



An Overview of *Bacillus* Species in Agriculture for Growth Promotion, Biocontrol and Dry Tolerance

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Abstract

Each year, millions of tons of chemicals and pesticides are applied to agricultural soils to support food production. However, this intensive use of chemical inputs depletes soil vitality, reduces moisture retention capacity, and raises significant environmental and health concerns. To mitigate these negative impacts, researchers worldwide are seeking alternative agricultural solutions that reduce reliance on chemical inputs. One promising approach is the application of rhizobacteria, which can restore soil health, control plant pathogens, and promote plant growth through various mechanisms. Notably, different *Bacillus* rhizobacteria species play key roles by producing hormones, enzymes, antibiotics, and siderophores that enhance plant growth and protect against pests. Additionally, *Bacillus* spp. form beneficial interactions with crops, boosting plant tolerance to environmental stresses. Despite their potential, the agricultural applications of these bacteria remain underexplored, with only a limited number of species currently in direct use, leaving much of their potential untapped. A deeper understanding of *Bacillus* spp. biology is essential to developing products that can drive sustainable biotechnological innovations in agriculture and industry. This article reviews the role of *Bacillus* spp. and the effective utilization of plant growth-promoting (PGP) strains in agricultural systems. It also highlights critical, yet understudied, aspects of rhizobacteria that should be prioritized in future research.

Keywords: *Bacillus*; Biocontrol; Biopesticide; Plant growth-promotion; Siderophores; Mineralization; Soil microbes

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1. Introduction

Bacillus spp. are non-pathogenic, gram-positive, soil-dwelling bacteria that commonly colonize the plant rhizosphere.^[1] These bacteria possess a vast array of molecular and genetic tools, making them highly adaptable and amenable to in vitro modification and research. They are widely used in various

industrial applications, such as food fermentation, hydrolytic enzyme production, sustainable agriculture, and as probiotics.^[2-5] To thrive in dynamic environments, *Bacillus* spp. secrete enzymes capable of degrading a wide range of substrates.^[1] Most volatile organic compounds (VOCs) produced by *Bacillus* spp. contribute to plant defense against pathogens.^[6] These bacteria form resilient spores that withstand abiotic stresses, including salinity, temperature fluctuations, drought, and nutrient deficiency.^[7] Additionally, they serve as versatile probiotics with strong inhibitory effects on harmful bacteria and fungi, while enhancing nutrient uptake.^[8]

In agriculture, various *Bacillus* species, such as *B. polymyxa*, *B. circulans*, *B. subtilis*, *B. pumilus*, *B. megaterium*, *B. coagulans*, *B. chitinolyticus*, *B. velezensis*, and *B. fusiformis*, are recognized as efficient biofertilizers and biocontrol agents.^[9,10] Research shows that applying *Bacillus* to compost can significantly increase its humus and carbon content, improving soil quality, enhancing phosphate (P)

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availability to plants, controlling phytopathogens, and promoting crop growth.^[11,12] Furthermore, *Bacillus* spp. contribute to reducing metal toxicity in soil by participating in bioremediation processes that mitigate environmental pollution.^[13] Strains isolated from solar salterns have demonstrated potential in biosorption-based heavy metal reclamation, including chromium (Cr), lead (Pb), and copper (Cu).^[14] *Bacillus subtilis* can persist in metal-rich environments and protect plants through mechanisms such as active removal, biotransformation, exclusion, precipitation, bioaccumulation, extrusion, and biosorption.^[15]

A wide range of microorganisms, including nematodes, bacteria, viruses, fungi, and protozoa, can cause plant diseases, leading to yield losses of 20-40% in agriculture.^[16,17] Although various methods are employed to reduce plant diseases, soil-borne pathogens often remain resistant, limiting the efficacy of these approaches.^[18] The increased use of synthetic pesticides, which negatively affect ecosystems and the environment, further threatens agricultural sustainability.^[16] Biocontrol agents, particularly *Bacillus* spp., are actively studied for their antagonistic action against plant diseases, offering a promising alternative to chemical pesticides.^[19] Advances in “Omic” technologies (genomics, transcriptomics, proteomics, and metabolomics) have enabled the investigation of gene clusters responsible for bioactive metabolite production, with particular interest in toxins and host-specific *Bt* proteins.^[13]

This review explores the mechanisms by which *Bacillus* spp. promote plant growth, control disease, and enhance phosphate availability. It serves as a valuable reference for researchers worldwide interested in the agricultural applications of *Bacillus* species.

2. *Bacillus* species in plant growth-promotion

Beneficial microbes known as plant growth-promoting rhizobacteria (PGPR) have been extensively studied for their significant impact on plant growth and development.^[20-23] These PGPRs enhance plant defenses against various diseases and are closely associated with the rhizosphere. Increasing evidence suggests that root-colonizing bacteria can influence

plant growth by producing phytohormones such as cytokinins, gibberellins, and auxins. In particular, *Bacillus* species are known to produce metabolites like auxins, cytokinins, and siderophores.^[22,24] While plants produce endogenous cytokinins, exogenous cytokinins can accelerate growth processes.^[25] Cytokinins stimulate protease and amylase activity, as well as the production of auxins like IAA (3-indole acetic acid), one of the most prominent auxins. IAA plays a key role in apical domain formation, cell proliferation, vascular tissue differentiation, and organ development.^[26,27]

