerance responsive gene, ERD15. In response to abiotic stressors, PGPR can modify the levels of the phytohormones

JA, ABA, BR, IAA, GAs, SA, CKs, and ET through different pathways. PGPR has ACC deaminase enzymes that convert ACC into α -ketobutyrate and ammonia, deplete ET ethylene level, and enhance abiotic stress tolerance in plants (Gupta and Pandey 2019; Misra et al. 2017). Potential traits of the mitigation of drought and heavy metal toxicity were shown by *B. cereus* and *B. haynesii*, isolated from *Vigna mungo* and *Phaseolus vulgaris*. Both were showing ACC-deaminase activity, EPS, and IAA production and tolerant to As, Ba, and Ni metals (Andy et al. 2023). The dual culture inoculation of arbuscular mycorrhizal fungus *R. irregularis* and *B. megaterium* in maize enhanced tolerance against drought and high temperature stress (Romero-Munar et al. 2023). *B. endophyticus* PB3, *B. altitudinis* PB46, and *B. megaterium* PB50 were compared to effectiveness in eliciting of drought tolerance in rice. *B. megaterium* PB50 was most effective as it improved the contents of water, total sugar, proteins, proline, phenolics, K, Ca, ABA, and IAA and upregulated the expression of stress-related genes (*LEA*, *RAB16B*, *HSP70*, *SNAC1*, and *bZIP23*) (Arun et al. 2020). The enhancement of antioxidant enzymes glutathione peroxidase and peroxidase as well as upregulation of genes associated with stress suppression, *B. butanolivorans* KJ40, can reduce the drought stress in pepper (Kim et al. 2022). When four varieties of wheat crop (V1: Akbar 2019; V2: Dilkash 2021; V3: Faisalabad 2008; and V4: Subhani 2020) seed were treated with *Bacillus subtilis* NA2, plants were found more tolerant to salinity stress in comparison to control (Gul et al. 2023). *Bacillus altitudinis* WR10 can improve the health of rice plant under high-salinity and low-phosphorus conditions. There are numerous examples of *Bacillus*-mediated tolerance against abiotic stresses in plants (Table 1.3).

1.13 *Bacillus*-Mediated ISR in Plants and Biotic Stress Tolerance

PGPR can mitigate biotic stress through the hyperparasitism, production of antimicrobial compounds (De Vrieze et al. 2018), ISR induction (Alizadeh et al. 2013; Martínez-Medina et al. 2017; Romera et al. 2019), and competition for nutrients and niche space (Recep et al. 2009; Vanitha and Ramjagathesh 2014; Lastochkina et al. 2019). The resistance induced against pathogens in plants by nonpathogenic antagonistic rhizobacteria is known as induced systemic resistance (ISR) in general (Ryu et al. 2004; Walters et al. 2005). *B. amyloliquefaciens*, *B. subtilis*, *B. pasteurii*, *B. cereus*, *B. pumilus*, *B. mycoides*, and *B. sphaericus* can significantly reduce the occurrence or impact of several diseases on a variety of hosts, through the ISR induction (Choudhary et al. 2007) (Table 1.4). Systemic acquired resistance (SAR) is mediated by SA and accretion of PR proteins, while ISR is mostly dependent on JA and ET signaling (Pieterse et al. 2001). The signaling pathway may be different and PGPR host specific. The pathogenesis-related (PR) gene may not be necessary for ISR to function because it is largely a JA- and ET-dependent mechanism

Table 1.3 *Bacillus*-mediated abiotic stress tolerance in different hosts and their effects on plants

