

Review

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Review

Potential of *Bacillus halotolerans* in Mitigating Biotic and Abiotic Stresses: A Comprehensive Review

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Abstract: *Bacillus halotolerans*, a halophilic bacterial species of the genus *Bacillus*, is emerging as a biological control agent with immense potential for sustainable agriculture, particularly in extreme conditions and environmental rehabilitation. This review summarizes the current state of research on *B. halotolerans*, emphasizing its diverse applications in the biocontrol of plant pathogens, plant growth promotion under salinity stress, nematode management, and bioremediation. *B. halotolerans* utilizes several mechanisms such as the production of siderophores and phytohormones, secretion of exopolysaccharides, and the release of antifungal and nematicidal compounds, which allows it to mitigate both abiotic and biotic stresses in various crops, including wheat, rice, date palm, tomato, and others. In addition, genomic and metabolomic analyses have revealed its potential for secondary metabolite production that improves its antagonistic and growth-promoting traits. Despite significant progress, challenges remain in translating laboratory results into field applications. Future research should focus on formulating effective bioinoculants and field trials, to maximize the practical utility of *B. halotolerans* for sustainable agriculture and environmental resilience.

Keywords: *Bacillus halotolerans*; biocontrol; abiotic stress; salt stress alleviation

1. Introduction

The increasing global demand for food security, coupled with the detrimental environmental effects of chemical plant protection products (cPPPs), has necessitated a shift toward more sustainable agricultural practices. While effective for controlling phytopathogens and enhancing yields, the widespread dependence of chemical inputs has resulted in severe ecological consequences, including soil and water pollution, harm to non-target organisms, and the development of resistant pathogens [1–4]. Public concerns about chemical residues in products have led to stricter regulations on cPPP usage, encouraging the exploration of biological alternatives. Biocontrol, a crucial component of integrated pest management (IPM) systems, represents a promising solution for reducing the negative impacts of phytopathogens while promoting sustainable and safe agricultural practices [5,6]. This approach includes the use of beneficial microorganisms such as *Bacillus* spp., known for their capacity to protect plants through competition and antagonism, to mitigate crop losses and improve yields, particularly in protected and organic vegetable production systems [7].

Among plant growth-promoting bacteria (PGPB), *Bacillus* species stand out due to their ability to colonize plant tissues endophytically without causing harm, offering a dual advantage in plant protection and growth promotion [8]. The genus includes a wide range of species such as *B. amyloliquefaciens*, *B. subtilis*, *B. velezensis*, *B. pumilus*, and *B. siamensis*, each recognized for their capabilities to produce enzymes, induce systemic resistance in plants, and synthesize antimicrobial metabolites [9]. These bacteria have also been extensively utilized in the production of commercial

biocontrol products, such as Serenade® and Rizhovital®, which are highly effective against foliar, soil-borne, and post-harvest pathogens [10]. The production of robust endospores by this Gram-positive bacterium further enhances their advantages over other bacterial biocontrol agents (e.g. *Pseudomonas* spp.), allowing for efficient production, extended shelf-life and easier formulation [11,12].

Members of *Bacillus* are known by the release of extensive arsenal of antimicrobial peptides, including iturin, fengycin, bacillomycin, and surfactin, which exhibit broad-spectrum biocidal activity against pathogens while inducing systemic resistance in plants [13–16]. Additionally, *Bacillus* species produce a variety of volatile and non-volatile compounds that synergistically combat phytopathogens [17]. These capabilities, coupled with the ability to activate plant defense enzymes such as peroxidase (POX), polyphenol oxidase (PPO), and phenylalanine ammonia-lyase (PAL), make *Bacillus* a cornerstone of modern biocontrol strategies [18,19].

Due to its unique physiological and ecological attributes, *B. halotolerans* has emerged as a particularly promising candidate for sustainable agriculture within this genus. This species is well-adapted to extreme environmental conditions, such as high salinity and drought, which are increasingly common in agricultural soils, particularly in arid and semi-arid regions [20]. *B. halotolerans* has demonstrated impressive biocontrol capabilities, producing a wide range of secondary metabolites, including antifungal lipopeptides, volatile organic compounds, and antioxidant enzymes that protect plants from both biotic and abiotic stresses [21–23]. Furthermore, its ability to enhance plant growth under stressful conditions has been observed in various crops, including wheat, tomatoes, and potatoes, making it a valuable tool in enhancing agricultural resilience and productivity [21,23–26]. This article presents a comprehensive review of the potential of *B. halotolerans* as a biocontrol agent in sustainable agriculture. It consolidates current research to showcase the physiological, biochemical, and molecular characteristics that make *B. halotolerans* uniquely suited for mitigating plant diseases and enhancing growth under stressful environmental conditions. The review also explores the diverse habitats of *B. halotolerans*, its ability to produce antimicrobial metabolites, and its role in alleviating abiotic stresses, such as salinity and drought. Furthermore, the article emphasizes the importance of this species in IPM strategies and its potential to reduce dependency on cPPP while ensuring crop productivity and environmental sustainability.

2. Morphological, Biochemical and Molecular Characteristics of *B. halotolerans*

B. halotolerans is a gram-positive, rod-shaped bacterium known for its adaptability to diverse and often extreme environmental conditions [27]. This species, previously classified as *Brevibacterium halotolerans*, has been reclassified through advanced molecular and biochemical tools, solidifying its position within the genus *Bacillus* [28]. It is an alkaliphilic organism capable of thriving in saline soils, which underpins its classification as a halotolerant species. Its historical classification and recent re-evaluation reflect ongoing efforts to establish its taxonomy, with strains like DSM 8802 and MS50-18A serving as references for its biochemical and genetic characterization [28,29].

Strains of *B. halotolerans* exhibit distinct morphological and biochemical profiles depending on their habitat and isolation source. For instance, strain LDFZ001 forms smooth, creamy colonies with regular edges on LB medium, and under light microscopy, it displays a rod-shaped structure typical of *Bacillus* species [30]. Similarly, strain DS5 presents as short rods with peritrichous flagella and forms milky white, opaque, and wrinkled colonies [31]. On TSA medium, Strain B-4359, from the Freshwater Bioresources Culture Collection (FBCC) in Korea, forms smooth, glossy light-brown colonies and is motile, with rod-shaped cells measuring approximately $0.84\text{--}1.49\text{ }\mu\text{m} \times 2.08\text{--}4.10\text{ }\mu\text{m}$ (width $\times$ length). Endospores from this strain are commonly observed after seven days of incubation, highlighting their robustness in adverse conditions [27].

