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Endospore-producing Endophytes: Structural Adaptations, Functional Roles, and Their Significance in Plant Growth and Stress Management

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Authors' contributions

This work was carried out in collaboration between both authors. Both authors read and approved the final manuscript.

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Review Article

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ABSTRACT

The primary genera of endospore-producing endophytes are *Bacillus* and *Clostridium*, both known for their robust survival strategies and diverse metabolic capabilities. Endospore-forming endophytic bacteria, particularly members of the genus *Bacillus*, are gaining increasing recognition for their multifaceted roles in sustainable agriculture. These microorganisms are capable of colonizing internal plant tissues and forming highly resistant endospores that ensure their survival under harsh environmental conditions. This review highlights the structural and functional aspects of bacterial endospores, including their formation, layers, and resistance mechanisms. Furthermore, it explores the significance of endophytic *Bacillus* spp. as plant growth-promoting

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agents through nutrient solubilization, phytohormone production, and disease suppression. The ability of these bacteria to alleviate biotic stresses through antimicrobial metabolites and systemic resistance, as well as their contribution to abiotic stress tolerance *via* antioxidant enzyme activation and ion homeostasis, is discussed in detail. The unique combination of persistence, adaptability, and beneficial plant interactions makes endospore-forming *Bacillus* spp. highly valuable for modern agricultural applications, especially under changing climatic conditions.

Keywords: Bacillus; endospore; endophytes; Plant Growth-Promoting Bacteria (PGPB); abiotic stress; biocontrol; ISR; nutrient solubilization; drought tolerance; salinity stress.

1. INTRODUCTION

Endospore-forming endophytic bacteria are a unique group of microbes that reside within the internal tissues of plants and possess the ability to produce highly resistant spores. Endospore-producing endophytic bacteria, particularly those belonging to the genera *Bacillus* and *Clostridium*, play a pivotal role in sustainable agriculture by enhancing plant growth through multifaceted mechanisms. These microorganisms colonize the internal tissues of host plants and form endospores that enable survival under adverse environmental conditions. Genera like *Bacillus* and *Paenibacillus* are well-known representatives that establish stable, beneficial relationships with their host plants, often enhancing plant growth and resilience. The formation of endospores allows these bacteria to withstand unfavourable environmental conditions while remaining viable within plant tissues, thereby ensuring their continued presence and contribution to plant health.

Research by Fira et al. (2018) and Ambawade and Pathade (2015) has emphasized the important role of endospore-forming endophytic bacteria in promoting plant growth, improving nutrient uptake, and enhancing tolerance to environmental stress. Additionally, their potential in suppressing a range of crop diseases has been demonstrated (Nandana and Anith, 2024; Sivapriya et al., 2024). Due to their resilience and multifunctional benefits, these bacteria are considered valuable agents for advancing sustainable agriculture and developing biotechnological solutions in plant-microbe interactions, particularly under the challenges posed by climate change.

2. ENDOSPORE

2.1 Endospore Structure

Endospores are highly resistant, dormant structures formed by certain bacteria to survive unfavourable environmental conditions. To observe endospores under the microscope, the Schaeffer-Fulton staining method is commonly used, which stains the endospore green with malachite green and the vegetative cell pink with safranin (Fig. 1).

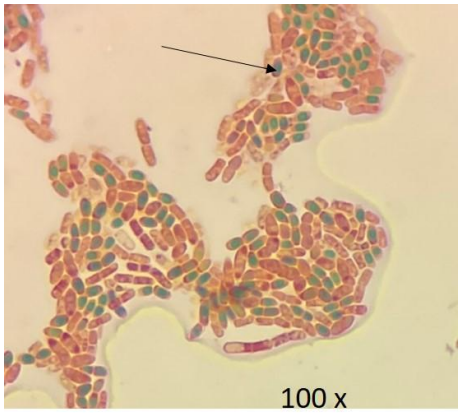

Fig. 1. Endospore-producing endophytic bacteria isolated from ginger visualized under 100× magnification using the Schaeffer–Fulton staining method. The green-stained structures (indicated by arrows) represent endospores stained with malachite green, while the surrounding vegetative cells appear pink due to safranin counterstaining