<i>Bacillus</i> strain	Host	Stress	Effects on host plant	Reference
<i>B. subtilis</i> QM3	Wheat (<i>Triticum aestivum</i> L.)	Metal (Pb) toxicity	Growth promotion, enhanced activity of antioxidant enzymes and decreasing the conc. of metal (Pb) in the plant roots	Hao et al. (2015)
<i>B. aryabhatai</i> RS341	Canola	Salinity	Decreased ACC content, depleted ET emission, and induced hydrolytic enzymes	Siddikee et al. (2015)
<i>B. subtilis</i> (LDR2)	Wheat	Salt and drought	Increased abscisic acid (ABA) and ACC deaminase under both stress conditions, modulation of <i>TaCTR1</i> and <i>TaDREB2</i> gene	Barnawal et al. (2017)
<i>B. Cereus</i> SA1	High temperature	Soybean	Enhanced antioxidant signaling, modulation of ABA and SA, decreased ROS formation	Khan et al. (2020)
<i>B. megaterium</i> WU-5 and <i>B. subtilis</i> WU-13	Salinity	<i>Capsicum annuum</i> L	Promoted biomass yield, high proline content and antioxidant enzyme activities	Wang et al. (2018)
<i>B. velezensis</i> 5113	Heat, old/freezing and drought stress	Wheat	Increased chlorophyll and GABA content, accumulation of stress metabolites, differential expression of more than 300 proteins	Abd El-Daim et al. (2019)
<i>B. aquimaris</i> strain 3.13	Water limitation	Jerusalem artichoke (<i>Helianthus tuberosus</i> L.)	IAA, EPS, ACC-deaminase producer, increased biomass of shoot and root, improved length, diameter, and surface of root	Namwongsa et al. (2019)
<i>B. pumilus</i> strain FAB10	Salinity	Wheat	Strong biofilm formation, enhanced amount of exopolysaccharides, IAA, ACC-deaminase activity and solubilized phosphate, alleviate stress	Ansari et al. (2019)
<i>Bacillus</i> sp. NBRI YN4.4	Alkaline stress	<i>Zea mays</i>	Improved chlorophyll content and soluble sugar and proline level in inoculated plats	Dixit et al. (2020)

(continued)

Table 1.3 (continued)

<i>Bacillus</i> strain	Host	Stress	Effects on host plant	Reference
<i>B. amyloliquefaciens</i> SN13	Arsenic (as) toxicity	<i>Oryza sativa</i> L. var. Saryu-52	Decreased accumulation of As, improved nutrient status, enhanced expression of genes related to the metabolism of carbohydrate and fatty acid	Joshi et al. (2023a, b)
<i>B. licheniformis</i> CH102	High temperatures and water deficits	<i>Arabidopsis</i>	Produce antibiotic and 2,3-butanediol antifungal compounds, increased chlorophyll content and antioxidant enzymes, increased proline and galactinol accumulation, overexpression of JA- and SA-related genes	Sukkasem et al. (2018)

(Romera et al. 2019; Alizadeh et al. 2013). ISR enables the whole plant to develop more resistance to pathogens. PGPR can induce transcription factor MYB72, hormones, and signal molecules such as auxins and nitric oxide (Zamioudis et al. 2015). The process of PGPR-induced ISR is not fully understood, although research findings suggested that VOCs and microbe-associated molecular patterns (MAMPS) are some of the significant elicitors. Phenylacetic acid (PAA), extracted from *B. fortis* IAGS162, was found potential ISR elicitor that significantly reduced Fusarium wilt disease and altered metabolite profile of tomato (Akram et al. 2016). *B. pumilus* INR7 induced ISR against bacterial spot caused by *X. axonopodis* pv. vesicatoria in pepper. The combination of INR7 and benzothiadiazole (BTH) leads to the enhanced expression of defense-related marker genes *CaPR1*, *CaTin1*, and *CaPR4* (Yi et al. 2013). PGPR strain *B. cereus* AR156 can provide resistance to a variety of diseases including *P. syringae* pv. tomato DC3000. NPR1-dependent activation of SA, JA, and ET signaling pathways and simultaneous expression of defense-related genes PR1, PR2, PR5, and PDF1.2 were observed when *Arabidopsis* was treated with AR156 (Niu et al. 2011). *B. subtilis* and *P. fluorescens* share same mechanism of ISR induction through the JA/ET and NPR1-dependent against *B. cinerea* but in case of *Pst* DC3000, *B. subtilis* elicit ISR induction relies on SA, JA/ET, and NPR1 while *P. fluorescens* was found depend on SA pathway only. ABA signaling is also very crucial along with JA/ET signaling in primed systemic immunity by beneficial bacteria against *Pst* DC3000, but not against *B. cinerea* (Nguyen et al. 2020). *B. proteolyticus* strain OSUB18 elicited the ISR against *P. syringae* and *Botrytis cinerea* in *Arabidopsis* plants. Plant treated with OSUB18 showed higher expression gene related to plant hormone SA (*PR1*, *PR2*, *PR5*, *EDS5*, and *SID2*) and JA (*PDF1.2*, *LOX3*, *JAR1*, and *COI1*) in comparison to the control (Yang et al. 2023a).