Biochemically, *B. halotolerans* displays a wide range of metabolic capabilities. It grows on diverse carbon sources, including glucose, cellulose, sucrose, lactose, fructose, and maltose [31]. It demonstrates remarkable salt tolerance, with some strains capable of thriving at NaCl concentrations up to 150 mM [32]. Notably, the KKD1 strain has been shown to grow at 13 % salinity in previous studies [23]. *B. halotolerans* exhibits impressive environmental adaptability and plant growth-

promoting traits. It can grow at temperatures ranging from 4 to 45°C, with optimal growth at 30°C [33], and thrives within a pH range of 5 to 9 [34]. Additionally, *B. halotolerans* produces various beneficial compounds such as indole-related compounds, acetoin, ammonia, and indole-3-acetic acid (IAA). It also demonstrates the ability to solubilize potassium and phosphorus, produce siderophores, chitinase, cellulase amylase, protease, ACC deaminase, and hydrogen cyanide [35,36]. These attributes contribute to its adaptability across various environmental conditions [31]. DSM 8802, a type strain, demonstrates the ability to form spores and grow on cellulose and glucose, a further showcase of the metabolic flexibility of this species [28].

The genomic architecture of *B. halotolerans* underscores its adaptability and biotechnological potential. Strain ZB201702, isolated from saline soil, has a circular genome of 4.15 Mb with a guanine-cytosine content of 43.81%, encoding 4,119 genes, including 30 rRNA and 85 tRNA genes [37]. Strain F29-3 with high similarity to *B. halotolerans* ATCC 25096 has a genome size of 4.2 Mb [38]. Similarly, MS50-18A, another well-characterized strain, exhibits genes involved in glycine/betaine uptake and bacilysin biosynthesis, critical for its saline stress tolerance and antifungal activity [29]. Advanced phylogenetic analysis using neighbor-joining trees has confirmed the close evolutionary relationships of *B. halotolerans* with other *Bacillus* species such as *B. mojavensis* and *B. subtilis* [30]. This is evident in strains like LDFZ001 and F29-3, which show genomic similarities within the *Bacillus* family [30,38].

B. halotolerans survives in extreme environments, including saline and arid soils, demonstrating remarkable resilience [20]. Strain MS50-18A, isolated from saline soil, and ZB201702 from arid regions exemplify the species' capacity to endure high salinity and alkalinity [29,37]. The Qinghai-Tibet Plateau, known for its low oxygen availability, low temperatures, and high salinity, has also been identified as a habitat for *B. halotolerans* [39]. Strains isolated from this region exhibit not only high stress tolerance but also biocontrol properties against plant pathogens. *B. halotolerans* has been isolated from different regions of the world and involved in the biocontrol of various crops (Figure 1).

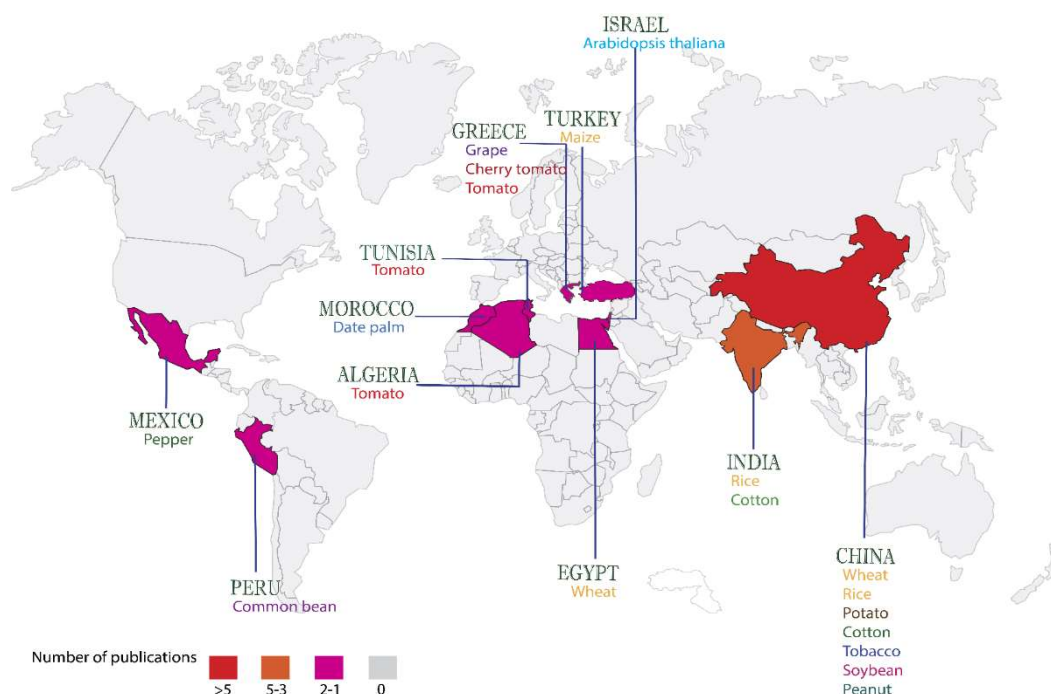


Figure 1. Global geographic distribution of *B. halotolerans* strains and their biocontrol of plant pathogens on the associated crops.

The stress tolerance mechanisms of *B. halotolerans* include the production of osmoprotectants, such as glycine and betaine, and its ability to regulate ion homeostasis, which are key for survival in saline and alkaline environments [24].

3. Biocontrol Mechanisms of *B. halotolerans*

3.1. Production of Antimicrobial Compounds

One of the key mechanisms behind the biocontrol effectiveness of *B. halotolerans* lies in its ability to produce a broad spectrum of antimicrobial compounds (AMCs) (Figure 2). These compounds, which include both ribosomally and non-ribosomally synthesized metabolites, play a crucial role in inhibiting pathogens and reducing plant diseases [40]. The potential of *Bacillus* species, particularly those in the *B. subtilis* group, to dedicate a significant portion of their genome, estimated by 4-5%, to the biosynthesis of AMCs highlights their importance in microbial antagonism [17]. Among the AMCs produced by *B. halotolerans* are lipopeptides such as surfactin, fengycin, and iturin [22]. These compounds exhibit potent antimicrobial activities, effective against a range of bacteria while showing strong antifungal properties [22,41]. For instance, *B. halotolerans* strain SpS5 synthesizes surfactin and mojavensin (Table 1), which have been shown to effectively control *Rhizoctonia solani*, a significant plant pathogen, under both laboratory and field conditions [42]. Similarly, strain KKD1, producing surfactin and fengycin, demonstrated its antifungal potential against *Fusarium graminearum* [39]. Strain Cal.l30, has been identified as a producer of several AMCs, including bacillaene, surfactin, fengycin, mojavensin, and bacillibactin. The ability of these compounds to inhibit plant pathogens like *Botrytis cinerea* enhances the potential of the strain as a biocontrol agent, making it a valuable candidate for plant protection [43]. In addition to lipopeptides, Cal.l30 synthesizes polyketides such as bacillaene and unique bioactive compounds like azelaic acid and L-dihydroantcapsin, the precursor of the antibiotic bacilysin (Table 1). Bacilysin is an important dipeptide with strong antibacterial and antifungal activity [43].

