



Phyostimulation and biocontrol potential of Gram-positive endospore-forming Bacilli

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Received: 22 October 2020 / Accepted: 2 August 2021 / Published online: 12 August 2021
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Abstract

Main conclusion The spore-forming *Bacillus* and *Paenibacillus* species represent the phyla of beneficial bacteria for application as agricultural inputs in form of effective phyto-stimulators, biofertilizers, and biocontrol agents.

Abstract The members of the genera *Bacillus* and *Paenibacillus* isolated from several ecological habitats are being thoroughly dissected for their effective application in the development of sustainable and eco-friendly agriculture. Numerous *Bacillus* and *Paenibacillus* species are reported as plant growth-promoting bacteria influencing the health and productivity of the food crops. This review narrates the mechanisms utilized by these species to enhance bioavailability and/or facilitate the acquisition of nutrients by the host plant, modulate plant hormones, stimulate host defense and stress resistance mechanisms, exert antagonistic action against soil and airborne pathogens, and alleviate the plant health. The mechanisms employed by *Bacillus* and *Paenibacillus* are seldom mutually exclusive. The comprehensive and systematic exploration of the aforementioned mechanisms in conjunction with the field investigations may assist in the exploration and selection of an effective biofertilizer and a biocontrol agent. This review aims to gather and discuss the literature citing the applications of *Bacillus* and *Paenibacillus* in the management of sustainable agriculture.

Keywords *Bacillus* · *Paenibacillus* · Mechanism · Spore formers · Biofertilizer · Biocontrol agent

Introduction

“The ultimate goal of farming is not the growing of crops but the cultivation and perfection of human beings”

- Masanobu Fukuoka

The current estimated global population is approximately 7 billion, which is expected to surge to 10 billion by the year 2055 (Ferreira et al. 2019). Agriculture plays a crucial role in the sustenance of the global economy. Ester Boserup, a Danish economist promulgated the concept of “agricultural intensification” which justifies a proverb—Necessity is the

mother of all inventions (Turner et al. 1977). According to Boserup’s theory of agricultural development, “the rise in the population would encourage experts to escalate food production”. In the twentieth century, the concept of the Green Revolution was introduced in India with a motive to enhance food production by employing irrigation and chemical formulations to constitute a self-sufficient India. Though it is exhilarating to ponder solutions that agriculture can provide to accomplish sustainable development goals, the world needs to practice them systematically instead of chasing magic bullet solutions which, in actuality, may not exist. The incessant and indiscriminate use of chemical fertilizers to increase agricultural productivity to feed the nation posed a negative impact on the environment and human health. Adding to the above-mentioned issue, the factors viz. climate change (abiotic stress), unequal food distribution, food spoilage and wastage, diseases (biotic stress), and use of agrochemicals contribute to the stress on agricultural productivity (Glick 2015). Unfortunately, the menace of “more demand and less supply” is once again in the headlines. Of the above-stated factors, insects, diseases,

Communicated by Gerhard Leubner.

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and weeds account for around 20–40% loss in global agricultural productivity (Savary et al. 2012). The traditional approaches such as crop rotation and breeding of resistant varieties seem to be impotent for controlling plant diseases. Moreover, the use of chemical formulations to sustain agricultural productivity pollutes the underground water, deteriorate soil quality and biodiversity, develops resistant races of pathogens, and foist danger to animal and human health due to their accumulation in the natural ecosystem (Heydari and Pessaarakli 2010; Ramakrishna et al. 2019). It is estimated that environmental pollution accounts for 40% of human death worldwide as a consequence of reduced food production, malnutrition, and incidences of diseases (<https://www.sciencedaily.com/releases/2007/08/070813162438.htm>). With the increase in awareness among the growers and consumers about the negative impact of aforementioned factors and practices, the emphasis is been made to bring into action a more sustainable and eco-friendly approach for food production—“Biorevolution”.

Soil is a complex mixture of organic matter, minerals, water, air, and microbes. The soil microbes play an indispensable role in maintaining the soil vitality and functionality, practicing the essential functions of nutrient cycling, maintaining plant diversity, decomposing soil organic matter, transforming toxic chemicals into their non-toxic forms (bioremediation) and enhance the overall quality and health of soil (Saxena et al. 2020). The natural soil inhabitants possess an ability to grow rapidly utilizing the wide range of nutrients secreted by plants, colonize its roots, secrete chemicals and enhance plant growth as well as crop yield while conferring protection against biotic and abiotic stresses (Goswami et al. 2016; Radhakrishnan et al. 2017). These natural growth stimulants and the succourer of plants are designated as plant growth-promoting bacteria (PGPB). The examples of bacteria belonging to this category include genera, *Bacillus*, *Paenibacillus*, *Pseudomonas*, *Rhizobium*, *Azotobacter*, *Burkholderia*, *Serratia*, *Enterobacter*, *Azospirillum*, and *Klebsiella*.

Plant growth-promoting bacteria

Plants are dependent on microorganisms ever since they edged out of aquatic habitat to the terrestrial ecosystem about a million years ago. The role of microorganisms in the evolution of plants has been highlighted by “The hologenome theory of evolution” (Rosenberg and Zilber-Rosenberg 2016). It proposes that a plant (host) growing under natural environmental conditions is associated with a well-structured and regulated community of symbiotic microbes (phytomicrobiome) that contributes to its morphology, anatomy, physiology, development, innate, and adaptive immunity (Backer et al. 2018; Rosenberg and Zilber-Rosenberg 2016). The associated microorganisms evolve through a

complex tripartite interaction between the host plant, soil microflora as well as the environment and promote the overall plant growth and productivity (Backer et al. 2018). The plants ooze approximately 5–30% of photosynthetically fixed carbon (photosynthates) through roots into the rhizosphere, a narrow layer of soil surrounding plant roots (Glick 2015; Kumar et al. 2006). These exudates serve as chemical attractants or repellents stimulating or inhibiting specific microbial communities, mediate the microbe–microbe and host-microbe interaction in the soil, help to cope with herbivores, and regulate chemical and physical properties of soil (Glick 2015; Zhang et al. 2017). The secretion of exudates in the soil establishes a gradient of intimacy between the bacteria and the plant roots, wherein the degree of interaction is inversely proportional to the distance between the interacting partners (Backer et al. 2018). It is a complex ecosystem consisting of bacteria (90,000,000), actinomycetes (4,000,000), fungi (200,000), algae (30,000), protozoa (50,000), nematodes (30), and arthropods (< 1) per gram of soil (Glick 2015). The relative abundance of bacteria in the rhizosphere is 10 to 1000 times higher than the bulk soil but with lower diversity in comparison to bulk soil (soil outside rhizosphere) (Lugtenberg and Kamilova 2009; Mhlongo et al. 2018). Besides being abundant in the soil, less than 1% of bacteria are reported to be cultivable (Glick 2012).

The microflora in the rhizosphere may interact positively (symbiotic), negatively (pathogenic), or remain neutral with the host. While PGPB enhances plant growth and protects them from biotic and abiotic stresses, pathogens negatively influence plant health (Glick 2015). The PGPB capable of actively colonizing plant roots or rhizosphere are termed plant growth-promoting rhizobacteria (PGPR) (Wu et al. 2005). The PGPR can be further classified into two groups based on their relationship with the plant: free-living and symbiotic bacteria or extracellular PGPR (present in rhizoplane or rhizosphere) and intracellular PGPR (present in root nodules) based on the residing sites (Hayat et al. 2010; Mustafa et al. 2019). Based on their functional characteristics, the PGPR can be classified into phytostimulators (bacteria producing substances that stimulate the growth of plants), biofertilizers (bacteria assisting plant in nutrient acquisition), biopesticides (microbes used to control pest, pathogens and weeds), and rhizomediators (microbes used in bioremediation) (Mustafa et al. 2019). The abundance of bacterial groups varies with the plant species, plant compartments, genotypes as well as biotic and abiotic factors (Compant et al. 2005; Trivedi et al. 2020; Ramakrishna et al. 2019). For instance, the phylogenetic analysis of Himalayan cold desert samples using 16S rRNA gene sequencing followed by restriction digestion analysis identified 31 genera belonging to phyla of Firmicutes (41%), Proteobacteria (37%), Actinobacteria (19%) and Bacteroidetes (3%) (Yadav et al. 2015). Another study reported the abundance

of Proteobacteria (49%), followed by Firmicutes (32%), Actinobacteria (12%) and Bacteroidetes (7%) in wheat using 16S rRNA amplification (Verma and Suman 2018). The dominant microbial phyla identified using high throughput sequencing (16S rRNA) and isotope probing in the root and rhizosphere soil of rapeseed oil (*Brassica napus*) were Proteobacteria, Actinobacteria, Bacteroidetes, Acidobacteria, Firmicutes, and Planctomycetes (Gkarmiri et al. 2017). Altogether, the phylum Actinobacteria, Firmicutes, Proteobacteria (alpha, beta, and gamma), Acidobacteria, and Bacteroidetes are the most abundant in the rhizosphere (Lagos et al. 2015; Ramakrishna et al. 2019; Rossmann et al. 2017). In the phylum Firmicutes, the common PGPB genera include *Bacillus* and *Paenibacillus*. The PGPB of phylum Proteobacteria includes *Pseudomonas*, *Enterobacter*, *Acinetobacter*, *Serratia*, *Rhizobium*, and *Bradyrhizobium* species (Mustafa et al. 2019). The phylum Bacteroidetes consist of *Flavobacteria* as one of the widely used PGPB (Hayat et al. 2010; Radhakrishnan et al. 2017; Ramakrishna et al. 2019). The members of *Bacillus* and *Pseudomonas* genera are the predominant PGPB, which have been extensively studied, explored and employed in agriculture (Hashem et al. 2019; Kumar et al. 2011). This review majorly focuses on the application of *Bacillus* and *Paenibacillus* species.