Table 1.4 *Bacillus*-mediated and ISR responses and biotic stress tolerance in plants

Strain	Mechanism	Reference
<i>B. subtilis</i> strain BEB-DN (BsDN)	ISR response against <i>Bemisia tabaci</i> , reduction in <i>B. tabaci</i> pupae transforming into adults in inoculated tomato plants	Valenzuela-Soto et al. (2010)
<i>B. subtilis</i> BBG111	ISR response against <i>R. solani</i> in <i>Oryza sativa</i> L., enhanced JA, ET, ABA, and IAA levels	Chandler et al. (2015)
<i>B. subtilis</i> SL18r	ISR in tomato plants against <i>B. cinerea</i> . Expression of <i>MSTRG18363</i> (lncRNAs) was increased, lncRNAs suppressed the miR1918, regulating the expression of <i>SIATL20</i>	Zhou et al. (2021)
<i>B. altitudinis</i> and <i>B. velezensis</i>	Reduce rice blast by direct and indirect antagonism, both strains were producing fengycin and iturin and elicit ISR	Lam et al. (2021)
<i>B. amyloliquefaciens</i> strain KPS46	ISR against <i>X. axonopodis</i> pv. glycines in soybean, accumulation of defense-related enzymes in leaf	Prathuangwong and Buensanteai (2007)
<i>B. subtilis</i> (UFLA285)	JA/ET-mediated ISR against <i>R. solani</i> , proline synthesis genes in cotton	Medeiros et al. (2011)
<i>B. subtilis</i> G1 and <i>B. amyloliquefaciens</i> FZB24 and 42	All the isolates increased total health status of tobacco plant and elicited ISR against TMV	Wang et al. (2009)
<i>B. cereus</i> BCM2	Reduced the number of <i>Meloidogyne incognita</i> galls and egg masses on tomato plant roots	Hu et al. (2018)
<i>B. cereus</i> AR156	ISR induction against <i>Pst</i> DC3000 in Arabidopsis. Priming with EPS evoked defense-related enzymes and genes <i>PRI</i> , <i>PR2</i> , and <i>PR5</i> and kinase (MAPK) cascade	Jiang et al. (2016a, b)
<i>B. subtilis</i> A15, <i>B. amyloliquefaciens</i> D29, <i>B. methylotrophicus</i> H8	ISR response in rice against BLB. All have strong biofilm formation tendency and produce bacillomycin, fengycin, iturin, and surfactin	Elshakh et al. (2016)
<i>B. safensis</i>	Resistance against <i>Bipolaris sorokiniana</i> , reduced disease index by 50%, accumulation of proline, increased antioxidant enzymes	Sarkar et al. (2018)
<i>B. cereus</i> AR156	Resistance to <i>Pst</i> DC3000 in Arabidopsis, upregulation of transcription factors, WRKY11 (JA signaling) and WRKY70 (SA signaling)	Jiang et al. (2016a, b)
<i>Bacillus</i> sp. BS107 (BS107)	Induce ISR through 2-aminobenzoic acid (2-AB) in tobacco against <i>Pectobacterium carotovorum</i> , upregulation of ISR marker genes, i.e., PR1a, PR1c, PR2, and PR4	Yang et al. (2011)
<i>B. subtilis</i> strain M4	Reduced disease incidence in cucumber and tomato caused by <i>C. lagenarium</i> and <i>P. aphanidermatum</i> , respectively	Ongena et al. (2005)

(continued)

Table 1.4 (continued)

Strain	Mechanism	Reference
<i>B. subtilis</i> K47, <i>B. cereus</i> K46, and <i>Bacillus</i> sp. M9	Promoted the ISR in <i>C. chinense</i> plants against pepper golden mosaic virus (PeGMV), interferes with the viral replication and upregulation of defense genes	Samaniego-Gómez et al. (2023)

1.14 Future Aspects

Putting together the information found in the literature, in conclusion, we saw that many *Bacillus* spp. are able to regulate plant growth, development, and tolerance against abiotic and biotic stresses, which certainly increases the importance of their practical application in an effort to boost agricultural productivity and sustainability. The findings from the literature show *Bacillus* genera have huge potential use as biofertilizers, biostimulants, biopesticides, and ISR elicitors against biotic stresses and defense against abiotic stress. Understanding their underlying mechanisms of physiochemical activity on host plants under various environmental and biotic stresses is crucial to maximizing the potential and application of PGPR in sustainable agricultural output.

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