The structural organization of spores remains largely conserved across all endospore-forming bacteria. Spore formation is a tightly regulated and intricate process involving multiple stages of assembly. A digital illustration of a *Bacillus subtilis* spore (Fig. 2) illustrates the complex architecture, particularly the spore coat, which consists of several distinct layers. This protective coat is made up of up to 25 different polypeptides, many of which are extensively cross-linked, contributing to the spore's resilience. The spore coat contributes to resistance against chemical and enzymatic challenges by functioning primarily as a selective permeability barrier (Driks, 1999). Located beneath the spore coat is a dense peptidoglycan layer, which may contribute up to 10% of the spore's total dry weight. This layer is composed of two distinct regions: a thin inner layer known as the primordial cell wall, and a thicker outer region called the cortex. The primordial cell wall constitutes only about 2–5% of the total peptidoglycan content in the spore. It helps maintain cellular integrity following germination and acts as a scaffold for peptidoglycan synthesis during the outgrowth phase (Atrih et al., 1996).

The cortex exhibits a distinct structural organization and features that are widely conserved among various spore-forming bacteria (Fig. 3). Notable characteristics include the presence of α-lactam modifications at approximately every alternate muramic acid residue and a low degree of cross-linking, with only about 2.9% of muramic acid residues being cross-linked in *B. subtilis* spores (Atrih & Foster, 2001). The low level of peptidoglycan cross-linking in spores is thought to be crucial for maintaining the specific architecture of this structural polymer. It is proposed that this reduced cross-linking represents a functional balance—providing sufficient wall stability to support core dehydration, while also allowing the necessary flexibility and degradability required for spore outgrowth. This structural property also facilitates cortex hydrolysis during germination, aiding in the transition of the spore from dormancy to active growth (Meador-Parton & Popham, 2000).

The spore core, or cytoplasm, houses all essential metabolic components of the cell, including the genomic DNA. In its dormant state, the core remains highly dehydrated, a condition that contributes significantly to the spore's heat resistance (Gerhardt & Marquis, 1989). Upon germination and rehydration, the enzymes within the core regain activity. The core is also rich in minerals such as Ca^{2+}, Mn^{2+}, and Mg^{2+}, which are primarily chelated with di Anexolinic acid, a spore-specific molecule. Additionally, the core contains a high concentration of small acid-soluble proteins (SASPs) that bind to DNA, playing a critical role in protecting it from UV damage (Setlow, 1994).

The inner membrane of dormant spores exhibits a highly compressed, polycrystalline structure and is significantly more viscous compared to the membrane of vegetative cells, to which it transitions during germination (Elmes et al., 1983). Modifications in the inner membrane have been found to influence germination behaviour, as the interaction of specific germinates with this membrane leads to changes in its fluidity (Skomurski et al., 1983).

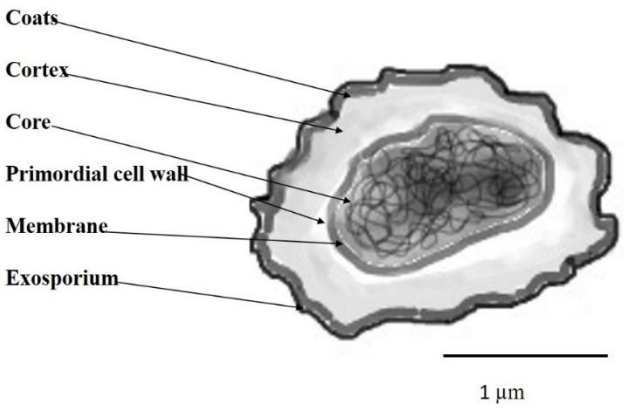

Fig. 2. Digitally illustrated representation of an endospore. The image highlights the endospore structure (Driks, 1999)