Distribution and taxonomy of *Bacillus* and *Paenibacillus*

The genus *Bacillus* (classified as Kingdom: Bacteria; Phylum: Firmicutes; Class: Bacilli; Order: Bacillales; Family: *Bacillaceae*) encompasses a diverse assemblage of low G + C, Gram-positive, rod-shaped, heterotrophic, and endospore-forming (a key distinguishing feature) bacteria (Slepecky and Hemphill 2006). *Paenibacillus*, on the other hand, emerged as a phylogenetically distinct group from Bacilli based on 16S rRNA gene sequences. They can be isolated from soil, humus, compost, rhizosphere, fermented food, and clinical specimens. The endospores formed in response to nutrient deprivation or environmental stresses can be easily dispersed by air to long distances irrespective of active growth. Thereby, they can be isolated from diverse terrestrial and aquatic habitats making them ubiquitous. They can be recovered from soil, rhizosphere, water, plant, insect, and animal gut with few being opportunistic or obligate pathogens viz. *Bacillus cereus*, *Bacillus thuringiensis*, and *Bacillus anthracis* (Gardener 2004; Jensen et al. 2003). *Bacillus* is one of the most studied and genetically explored bacterial genus with genome sequences of 253 species available to date (<https://www.ncbi.nlm.nih.gov/genome/?term=bacillus>) and 93 validly published names (<https://lpsn.dsmz.de/genus/bacillus>). Formerly, the taxonomy and classification of *Bacillus* species were governed by traditional

phenotypic approaches such as its niche, morphology, nutrition, ecophysiology, and biochemical characteristics (Kumar et al. 2011; Ravel and Fraser 2005). The use of 16S rRNA/DNA gene cataloging substantiated the phylogenetic resolution over traditional classification that was a mystifying and unsystematic procedure (Zeigler and Perkins 2015). This led to the assignment of numerous species to genus *Bacillus* despite lacking phenotypic and biochemical properties parallel with the type strain *Bacillus subtilis*. Also, a high level of similarity and multiple copies of the 16S rRNA gene restricts the complete resolution of closely related species (Ash et al. 1991; Khurana et al. 2020). With the advent of next-generation sequencing technology, comparative genomics and the increased accessibility of whole-genome sequences in the databases, it has now become possible to distinguish between two closely related *Bacillus* species based on whole-genome comparisons or employing multiple phylogenetic markers (Fan et al. 2017). Several strains taxonomically classified as *B. subtilis* or *Bacillus amyloliquefaciens* are now designated as strains of *Bacillus velezensis*. The model strain for Gram-positive PGPR and biocontrol, *B. amyloliquefaciens* subsp. *plantarum* FZB42 based on phylogenomic analysis has been reclassified to *B. velezensis* (Fan et al. 2018). The comparative genome analysis carried out by Chun et al. (2019) between the members of *B. amyloliquefaciens* group viz. *B. velezensis*, *Bacillus siamensis*, and *B. amyloliquefaciens* revealed the similarity in their genomic and metabolic features, however, certain unique features were also annotated. For instance, the core genome of all the members encoded gene clusters associated with the metabolism of xanthine, uric acid and diverse carbon sources whereas the core genome of *B. velezensis* encoded more genes associated with the biosynthesis of antimicrobial compounds as well as D-galacturonate and D-fructuronate metabolism. With this reference, Dunlap (2019) proposed the use of sugar kinase gene primers as a rapid screening strategy to determine the identity of *B. velezensis* circumventing genome sequencing. Using comparative genomics approach, Bhandari et al. (2013) determined several conserved indels (insertion and deletions) specific for *B. subtilis* and *B. cereus* clade. Similarly, Patel and Gupta (2020) proposed six new genera to redesignate the members previously classified under genus *Bacillus* viz. *Peribacillus*, *Cytobacillus*, *Mesobacillus*, *Neobacillus*, *Metabacillus*, and *Alkalihalobacillus* using phylogenomic and comparative genomic approach. Overall, to obtain a comprehensive taxonomic insights into the genus *Bacillus*, the classical microbiology combined with comparative genome analysis including the combination of tools such as digital DNA–DNA hybridization (dDDH), Average Nucleotide Identity (ANI), Average amino acid identity (AAI), and Tetra-Nucleotide Analysis (TNA) appears to be a more realistic approach (Fan et al. 2017).

Bacillus and Paenibacillus as PGPB

The heterogeneity in the physiology and nutrient utilization, the ability to form endospores, production of peptide antibiotics and signal molecules, extracellular enzymes, and physiochemical growth optima confer the species of the genera *Bacillus* and *Paenibacillus* an ecological advantage for survival and successful colonization over a wide range of habitats (Gardener 2004; Hong et al. 2009; Tiwari et al. 2019).

For decades, Bacilli have been explored as plant growth-promoting agents owing to their excellent colonization and sporulation abilities, good secretion system and few other characteristics mentioned previously (Jama et al. 2018). The crystal insecticidal toxin-producing gene of the entomopathogenic bacterium, *B. thuringiensis* (Bt) has revolutionized insect pest management for many economically important crops reducing the environmental and ecological issues associated with the use of chemical fertilizers (Rani et al. 2019). Besides *B. thuringiensis*, a mosquito toxic bacterium, *B. sphaericus* is reported to produce a parasporal crystal protein (Mtx) contributing to the above-stated fact (Feto 2016; Neto et al. 2020). Consequently, several findings indicated the development of

resistance in insects against 'Bt' toxin imposing a challenge in the management of unwanted organisms in the future and exploitation of more natural enemies to combat the same (Feto 2016). The Bacilli reported as PGPB include *B. subtilis*, *Bacillus megaterium*, *B. amyloliquefaciens*, *B. velezensis*, *Bacillus macerans*, *Paenibacillus* sp. and have been employed commercially for growth promotion or biocontrol applications in the crops such as wheat, barley, peas, soybean, maize, and potato (Liu et al. 2017; Rai et al. 2020; Rybakova et al. 2017; Sansinenea 2019). A systematic comprehension of plant growth promotion mechanism is essential to manipulate the rhizospheric microflora to exploit the processes that may enrich the productivity of the plant. The Bacilli candidates can affect plant growth by employing direct or indirect mechanisms discretely or in conjunction during the life cycle of a plant (Fig. 1). These PGPs may act directly by elevating the plant growth through modulation of growth hormones or facilitating nutrient acquisition resulting in soil amelioration and indirectly by contending the growth of deleterious microbes (Glick 2015; Rani et al. 2019). For instance, *Bacillus pumilus* LZP02 could promote the growth of rice by augmenting carbohydrate metabolism and phenylpropanoid biosynthesis as suggested by proteomic, transcriptomic and metabolomic studies (Liu et al. 2020), while

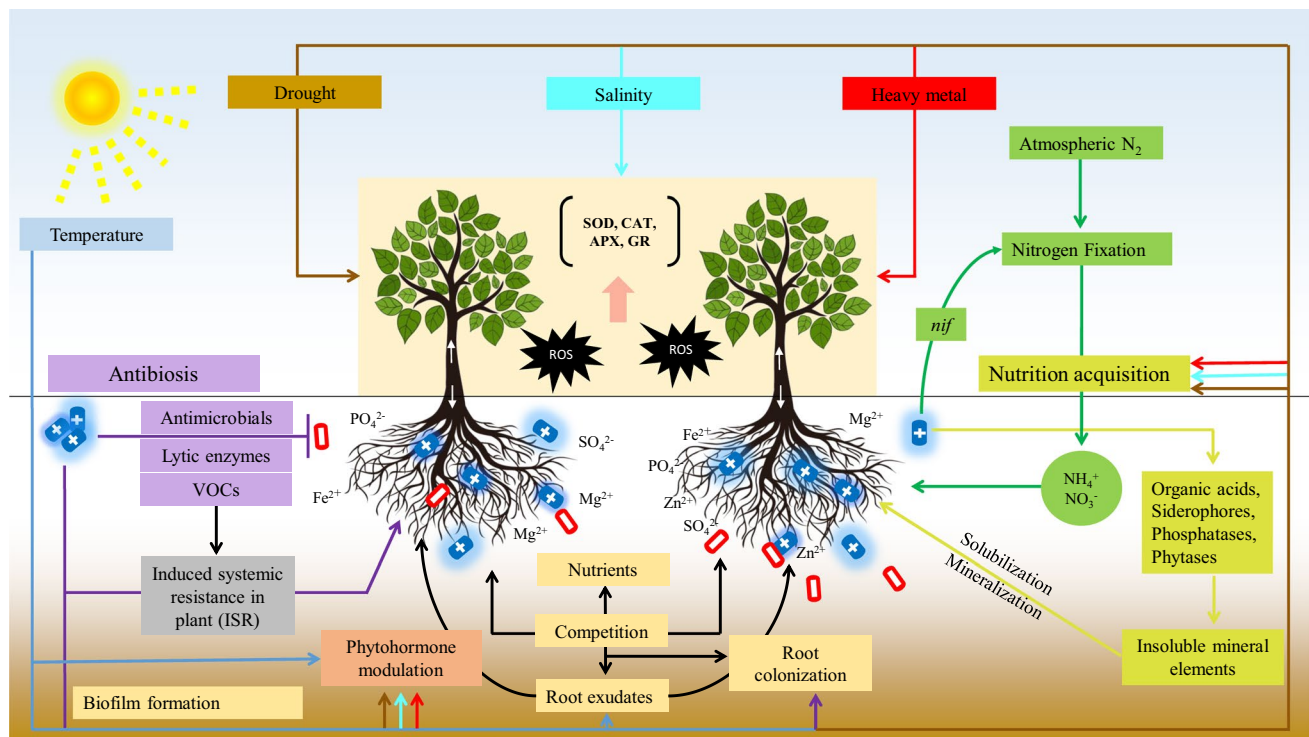


Fig. 1 Schematic representation of direct and indirect mechanisms of plant growth promotion. The plant growth-promoting bacteria are denoted as blue rods with positive signs whereas the pathogens are denoted as red rods with a negative sign. The color frames and the

arrows in different colors represent different mechanisms and the influence of various direct or indirect factors (highlighted in different colors) on plant growth. *SOD* superoxide dismutase, *CAT* catalase, *APX* ascorbate peroxidase, *GR* glutathione reductase

the application of *Bacillus velezensis* F21 in watermelon could confer resistance to *Fusarium oxysporum* infection owing to the induction of defense-related genes as well as induction of MAPK and phytohormone related signaling pathways (Jiang et al. 2019). The mode of action of *Bacillus* as PGPB are discussed in detail below:

Mechanism of action

Direct mechanism

The direct mechanism of the PGPB executed inside the plant influence the balance of plant growth regulators, thereby facilitating the proliferative and adaptive capacity of the host plant (Glick 2015; Goswami et al. 2016) as well as facilitates the acquisition of nutrients, which are essential for proper growth, development and physiological processes of the plants.