Moreover, *Bacillus* spp. act as a barrier against harmful microorganisms by inducing plant defense mechanisms. For instance, *Bacillus licheniformis* synthesizes phytohormones that solubilize phosphate and fix atmospheric nitrogen, promoting plant growth.^[28] Due to its ability to solubilize fixed phosphate and fix nitrogen, *Bacillus megaterium* has been proposed as a promising biofertilizer.^[29] *Bacillus* spp. enhance crop development and productivity through phytohormone synthesis, mitigation of abiotic stress, and improved nutrient availability. Additionally, antimicrobial peptides produced by *Bacillus* species hold promise for therapeutic applications, exhibiting rapid, broad-spectrum pathogen-killing properties. As microbial resistance to common antibiotics rises, there is a growing need for antimicrobial peptides to prevent and treat bacterial infections, offering both protection and ecological sustainability.^[30]

Phosphorus is essential for various physiological processes in plants, including photosynthesis and cell proliferation.^[31] While phosphate fertilizers are commonly used, they quickly become immobilized in the soil, rendering them inaccessible to plants.^[32] Overuse of chemical fertilizers also risks environmental contamination.^[33] However, employing specific *Bacillus* strains with the ability to solubilize insoluble phosphate can reduce the need for chemical fertilizers (Fig. 1).

3. *Bacillus* species as a phosphate solubilizer

In order to solubilize bound phosphate, microbes release organic acids that lower the pH of the surrounding environment. This acidification facilitates the chelation of metal ions, allowing microbes to compete with phosphate for adsorption sites. As a result, phosphate is released by forming soluble complexes with metal ions. At low pH, the most soluble form of phosphate is H_2PO_4^- (the monovalent anion); however, at higher pH levels, this monovalent form can convert into less soluble divalent and trivalent forms. The production of organic acids by microbes aids in converting these divalent and trivalent ions into more soluble monovalent forms by reducing the pH. Numerous studies indicate that phosphate-solubilizing bacteria, including various *Bacillus* species, release organic acids such as oxalic acid, gluconic acid, and tartaric acid. These acids contribute to soil acidification and enhance phosphate solubilization.^[34] Several mechanisms are involved in the ability of *Bacillus* species to solubilize phosphate sources (Fig. 2).

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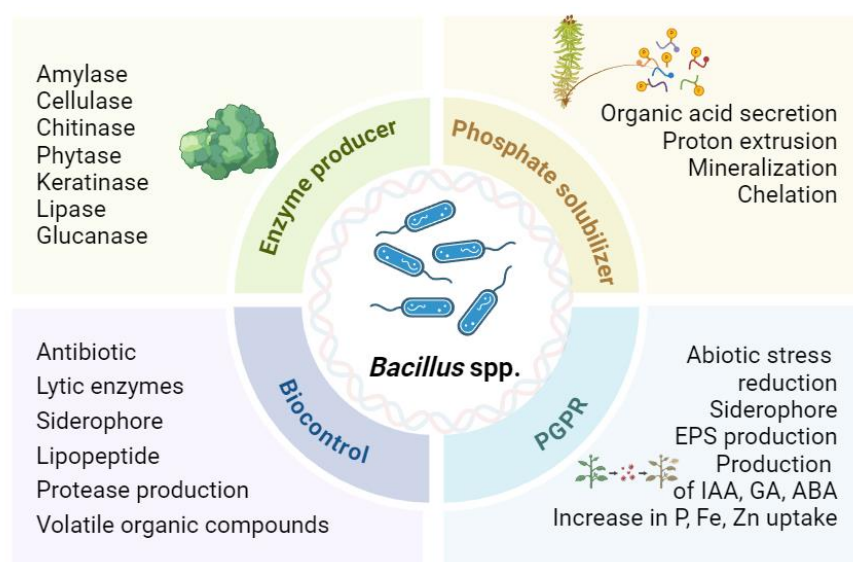


Fig. 1 Application of *Bacillus* species and their mode of action for plant growth. Those bacteria can be utilized as biofertilizers, biopesticides, and bio-insecticides, with some species also being suitable for both applications.

4 Mechanism of phosphate solubilization

4.1 Non-living phosphate mobilization mechanisms

Production of organic acids: The generation of organic acids is the primary mechanism by which inorganic phosphate is solubilized. *Bacillus* spp., as phosphate-solubilizing microorganisms, produce a range of acids, including oxalic, gluconic, formic, citric, propionic, lactic, succinic, glycolic, acetic, and 2-ketogluconic acids, as well as pyruvic, malic, fumaric, and alpha-ketoglutaric acids.^[35-37] These organic acids solubilize rock phosphate by lowering the pH of the medium, a process observed by multiple studies, as *Bacillus* spp. tend

to thrive in liquid media where organic acids accumulate.^[38-40] Phosphate-solubilizing microbes, including *Bacillus* spp., produce several types of acids in liquid environments, such as tricarboxylic hydroxy acids (e.g., citric acid), monocarboxylic hydroxyl acids (e.g., gluconic acid), and dicarboxylic hydroxy acids (e.g., malic acid). Among these, gluconic acid is frequently identified as the predominant acid used by bacteria for phosphate mobilization.^[36,41]

Chelation creation: Chelating substances play a crucial role in phosphate solubilization. Carboxyl and hydroxyl acids, such as humic acid, fulvic acid, and 2-ketogluconic acid, act