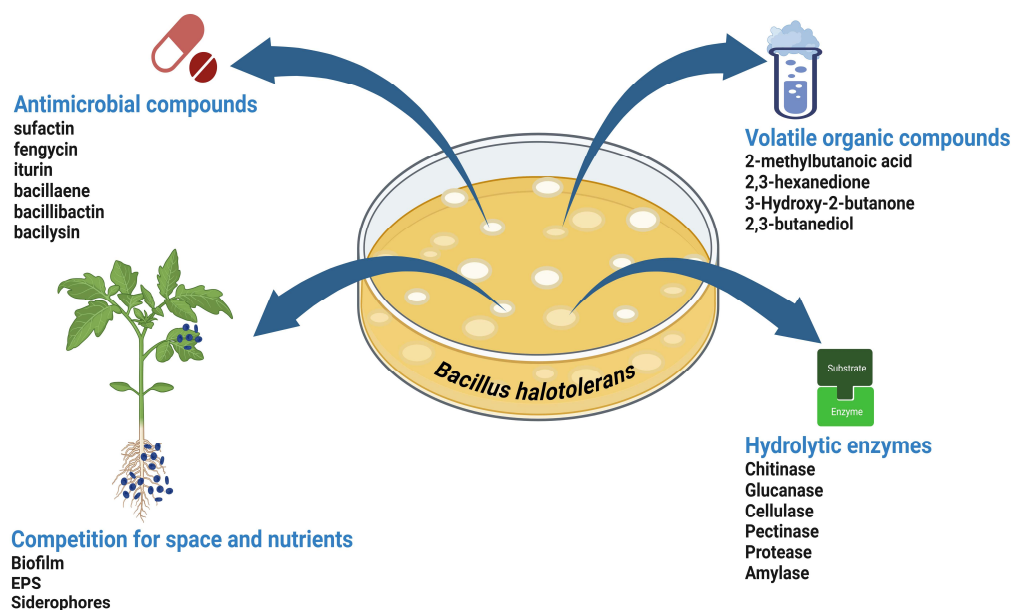


Figure 2. Mechanisms of action of *B. halotolerans* against phytopathogens.

The genomic basis for AMCs production in *B. halotolerans* underscores its biocontrol capabilities. Strain QTH8, for example, harbors biosynthetic gene clusters (BGCs) that encode enzymes responsible for the synthesis of surfactin, fengycin, and iturin. These genes (e.g., *srfAA*, *srfAB*, *fenD*, *spaS*, *bmyB*, *bacA*, and *ituC*) enable the strain to combat pathogens like *Fusarium pseudograminearum*, which causes crown rot in wheat [22]. Similarly, strain HGR5 contains a wide array of BGCs encoding compounds such as bacillaene, subtilosin, and bacillibactin, which are active against pathogens like *F. graminearum*, *Alternaria alternata* and *Phytophthora infestans* [55]. In many cases, the effectiveness of *B. halotolerans* as a biocontrol agent is attributed to the wide range activity of its AMCs. For example, strain *B. halotolerans* VT-5 produces a variety of bioactive compounds, including phenolic derivatives

and diketopiperazines, which exhibit significant antimicrobial properties. This strain has demonstrated the ability to reduce the effects of human pathogens like *Pseudomonas aeruginosa* and *Staphylococcus aureus* [41]. A study on the strain AQ11M9, which acts as an antagonist against the human pathogen *Candida auris*, identified the presence of clusters for fengycin and surfactin [58]. Analysis of the secondary metabolite secretome from *B. halotolerans* isolates BFOA1 to BFOA4 using LC-HRMS identified a variety of compounds with known plant growth promotion (PGP), antimicrobial, herbicidal, and insecticidal activities. However, examination of their genomes revealed a strong presence of PGP abilities and secondary metabolite gene clusters, particularly four clusters: subtilosin A, bacillibactin, bacillaene, and bacilysin [33].

B. halotolerans exemplifies a robust biocontrol agent with a remarkable ability to produce diverse AMCs, including lipopeptides, polyketides, and bacteriocins. The production of volatile organic compounds (VOCs) by *B. halotolerans* plays a significant role in its biocontrol ability (Figure 2). VOCs are low-molecular-weight, naturally occurring, hydrophobic substances with the ability to diffuse through the environment, enabling long-distance effects without direct contact with the target pathogens or plants [59,60]. This property makes them particularly advantageous for biofumigation, where direct application is impractical or undesirable. VOCs produced by *Bacillus* species have been shown to suppress the growth of plant pathogens, stimulate plant defenses, and promote plant growth [61,62].

Table 1. Review of the efficacy of *B. halotolerans* strains against various plant pathogens and their modes of action on different crops.

Crop	<i>B. halotolerans</i> strains	Targeted pathogens	Modes of action	References
Tomato	RFP1, RFP10, RFP57, RFP74	<i>Alternaria</i> spp., <i>Bipolaris</i> spp., <i>F. oxysporum</i> f.sp. <i>lycopersici</i> , <i>Ascochyta</i> sp.	CWDEs, VOC and antimicrobial production	[44,45]
	LYSX1	Root-knot nematode (<i>Meloidogyne javanica</i>)	Induced systemic resistance (ISR), nematocidal activity	[46]
	Gb67	-	VOCs (acetoin, 2,3-butanediol), enhanced root/shoot growth, reduction of salinity stress impact	[32]
	Cal.l.30, Cal.f.4	<i>Botrytis cinerea</i>	VOC-mediated suppression, production of surfactin analogs	[43]
	NYG5	<i>M. phaseolina</i> , <i>R. solani</i> , <i>P. aphanidermatum</i> , <i>S.sclerotiorum</i> , <i>A. tumefaciens</i> , etc.)	VOC production (e.g., 2-methylbutanoic acid), nematocidal activity against <i>M. javanica</i>	[47]
Wheat	KKD1	-	Enhanced soil fertility under saline conditions, phosphate solubilization, soil pH stabilization, nutrient cycling	[23]
	MSR-H4	-	Nitrogen fixation, phosphate solubilization, and improving root-shoot K ⁺ /Na ⁺ ratios under saline conditions	[24]