Nutrient acquisition The growth and development of the plant are largely dependent on the concentration and amalgamation of the nutrients present in the soil. The nutrients can be classified into two categories based on their abundance in the plant: macronutrients (nitrogen, potassium, calcium, magnesium, phosphorous, and sulfur) and micronutrients (iron, chlorine, manganese, zinc, copper, molybdenum, and boron) (Kirkby 2012; Ramakrishna et al. 2019). Owing to the suboptimal concentrations and/or insoluble forms of such nutrients, plants face significant challenges in acquiring them from the environment. Nonetheless, the evolution of plant species with mutually beneficial PGPB aids the bioconversion and bioavailability of inert and insoluble nutrients. For instance, Bisht et al. (2020) described the role of *Paenibacillus lentimorbus* B-30488 and *B. amyloliquefaciens* SN13 in overcoming the nutrient starvation stress in rice plants through modulation of organic acid, amino acid, and carbohydrates (Bisht et al. 2020). The PGPBs may even improve the root architecture of the host plant, augmenting the surface area accessed by the roots for the procurement of water and nutrients from the soil (Trivedi et al. 2020). Such PGPBs are designated as “Biofertilizers” as they supply nutrients to the plants (Lugtenberg and Kamilova 2009).

Nitrogen is the most abundant element constituting ~78% of the atmosphere, however, plants are capable of utilizing only reduced forms of nitrogen such as ammonium and nitrates limiting its availability. The cooperation or compromise exists between the plant (eukaryote) and the nitrogen-fixing bacteria (prokaryote). The prokaryote delivers the fixed nitrogen to the eukaryote in the reciprocity of fixed carbon released as root exudates by plants (Govindasamy et al. 2010). Zhang et al. (2019) described the influence of root microbiota on nitrogen utilization efficiency and the growth of rice cultivars. In this study, the ‘indica’ variety of

rice recruited diverse nitrogen metabolizing bacteria compared to ‘japonica’ variety leading to better nitrogen utilizing capacity and growth. For identifying nitrogen-fixing bacteria from a particular niche, microbial bioassay (direct) or acetylene reduction assay (indirect) is carried out (Das and De 2018). Besides, the presence of a gene marker *nifH* validates the nitrogen-fixing capability of bacteria. Ding et al. (2005) investigated the isolates of wheat, maize, ryegrass, and willow rhizosphere for the presence of *nifH* gene to determine the nitrogen-fixing capabilities of *Bacillus* and *Paenibacillus* genera. Seldin et al. (1984) screened the isolates of Brazilian soil for their nitrogen-fixing abilities based on acetylene reduction assay of which maximum belonged to *Paenibacillus* species. A novel bacterium *Bacillus azotofixans* isolated from Brazilian soil and grassroots exhibited higher nitrogen-fixing capability than other species of *Paenibacillus* (*Paenibacillus macerans* and *Paenibacillus polymyxa*) isolated from a similar source (Seldin et al. 1984). An endophytic diazotroph *P. polymyxa* P2b-2R was reported to colonize and promote the growth of oilseed crop canola under nitrogen limiting conditions (Puri et al. 2016). A recent study described the growth promotion of wheat, maize, and cucumber upon treatment with a diazotrophic *Paenibacillus beijingensis* BJ-18 that induces the gene expression and the activity of enzymes involved in nitrogen uptake and utilization (Li et al. 2019). *Bacillus licheniformis*, *B. cereus*, *B. megaterium*, *B. macerans*, *B. azotofixans*, and *Paenibacillus* sp. are reported as efficient nitrogen fixers supporting the progression of crop plants in agriculture (Saxena et al. 2020; Seldin et al. 1984; Tiwari et al. 2017). However, the genome studies of *Bacillus* (5216) and *Paenibacillus* (396) strains carried out by Ali et al. (2021) revealed the dominance of nitrogen-fixing ability in *Paenibacillus* over *Bacillus*.

Phosphorous (P) is the second limiting nutrient (400–1200 mg/kg of soil) essential for the growth and development of the plants, after nitrogen. Plants utilize P from the soil solution as HPO_4^{-2} and $\text{H}_2\text{PO}_4^{-1}$, however, the soluble form of P exists at a concentration of less than 1 ppm (Glick 2012; Hayat et al. 2010). A major proportion of soil P is present in an insoluble form such as apatite (inorganic) or as inositol phosphate, phosphomonoesters and phosphodiester (organic) hampering its availability to the plants. The chemical fertilizers amended in the soil often fail to serve the crops with P owing to the transformation of soluble P into immobilized recalcitrant form soon after its application (Glick 2012). Moreover, the process of P fixation and solubilization is controlled by soil pH and its type (Hayat et al. 2010). The mineralization and solubilization of P by PGPB can overcome the aforementioned problem. The role of soil pH on the mode of action of phosphate solubilizing bacteria (PSB) was demonstrated by Mpanga et al. (2020). In moderately acidic soil, the *B. velezensis* FZB42 (formerly known as *B. amyloliquefaciens*) inoculation resulted in higher growth of

maize plants by enhanced availability of P through solubilization of rock P by acidification of the rhizosphere (Mpanga et al. 2020). On the other hand, in alkaline soil, the inoculant FZB42 promoted the maize plant growth by inducing root proliferation and thus facilitating the acquisition of low concentration of soluble P (Mpanga et al. 2020). The organic acids and acid phosphatases produced by PSB play a key role in the mineralization of organic and inorganic form of P (Glick 2012; Oteino et al. 2015; Rodríguez and Fraga 1999). At a low level of P in soil, several heterotrophic bacteria in the presence of labile carbon immobilize soil P and serve as a source of P to plants (Govindasamy et al. 2010). The organic acids secreted by PSB chelates the cations of insoluble phosphate salts and release the phosphate anions which are soluble and bioavailable. The major organic acids produced by PSB include gluconic acid, 2-ketogluconic acid, oxalic acid, malonic acid, and succinic acid (Billah et al. 2019; Govindasamy et al. 2010). The bacteria belonging to genera *Bacillus*, *Paenibacillus*, *Pseudomonas*, *Rhizobium*, *Erwinia*, and *Serratia* are reported as PSB (Prakash and Arora 2019; Ramakrishna et al. 2019). Of all, strains of *Bacillus*, *Pseudomonas*, and *Rhizobium* are the most efficient PSB (Hayat et al. 2010). The bacterium *P. polymyxa* with P-solubilizing activity of 2635 µg/mL elevated the growth of *Zea mays* under abiotic stress (Din et al. 2020). Similarly, the growth and oil yield of *Mentha arvensis* were found to be enhanced by co-inoculating PSB *Bacillus* sp. with tricalcium phosphate (Prakash and Arora 2019). The inoculation of N₂-fixing and P-solubilizing *Bacillus* sp. in sugar beet and barley fields enhanced the leaf, root, and sugar yield of sugar beet as well as grain and biomass yield of barley, respectively (Sahin et al. 2004). The PSB, *B. thuringiensis* isolated from acidic soil has been reported to increase the growth and crude protein content of groundnut (Wang et al. 2014). *B. licheniformis* UBPSB-07 increased the overall growth of *Vigna radiata* by increasing the bioavailability of soil P by the production of acid phosphatases (Thomas et al. 2018). The extracellular enzyme phytase in the culture filtrate extract of *B. amyloliquefaciens* FZB45 stimulated the growth of maize seedlings in the presence of phytate under phosphate limiting conditions whereas phytase mutant strain did not promote plant growth (Idriss et al. 2002). A plant growth-promoting bacterium *Bacillus aryabhatai* isolated from the roots of the chickpea rhizosphere is reported to produce a novel phytase enzyme that was found to be effective in improving germination and growth of chickpea seedlings under phosphate limiting conditions (Roy et al. 2017).

Potassium (K) is the third important component of plant nutrients after nitrogen and phosphorous. A major proportion (~98%) of K in the soil exists in an insoluble form of rocks and minerals (feldspar and mica) reducing its availability to the crop plants (Yasin et al. 2016; Saha et al. 2016a, b). K is essential for early growth and development of proteins,

phloem transport, tropism, regulation of stomatal aperture as well as the biotic and abiotic stress tolerance. (Yasin et al. 2016; Sharma et al. 2016). Soil microorganisms playing a pivotal role in K cycling include *Pseudomonas*, *Burkholderia*, *Paenibacillus*, *Bacillus*, *Agrobacterium*, *Rhizobium*, and *Acidithiobacillus* (Yasin et al. 2016; Saha et al. 2016a, b; Sattar et al. 2019; Saxena et al. 2020). The solubilization of K by potassium solubilizing/dissolving bacteria (KSM/KDB) can occur by various mechanisms such as direct secretion of acids, indirect chelation of cations bound to the insoluble form of K, exchange reactions, metal complexing ligands, the release of phytohormones, polysaccharide secretion or by biofilm formation (Sattar et al. 2019). Saha et al. (2016a, b) demonstrated the K solubilizing abilities of *B. licheniformis* BHU18 and *Paenibacillus azotoformans* isolated from wheat. Moreover, it was found to resist various regimes of pH making it an efficient biofertilizer in acidic and alkaline soils. *Bacillus edaphicus* NBT solubilized feldspar and illite minerals and increased the K uptake by wheat owing to its ability to produce organic acids and capsular polysaccharides (Sheng and He 2006). *B. edaphicus* NBT also promoted the growth of cotton and rape seeds under K deficient conditions (Sheng 2005). The KSB, *B. pseudomycoloides* facilitated the uptake of K in tea plants grown in soil amended with mica waste. Shen et al. (2016) demonstrated the potential of a plant growth-promoting (PGP) bacterial complex (*B. amyloliquefaciens* XD-N-3, *Bacillus pumilus* XD-P1, and *Bacillus circulans* XD-K2) endowed with an excellent enhancement of NPK bioavailability in improving the growth as well as imparting stress tolerance to the Kiwi fruit.