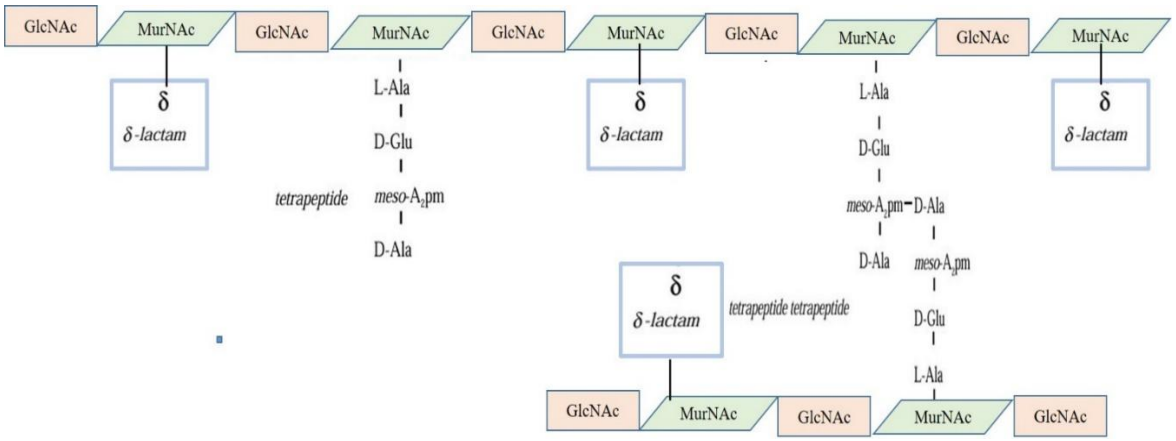

Fig. 3. The distinct structural organization in cortex. Notable characteristics include the presence of α-lactam modifications at approximately every alternate muramic acid residue and a low degree of cross-linking (Atrih & Foster, 2001)

2.2 Endospore Formation

Endospore formation in bacteria, particularly in *Bacillus* and *Clostridium* species, is a highly coordinated developmental process that is triggered by environmental stress, such as nutrient limitation. The process is initiated by the activation of the master regulator Spo0A, a response regulator that becomes phosphorylated through a complex phosphorelay system involving multiple kinases (Hoch, 1993). Once phosphorylated, Spo0A~P activates the expression of genes required for sporulation and represses genes involved in vegetative growth.

Sporulation begins with asymmetric cell division, generating a smaller forespore and a larger mother cell. The forespore is then engulfed by the mother cell membrane, forming a double-membraned structure. Protective layers such as the cortex, composed of loosely cross-linked peptidoglycan, and the multi-layered spore coat are sequentially synthesized. Meanwhile, the spore core dehydrates and accumulates dipicolinic acid and calcium ions, contributing to heat resistance and dormancy. Finally, the mother cell undergoes programmed lysis, releasing the mature endospore into the environment. The spore remains metabolically inactive yet highly resilient, capable of germinating into a vegetative cell when conditions become favourable.

2.3 Spore Resistance Mechanisms

Bacterial spores have evolved as a robust survival strategy, enabling them to endure extreme environmental conditions (Fig. 4). Compared to their vegetative forms, spores exhibit significantly enhanced resistance. The molecular basis of their heat resistance is complex and involves multiple factors. Proteins and enzymes are believed to be the primary targets during heat-induced spore killing (Belliveau et al., 1992). Interestingly, enzymes extracted from spores lose activity at much lower temperatures than the same enzymes within intact spores, highlighting the protective nature of the spore structure. However, the specific enzymes and proteins that serve as the key targets for thermal inactivation remain unclear.

3. ENDOSPORE-FORMING ENDOPHYTES AS PLANT GROWTH PROMOTERS

Species of the genus *Bacillus*, commonly found in soil, are frequent endophytes known for their significant contributions to plant growth and development. These bacteria influence plant physiology by producing phytohormones or growth regulators that, even in low concentrations, can stimulate, suppress, or alter plant growth. *Bacillus* spp. enhance plant health through multiple strategies, including the suppression of phytopathogens. For example, *Bacillus subtilis* SWR01 demonstrates traits such as swarming motility and chemotaxis, which are vital for efficient root colonization (Gao et al., 2018). Moreover, the ability to form biofilms often induced by seed and root exudates—further supports their successful establishment in the rhizosphere and endosphere (Zhang et al., 2016).