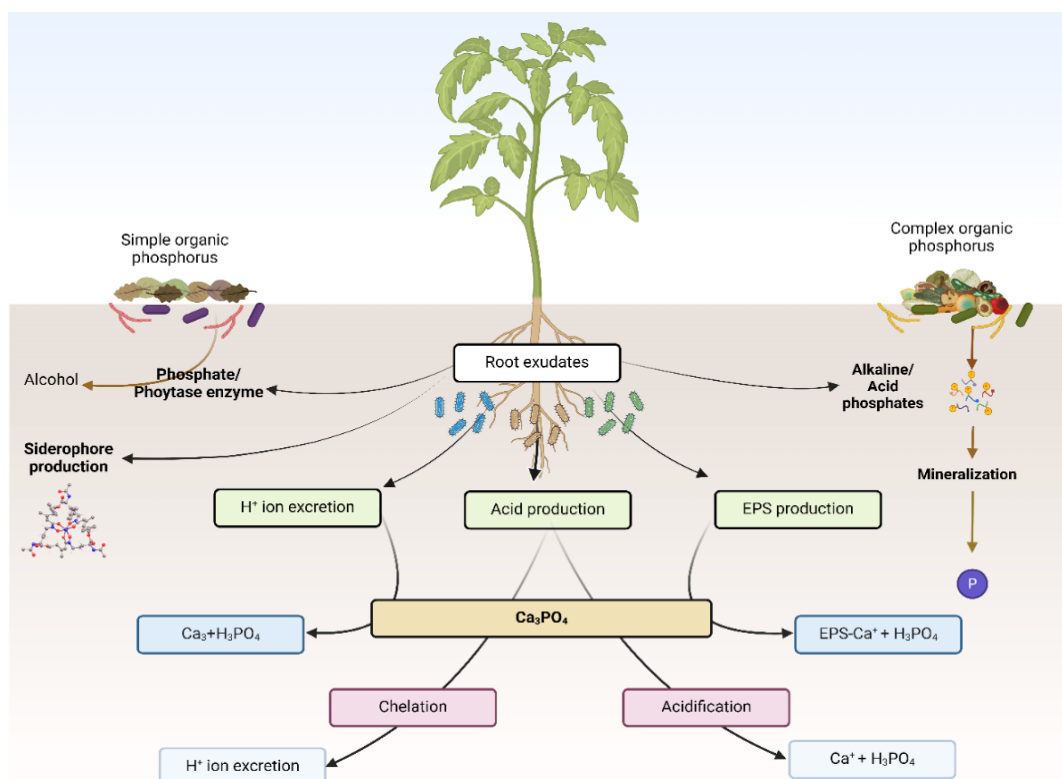


Fig. 2 Overall mechanisms of organic and inorganic phosphate mobilization by dint of *Bacillus* spp.

as effective chelators of cations like calcium, aluminum, and iron, transforming phosphate into soluble forms.^[42] These acids can efficiently solubilize inorganic phosphate complexed with aluminum, calcium, and iron.^[43] Microorganisms release fulvic and humic acids during the decomposition of plant material.^[44] The ability of *Bacillus* species to secrete 2-ketogluconic acid has been well-documented.^[36,44,45] while *Bacillus megaterium* and *Bacillus aryabhattai* are known to produce humic acid.^[46,47] Additionally, *Bacillus acidiceler* generates fulvic acid, a potent chelator of calcium.

Proton extrusion: Phosphate solubilization can also occur without the production of organic acids through the acidification of the medium due to H⁺ excretion. This process is driven by the release of anions in conjunction with organic acids, respiratory production of H₂CO₃, and the absorption of NH₄⁺, all contributing to H⁺ excretion.^[48,49] The nitrogen availability in the environment significantly influences proton release, with NH₄⁺ being more effective than NO₃⁻ in lowering pH.^[50] Studies suggest that *Bacillus* species supplied with NH₄⁺-N in their nutrient medium exhibit an increased capacity for proton extrusion, further enhancing phosphate solubilization.^[51]

Exopolysaccharide production: Exopolysaccharides (EPS) produced by microorganisms are thought to indirectly influence phosphate solubilization.^[52] Microbial EPS, often released under stress, can bind with various metals in the soil, affecting the solubility of metal phosphates.^[53] For instance, the solubilization of tricalcium phosphate has been observed in the presence of microbial EPS along with organic acid anions.^[54] A notable correlation exists between EPS content and the rate of phosphate solubilization, although further research is needed to fully understand their role in soil processes. Several *Bacillus* species, including *Bacillus licheniformis*, *Bacillus amyloliquefaciens*,^[55] *Bacillus cereus*,^[56] and *Bacillus thuringiensis*,^[57] have been shown to produce EPS.^[58–60]

Siderophore production: Microorganisms with a high affinity for iron chelation release compounds known as siderophores.^[61] These siderophores – whether hydroxamate, carboxylate, or catecholate types – contain six oxygen electron donor groups, allowing them to chelate metal ions such as Cu²⁺, Pb²⁺, Zn²⁺, and Al³⁺.^[62] Various *Bacillus* species, including *Bacillus subtilis*,^[63] *Bacillus tequilensis*,^[64] *Bacillus cereus*,^[65] *Bacillus velezensis*,^[66] *Bacillus licheniformis*,^[67] and *Bacillus megaterium*,^[68] are capable of producing siderophores. While siderophores contribute to the dissolution of iron phosphates in soil, the direct link between siderophore production and phosphate solubilization remains unclear and warrants further investigation.