Another important micronutrient essential for the proper growth and development of a plant is zinc. It plays a role in carbohydrate metabolism, auxin metabolism and acts as an antioxidant (Kamran et al. 2017). The bacterial genera *Pseudomonas*, *Bacillus*, *Rhizobium*, *Azospirillum*, and *Pantoea* possess the ability to solubilize zinc by chelation or reducing the pH of the surrounding environment (Saxena et al. 2020). *Bacillus* sp. ZM20 and *B. cereus* produced lactic acid and acetic acid in culture media amended with zinc oxide resulting in its solubilization due to a reduction of surrounding pH (Mumtaz et al. 2019). Khande et al. (2017) demonstrated the role of zinc solubilizing *Bacillus* strains in biofortification and an increase in the yield of soybean and wheat. Zaheer et al. (2019) evaluated the positive influence of indole acetic acid (IAA) and organic acid-producing *Bacillus* sp. AZ17 capable of solubilizing P and Zn on the growth of chicken pea under field conditions. A multi propitious isolate of cow dung, *B. megaterium* CDK25 showed higher solubilization of zinc (~20 ppm) and displayed PGP attributes such as phosphate solubilization, phytase, IAA, and siderophore secretion resulting in enhanced growth, nutrient uptake and yield of *Capsicum annum* at pot scale

(Bhatt and Maheshwari 2020). The application of *Bacillus* sp. ZM20, *B. aryabhatai* ZM31 and S10 and *B. subtilis* ZM63 promoted the growth and increased the bioavailability and concentration of zinc in maize (Mumtaz et al. 2017).

Modulation of phytohormones The plants, being sessile are vulnerable to several biotic and abiotic stresses causing physiological, biochemical, and molecular changes. This affects the overall growth and productivity of food crops. However, the plants have evolved numerous complex sophisticated mechanisms to deal with such stresses. The plant hormones are small endogenous, low molecular weight molecules that hold a role in growth, development, physiological processes, homeostasis, and retaliation against environmental stresses (Checker et al. 2018). It includes auxin, cytokinin (CKs), gibberellic acid (GA), abscisic acid (ABA), salicylic acid (SA), jasmonic acid (JA), ethylene (ET), and brassinosteroids (Duca and Glick 2020; Glick 2015). The plant rhizosphere is a nutrient-rich milieu consisting of various sugars, amino acids, secondary metabolites, and organic compounds that attract microbes. The microbial inhabitants in reciprocation alleviate the stress responses by modulating the nutritional and hormonal levels in plants and inducing systemic tolerance to stress (Egamberdieva et al. 2017; Ortíz-Castro et al. 2009). For instance, the bacterium *B. amyloliquefaciens* SN-13 modulated the expression of stress response genes on the exogenous application of phytohormones (ABA, SA, JA, and ethylene) in rice seedling conferring tolerance to abiotic stresses. (Tiwari et al. 2017).

Auxin and cytokinin

Auxins, the first plant hormone to be discovered, are low molecular weight organic compounds constituting an important and diverse group of plant hormones. They are recognized to promote cell division, elongation, and differentiation processes in plants (Goswami et al. 2016). They are also reported to play a role in mediating and improving plant tolerance to biotic and abiotic stresses (Checker et al. 2018). IAA is a predominant and the most widely explored hormone of this class. IAA regulates bacterial physiology, adaptation to stress and microbe-microbe interaction (Duca and Glick 2020). IAA biosynthesis in bacteria can be tryptophan dependent or independent. The tryptophan-dependent pathways include indole-3-acetamide (IAM), indole-3-pyruvic acid (IPyA), indole-3-acetonitrile (IAN), tryptamine (TAM), and tryptophan side chain oxidase (TSO) pathways whereas no enzymes or genes involved in tryptophan independent pathways for IAA synthesis have been identified (Liu et al. 2019). Approximately, 80% of microbial flora in the plant rhizosphere synthesizes auxins and hence can alter the physiological responses in the plant (Goswami et al. 2016). The bacteria belonging to *Bacillus* and *Paenibacillus*

genera are reported to synthesize plant hormones influencing the host plant. The IAA produced via the tryptophan-dependent pathway by *B. amyloliquefaciens* FZB42 (now *B. velezensis* FZB42) is demonstrated to stimulate the growth of duckweed fronds under in vivo conditions. The presence of IAA in FZB42 was identified using high-performance liquid chromatography and gas chromatography–mass spectrometry whereas the pathway for the production of IAA was elucidated by constructing *trp* mutants (Idris et al. 2007). The application of *B. amyloliquefaciens* SQR-9 increased the secretion of tryptophan three to fourfold from the roots of cucumber, which resulted in enhanced synthesis of IAA via IAN pathway and served as a major trait for PGP. This study highlighted the importance of plant–microbe chemical communication in the better growth of the plant (Liu et al. 2016). Zerrouk et al. (2020) explored the effect of a multi-plant hormone (auxin, phenylacetic acid, and cytokinin) producing bacterium *Bacillus toyonensis* Bt04 on the growth and stress-induced response in maize. The study underlined the role of auxin transport and signaling in the growth and development of roots and mitigation of aluminum stress. In a similar manner, Asari et al. (2017a, b) demonstrated the role of auxin and cytokinin in the modulation of root architecture of *Arabidopsis thaliana*, wherein the synthesis of auxins was found to be stimulated by supplementation of root exudates and tryptophan. *Bacillus altitudinis* WR10 produced IAA, which improved iron stress response in wheat by elevating the expression of iron sequestering protein ferritin (Sun et al. 2017). A plant growth-promoting rhizobacterium *P. polymyxa* CF05 isolated from *Cryptomeria fortunei* eliciting defence response in tomato was reported to produce IAA in media supplemented with tryptophan suggesting its synthesis via tryptophan-dependent pathway (Mei et al. 2014). Similarly, several strains of *P. polymyxa* reported as efficient PGPB and biocontrol agents are known to possess genes for the synthesis of IAA (Eastman et al. 2014).

Cytokinins (CKs), another class of phytohormones, are involved in cell proliferation, differentiation, and inhibition of premature leaf senescence. They are necessary for the proper development of roots in coordination with auxins (Schaller et al. 2015). Several *Bacillus* species are reported to promote growth and mitigate stress responses in plants by producing cytokinin. The growth, concentration of chlorophyll and carotenoids in the leaves and the endogenous hormones (auxin, cytokinin, ABA) of lettuce plants were positively influenced by the application of cytokinin-producing *B. subtilis* (Arkipova et al. 2005). An endophyte of cocoa plant *B. amyloliquefaciens* LKM-UL exhibiting antifungal activity against *Phytophthora palmivora* was reported to produce 1-naphthalene acetic acid (NAA), tryptamine, 3-indole propionic acid (IPA), indole-3-butyric acid (IBA), gibberellic acid (GA), trans-zeatin, and kinetin (Hamzah et al. 2017). The inoculation of *Platycladus orientalis* seedling

with cytokinin-producing *B. subtilis* led to the increase in shoot length, relative water content and leaf water potential of *P. orientalis* as well as conferred better resistance to drought conditions in comparison to the control (Liu et al. 2013). The inoculation of tomato seedling with cytokinin-producing *B. amyloliquefaciens* stimulated the plant growth by altering the growth parameters such as plant height, root length, shoot, and root dry weight, the proliferation of lateral roots, and yield up to 42 and 12.7% at 50 and 25% water holding capacity (irrigation stress parameters), respectively (Selvakumar et al. 2018).

Abscisic acid, Gibberellic acid, and Ethylene

Abscisic acid (ABA) plays role in seed germination, seed dormancy and seed development. It controls the growth and water content of the plant under stress conditions (Egamberdieva et al. 2017). The inoculation of ABA-producing *B. subtilis* enhanced the growth of *A. thaliana* by mitigating the cadmium-induced oxidative stress and photosynthetic inhibition via iron-regulated transporter *IRT1* (Xu et al. 2018). The endogenous level of plant hormones plays a pivotal role in the growth-promoting activity of rhizobacteria. The inoculation of *B. megaterium* in the tomato plant failed to stimulate the growth of tomato seedlings in ABA-deficient mutant plants due to the increasing level of ethylene and pathogenesis-related genes suggesting the importance of abscisic acid in plant growth (Porcel et al. 2014). The inoculation of *B. licheniformis* SAO3 conferred alkaline stress tolerance and regulated the accumulation of iron and sodium by increasing the ABA level in the Chrysanthemum plant (Zhou et al. 2017). The treatment of Chinese cabbage with *B. aryabhattai* H26-2 and *B. siamensis* H30-3 increased the plant growth and stress tolerance (heat and drought) by increasing leaf abscisic level and reducing the stomatal opening and wilting (Shin et al. 2019). Kim et al. (2017a, b) reported the salt stress tolerance ability of soybean crops owing to the production of ABA, GA, and phosphate solubilization ability of a soil isolate *B. amyloliquefaciens* H-2-5 (Kim et al. 2017a, b).

GA influences seed germination, stem elongation, flowering, and fruit settling in higher plants. GAs are reported to be produced by *B. pumilus*, *B. licheniformis*, *B. velezensis*, and *B. subtilis* (Goswami et al. 2016; Saxena et al. 2020). A gibberellin-producing isolate of Kimchi food, *Bacillus methylotrophicus* KE2, alleviated the germination of *Lactuca sativa*, *Cucumis melo*, *Glycine max*, and *Brassica juncea*. It also stimulated the growth and nutritional value of lettuce (Radhakrishnan and Lee 2016). The stimulation of stem elongation of alder seedlings on the application of two rhizobacteria, *B. pumilus* and *B. licheniformis* was attributed to the production of a mixture of GA₁, GA₃, GA₄, and GA₂₀ (Gutierrez-Maneroa et al. 2001). *B. pumilus* CJ-69, *Bacillus*

macroides CJ-29 and *B. cereus* MJ-1 producing nine different types of GA, identified using Gas chromatography-mass spectroscopy, promoted the growth of red pepper plug seedlings (Joo et al. 2004). Shahzad et al. (2016) studied the effect of GA produced by rice endophytic bacterium *B. amyloliquefaciens* RWL-1. The rice plants treated with RWL-1 exhibited higher growth owing to the upregulation of several forms of endogenous GA and SA in comparison to seedlings treated with exogenous GA.