	JK-25	<i>Bipolaris sorokiniana</i> , <i>F. oxysporum</i> , <i>F. graminearum</i> , <i>Rhizoctonia zeae</i>	surfactin production, CWDEs; reduced antioxidant activity; siderophore	[21]
	QTH8	<i>F. graminearum</i> , <i>B. cinerea</i> , <i>F. pseudograminearum</i> , <i>S. sclerotiorum</i> , <i>Phytophthora nicotianae</i> ,	iturin, surfactin, fengycin; lipopeptides biosynthesis genes; growth promotion (ISR, AMCs)	[22]
Maize	B7, B18, B14	-	Biofilm and exopolysaccharide production, increased chlorophyll under saline conditions	[48]
Potato	SpS5	<i>Rhizoctonia solani</i>	Biofilm formation, CWDEs	[42]
	Q2H2	<i>F. oxysporum</i> , <i>F. graminearum</i> , <i>R. solani</i> , <i>Stemphylium solani</i>	surfactin, fengycin, bacillaene, subtilisin A; VOCs; phosphate solubilization; nitrogen fixation; IAA and NH ₃ and biofilm	[49]
	F29-3	<i>R. solani</i>	fengycin via NRPS genes; antagonistic properties; pathogen suppression in field trials	[38]
Soybean	Ba2-6	<i>Heterodera glycines</i> (soybean cyst nematode)	Juvenile nematode mortality, antibiosis, ISR, root colonization	[50]
Peanut	B28	not specified	Benzoic acid breakdown, reduce continuous cropping stress	[51]
Lily	LBG-1-13	<i>B. cinerea</i> , <i>Botryosphaeria dothidea</i> , <i>F. oxysporum</i>	ACC deaminase activity, IAA and siderophore production, ISR and salt/drought tolerance	[52]
Cotton	SSVP2	Soil-borne nematodes	ACC deaminase production, mineral solubilization (P, K), and nematicidal activity	[53]
	Y6MSR-H4	<i>Verticillium dahliae</i>	β-glucanase activity; enhanced resistance in cotton in the field	[54]
Date palm	BFOA1–BFOA4	<i>F. oxysporum</i> f. sp. <i>albedinis</i> , <i>F. solani</i> , <i>F. acuminatum</i> ,	Antagonism via AMCs (pulegone, 2-undecanone, germacrene D); salt and drought tolerance; auxin and biofilm production; nutrient solubilization, nitrogen fixation	[33]

		<i>B. cinerea</i> , <i>A. alternata</i> , <i>Phytophthora infestans</i> , <i>Rhizoctonia bataticola</i>		
Not specific d	HGR5	<i>F. graminearum</i> , <i>P.</i> <i>infestans</i> , <i>A. alternata</i>	fengycin, subtilosin, bacilysin; CWDEs (chitinase, cellulase, xylanase); plastic degradation	[55]
Wheat, Rice, Maize	LDFZ001	<i>R. solani</i>	Antifungal activity via phosphopantetheinyl transferase (SFP) and major facilitator superfamily (MFS) genes; two chitosanases; diverse biosynthetic gene clusters (NRPS, PKS).	[30]
Pepper	MS50-18A	<i>Phytophthora capsici</i> , <i>F.</i> <i>solani</i> , <i>R. solani</i> , <i>F.</i> <i>oxysporum</i>	AMCs and auxin production	[29]
Tomato , Grapes, <i>A.</i> <i>thaliana</i>	Hil4	<i>B. cinerea</i>	AMCs; ISR elicitors; Mojavensin cluster; secretome extracts; promotes plant growth and mitigates gray mold disease	[35]
Comm on bean	IcBac2.1	<i>R. solani</i> , <i>F. oxysporum</i> , <i>S. sclerotiorum</i>	Amphiphilic compounds with inhibitory activity; field efficacy against <i>S. sclerotiorum</i> ; plant growth promotion	[56]
Apple	Pl7	<i>Botryosphaeria dothidea</i>	CWDEs production, induction of plant secondary metabolite biosynthesis and plant- pathogen interaction	[34]
Rice	AD9	not specified	High NH ₃ and phosphate solubilization; salinity reduction via enzymes (SOD, CAT)	[57]
Strawb erries	KLBC XJ-5	<i>Botrytis cinerea</i>	Enhancement of disease resistance compounds (phenols, flavonoids), induction of plant defense enzymes (polyphenol oxidase, phenylalanine ammonia lyase)	[26]
not specific d	DMC8	<i>R. solani</i> , <i>P.</i> <i>aphanidermatum</i> , <i>M.</i> <i>phaseolina</i>	CWDEs (protease, chitinase), siderophores, NH ₃ , IAA; nitrogen fixation; phosphate solubilization.	[2]

In *B. halotolerans*, specific VOCs have been identified as key antifungal agents. For instance, strain NYG5 emits VOCs that effectively inhibit various phytopathogenic fungi, including *Macrophomina phaseolina*, *Rhizoctonia solani*, *Pythium aphanidermatum* and *Sclerotinia sclerotiorum*, as well as bacterial pathogens such as *Agrobacterium tumefaciens*, *Xanthomonas campestris*, *Clavibacter michiganensis*, and *Pseudomonas syringae* [47]. Analyzing VOC profiles of *B. halotolerans* have revealed a range of bioactive compounds. VOCs such as 2-methylbutanoic acid and 2,3-hexanedione were identified as primary contributors to these inhibitory effects, with 2,3-hexanedione exhibiting strong nematocidal activity against *Meloidogyne javanica* [47]. Strain Gb67 produces 3-hydroxy-2-butanone (acetoin) and 2,3-butanediol, which are associated with stress-induced defense regulation and plant growth promotion under salinity stress [32]. Additionally, strain Cal.1.30 has demonstrated VOC-mediated suppression of *B. cinerea*, attributed to compounds such as C13 and C15 surfactin analogs [43]. Moreover, *Brevibacillus halotolerans* B-4359 produced VOCs that demonstrated significant efficacy against the mycelial growth of *Colletotrichum acutatum* [27]. The diversity and bioactivity of VOCs enable *B. halotolerans* to target a wide spectrum of pathogens [47]. VOCs produced by *B. halotolerans* not only inhibit the growth of pathogens but also enhance plant physiological traits, such as root and shoot length, biomass, and photosynthetic ability. These effects are often attributed to the production of VOCs in conjunction with other plant growth promoting traits like ACC-deaminase activity and exopolysaccharide production [32]. The ability of *B. halotolerans* to produce VOCs is further exemplified in its environmental adaptability. When cultured in various growth media, its VOC profiles adapt to the conditions, producing compounds like 2-ethyl-1-hexanol and 6-methyl-2-heptanone, which demonstrate flexibility and effectiveness across diverse agricultural settings [47].