Mineralization: The processes of immobilization and mineralization of soil organic phosphorus (P) are essential to the phosphorus cycle in agricultural soils.^[42] Mineralization involves microorganisms breaking down phosphorus-rich plant compounds, such as nucleic acids, phospholipids,

polyphosphates, and phytic acid, thereby transforming insoluble organic phosphate into plant-available forms.^[69] Phosphate-solubilizing microorganisms (PSMs) produce enzymes like phosphatases, particularly phytase, which facilitate the mineralization of organic P in soil by hydrolyzing organic compounds and releasing inorganic phosphate that plants can absorb. Acidic and alkaline phosphatases are key enzymes in this process, converting organic phosphate into an inorganic form.

To further mineralize organic phosphates, soil microorganisms such as *Streptomyces* and *Bacillus* spp. secrete extracellular enzymes like phosphodiesterase, phytase, and phospholipase.^[45,70] Siderophores produced by *Bacillus* spp. can also enhance the hydrolysis of plant phosphorus, increasing its bioavailability in the soil.^[71] Additionally, PSMs are reported to stimulate extensive root system development, improving phosphorus absorption from a larger soil area.^[72] The solubilization of both organic and inorganic P through inoculation with phosphate-solubilizing bacteria (PSB) like *Bacillus* spp. can significantly enhance crop yields.^[42,73]

4.2 Organic phosphate solubilization mechanisms

Organic phosphate compounds in soil, such as nucleic acids, phosphonates, cellulose, phospholipids, polyphosphates, and sucrose phosphates, are made available through the action of microbe-derived enzymes, including phosphohydrolase, phosphonatease, and phytase.^[74] Soil-dwelling *Bacillus* and *Streptomyces* species release extracellular enzymes like phosphodiesterases, phytases, and phospholipases, which play crucial roles in phosphate solubilization.^[45] Phosphatase enzymes, for instance, break the ester bonds in high-molecular-weight organic compounds, releasing essential phosphate ions and transforming these compounds into lower molecular weight forms.^[75] Phytase specifically targets myo-inositol phosphate complexes, such as phytic acid, while phosphonatease hydrolyzes ester bonds in phosphonates like phosphonyl pyruvate and phosphonoacetate, releasing phosphate ions and organic compounds (e.g., hydrocarbons) that can be assimilated by microorganisms.

5. *Bacillus* species as nitrogen fixers

Rhizobacteria play a critical role in the localization and stimulation of key elements such as nitrogen (N₂), phosphorus (P), and iron (Fe) within the rhizosphere. Plants cannot directly utilize atmospheric N₂, relying instead on symbiotic relationships with microorganisms to access this essential nutrient. Several *Bacillus* species, including *Bacillus subtilis*, *Bacillus circulans*, and *Bacillus megaterium*, have demonstrated the ability to fix atmospheric nitrogen, making N₂ bioavailable for plant use. Through biological nitrogen fixation, these bacteria convert atmospheric nitrogen into ammonia (NH₃), which plants can assimilate. This process enhances nitrogen availability in the soil and supports the establishment of other nitrogen-fixing organisms within the rhizosphere. Additionally, *Bacillus* spp. promote nodulation,

especially in leguminous plants, further facilitating symbiotic nitrogen fixation. This nitrogen-fixing capability is particularly beneficial in nitrogen-deficient soils, reducing reliance on synthetic nitrogen fertilizers and supporting more sustainable agricultural practices.^[76]

6. *Bacillus* species as a phytohormones producer

Plants associate with numerous microorganisms that produce essential phytohormones crucial for their growth and development.^[77] Key *Bacillus* species, including *Bacillus amyloliquefaciens*, *Bacillus licheniformis*, *Bacillus pumilus*, *Bacillus subtilis*, and *Bacillus tequilensis*, are consistently found in the rhizosphere, where they positively influence crop growth and health.^[21] These species, located in the rhizosphere, significantly impact plant extension and robust growth.^[78] Phytohormones, or plant growth regulators, such as auxins, cytokinins (CK), abscisic acid, gibberellic acid, and salicylic acid, are indispensable for crop growth and development. Though secreted in low concentrations, they play critical roles in regulating various plant processes. Additionally, these hormones act as signaling molecules, helping plants activate defenses against both biotic and abiotic stressors.^[79]

Notably, *Bacillus aryabhattai*, isolated from rhizospheric soil in South Korea, has been shown to significantly enhance plant growth and improve heat tolerance by synthesizing abscisic acid, IAA, and gibberellic acid.^[80] By modulating phytohormone levels and increasing nutrient bioavailability, *Bacillus* species, known for their phytohormone production, exert a profound positive influence on crop proliferation and maturation.^[21] Table 1 lists a summary of the array of phytohormones produced by various *Bacillus* species and their respective effects on crops.

Table 1. Different phytohormones are assembled by the dint of *Bacillus* spp.

<i>Bacillus</i> species	Phytohormone	Reference
<i>B. subtilis</i>	IAA	[80,81]
<i>B. subtilis</i>	CK	[82]
<i>B. tequilensis</i>	IAA, GA, ABA	[24]
<i>B. amyloliquefaciens</i>	ABA	[21]
<i>B. licheniformis</i>	IAA	[83]
<i>B. licheniformis</i>	ABA	[21]
<i>Bacillus velezensis</i>	IAA	[10]
<i>B. megaterium</i>	IAA	[84]
<i>B. cereus</i>	IAA	[85]
<i>B. aryabhattai</i>	IAA, GA, ABA	[80]

Note: IAA, ndole acetic acid; GA, Giberalllic acid; ABA, Absciscic acid; CK, Cytokinin.