Ethylene hormone modulates the growth of plants but the environmental change inducing ethylene production in plants can impede growth and cause senescence (Saxena et al. 2020). The PGPB that produces 1-aminocyclopropane-1-carboxylate (ACC) deaminase enzyme hydrolyzes a precursor of ethylene, ACC to ammonia and alpha-ketobutyrate (which can be utilized by PGPB for its growth) thus regulating the level of ethylene. Glick (2014) proposed a model describing the interplay of plant and bacterial IAA in mediating the level of ethylene in the plant under stress conditions. Briefly, the plant endogenous IAA and the IAA synthesized by ACC deaminase-producing PGPB stimulate plant cell proliferation, elongation, exudation (due to loosening of the plant cell wall), and transcription of plant ACC synthase. The plant ACC exuded along with other root exudate components can be cleaved by the ACC deaminase of PGPB, thereby lowering the endogenous or IAA-stimulated ACC and ethylene level. Such plants have longer roots and shoot as well as exhibit better resistance to ethylene stress. Gupta and Pandey (2019) described plant growth-promoting features and reduction of stress-induced ethylene in *Phaseolus vulgaris* plant by the action of ACC deaminase activity of *Paenibacillus* sp. Similarly, the three indigenous salt-tolerant *Bacillus* spp. (two *B. subtilis* and *Bacillus safensis*) promoted the growth of *Zea mays* by efficient colonization and modulation of ACC, ACC oxidase, and ACC synthase (enzymes involved in the synthesis of ethylene). It also altered the profile of defense-related enzymes, chlorophyll content, proline, and sugar content of maize (Misra and Chauhan 2020). The study carried out by Barnawal et al. (2013) defines the role of *B. subtilis* LDR-2 in reducing the level of ethylene under the condition of drought stress through the production of ACC deaminase enzyme. This led to the establishment of a favorable environment for the colonization of arbuscular mycorrhizal fungi (AMF) and enhanced rhizobial root nodulation resulting in amelioration of nutrient uptake and plant growth. Interestingly, the spore-forming bacteria associated with AMF, *B. aryabhattai* S210B15 enhanced the seed germination and salinity tolerance of maize seedling that was attributed to the ACC deaminase enzyme (Selvakumar et al. 2017). Genome studies illuminate the biosynthetic potential of the bacteria. Although several studies have reported the production of ACC deaminase

by *Bacillus* and *Paenibacillus* species, a recent investigation using the genome analysis of *Paenibacillus* ($n = 396$) and *Bacillus* species ($n = 5216$) revealed the absence of ACC deaminase gene (*acdS*) in these genomes (Ali et al. 2021). The contradiction in the phenotypic and genome analysis results is difficult to explain. The low-level ACC deaminase activity showed by *Bacillus* may represent non-specific activity of D-cysteine desulphydrase-like enzymes (Nascimento et al. 2014).

Several strains of *Bacillus*, known to produce more than one plant hormone are reported to modify the growth and stress responses in the plant. The application of *B. megaterium* A12 altered the concentration of ABA, SA, GA and ethylene leading to enhanced growth, photosynthetic ability and salinity stress in tomatoes (Akram et al. 2019). The bacterium *Bacillus tequilensis* SSB07 producing IAA, GA and ABA alleviated the shoot length, leaf area, biomass, and photosynthetic pigments of soybean under normal and heat stress conditions along with modulation of the endogenous hormones of the soybean plant (Kang et al. 2019). An isolate of soybean rhizosphere, *B. aryabhatai* SRB02 producing a high amount of IAA, CKs, GA, and ABA stimulated the shoot and root growth as well as attributed heat stress tolerance to soybean plant (Park et al. 2017).

Indirect mechanism

The indirect mechanism of plant growth promotion is generally executed outside the host plant. *Bacillus* and *Paenibacillus* are the two most widely exploited bacterial genera for the biological control of plant pathogens and pests. This is ascribed to their ability to produce diverse forms of antibiotics, hydrolytic enzymes and volatile organic compounds that have a direct inhibitory effect on other competitive/pathogenic microorganisms. Besides this, the competition for essential nutrients, habitat and induction of defense responses in plants (ISR) fall under the category of the indirect mechanism of PGP (Lo 1998).

Antibiosis There are numerous reports on the production of an array of antimicrobial metabolites by *Bacillus* sp. active against a wide range of bacterial and fungal plant pathogens and have been employed in commercial formulations (Table 1). These metabolites mainly fall under the category of non-ribosomal peptides (NRPs), ribosomal peptides, polypeptides (PKs), and volatile organic compounds based on their chemical nature and biosynthetic pathway. The PGP and biocontrol activity of *B. velezensis* RB.DS29 against a *Phytophthora* oomycete was attributed to the production

Table 1 Examples of Bacilli based commercial biocontrol formulations employed in agriculture

Product	Microbial agent	Target pathogen	Crop	Mode of application	Company
Biosubtilin	<i>B. subtilis</i>	<i>Fusarium</i> , <i>Macrophomina</i> , <i>Alternaria</i> , <i>Cercospora</i> , <i>Rhizoctonia</i> , <i>Erysiphae</i>	Cotton, Pulses, Paddy, Groundnut, Fruits, Vegetables and plantation crops	Seed treatment, soil application, foliar spray, seedling dipping	Biotech International Ltd. India
Kodiak	<i>B. subtilis</i>	<i>Rhizoctonia</i> spp., <i>Fusarium</i> spp.	Cotton	Seed dressing	Gustafson, Inc., Plano, TX USA
Ballad	<i>B. pumilus</i>	<i>Rhizoctonia</i> , <i>Puccinia</i> , <i>Erysiphae</i> , <i>Sclerotinia</i> , <i>Xanthomonas</i> , <i>Cercospora</i> , <i>Peronospora</i>	Sugar beet, cereals, oil plant	Ground and aerial spray	AgraQuest Inc. USA
Yield Shield	<i>B. pumilus</i>	<i>Rhizoctonia solani</i> , <i>Fusarium</i>	Soybean	Seed	Bayer CropScience USA
Companion	<i>B. subtilis</i>	<i>Colletotrichum</i> , <i>Rhizoctonia</i> , <i>Sclerotinia</i> , <i>Fusarium</i> , <i>Pythium</i> , <i>Phytophthora</i>	Cotton, bean, soybean, pea	Foliar spray, soil drench	Growth Products, Ltd. USA
Eco Guard	<i>B. licheniformis</i>	<i>Sclerotinia homoeocarpa</i> , <i>Colletotrichum graminicola</i> , <i>R. solani</i>	Golf Course greens, tees, fairways, ornamental turfgrass, lawns and sports turf	Foliar spray, soil drench	Novozymes, Biologicals, Inc. USA
RhizoVital 42	<i>B. amyloliquefaciens</i>	Soil borne pathogens	Potato, corn, strawberry, tomato, cucumber, ornamental plants	Drenching, spraying, Dipping	ABiTEP GmbH Germany
Sonata	<i>B. pumilus</i>	<i>Alternaria</i> , <i>Botrytis</i> , Powdery mildew fungi	Apple, onion, strawberry,	Ground, foliar spray	AgraQuest, Inc. USA, Mexico, Peru, Switzerland, Germany

of seven different antifungal compounds and hydrolytic enzymes viz. chitinases and beta-glucanases (Trinh et al. 2019). Non-ribosomal peptides and polyketides are a group of secondary metabolites synthesized by giant multi-domain non-ribosomal peptide synthetases. The members belonging to this class majorly include surfactin, iturins, fengycins, gramicidin, tyrocidine, bacitracin, difficidin, bacilysin, and bacillaene exhibiting antifungal and antibacterial activities (Caulier et al. 2019; Sumi et al. 2015). The heat-labile and ultraviolet resistant complex lipopeptides produced by *B. velezensis* BM21 inhibited the conidial germination and caused mycelial deformities in *F. graminearum*, a causative agent of corn stalk (Wang et al. 2020a, b). The antifungal metabolites belonging to iturin family viz. iturin, bacillomycin D, bacillomycin F, bacillomycin L, mycosubtilin, and mojavensin act on the fungal cell wall and are reported to be diversified across *B. subtilis* group (Dunlap et al. 2019). Iturins produced by *B. subtilis* displayed antifungal activity against *Aspergillus carbonarius* by interfering with multiple pathways such as alteration of osmotic pressure, energy metabolism, transportation, and oxidation–reduction processes of the fungus apart from affecting membrane permeability (Jiang et al. 2020). Similarly, studies on the effect of iturin produced by *B. subtilis* WL-2 on *P. infestans* using a scanning electron microscope and transmission electron microscope revealed the induction of oxidative stress and mitochondrial damage in addition to cell structure disruption (Wang et al. 2020a, b). It is noteworthy to mention that the antifungal activity of Bacillomycin D produced by *B. velezensis* HN-2 against *Colletotrichum gloeosporioides* was found to be superior in comparison to commercial fungicides prochloraz and mancozeb (Jin et al. 2020). Farzand et al. (2019) described a correlation between the presence of antifungal genes and the antifungal activity by screening 47 different Bacilli for the production of NRPs and PKs using molecular markers (surfactin, iturin, fengycin, bacilysin, bacillomycin, bacillibactin, bacillaene) and characterization using LC–MS analysis. A study on banyan endophyte, *B. subtilis* K1 for the production of the different antifungal compounds revealed the heterogeneity in lipopeptides of surfactin and fengycin family (Pathak et al. 2012, 2014). These metabolites exhibited excellent antifungal activity against 11 different fungal pathogens electing it as a biocontrol candidate. The antifungal activity of *B. velezensis* GH1-13, a potent PGPB and biocontrol agent against an array of phytopathogenic fungi was attributed to the production of surfactin (Park et al. 2019). Fengycins produced by strain *B. velezensis* FZB42 reduced the pathogenicity of *Fusarium graminearum* by altering its cell structure and permeability, conidial germination, DNA synthesis and reduction in the synthesis of toxic secondary metabolites (Hanif et al. 2019). The surfactins are known to retain their antifungal activity at high temperatures (up to 121 °C), and over a wide pH range