3.2. Cell Wall Degrading Enzymes

The activity of hydrolytic cell wall degrading enzymes (CWDEs) is a cornerstone of the biocontrol potential of *B. halotolerans* (Figure 2) [63]. These enzymes directly target and degrade the structural components of pathogen cell walls, thereby inhibiting the growth and development of harmful microorganisms [64]. The arsenal of hydrolytic CWDEs produced by *B. halotolerans* includes chitinases, glucanases, proteases, cellulases, lipases, and amylases, each playing a certain role in pathogen suppression [63].

Chitinases, one of the most prominent enzymes produced by *B. halotolerans*, are particularly effective against fungal pathogens. They hydrolyze β -(1,4)-glycosidic bonds in chitin, a critical component of fungal cell walls, producing N-acetylglucosamine and other oligosaccharides that disrupt cell wall integrity [26]. The breakdown products of chitin also act as elicitors of plant defense, inducing systemic resistance against further pathogen attacks [63,65]. Glucanases, particularly β -1,3-glucanases, complement chitinase activity by degrading glucans, another key component of fungal cell walls, further weakening fungal structures and facilitating cell lysis [34].

Proteases produced by *B. halotolerans* target glycoproteins in pathogen membranes, while cellulases and lipases break down cellulose and lipids, respectively, attacking structural and metabolic components of pathogens [63]. The multifunctional nature of these enzymes enables *B. halotolerans* to combat a diverse array of plant pathogens, including fungal, bacterial, and oomycete species [26,63]. Furthermore, strain JK-25 produces cellulase, enzyme critical for degrading the structural polysaccharides of oomycete pathogens [21]. The strain Pl7 of *B. halotolerans* with remarkable antagonistic effects against *Botryosphaeria dothidea*, the causal agent of apple ring rot, exhibited antifungal activity through the production of CWDEs, including protease, β -1,3-glucanase, and cellulase [34]. Another strain, KLBC XJ-5, has been reported to produce high levels of chitinase, supported by the presence of the glycoside hydrolase 18 (GH18) family chitinase genes, underscoring its ability to suppress fungal pathogens [26].

The enzymatic versatility of *B. halotolerans* is further demonstrated by its adaptability to environmental conditions. For example, strain DS5 produces alkaline protease (Prot DS5), which is particularly effective in high-pH environments, while strain RFP74 shows enhanced amylase production, enabling it to target starch-rich residues often associated with fungal spore development

[31,45]. Lipase activity in strains like VSH 09 and RCPS2 has also been documented, providing additional biocontrol mechanisms against pathogens that rely on lipid-based cellular components [66,67].

Beyond pathogen suppression, the CWDEs of *B. halotolerans* contribute significantly to plant health and growth. Hydrolytic enzymes like cellulase and β -glucosidase enhance carbon cycling in the soil, while protease and phosphatase release nitrogen and phosphorus, enriching soil nutrient availability [65]. These dual benefits of pathogen suppression and plant growth promotion make *B. halotolerans* a highly versatile biocontrol agent.

Additionally, hydrolytic enzyme activity has been linked to the ability of *B. halotolerans* to form robust biofilms on plant roots, enhancing colonization and persistence in the rhizosphere. This property enables the sustained release of enzymes in close proximity to pathogens, maximizing their biocontrol efficacy while simultaneously promoting plant growth [63].

3.3. Root Colonization and Competition for Space and Nutrients

The ability of *B. halotolerans* to compete with other microorganisms and efficiently colonize plant roots is fundamental to its role as a biocontrol agent (Figure 2). Root colonization ensures the bacterium's proximity to the plant, enabling direct interactions with pathogens and promoting plant health [68]. Tian et al. emphasized the importance of efficient root colonization for beneficial rhizobacteria, allowing them to exert plant growth promoting and protective effects [69]. Additionally, Li et al., identified robust root colonization as a critical factor for the biocontrol of soil-borne pathogens such as *Verticillium dahliae*, causal agent of verticillium wilt of cotton [68]. Plants actively recruit beneficial bacteria in the rhizosphere by secreting specific compounds, for example strigolactones and flavonoids in their exudates, which attract microbes like *B. halotolerans* [70–72].

In addition, *B. halotolerans* exhibited strong biofilm-forming capabilities, a trait that significantly enhances its root colonization potential [73]. Biofilms are structured communities of bacterial cells embedded in a self-produced extracellular polymeric matrix, which protects the bacteria from environmental stresses and helps in adhesion to surfaces, including plant roots [74]. Biofilms formed by *Bacillus* spp. can protect plants against pathogens and improve plant resilience to abiotic stresses [73]. For instance, biofilm production by *B. halotolerans* has been associated with increased tolerance to salinity, as observed in strains such as B7 and B18, which formed robust biofilms under salt stress [48].

The release of Extracellular Polymeric Substances (EPS) also plays a critical role in root colonization. EPS helps bacteria adhere to root surfaces, improves soil aggregation, and enhances the plant's water and nutrient uptake [75]. In saline conditions, EPS can bind toxic ions like Na^+ , restricting their influx into plant roots and promoting water retention [76]. These properties are particularly advantageous in challenging environments, making *B. halotolerans* a promising candidate for biocontrol in saline soils. For instance, the antibacterial activity of EPS produced by the marine bacterium *B. halotolerans* against clinical strains of *Pseudomonas aeruginosa* and *Serratia marcescens* was reported [77]. *B. halotolerans* strain DT1 isolated from dried cabbages of Tianjin was capable of producing exopolysaccharides that could potentially be used as food additive in high-fat food products [78].

Competition with other microorganisms is another essential aspect of *B. halotolerans*' biocontrol mechanism. By rapidly colonizing root surfaces and forming biofilms, *B. halotolerans* can outcompete harmful pathogens for space and nutrients [79]. Additionally, root exudates can stimulate the production of antimicrobial compounds and surfactants, further aiding in the displacement of competitors. For example, surfactin production has been shown to trigger biofilm formation by *B. subtilis* UMAF6614 and enhance the bacterium's colonization capacity [80].