7. *Bacillus* species equally ecological difficulty controlling

With ongoing global changes in weather patterns, adverse environmental conditions have significantly reduced the growth, development, and yield of nearly all crops.^[86,87] Salt intolerance and groundwater depletion are among the major challenges facing modern agriculture. Freshwater resources

are becoming increasingly scarce, and drought—expected to worsen due to climate change—presents one of the most significant environmental challenges to agricultural productivity. In the coming decades, reduced crop irrigation may be necessary to conserve this vital resource. Additionally, prolonged irrigation practices have led to soil salinization, with 20% to 50% of irrigated agricultural land already affected by salt.

Certain *Bacillus* species possess the ability to alleviate abiotic stress that would otherwise limit crop yields. For instance, *Bacillus subtilis* has been shown to enhance plant tolerance to both drought and salt stress. Studies demonstrate that *Bacillus amyloliquefaciens* can increase salt tolerance in rice,^[88] while *Bacillus pumilus* enhances proline content in rice seedlings, improving plant health under various stress conditions. Recent research also indicates that *B. subtilis* can regulate gene expression to increase resistance to salt and drought stress by upregulating genes involved in the production of abscisic acid (ABA), a key stress hormone, and independently enhancing osmotic stress tolerance.^[89] Specifically, *B. subtilis* helps plants manage drought-induced damage by increasing osmoprotectant production and modulating the Na⁺ importer HKT1 protein in plant organs based on their specific needs.^[89] Furthermore, many *Bacillus* species can release volatile organic compounds (VOCs) that play a critical role in reducing abiotic stress.^[90] Additionally, gibberellic acids (GAs) produced by certain *Bacillus* species provide protective benefits, aiding in adaptation to abiotic stress and heavy metal detoxification in plants.^[91]

8. *Bacillus* as biocontrol agent (BCA)

A wide variety of microorganisms, including fungi, protozoa, viruses, bacteria, and nematodes, can cause numerous plant diseases, significantly impacting agricultural productivity and increasing crop losses.^[16] Various pathogenic diseases account for 20–40% of agricultural output deficits.^[17] Management strategies such as crop rotation, the use of less vulnerable cultivars, and insecticides have been traditionally employed to mitigate the occurrence of plant diseases. However, the excessive use of chemical pesticides has led to reduced effectiveness due to the development of resistance to soil-borne pathogens, negative environmental effects, ecosystem disturbances, and a decline in agricultural sustainability.^[19]

Currently, research is increasingly focusing on environmentally sustainable alternatives for integrated crop management systems (ICMS) to control plant diseases and improve agricultural productivity.^[92] A key component of an ICMS is biological control, which involves identifying microorganisms with antagonistic properties, studying their mechanisms of action, and developing new biocontrol agents.^[93] Among the most studied components of biological control are *Bacillus* species, which have been shown to effectively suppress plant diseases by competing with or inhibiting pathogens.^[21] *Bacillus* spp. combat plant pathogens through several mechanisms, including competition for

Table 2. Different mechanisms of plant pathogen inhibition by *Bacillus* spp.

Biocontrol agents	Antibiotics/mode of action	Target pathogen	Target diseases and/crops	References
<i>B. subtilis</i>	Bacillomycin D	<i>Aspergillus flavus</i>	Aflatoxin contamination	[95]
	Mycosubtilin	<i>Pythium</i> , <i>Aphanidermatum</i>	Damping off	[96]
	Iturin A	<i>Botrytis cinerea</i> and <i>R. solani</i>	Damping off	[78, 97]
	Surfactin, fengycin	<i>Fusarium graminearum</i>	Head blight of wheat	[98]
	Fengycin, iturin	<i>Pythium ultimum</i>	Damping of bean	[99]
	Iturin, dicidin, surfactin, plipastatin, bacillomycin	<i>Gaeumannomyces graminis</i> var. <i>tritici</i>	Take all of wheat	[100]
<i>B. amyloliquefaciens</i>	Bacillomycin, Fengycin	<i>Fusarium</i> , <i>Oxysporum</i>	Wilt	[101]
	Bacteriocins, fengycin, surfactin	<i>Fusarium oxysporum</i> , <i>Fusarium avenaceum</i> , <i>Mucor</i> sp.	Occur diseases of field and vegetable crops	[102]
	Surfactin, iturin, fengycin, Siderophore	<i>Sclerotinia sclerotiorum</i>	White mold of common bean	[103]
<i>B. cereus</i>	Zwittermicin A	<i>Phytophthora medicaginis</i> and <i>P. aphanidermatum</i>	Damping off	[104]
<i>B. licheniformis</i>	Surfactin	<i>Magnaporthe grisea</i>	Blast disease of rice	[105]
<i>B. pumilus</i>	Lipopeptides	<i>Pseudomonas syringae</i> pv. <i>aptata</i>	Leaf spot disease of sugar beet	[106]
<i>B. velezensis</i>	Chitinase, Protease, Cellulase, Glucanase	<i>Botrytis cinerea</i>	Gray mold disease of pepper	[107]

resources, antibiotic production, siderophore secretion, and inducing systemic resistance in plants. These actions disrupt pathogen growth and development, reducing the incidence of plant diseases. The different mechanisms used by *Bacillus* spp. to suppress pathogens are summarized in Table 2.^[94]