(5–9) (Sarwar et al. 2018). Similarly, the antibacterial compounds produced by *Paenibacillus peoriae* NRRL BD-62 endured the action of high temperature, organic solvents, hydrolytic enzymes and a wide pH range (Weid et al. 2003). The members of the genus *Bacillus* being genetically elastic can serve as a model for genetic modification of lipopeptides with improved qualities. Gao et al. (2017) genetically modified a lipopeptide non-producer *B. subtilis* pB2-L into a surfactin and plipastatin co-producer, which then exhibited strong antifungal activity against *F. oxysporum*. Besides displaying excellent antifungal activity, iturins are reported to manifest antibacterial activity against phytopathogenic bacteria *Xanthomonas campestris* and *Pectobacterium carotovorum* (Zerriouh et al. 2011). Difficidin, a polyketide and Bacilysin, the NRP exhibit antibacterial activity against *Xanthomonas oryzae* by downregulating the expression of genes encoding cell wall and protein synthesis, cell division and virulence (Wu et al. 2015). Several NRPs, PKs, and peptide metabolites synthesized by *Bacillus* (viz. bacillaene, difficidin, macrolactin, surfactin, fengycin, iturin, mojavensin, bacillomycin, mycosubtilin, etc.) and *Paenibacillus* species (viz. polymyxin, paenimacrolidin, paenilamicin, polypeptin, fusaricidin, etc.) are known to be active against several plants and human pathogens (Olishevskaya et al. 2019). The polymyxin P produced by *P. polymyxa* inhibits Gram-negative bacteria, *Erwinia amylovora* and *Erwinia carotovora* targeting its cell wall (Niu et al. 2013). The fusaricidins produced by *P. polymyxa* reduces chitin, ergosterol, NADP/NADPH, and ATP levels in *Fusarium moniliforme* in addition to disruption of the fungal cell wall, cell membrane, and cytoskeleton (Han et al. 2017).

Lytic enzymes The microbes inhabiting the rhizosphere secrete an array of hydrolytic enzymes that drive the process of mineralization and decomposition of the complex organic compounds present in the soil or secreted by plants (via root exudates) into accessible nutrient elements. Therefore, the microbes are considered as a pre-eminent character in the maintenance of soil structure and the affluent biogeochemical cycle. The microbial hydrolytic enzymes or antifungal proteins also play a promising role in the suppression of competing microbes and plant pathogens (Table 2). These proteins distort the fungal cell envelope, create pores, and inactivate the ribosomes (Hong and Meng 2003). Although the fungal cell wall composition varies with species, a typical fungal cell wall consists of chitin, glucans (β -1, 3 glucans) and glycoproteins (Kang et al. 2018). The enzymes, chitinases, glucanases, proteases, and lipases active against fungal pathogens are reported to be produced by *B. subtilis*, *B. velezensis*, *B. cereus*, *B. thuringiensis*, *B. licheniformis*, *B. pumilus*, etc. (Saxena et al. 2020). The purified enzyme, β -1,3-1,4-glucanase obtained from *B. velezensis* displayed antifungal activity against *Cryphonectria parasit-*

Table 2 The mechanism of action of a few species of *Bacillus* under in vivo conditions

Biocontrol agent	Source	Target pathogen	Mechanism	Crop	References
<i>B. velezensis</i> OEE1	Olive root	<i>Verticillium dahlia</i>	Antibiosis	Olive	Azabou et al. (2020)
<i>B. velezensis</i> BM21	Corn Rhizosphere	<i>F. graminearum</i>	Antibiosis	Corn	Wang et al. (2020a, b)
<i>B. safensis</i> B21	<i>Osmanthus fragrans</i>	<i>M. oryzae</i>	Antibiosis	Rice	Rong et al. (2020)
<i>B. amyloliquefaciens</i> VB7	Lilium rhizosphere	<i>B. cinerea</i>	Antibiosis, ISR	Lilium	Nakkeeran et al. (2020)
<i>Bacillus</i> spp.	-	<i>Phyllosticta citricarpa</i>	Antibiosis	<i>Citrus sinensis</i>	Kupper et al. (2020)
<i>Bacillus flexus</i> KLBMP 4941	<i>Limonium sinense</i> rhizosphere	-	ISR	<i>Limonium sinense</i>	Xiong et al. (2020a, b)
<i>B. toyonensis</i> COPE52	Blueberry endophyte	<i>B. cinerea</i>	ISR, antibiosis, lytic enzymes	Tomato	Rojas-Solis et al. (2020)
<i>B. subtilis</i> TE3	Wheat	<i>Bipolaris sorokiniana</i>	Antibiosis	Wheat	Rodríguez et al. (2019)
<i>B. velezensis</i>	Tomato crown	<i>V. dahlia</i>	Antibiosis, lytic enzymes, ISR	Tomato	Dhouib et al. (2019)
<i>B. mojavensis</i> PB-35	Soybean rhizosphere	<i>R. solani</i>	Antibiosis, ISR, lytic enzymes, nutrient acquisition	Soybean	Prajakta et al. (2019)
<i>B. licheniformis</i> GL174	Grapevine endophyte	<i>Phaeoacremonium aleophilum</i> , <i>Phaeoaniella</i> spp., <i>Botryosphaeria</i> spp., <i>B. cinerea</i> , <i>Sclerotinia sclerotiorum</i> and <i>Phytophthora infestans</i>	Antibiosis, lytic enzymes,	Grapevine	Nigris et al. (2018)
<i>B. amyloliquefaciens</i>	<i>Curcuma longa</i>	<i>Fusarium</i> spp., <i>R. solani</i> , <i>Colletotrichum capsici</i>	Antibiosis, phytohormone modulation, nutrient acquisition	<i>Capsicum annuum</i>	Passari et al. (2018)
<i>Bacillus</i> sp. SJ-5	Soybean rhizosphere	<i>R. solani</i> , <i>F. oxysporum</i>	ISR, antibiosis	Soybean	Jain et al. (2017)
<i>B. subtilis</i> AH18, <i>B. licheniformis</i> K11	Soil	<i>Phytophthora capsici</i>	Antibiosis	Red pepper	Lim and Kim (2010)
<i>B. amyloliquefaciens</i>	Vegetable crop rhizosphere	<i>Colletotrichum truncatum</i>	Antibiosis, ISR	Chilli	Gowtham et al. (2018)
<i>B. subtilis</i> BN1	-	<i>M. phaseolina</i>	Antibiosis, lytic enzymes,	<i>Pinus roxburghii</i>	Singh et al. (2008)

ica and *Cylindrocladium quinqueseptatum* by distorting the mycelial morphology (Xu et al. 2016). The lytic enzymes produced by *B. licheniformis* MH48 inhibited the foliar pathogen *Camellia oleifera* by 50% (Won et al. 2019). The antifungal activity of *B. pumilus* MSUA3 against *F. oxysporum*, *R. solani*, and *Fagopyrum esculentum* was ascribed to the co-production of chitinase and surfactin (Agarwal et al. 2017). The mass spectroscopic analysis of purified antifungal protein of *B. licheniformis* W10 revealed the potential of a serine protease in the biocontrol of fungal pathogens (Ji et al. 2020). Similarly, Guleria et al. (2016) evaluated the role of purified alkaline protease from *B. amyloliquefaciens* SP1 in biocontrol of *F. oxysporum* under in vitro conditions. Several *Paenibacillus* species also secrete lytic enzymes to curb the damage caused by pathogens. Yu et al. (2019) proposed the broad-spectrum antifungal activity of *Paeni-*

bacillus terrae NK3-4 against several fungal pathogens viz. *Magnaporthe oryzae*, *Exserohilum turcicum*, and *R. solani* and a bacterial pathogen *X. campestris* under field conditions that were attributed to secretion of β -1, 3 glucanases. The partially purified chitinase obtained from *Paenibacillus ehimensis* MA2012 inhibited the conidial germination of *C. gloeosporioides* under in vitro conditions (Seo et al. 2016). Also, the crude enzyme extract consisting of chitinase, cellulase, glucanase, and protease activities prepared from *P. ehimensis* KWN38, isolated from the pepper field, distorted the hyphal morphology of *R. solani*, *F. oxysporum* f.sp. *lycopersici*, and *Phytophthora capsici* (Naing et al. 2014). The extracellular proteases, chitinases, cellulases and pectinases secreted by *Paenibacillus* sp. B2 probably caused disorganization of hyphal content and cell death of *Phytophthora parasitica* and *F. oxysporum* (Budi et al. 2000).