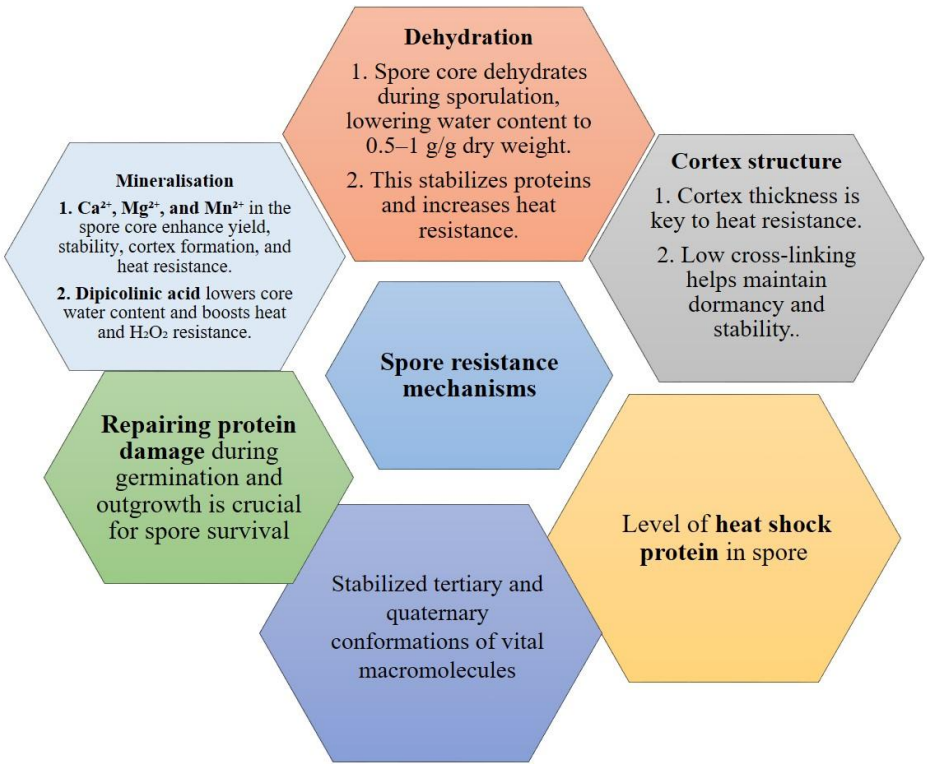

Fig. 4. Spore resistance mechanisms for surviving extreme environmental conditions (Belliveau et al., 1992)

One of the key roles of *Bacillus* species in plant-microbe interactions is their ability to solubilize nutrients and enhance nutrient uptake. These bacteria can convert complex nutrient forms into simpler, bioavailable forms for plant absorption. Studies have revealed that both *Bacillus* and *Paenibacillus* species carry the nifH gene, which is associated with nitrogen fixation (Ding et al., 2005). *Bacillus* spp. also contribute to phosphorus availability by producing organic acids such as gluconic, acetic, succinic, and propionic acids (Saied et al., 2018). Certain strains, including *B. amyloliquefaciens* NBRI-SN13, have demonstrated efficient tricalcium phosphate solubilization (Nautiyal et al., 2013). In addition, species like *B. megaterium* and *B. cereus* have been shown to solubilize phosphorus from organic sources such as poultry and fish bones (Saeid et al., 2018). *Bacillus* species can dissolve potassium from insoluble minerals through the production of organic acids, which enhance mineral solubilization by providing protons or complexing calcium ions (Teotia et al., 2016).

Bacillus species are also known for producing phytohormones such as auxins, gibberellins, and cytokinins, which play a vital role in promoting plant growth and increasing crop yield (Miljakovic et al., 2020). Some strains synthesize ACC deaminase, an enzyme that lowers ethylene levels in plants, thereby enhancing growth under stress conditions (Xie et al., 2021). The production of growth regulators like gibberellic acid (GA_3) and indole-3-acetic acid (IAA) by *Bacillus* spp. improves nutrient uptake and stimulates plant development (Shafi et al., 2017). These phytohormones contribute to better nutrient absorption and strengthen plant defence against both biotic and abiotic stresses. Endophytic strains such as *Bacillus subtilis*, *B. methylotrophicus*, and *B. cereus* are capable of producing ammonia, solubilizing essential nutrients, and fixing atmospheric nitrogen (Hassan et al., 2017). Species like *B. amyloliquefaciens* and *B. velezensis* are well-known for their gibberellin production, which promotes plant growth by enhancing seed germination and related developmental processes (Shahzad et al., 2020). In addition, the synthesis of cytokinins by these bacteria contributes to root system development by stimulating lateral root elongation and increasing root hair formation (Asari et al., 2017).