8.1 Antibiosis

Secondary metabolites, commonly referred to as antibiotics, are produced by bacteria and fungi and exhibit inhibitory effects on other organisms. These metabolites are highly effective against diseases and competitors, often preventing adhesion and inhibiting the production of extracellular virulence factors.^[108] Under favorable conditions, particularly in soil environments, microorganisms can induce physiological changes in other organisms and act as biocontrol agents, reducing the severity of plant diseases or preventing their onset.^[109] Certain bacteria, such as *Bacillus* species, are especially valuable due to their biocontrol properties. Various

strains of *Bacillus* not only promote plant growth but also protect against plant diseases by producing an array of metabolites, exotoxins, and enzymes with nematocidal activities.^[110–113]

Among the most studied *Bacillus* metabolites are oligopeptide antibiotics, including iturin, surfactin, and fengycin.^[114] These compounds possess potent antifungal and antibacterial properties, making them effective tools for controlling plant pathogens. Recent molecular research has shown that *Bacillus* spp. can secrete a diverse range of previously unidentified metabolites with potential antibacterial activities. The antibiotic-producing capabilities of *Bacillus* spp. position them as promising candidates for developing antifungal agents, particularly for managing post-harvest diseases. For example, *Burkholderia cepacia* produces the pyrrolnitrin antibiotic, which is effective against pathogens like *Penicillium expansum*, *Botrytis cinerea*, and *Penicillium digitatum*.^[115]

Additionally, *Bacillus subtilis* and other *Bacillus* species produce a variety of antibiotics, such as amylocyclin, subtilin, plantazolicin, ericin, mersacidin, amylolysin, subtilosin, and bacteriocins.^[116-119] These compounds have shown significant potential as biocontrol agents in agricultural settings. Furthermore, cyclic lipopeptides (cLPs) such as iturin and surfactin, produced by *Bacillus licheniformis*, *Bacillus pumilus*, and *Bacillus subtilis*, include bioactive secondary metabolites like lichenysin and pumilacidin. These lipopeptides exhibit strong antifungal and antimicrobial properties, making them valuable for controlling plant pathogens and enhancing crop protection.

8.2 Parasitism

A distinctive type of biocontrol agent (BCA) directly eliminates or inhibits pathogen growth by targeting the pathogen during its parasitism stage. *Bacillus* species, known for their biocontrol capabilities, can employ parasitism to combat various plant pathogens. These bacteria exhibit antagonistic properties against a wide range of plant pathogens, including *Magnaporthe oryzae*, *Fusarium graminearum*, *Blumeria graminis*, *Colletotrichum acutatum*, *Fusarium oxysporum*, and *Zymoseptoria tritici*.^[107,120-126] Additionally, studies have shown that *Bacillus* spp. exhibit antagonistic activity against *Pythium aphanidermatum* and *Phytophthora infestans*.^[127,128] Under in vitro conditions, *Bacillus velezensis* has demonstrated the ability to inhibit the growth of various fungi, including *Colletotrichum gloeosporioides* and *F. oxysporum*.^[129]

Beyond their activity against fungal pathogens, *Bacillus* species are also effective against viral plant diseases. For example, *Bacillus amyloliquefaciens* Ba13 has been shown to suppress tomato yellow leaf curl virus,^[130] while *B. amyloliquefaciens* 5B6 can inhibit cucumber mosaic virus, which affects tobacco and pepper plants.^[131]

8.3 Bacterial lytic enzymes and additional microbial byproducts

Fungal cell walls are composed of proteins, lipids, cellulose, glucan, chitin, and chitosan. *Bacillus* species produce hydrolytic enzymes with antimicrobial properties, such as fungal cellulase, which can degrade the cell walls of both bacteria and yeasts.^[132] A key enzyme, bacterial chitinase, hydrolyzes chitin – a major component of fungal cell walls – making it a valuable biocontrol agent against various plant diseases, especially those caused by phytopathogenic fungi.^[133,134] Similarly, *Bacillus* spp. that secrete chitosanase can act as biocontrol agents to prevent fungal infections, as fungal cell walls also contain chitosan.^[135] Another enzyme, glucanase, produced abundantly by *Bacillus* spp., has been isolated from *Bacillus subtilis*, *Bacillus brevis*, and *Bacillus halodurans*.^[136] Additionally, these species synthesize other enzymes, such as cellulase and protease, which contribute to fungal cell wall degradation upon pathogen contact.^[137]

Research has shown that *B. subtilis*, which secretes

chitinase, is effective against *Rhizoctonia solani*. Meanwhile, *Bacillus amyloliquefaciens*, known for its protease production, demonstrates activity against *Fusarium oxysporum*, *Clavibacter michiganensis*, and *Fusarium verticillioides*, which causes maize stem rot.^[137-139] Furthermore, *Bacillus velezensis* has been shown to successfully suppress pepper dark mold disease caused by *Botrytis cinerea*.