Siderophores Iron is an essential micronutrient for most life forms including microbes and pathogens dwelling in the rhizosphere. In nature, iron exists in an oxidized ferric state (Fe^{3+}), which is insoluble at neutral and basic pH, hence reducing its bioavailability (Kramer et al. 2019). The microbes have evolved certain iron uptake systems or secrete certain molecules to acquire this limiting nutrient. Siderophores are the low molecular weight metabolites secreted by bacterial cells to sequester iron from the extracellular environment as well as confer a survival advantage over other competing organisms for colonization in their respective environmental niche (Table 2). The siderophore-producing bacteria belong to the genus *Pseudomonas*, *Bacillus*, *Paenibacillus*, *Rhizobium*, and *Agrobacterium*. Based on iron-binding moieties, the siderophores are majorly classified into carboxylates, hydroxamates, and catecholates (Ellermann and Arthur 2017). The rhizosphere inhabiting species of *Bacillus* are reported to produce catecholate and hydroxamate type siderophores. Under Fe-deficient conditions, *B. velezensis* FZB42 produces a catechol type siderophore, bacillibactin, which was determined using matrix-assisted laser desorption/ionization coupled to time of flight (MALDI-TOF) mass spectroscopy and genome analysis (Chowdhury et al. 2015a, b). Yu et al. (2011) detected the reduction in the biocontrol efficiency of *B. subtilis* CAS15 on wilt causing fungus *F. oxysporum* by supplementation of iron in pot culture assay signifying the role of bacillibactin siderophore produced by *B. subtilis* CAS15 in suppressing the fungus. *B. subtilis* CTS-G24 exhibiting biocontrol activity against *F. oxysporum* and *Macrophomina phaseolina* was reported to produce hydroxamate type of siderophore (Patil et al. 2014). Several strains of *Paenibacillus* established as PGPB and biocontrol agents are recognized to produce siderophores. The deficiency of iron in the plant results in interveinal chlorosis affecting the growth of the plant. The two siderophore-secreting bacteria *Paenibacillus illinoisensis* and *Bacillus* sp. isolated from the rhizosphere of peanut enhanced the chlorophyll and iron content in leaves along with improvement of other PGP characteristics such as root activity, quality of kernels, plant biomass and NPK content of peanut in comparison to the controls under pot and field trials (Liu et al. 2017). Numerous reports on genome analysis of *Bacillus* and *Paenibacillus* sp. reveal the presence of genes that contribute to the production of various types of siderophores (Bhattacharyya et al. 2017; Eastman et al. 2014; Kim et al. 2017a, b; Niazi et al. 2014; Seo et al. 2016).

Volatile organic compounds The microbes inhabiting the rhizosphere secrete certain chemical messengers dialing the gene expression in the interacting partners to establish a mutualistic or symbiotic relationship. Volatile organic compounds (VOCs) are small, low molecular weight lipophilic entities with a low boiling point and high vapor pressure

that are secreted by PGPB as long-distance signaling molecules mediating plant development and physiology. Also, they are known to serve as a nutrient source, induce resistance in plants, and suppress plant colonization by pathogens (Schulz-Bohm et al. 2017). The efficient PGPBs *B. subtilis* GB03, and *B. amyloliquefaciens* IN937a are reported to exhibit 2, 3-butanediol and acetoin mediating plant–microbe interaction (Ryu et al. 2003). The VOCs benzaldehyde and diacetyl secreted by three different strains of *B. velezensis* amidst 15 different VOCs were found to be active against *Botrytis cinerea*, *Monilinia fructicola*, *Monilinia laxa*, *Penicillium italicum*, *Penicillium digitatum*, and *Penicillium expansum* under in vitro conditions and on fresh fruit (Calvo et al. 2020). The *B. subtilis* CF-3 inhibited the germination of *C. gloeosporioides* spores, disrupted hyphal morphology, and abridged the cell membrane integrity through the production of 2,4-di-tert-butylphenol along with the induction of defense response in litchi (Zhao et al. 2019). The head-space solid-phase microextraction/gas chromatography–mass spectrometry led to the identification of eleven VOCs displaying antibacterial activity against *Clavibacter michiganensis* subsp. *sepedonicus*, the causative agent of bacterial ring rot of potato (Rajer et al. 2017). The role of dimethyl disulfide produced by *Bacillus* sp. B55 in the sulfur acquisition and metabolism mediated growth promotion of *Nicotiana attenuata* has been reported (Meldau et al. 2013). In addition to antifungal activity against a wide range of fungal pathogens, VOCs of *B. amyloliquefaciens* are demonstrated to induce resistance mechanisms and promote the growth of *A. thaliana* (Asari et al. 2016). The incorporation of root exudates in culture media is known to enhance plant growth even at a low density of PGPB. For instance, Raza et al. (2015) showed that the incorporation of root exudates and organic fertilizer in the agar medium enhanced the antifungal activity of VOCs released by *P. polymyxa* WR-2. Hydrogen cyanide, a VOC produced by *B. megaterium* CtST3.5 inhibited the growth of *Agrobacterium tumefaciens*, and a nematode, *Meloidogyne incognita* under in vitro conditions (El-Rahman et al. 2019). Rybakova et al. (2017) described the aerial antagonistic communication between *P. polymyxa* Sb3-1 and *Verticillium longisporum* via 40 different VOCs, which inhibited the fungus and also enhanced the growth of oilseed rape. Certain species of *Paenibacillus* are known to produce VOC (mainly 2,3-butanediol and acetoin) inducing the resistance and growth in experimental plants (Lee et al. 2012). The VOCs produced by *P. ehimensis* KWN38 inhibited the growth of phytopathogens *R. solani*, *F. oxysporum* f.sp. *lycopersici* and *P. capsici* (Naing et al. 2014). A recent study described the inhibition of conidial structure and morphological changes in the *Alternaria solani* through the VOCs secreted by a biocontrol agent, *B. subtilis* (Zhang et al. 2020).

Induced systemic resistance Certain bacteria activate the defense responses (ISR) in the plants before infection by pathogens, consequently reducing the incidences or severity of the disease. This activation is accompanied by the secretion of antimicrobial compounds viz. coumarin and benzoxazinoids, which incentivizes the colonization of strains that induce systemic resistance, thus demonstrating the manipulation of plant defense responses by establishing a stable microbial community proffering shield over generations (Trivedi et al. 2020). The genera well-characterized and documented for stimulation of ISR in plants include *Pseudomonas* and *Bacillus* sp. (Table 2) (Mustafa et al. 2019). Kloepper et al. (2004) had illustrated the description and mechanism of ISR by several reported strains of *Bacillus*. The antimicrobial lipopeptides secreted by *Bacillus* are known to be the elicitors of ISR in plants. For instance, the lipoxygenase pathway in infected leaves of tomato was triggered upon treatment with the surfactin and fengycin metabolites produced by multiple strains of *Bacillus* (Ongena et al. 2007). The treatment of lipopeptide extracts obtained from *B. amyloliquefaciens* on roots of *Arabidopsis* elicited the jasmonic acid-dependent host response for biocontrol of fungal pathogens (Asari et al. 2017a, b). Further, the microbial formulation based on *B. amyloliquefaciens* was shown to induce the defense response in the tomato plant in a dose-dependent manner (Dimopoulou et al. 2019). The estimation of defense-related enzymes and marker genes encoding phytohormones were useful in characterizing the role of antagonistic *B. amyloliquefaciens* CM-2 and T-5 in the induction of defense responses in tomato (Tan et al. 2013). Generally, the ISR by PGPB induces jasmonic acid (JA)/ethylene (ET) in plants, however, few *Bacillus* sp. are reported to induce both JA/ET and salicylic acid (SA) signaling pathways. The bacterium *B. cereus* AR156 has been shown to elicit ISR in *A. thaliana* by modulation of the JA pathway and SA pathway through the transcriptional factors WRKY11 and WRKY70, respectively (Jiang et al. 2016a, b). The extracellular polysaccharide of PGPB strain AR156 sensed as microbe-associated molecular patterns (MAMPs) by *Arabidopsis* led to the induction of defense-related enzymes, callose deposition and H₂O₂ accumulation (Jiang et al. 2016a, b). Wu et al. (2018) demonstrated the synergistic action of extracellular metabolites, antimicrobial compounds, VOCs and exopolysaccharides in ISR against *Pseudomonas syringae* and *B. cinerea* by operating both the signaling pathways. Conversely, an application of cyclic depsipeptide, produced by *P. polymyxa* E681, on *A. thaliana* upregulated the pathogenesis-related genes in comparison to control implying the involvement of the SA signaling pathway in ISR (Lee et al. 2013). *P. polymyxa* BFKC01 stimulated defense response and activation of the phenolic compound biosynthetic pathway in *Arabidopsis*. This increased the abundance of phenolic compounds in root exudates inoculated with the strain

facilitating the acquisition of iron under alkaline conditions. This study portrays the role of strain BFKC01 in the elicitation of ISR as well as sequestration of Fe under limiting conditions (Zhou et al. 2016).

Competition The microbes inhabiting the rhizosphere are often under famine conditions interrupted by the short events of nutrient richness (feast) following the secretion of root exudates. To thrive in the rhizosphere, the microbes need to compete with their neighbors for habitat and resources. If one organism inhibits the other through resource consumption, then it is considered passive competition, whereas the direct and active confrontation of two organisms damaging one another is termed active competition (Bauer et al. 2018).

The rhizosphere being a rich source of nutrients attracts a vast diversity of beneficial as well as pathogenic microorganisms. The successful colonization of the bacteria on the surface of the root is primary and a crucial step in executing the protective role of PGPB against soil-borne pathogens. The process of root colonization by PGPB depends on the attributes of both, the plant and the bacterium and is influenced by numerous biotic and abiotic factors. The chemotactic movement of the bacteria towards the secreted root exudates facilitated by active motility illustrates the events involved in root colonization. For instance, the organic acids exudated by the root of the banana influenced the recruitment and colonization of *B. amyloliquefaciens* NJN-6 by mediating the chemotactic response and biofilm formation (Yuan et al. 2015). Similarly, the organic acids, amino acids and sugars of maize root exudates induced chemotactic response, swarming motility, biofilm formation in *B. velezensis* S3-1 demonstrating the interaction between plant and *Bacillus*, interceding successful colonization (Jin et al. 2019). Extensive research on the use of root colonizing *Bacillus* species for PGP and suppression of pathogens has been carried out. *In planta* *B. amyloliquefaciens* completely inhibited the colonization of *Ralstonia solanacearum* on tomato roots highlighting the process of competitive exclusion (Tan et al. 2016). The disruption of gene *abrB*, which is a negative regulator of chemotaxis and biofilm formation, significantly improved the root colonizing and biocontrol activity of *B. amyloliquefaciens* SQR9 (Weng et al. 2013). Moreover, the role of proteins involved in biocontrol, detoxification, biofilm formation, cell motility and chemotaxis, transport, and degradation of plant polysaccharides in the root colonization process is well documented in *B. amyloliquefaciens* SQR9 (Qiu et al. 2014). The quorum-sensing molecules secreted in an environment by certain beneficial and pathogenic bacteria to sense the quality of an ecological niche and act as an inducer molecule for the plant to secrete defensive secondary metabolites for disrupting the quorum-sensing signals of pathogenic bacteria (Hartmann et al. 2014). Recently, Xiong et al. (2020a, b) highlighted the role of a quorum-sensing