4. Plant Growth-Promoting Effect of *Bacillus halotolerans* in Alleviation of Abiotic and Biotic Stresses

4.1. Production of Indole-3-Acetic Acid

The production of indole-3-acetic acid (IAA), a key auxin, is a central mechanism by which *B. halotolerans* contributes to plant growth promotion [81] (Figure 3). This phytohormone regulates a wide range of physiological processes in plants, including cell elongation, division, and differentiation, as well as root and shoot development [82]. IAA production by rhizobacteria significantly enhances plant growth and resilience under various environmental conditions [83].

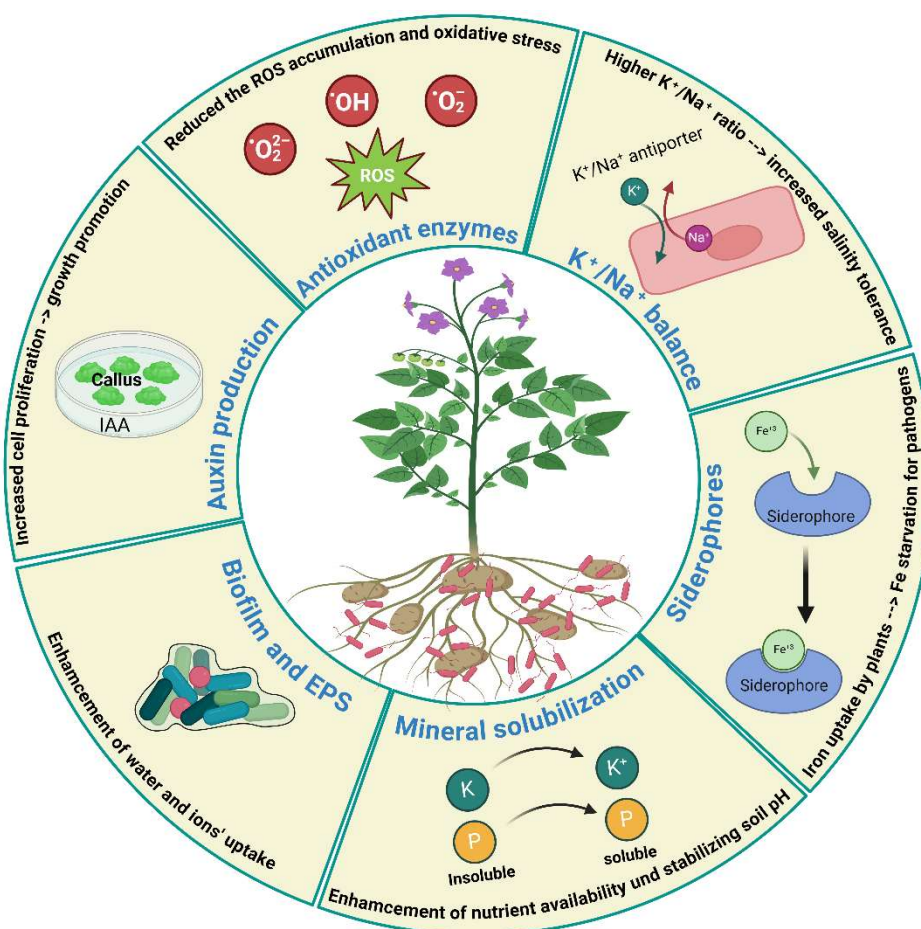


Figure 3. Actions of *B. halotolerans* in plant growth promotion and mitigating abiotic and biotic stresses. Key processes include the production of EPS to stabilize soil and reduce salt stress, synthesis of phytohormones like indole-3-acetic acid (IAA) to enhance root architecture, and the modulation of the K^+/Na^+ balance to prevent ion toxicity. Additional mechanisms, such as nitrogen fixation, phosphate solubilization, and siderophore production, improve nutrient availability and uptake, while biofilm formation aids in root colonization, protecting plants from abiotic stress and boosting growth.

Several reports documented the critical role of IAA synthesis pathways in the plant growth-promoting properties of rhizobacteria [82,84,85]. *Bacillus* species utilize both tryptophan-dependent and -independent pathways for IAA biosynthesis [85]. For instance, the *ipdC* gene, involved in the tryptophan-dependent indole-3-pyruvic acid (IPyA) pathway, played a significant role in bacterial IAA production [84]. Mutants deficient in this gene exhibited reduced colonization capabilities and a diminished ability to promote plant growth. Furthermore, modulation of IAA production under various conditions demonstrated the versatility of *Bacillus* strains. For example, *B. velezensis* strain MOST-IAA produced IAA at optimal levels when cultured with specific carbon and nitrogen sources under controlled pH and temperature, enhancing barley root growth [83].

Similarly, *B. halotolerans* strains isolated from challenging environments, such as saline or heavy metal-contaminated soils, exhibited robust IAA production and other plant growth-promoting traits,

such as phosphate solubilization, nitrogen fixation and ACC deaminase production ensuring their suitability as bioinoculants in stress-prone agricultural systems [86,87]. In addition to enhancing root and shoot development, IAA-producing *B. halotolerans* strains improved rhizosheath formation, as seen in barley plants under drought conditions [81]. This enhanced rhizosheath formation facilitated better water and nutrient uptake, leading to improved drought tolerance [88,89]. Furthermore, multi-trait halotolerant *Bacillus* strains, including *B. halotolerans*, mitigate salinity stress by producing IAA along with other phytohormones and stress-tolerant molecules (e.g. gibberellins, cytokinins), thereby enhancing crop resilience and productivity [2,52,53,90].

4.2. Siderophore Production

Siderophores, low-molecular-weight iron-chelating molecules, are critical secondary metabolites produced by a wide range of microorganisms including *B. halotolerans* to enhance plant growth under iron-limited conditions [91] (Figure 3). These compounds bind ferric iron (Fe^{3+}) in the rhizosphere, increasing its solubility and facilitating its uptake. This mechanism is particularly beneficial in iron-deficient soils, such as calcareous and alkaline environments, where the availability of ferric iron is limited [92].

The siderophores produced by *B. halotolerans* and related species, such as bacillibactin and catecholate-type siderophores, have been widely documented for their role in promoting plant growth and controlling pathogens. For example, *B. halotolerans* JK-25 produces siderophores that inhibit fungal pathogens like *Bipolaris sorokiniana* and improve wheat growth under stress conditions [21]. Similarly, the strains LBG-1-13 of *B. halotolerans* demonstrated siderophore production alongside phosphate solubilization and ACC deaminase activity, enhancing the growth of lily plants under salt and drought stress [52].