8.4 Siderophore production

Siderophores are low-molecular-weight compounds with a strong affinity for iron (Fe) and have shown significant potential in managing phytopathogens. Siderophore-producing biocontrol bacteria, such as *Bacillus* species, can inhibit the growth, metabolic activity, and spread of phytopathogens – responsible for numerous plant diseases – through Fe chelation.^[140,141] Beyond iron chelation, siderophores facilitate the extraction and solubilization of iron from crystals and organic compounds, creating competition for iron and subsequently reducing its availability to phytopathogens.

Bacillus species produce more siderophores than many other bacteria commonly found in the rhizosphere of crops like maize.^[142] They generate a wide range of siderophores (iron carriers), including pyochelin, schizokinen, and petrobactin.^[143] Among the most notable is bacillibactin, a siderophore produced by *Bacillus subtilis*, *Bacillus cereus*, and *Bacillus thuringiensis*.^[144] *Bacillus subtilis*, a bacillibactin producer, has been shown to enhance pepper growth and yield while simultaneously reducing the incidence of *Fusarium* wilt.^[145] Additionally, *Bacillus subtilis* has been used as an effective biocontrol agent against *Bipolaris sorokiniana*, the causal agent of leaf spot disease in various crops.^[146]

8.5 Host resistance induction

Beneficial bacteria with diverse mechanisms can induce host plants to develop resistance to diseases, effectively triggering plant defense mechanisms.^[147,148] One of the primary defense strategies employed by plants is induced systemic resistance (ISR), a process stimulated by non-pathogenic rhizobacteria and influenced by both biotic and abiotic factors. ISR enables plants to activate their defense systems against a wide range of pathogens. *Bacillus* species are well-studied rhizobacteria known for protecting plants by enhancing immune responses and increasing resistance to numerous phytopathogens through ISR.^[149-152] Several *Bacillus* species, including *Bacillus amyloliquefaciens*, *Bacillus atrophaeus*, and *Bacillus cereus*, have been shown to combat bacterial, fungal, and viral infections by inducing ISR. These species produce specific protein elicitors to defend plants against pathogens such as *Botrytis cinerea* and tobacco mosaic virus. For example, the AMEP 412 protein from *Bacillus* sp. induces resistance in tobacco against *Pseudomonas syringae* pv. *tomato*, while *Bacillus amyloliquefaciens* produces the PeBA1 protein, which enhances tobacco resistance.^[153,154]

In addition to protein elicitors, *Bacillus* species release

volatile organic compounds (VOCs) that contribute to plant protection. *Bacillus subtilis*, a producer of VOCs, has been shown to reduce pathogen infection in *Arabidopsis thaliana* seedlings by triggering the plant's immune response.^[155] Similarly, VOCs from *Bacillus amyloliquefaciens* reduce *Xanthomonas axonopodis* spot infestations in peppers,^[156] and *Bacillus megaterium* has been shown to suppress plant blotch caused by *Mycosphaerella graminicola*.^[125] Furthermore, *Bacillus cereus* has been reported to decrease the incidence of *Botrytis cinerea* infections through ISR,^[157] while *Bacillus amyloliquefaciens* enhances salicylic acid-mediated defenses against tomato spotted wilt virus.^[158] Since antioxidant defense enzymes are crucial for protecting plants from blight,^[159] *Bacillus* species stimulate the production of enzymes like peroxidase (POX), phenylalanine ammonia-lyase (PAL), and superoxide dismutase (SOD), all of which contribute to the ISR process in plants.

9. Abiotic stresses in crops mediated by *Bacillus* spp.

In their natural ecosystems, plants frequently encounter various abiotic stressors, including salinity, drought, extreme temperatures (heat and cold), flooding, heavy metal contamination, waterlogging, and ultraviolet radiation. These stressors severely affect plant growth and survival, posing significant threats to the sustainability of global crop yields. The intensification of climate change has worsened these conditions, leading to an alarming increase in crop losses due to abiotic stresses. As immobile organisms, plants are unable to escape unfavorable conditions and must instead rely on internal stress responses. The effectiveness of these responses

depends on factors such as the severity and duration of the stress, as well as the plant's developmental stage. Understanding the most common abiotic stress factors and plant responses is essential to mitigating crop losses and promoting agricultural sustainability.^[160]

A key aspect of plant survival in harsh environments is their association with beneficial bacteria that enhance growth and stress resistance. In drought- and salt-affected soils, plants often form symbiotic relationships with bacteria capable of improving their resilience to these stressors. Species within the genus *Bacillus* are particularly notable for their ability to thrive in extreme soils and provide protective benefits to their plant hosts. These bacteria possess mechanisms that allow them to adapt to high osmolarity and salinity levels, enabling survival in challenging environments. Studies have shown that certain *Bacillus* species can alleviate salinity and drought stress in a variety of plants, including wheat, maize, chickpea, *Arabidopsis thaliana*, sweet basil, lettuce, *Acacia gerrardii*, strawberry, radish, *Lactuca sativa*, pepper, eggplant, and rice. The mechanisms through which *Bacillus* species and other plant-associated bacteria promote plant growth under abiotic stress are multifaceted. These mechanisms include phytohormone production, 1-Aminocyclopropane-1-Carboxylate (ACC) deaminase activity, enhanced nutrient availability, increased root biomass and morphology, induction of antioxidant enzymes, osmolyte accumulation, ion homeostasis, and stress-responsive gene induction (Fig. 3).^[161] The rapid increase in the global population, coupled with environmental instability, has intensified the need for sustainable solutions to enhance agricultural productivity.