Siderophore production by *Bacillus* species plays a key role in enhancing iron availability to plants. These compounds chelate ferric iron (Fe^{3+}) and

convert it into the more plant-accessible ferrous form (Fe^{2+}) (Wilson et al., 2016). Notably, species such as *B. anthracis*, *B. thuringiensis*, and *B. subtilis* have been reported to produce siderophores (Ramadoss et al., 2013; Goswami et al*.,* 2014).

Overall, *Bacillus* species play a crucial role in promoting plant growth and development through multiple direct and indirect mechanisms. Their capacity to form resilient endospores contributes to long-term stability and ease of formulation, making them ideal candidates for commercial bioinoculants aimed at enhancing crop productivity and resistance to pathogens.

4. ENDOPHYTIC *Bacillus* AND BIOTIC STRESS MITIGATION

4.1 Mechanisms

Pathogenic microbes pose a major threat to plant health, often leading to significant crop losses. Endophytic bacteria, particularly *Bacillus* species, help combat these threats by secreting bioactive compounds into the rhizosphere, indirectly supporting plant growth. These bacteria suppress a wide range of bacterial, fungal, and viral pathogens through the production of siderophores, antibiotics, hydrogen cyanide, pyoluteorin, pyrrolnitrin, and cell wall–degrading enzymes such as chitinases, cellulases, and proteases (Olanrewaju et al., 2017).

Bacillus species synthesize both ribosomally produced antibiotics (bacteriocins) and non-ribosomally produced compounds such as lipopeptides and polyketides, enabling broad-spectrum disease suppression (Miljakovic et al., 2020). Bacteriocins like amylolysin, amysin, and subtilin have been identified in various *Bacillus* strains and are key contributors to their antimicrobial effects (Abriouel et al*.,* 2011). For instance, *Bacillus subtilis* BSn5 demonstrates strong activity against *Erwinia carotovora* subsp. *carotovora* and produces antifungal agents like iturin A, which effectively inhibit fungal pathogens (Cho et al., 2003).

Bacillus amyloliquefaciens RWL-1 has been shown to enhance disease resistance in tomato plants against *Fusarium oxysporum* f. sp. *lycopersici* by stimulating amino acid biosynthesis and strengthening plant defence responses (Shahzad et al., 2020). Various *Bacillus* species produce cyclic lipopeptides such as iturin, bacillomycin, fungicin, and surfactin, which disrupt pathogen cell membranes (Fira et al*.,* 2018). In addition, these bacteria secrete lytic enzymes including chitinases, glucanases, cellulases, lipases, and proteases that degrade the cell walls of fungal and bacterial pathogens (Tran et al*.,* 2022). *Bacillus* spp. also trigger induced systemic resistance (ISR), leading to a broad-spectrum defence response in plants (Li & Zou, 2017). Species such as *B. amyloliquefaciens*, *B. subtilis*, *B. pasteurii*, *B. cereus*, *B. pumilus*, *B. mycoides*, and *B. sphaericus* have demonstrated ISR-mediated protection against a wide range of plant pathogens, including leaf-spotting bacteria and fungi, systemic viruses, root-knot nematodes, crown-rot, stem blight, blue mold, and late blight diseases (Caulier et al*.,* 2019).