In agricultural applications, siderophore production has shown significant benefits in improving crop iron nutrition. *B. halotolerans* strains isolated from rhizospheric soils of various crops demonstrated notable siderophore production, reducing chlorosis symptoms and enhancing biomass production [93]. These strains not only improve iron bioavailability but also promote the uptake of other essential nutrients by solubilizing phosphate or producing EPS contributing to sustainable agricultural practices [94].

In addition to nutrient facilitation, siderophore-producing *B. halotolerans* strains possess antifungal properties. For instance, *B. halotolerans* Jk-25 have been shown to inhibit the growth of *B. sorokiniana* and other soil-borne pathogens, thereby serving a dual role in nutrient cycling and pathogen suppression [21]. Similarly, *B. halotolerans* BFOA1–BFOA4 inhibited four major pathogens *Botrytis cinerea*, *A. alternata*, *P. infestans*, and *Rhizoctonia bataticola* [33]. The adaptability of *B. halotolerans* to abiotic stresses, such as drought and salinity, further amplifies its significance as a bioinoculant. Under these conditions, siderophore production helps in mitigating stress impacts by improving root architecture, maintaining soil moisture, and enhancing micronutrient uptake [36].

4.3. ACC Deaminase Activity

The production of 1-aminocyclopropane-1-carboxylate (ACC) deaminase can lead to plant growth promotion, especially under abiotic stress conditions (Figure 3). ACC deaminase catalyzes the breakdown of ACC, the direct precursor of ethylene in plants, into α -ketobutyrate and ammonia [95]. This activity reduces ethylene levels, which are often elevated under adverse stress conditions like salinity, drought, and heavy metal, thereby alleviating the growth-inhibitory effects of ethylene [96].

Several reports demonstrated the efficacy of ACC deaminase-producing *B. halotolerans* strains in enhancing plant tolerance to abiotic stresses. For instance, strain LBG-1-13 exhibited ACC deaminase activity and promoted plant growth under salt and drought stress, with notable improvements in root and shoot development in lily plants cultivated under these conditions [52]. Additionally, strain B5 of *B. halotolerans* isolated from salt-contaminated soils have shown robust ACC deaminase activity, further confirming their potential as stress-alleviating bioinoculants [97]. The role of ACC deaminase

in plant stress response is further supported by its impact on physiological parameters [86]. ACC deaminase activity has been linked to increased chlorophyll content, enhanced root and shoot biomass, and improved osmotic balance under salinity stress [86,95]. For example, in maize plants treated with halotolerant strains of *B. halotolerans*, stress-induced ethylene levels were reduced, leading to better water retention and improved nutrient uptake [96].

Moreover, the presence of ACC deaminase-producing strains in the rhizosphere not only promotes plant growth but also enhances the plants' ability to withstand biotic stresses, such as soil-borne infections [53]. Multi-trait bacterial isolates, including *B. halotolerans*, show a combined effect of ACC deaminase activity and other plant growth-promoting traits like mineral solubilization and IAA production, which synergistically improve plant growth under stress conditions [53].

4.4. Nitrogen Fixation and Mineral Solubilization

B. halotolerans has the ability to fix atmospheric nitrogen and solubilize essential minerals, such as phosphorus, potassium, and zinc [20,23,24]. These traits enable the bacterium to enhance soil fertility and provide plants with bioavailable nutrients under both normal and stress conditions [98]. Nitrogen fixation is a crucial process that converts atmospheric nitrogen into ammonia, a form usable by plants [98,99]. Extremophilic strains of *B. halotolerans* have been identified as nitrogen-fixing bacteria due to the presence of the nitrogenase enzyme [20]. These strains, isolated from diverse environments, have demonstrated the ability to enhance soil nitrogen levels and contribute to plant growth even under saline and nutrient-deficient conditions [20]. Similarly, *B. halotolerans* MSR-H4 was shown to fix nitrogen effectively, contributing to improved wheat growth under salt stress [24].

In addition to nitrogen fixation, *B. halotolerans* exhibits strong mineral solubilization activities (Figure 3). Strains such as SSVP2 and KKD1 have demonstrated the ability to solubilize phosphorus, a vital nutrient for plant development [23,53]. The production of phosphatases by *B. halotolerans* converts insoluble phosphate into soluble forms like H_2PO_4^- , enhancing its availability for plant uptake, especially under saline conditions [23,53]. Other strains, including ADCN (AD9), have been shown to solubilize phosphate even at high salt concentrations, further highlighting the salt tolerance of this bacterium [57]. Potassium and zinc solubilization are additional characteristics of *B. halotolerans*. The solubilization of potassium and zinc enhances nutrient cycling in the rhizosphere, thereby improving plant growth and health [100–102]. Strains SSVP2 and ADCN have been noted for their ability to solubilize potassium, with zinc solubilization also observed in some extremophilic *B. halotolerans*, resulting in clear zones on mineral solubilization assays [20,53].

Through these mechanisms, *B. halotolerans* not only enhances nutrient availability but also stabilizes soil pH, as evidenced by the strain KKD1, which maintained optimal pH levels in saline soils, creating a favorable environment for plant growth [23]. These attributes position *B. halotolerans* as a key player in sustainable agriculture, offering eco-friendly alternatives to chemical fertilizers.

4.5. Improving K^+/Na^+ Balance in Plants

Maintaining an optimal K^+/Na^+ balance in plants is critical for mitigating salt stress and ensuring normal metabolic activities [103] (Figure 3). *B. halotolerans* strains have been shown to play a key role in improving the ionic balance under saline conditions. For instance, plants treated with *B. halotolerans* demonstrated a significantly higher K^+/Na^+ ratio and reduced sodium accumulation in roots and shoots [104]. This improved ionic homeostasis correlates with enhanced plant growth and resilience in saline environments [24,104].

4.6. Induction of Antioxidant Enzymes

B. halotolerans is also known to elicit the production of antioxidant enzymes, which serve as the first line of defense against oxidative stress caused by abiotic and biotic stressors [105] (Figure 3). These enzymes, including superoxide dismutase (SOD), peroxidase, polyphenol oxidase, and phenylalanine ammonia lyase, have been shown to reduce the accumulation of reactive oxygen

species (ROS), thereby minimizing cellular damage and enhancing plant survival under stress conditions [106]. For instance, plants treated with the strain KLBC XJ-5 of *B. halotolerans* exhibited significantly higher antioxidant enzyme activities, which contributed to reduced grey mold decay in postharvest strawberries and improved overall plant resilience [26].