signal molecule “autoinducer-2” encoded by *luxS* gene in regulating the process of biofilm formation, motility and root colonization ability of strain SQR9. Bais et al. (2004) demonstrated the root colonization of *B. subtilis* 6051 through surfactin production and biofilm formation with subsequent biocontrol of a bacterial pathogen *P. syringae*. The process of priming and colonization of rhizoplane, cortex and xylem vessels of eggplant with *B. cereus* strain XB177R played a crucial role in the suppression of wilt causing *R. solanacearum* (Achari and Ramesh 2019). The isolate *B. subtilis* with antifungal activity successfully colonized the roots of cotton over a wilt causing fungus, *F. oxysporum* (Zhang et al. 1996). Over and above this, the lipopeptides secreted by *Bacillus* to control pathogens and trigger defense responses in plants assist in the process of root colonization. Aleti et al. (2016) defined the role of surfactins produced by a fungal antagonist *B. atrophaeus* 176 s in facilitating biofilm formation and root colonization in the gnotobiotic environment. The dynamics of *B. amyloliquefaciens* antifungal metabolites i.e., iturin, fengycin and surfactin in the development of biofilm on the roots was assessed using MALDI-MSI imaging (Debois et al. 2014). A potent biocontrol agent *P. polymyxa* SQR-21 modulates the root exudates of watermelon to reduce the germination of *F. oxysporum* conidia (Ling et al. 2011). The manipulation of root exudates to control the pathogen proliferation can be considered as a mutualistic interaction between the PGPB and plant to inhibit the colonization of competing microbe or pathogen. The struggle for nutrients is generally considered to be the most extensive form of competition contributing to an indispensable role in disease suppression (Lo 1998). The phenomenon of secreting extracellular enzymes, chelating molecules i.e., siderophores, organic acids discussed earlier serve as the tools to sequester nutrients from the environment.

Bacillus as stress regulator

The global climate alterations accelerate the concurrence of various biotic (pathogens) and abiotic (temperature, salinity, drought, and waterlogging) stress on the growth and productivity of the crop plants affecting the food quality as well as imposing a threat to global food security. The application of PGPB offers an effective, eco-friendly and sustainable agricultural management approach that under stress conditions modulates the local and systemic resistance mechanism in the host plant (Meena et al. 2017). The Gram-positive spore-forming Bacilli prove to be a valuable resource due to their inherent ability to resist harsh environmental conditions.

The conditions of drought and salinity cause osmotic stress and oxidative damage to the plants (Nxele et al. 2017). The application of *B. subtilis* GOT9 increased

the drought and salt tolerance in *A. thaliana* and *Brassica campestris* by inducing the drought and stress tolerance genes as well as the lateral root growth for enhanced uptake of water and nutrients (Woo et al. 2020). An ACC deaminase-producing and PGP bacterium, *B. licheniformis* HSW-16 protected the wheat plants from salinity stress by reducing the accumulation of sodium and potassium ions, producing exopolysaccharides to sequester the excess sodium ions and increased accumulation of osmolytes such as sugar and protein (Singh and Jha 2016). Recently, Gowtham et al. (2020) reported the induction of drought tolerance by an ACC deaminase-producing bacterium, *B. subtilis* SF 48, which caused an increase in superoxide dismutase activity, ascorbate peroxidase activity, proline content and reduction in malondialdehyde; conferring protection to the plants against osmotic stress and oxidative damage caused during drought conditions. Wang et al. (2019) emphasized the importance of the biofilm-forming ability of *B. amyloliquefaciens* 54; abscisic acid pathway in regulating stomatal closure, defence response, elevated antioxidant enzymes and stress responsive genes in conferring drought tolerance to tomato. Likewise, *B. pumilus* modulated antioxidants accumulation, growth, metabolism and related protein expression of *Glycyrrhiza uralensis* Fisch., resulting in its growth improvement upon exposure to drought conditions (Xie et al. 2019).

The issue of global warming has imposed temperature stress on crops. Increased temperature affects plant growth, development and productivity, photosynthesis, respiration, membrane permeability, homeostasis, and hormonal signaling (Bita and Gerats 2013). The production of exopolysaccharide and ACC deaminase by a thermotolerant *B. cereus* mitigated the adverse effect of heat and promoted the growth by improving the physiological and biochemical characteristics of the tomato plant (Mukhtar et al. 2020). *B. cereus* SA1 producing gibberellin, IAA and organic acids enhanced the biomass, chlorophyll content, antioxidant enzymes, amino acid content, and potassium gradient in soybean under thermal stress (Khan et al. 2020a, b). The application of the same strain, i.e., SA1 along with humic acid reduced the damage caused by heat stress in tomato seedling (Khan et al. 2020a, b). The genome analysis of *Bacillus* spp. and *B. velezensis* revealed the presence of genes encoding functions associated with cold stress response, osmoregulation, membrane transport, and signal transduction and also established the role of phytohormones in improving plant growth under cold stress (Zubair et al. 2019). The exposure of wheat seedling to different stress conditions, i.e., heat, cold and drought after treatment with *B. velezensis* 5113 revealed the intersection of proteins involved in conferring tolerance to various stress conditions (Abd El-Daim et al. 2019).

Significance of conducting in vivo biocontrol trials and elucidation of the mode of action

Evaluation of the antagonistic or plant growth-promoting activities of bacteria under in vitro conditions is the most preferable strategy for the selection of bacterial agents. Over hundreds of strains with no in vitro activities are actually discarded before *in planta* tests. A recently published article with the support of a case study showed that the strains with poor in vitro antagonistic activity could display better efficacy *in planta* over the good antagonistic bacteria. This may be due to the inability of the selected bacteria to colonize roots, prevailing dynamic biotic components and the soil properties. The authors finally suggest that the in vitro and *in planta* combinatorial studies may be a more effective approach for the selection of an effective biocontrol agent (Manzoni et al. 2019; Meldau et al. 2012). In addition, the exploration of the mechanism governing the beneficial effect in situ or in the field would harness the true potential of the microorganism. Several studies have been conducted to assess the mechanism of PGP or biocontrol in nature or under field conditions. To illustrate, Liu et al. (2021) with the help of transcriptomics studies demonstrated that pepper stimulates chemotaxis, biofilm formation, quorum sensing, polymyxin biosynthesis genes in the strain SC2, whereas strain SC2 induces systemic resistance in pepper by upregulating the expression of early defense signaling genes. Similarly, the tripartite interaction studies carried out between PGPB *B. subtilis* MBI 600, the pathogen *Botrytis cinerea* and the host plant cucumber revealed the induction of immunity genes in cucumber as well as induction of detoxification transporters (ABC and MFS transporters) in *B. cinerea* upon *B. subtilis* MBI 600 treatment (Samaras et al. 2021). *B. subtilis* RH5 could effectively promote plant growth and inhibit the growth of *Rhizoctonia solani* through the production of defense-related antioxidant enzymes such as polyphenol oxidase (PPO), phenylalanine lysase (PAL) and peroxidase (Jamali et al. 2020). The priming of rape oilseed with *B. amyloliquefaciens* 5113 led to the induction of systemic resistance against *B. cinerea* via JA dependent *PDF 1.2* expression (Sarosh et al. 2009). In similar lines, the combination of confocal microscopy, mass spectroscopy and expression studies using mutants revealed that the nonribosomally synthesized secondary metabolites produced by FZB42 in the lettuce rhizosphere induced systemic resistance in plants against *R. solani* via JA dependent *PDF 1.2* expression (Chowdhury et al. 2015a, b).

Conclusion

The rising population and diminishing arable land have built a challenge for researchers to develop alternatives tools to replace the detrimental chemical fertilizers and pesticides to satisfy global hunger. Besides, global warming has paved the evolution of extreme climate, further impacting the vision of sustainable agriculture development and management. The microbial communities inhabiting the rhizosphere have functioned as natural fertilizers, pesticides, and stimulators long before the practice of microbial inoculants came into existence. Therefore, the “Biorevolution” can be foreseen as a promising approach to replenish agricultural practices and improve productivity by employing microbes to promote plant growth and impart protection against diseases as well as pests. The members of the genus *Bacillus* persisting as the zymogenous flora and *Paenibacillus* in the soil have been isolated from varied sources and developed as biofertilizer, biopesticide, phyto-stimulant, and rhizomediator. These applications of Bacilli are attributed to their ability to produce resistant spores enabling them to endure harsh environmental factors for an extended period, produce an array of antimicrobial peptides to compete and conquest over competing microbes, display genetic and metabolic diversity to exploit and thrive on a wide range of nutrients and habitats. To harness an effective biofertilizer and a biocontrol agent, the mechanism of action needs to be dissected. The mode of action of all agricultural bio-inoculants shares homology and its impact on the host is the confluence of more than one action. For instance, PGPB can employ either direct or indirect or a combination of both the mechanism to portray its beneficial effect. With the advent of high throughput technologies, the study of the ecology and tripartite interaction between the host, PGPB and the pathogen can be easily elucidated. It can simplify the process of selection and construction of efficient bio-inoculants.

Numerous reports describe the in vitro biocontrol potential and PGP traits of *Bacillus* and *Paenibacillus* species under laboratory conditions, however, the actual number logarithmically reduces when practiced under field conditions. The factors responsible for such discrepancies include phase variation (Broek et al. 2005), the effect of environmental factors on microbial metabolite synthesis and regulation, the concentration and effectiveness of metabolites in the soil, the presence of competing microbes and the development of resistance to antagonists. The suggestible approach to overcome these shortcomings is to rail the laboratory experiments with the field studies. Also, the tripartite interaction studies comprising the host plant, PGPB, and the pathogens have significantly contributed to our understanding of the multifarious interactions, which will held in developing better strategies for improving crop yield. Moreover, the use of

microbial consortium/mixture with intersecting avalanche of the mechanisms may help in containing the development of resistance.

Author contribution statement RS performed a literature survey and framed the manuscript. HRK critically reviewed and edited the final manuscript. Both the authors have approved the final version of the manuscript.

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