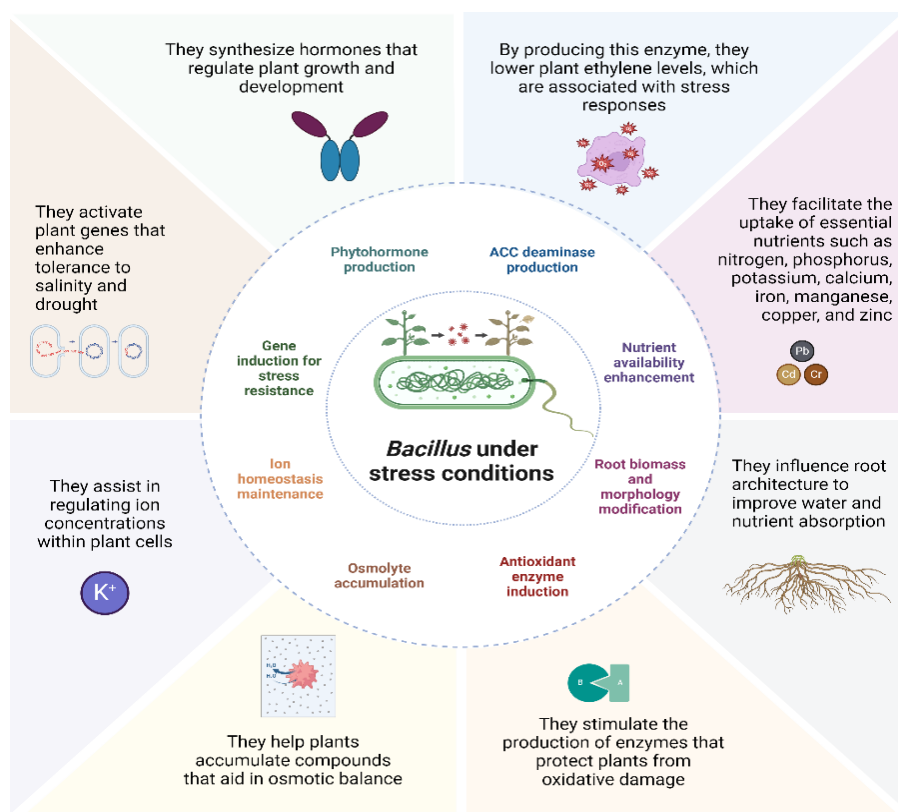


Fig. 3 Role of *Bacillus* spp. in enhancing plant stress tolerance mechanisms.

Traditional reliance on synthetic fertilizers to meet food demand has led to adverse environmental consequences, sparking growing interest in eco-friendly alternatives. As a result, future research is increasingly focused on developing biocontrol products and biofertilizers, with *Bacillus* species emerging as promising candidates due to their versatile genetic makeup, which includes compatible genetic tools, promoters, and plasmid expression systems.^[162]

Despite their potential, *Bacillus* spp. has not garnered as much research attention as other microorganisms, such as *Escherichia coli*. Challenges such as the complexity of field environments, variability in climatic conditions, and a lack of comprehensive studies on their mechanisms of action have hindered the widespread utilization of *Bacillus* in agriculture. Additionally, difficulties in formulating stable biological products and quantifying the low concentrations of active substances produced by these bacteria present further obstacles.^[163,164] Advances in biotechnology could address these challenges by enhancing the stability of *Bacillus*-based products and improving their ability to colonize plant roots effectively. Expanding our understanding of the distribution, diversity, and functional mechanisms of *Bacillus* spp. will facilitate the development of more efficient biofertilizers tailored to specific crops.^[165,166]

In-depth studies on root colonization are essential, as is the development of characterization techniques to distinguish introduced *Bacillus* strains from native microbial communities, further optimizing their application.^[167]

10. Conclusion and perspectives

Bacillus species present promising, sustainable solutions for enhancing agricultural productivity through biofertilization, growth promotion, and microbial management. These bacteria produce resilient endospores and beneficial compounds that help plants withstand stressful environments, improve crop yields, and combat pests through mechanisms like phosphate solubilization and hormone stimulation. Despite their efficacy, their inconsistent results across diverse environmental conditions remain a limitation to widespread application. Factors like soil variability and climatic conditions impact their performance, making it essential to refine their application for consistency.

Soil inoculation with *Bacillus* spp. enhances phosphorus availability by solubilizing otherwise inaccessible forms of phosphorus and releasing growth-promoting hormones, which collectively accelerate plant development. *Bacillus* species also bolster nitrogen fixation and produce antimicrobial agents like hydrogen cyanide, contributing to natural biocontrol processes. However, challenges such as stabilizing *Bacillus* formulations and accurately quantifying their active components persist. Advances in biotechnology could improve product stability and facilitate root colonization by these bacteria.

Future research is critical to optimizing the use of *Bacillus* spp. in biofertilizers and biocontrol agents, with an emphasis

on selecting strains best suited for specific crops and climates. Improved understanding of *Bacillus* spp. diversity and root colonization processes will also aid in developing formulations that enhance plant resilience to both abiotic and biotic stresses. Integrating insights from biotechnology, physiology, and molecular biology will pave the way for managing environmental stressors more effectively, fostering more sustainable agricultural practices.

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Conflict of Interest

There is no conflict of interest.

Supporting Information

Not applicable.

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