5. Additional Applications of *B. halotolerans*

5.1. Nematode Management

Plant-parasitic nematodes (PPNs) are microscopic non-segmented worms that parasitize plant roots and other tissues, causing significant damage to crops worldwide. Root-knot nematodes (*Meloidogyne* spp.), in particular, are recognized as one of the most destructive genera, responsible for severe yield losses in vegetables and cereals globally.

Species within the *Bacillus* genus, offer promising eco-friendly solutions for nematode management. *Bacillus* spp. employ multiple mechanisms, including the production of VOCs, antibiotics, and enzymes, to inhibit nematode development and reproduction directly [107]. Additionally, they can enhance plant resistance to nematodes through induced systemic resistance (ISR) and biofilm formation, which acts as a physical barrier to nematode invasion [108]. *B. halotolerans* has shown remarkable potential as a biocontrol agent against PPNS. Recently, *B. halotolerans* strains demonstrated strong nematicidal activity against *Meloidogyne incognita* and *M. javanica* [46]. In the latter study, the authors found that strain LYSX1 was highly effective in inhibiting egg mass hatching and reducing juvenile nematode survival in a dose-dependent manner. Similarly, *B. halotolerans* strain Ba2-6 achieved 93.85% mortality of *Heterodera glycines* juveniles in greenhouse and field trials, highlighting its efficiency as a BCA for soybean crops [50]. In tomato crops, *B. halotolerans* not only suppressed nematode populations but also enhanced plant growth and yield [109]. The effectiveness of *B. halotolerans* in nematode management is attributed to its ability to produce nematicidal compounds and induce systemic resistance in plants. These compounds disrupt nematode development, interfere with feeding site formation, and suppress reproduction [110].

5.2. Bioremediation

Heavy metals are persistent environmental pollutants due to their non-biodegradable nature and ability to accumulate in ecosystems, posing serious threats to both plant and human health [111]. They originate from both natural sources, such as soil erosion and volcanic activity, and anthropogenic sources, such as mining, fossil fuel combustion, and industrial waste [112]. Bioremediation is an eco-friendly and cost-effective approach to mitigate environmental contamination caused by toxic substances such as heavy metals, hydrocarbons, and aromatic pollutants. This process includes the ability of microorganisms to detoxify or remove harmful contaminants through mechanisms such as biosorption, bioaccumulation, and bioprecipitation [113]

Bacillus species, known for their tolerance and ability to grow in extreme conditions, are widely studied for bioremediation. They degrade hydrocarbons, solubilize heavy metals, and restore soil fertility [113]. For example, *B. halotolerans* strain 1-1 has been identified as a potent crude oil-degrading bacterium, demonstrating its ability to bioremediate hydrocarbon-contaminated soils effectively [114]. Similarly, *B. halotolerans* B28 has shown the capacity to degrade benzoic acid, an aromatic pollutant found in soils affected by continuous cropping, thus mitigating its inhibitory effects on crop growth [51].

Additionally, *B. halotolerans* has been isolated from lead- and zinc-contaminated soils, where it exhibited plant growth-promoting traits such as phosphate solubilization, siderophore production, and nitrogen fixation, enhancing both plant health and soil quality under toxic conditions [115]. These features highlight the dual role of *B. halotolerans* in promoting plant growth and remediating contaminated environments, making it a valuable bioresource for sustainable agriculture and environmental restoration.

6. Conclusion and Future Perspectives

B. halotolerans has emerged as a versatile and promising PGPR and BCA, particularly under challenging conditions such as salinity stress. Its ability to produce phytohormones, volatile organic compounds, hydrolytic enzymes, and stress regulators like ACC-deaminase and exopolysaccharides underscores its potential in enhancing crop productivity and soil health. Additionally, some strain of *B. halotolerans* demonstrates significant applications in bioremediation of heavy metals and other environmental pollutants, positioning it as an eco-friendly solution to mitigate soil and water contamination and restore ecosystem balance.

However, while numerous studies highlight its efficacy under controlled laboratory conditions, further research is needed to establish its full potential under natural and field settings. Rigorous pot and field trials are crucial to validate its biocontrol and growth-promoting efficiency across different crops and environmental conditions [32,53]. Moreover, understanding the ecological impact of *B. halotolerans* on soil microbial communities and ecosystem dynamics will provide insights into its long-term sustainability and practical application.

Future research should also focus on unraveling the molecular mechanisms underlying plant-microbe interactions, particularly in response to abiotic and biotic stressors, to enhance our understanding of their “molecular dialogue” [116]. This knowledge will pave the way for designing innovative microbial formulations and bioinoculants tailored for saline soils, bioremediation, and disease management [117,118]. The development of advanced technologies, such as next-generation sequencing (NGS), will allow researchers to uncover the complex biodegradation pathways and stress alleviation mechanisms of *B. halotolerans* [113]. By integrating *B. halotolerans* into sustainable agricultural practices, its applications as biofertilizers, biopesticides, and phytoremediators can mitigate the adverse effects of salinity, enhance crop resilience, and improve soil fertility. The continued exploration of this bacterium holds great promise for addressing global challenges in food security and environmental sustainability.

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Abbreviations

The following abbreviations are used in this manuscript:

ACC	1-aminocyclopropane-1-carboxylate
AMCs	Antimicrobial Compounds
BCA	Biological Control Agent
BGCs	Biosynthetic Gene Clusters
CAT	Catalase
cPPPs	chemical Plant Protection Products
CWDEs	Cell Wall Degrading Enzymes
EPS	Extracellular Polymeric Substances
FBCC	Freshwater Bioresources Culture Collection
IAA	Indole-3-Acetic Acid
IPM	Integrated Pest Management
ISR	Induced Systemic Resistance

LB	Luria-Bertani medium
MFS	Major Facilitator Superfamily
NGS	Next Generation Sequencing
NRPS	Non-Ribosomal Peptide Synthetases
PAL	Phenylalanine Ammonia-Lyase
PGPB	Plant Growth-Promoting Bacteria
PKS	Polyketide Synthase
PPNs	Plant-Parasitic Nematodes
POX	Peroxidase
PPO	Polyphenol Oxidase
ROS	Reactive Oxygen Species
rRNA	Ribosomal Ribonucleic Acid
SOD	superoxide dismutase
tRNA	Transfer ribonucleic acid
TSA	Tryptic Soy Agar
VOCs	volatile organic compounds

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