4.2 Biocontrol of Foliar Diseases

Various studies have reported the effectiveness of *Bacillus subtilis* and related endospore-forming bacteria in controlling foliar diseases. *In vitro* evaluations have shown that *Bacillus* species can suppress the growth of leaf spot pathogens by inducing structural changes in fungal hyphae, such as granulation, coiling, and cytoplasmic damage (Analia & Cecilia, 2007). In field experiments, *B. subtilis* treatments led to a 75% reduction in bean rust severity, performing comparably or even better than the commonly used fungicide mancozeb (Baker et al., 1985). Research on Cercospora leaf spot in sugar beet indicated that using bacterial isolates from the phyllosphere, applied at concentrations of 1×10^6 CFU/mL or higher, significantly lowered disease levels when sprayed three days before pathogen inoculation. Although this approach was less effective than chemical fungicides, treated plants consistently showed reduced disease incidence compared to untreated controls (Collins & Jacobsen, 2003).

Commercial formulations of *B. subtilis*, such as FZB24® and Phytovit®, have also shown strong potential against major foliar diseases of tomato, including early and late blight, powdery mildew, and leaf mold. Culture filtrates from *B. subtilis* notably decreased the biomass of *Phytophthora infestans* in tomato leaves by 83% and led to more than 70% reduction in disease severity (Sultan, 2012). A plant growth-promoting strain, *B. subtilis* UD1022, was found to enhance resistance in *Arabidopsis thaliana* by blocking stomatal entry of *Pseudomonas syringae* through induced stomatal closure (Kumar et al., 2012). This effect was also observed in crops like

romaine lettuce and spinach, where the strain helped limit pathogen entry (Markland et al., 2013). Collectively, these findings emphasize the role of endospore-forming bacteria, particularly *B. subtilis*, as promising biocontrol agents capable of reducing foliar disease severity and enhancing plant defence mechanisms across a range of crops.

4.3 Biocontrol of Root Diseases

Several studies have demonstrated the potential of *Bacillus subtilis* strains in managing soilborne plant pathogens. Backman et al. (1997) reported that 60–75% of cotton seeds in the US were treated with *B. subtilis* GB03 (Kodiak®), and while its performance was inconsistent, it showed a 22% reduction in *Fusarium* root rot in beans and an 81% increase in chickpea stand. Chen et al. (2013) identified six out of 60 *B. subtilis* isolates that exhibited over 50% control efficacy against *Ralstonia solanacearum* in tomato. These strains also formed strong biofilms and carried genes linked to biofilm and matrix production. Similarly, *B. subtilis* EU07 showed 75% disease reduction in tomatoes infected by *Fusarium oxysporum* f.sp. *radicis-lycopersici*, outperforming QST 713, which had only 52% reduction (Baysal et al., 2008). The EU07 strain contained a unique YrvN protein associated with protease activity, which could serve as a marker for selecting potent biocontrol strains.

In canola, *B. subtilis* QST 713 (Serenade®) successfully suppressed *Plasmodiophora brassicae* infection when applied twice, with enhanced resistance observed through increased expression of defence-related genes (Lahlali et al., 2013). Asaka and Shoda (1996) demonstrated that *B. subtilis* RB14 effectively controlled damping-off in tomato caused by *Rhizoctonia solani*, primarily due to the production of iturin A. Brewer and Larkin (2005) noted that while none of the 28 tested biocontrol agents completely managed stem canker and black scurf in potato, *B. subtilis* GB03 and some fungal strains reduced canker severity by 40–49%. Additionally, combining *B. subtilis* with *Trichoderma virens* provided better disease suppression than individual applications.

4.4 Biocontrol of Post-harvest Diseases

Research across various crops has highlighted the efficacy of *Bacillus subtilis* strains in managing postharvest diseases. Liu et al. (2011) evaluated several *B. subtilis* strains and sodium bicarbonate, both individually and in combination, for controlling ring rot in pears caused by *Botryosphaeria berengeriana*. All treatments significantly suppressed pathogen growth both *in vitro* and on fruit, with the combined treatment showing enhanced effectiveness in both preventive and curative applications. Similarly, Korsten et al. (1997) demonstrated that *B. subtilis* (B246), along with *B. cereus* (B247 and B249) and *B. licheniformis* (B248), exhibited strong antagonism against a range of avocado postharvest pathogens such as *Colletotrichum gloeosporioides*, *Phomopsis perseae*, *Drechslera setariae*, *Pestalotiopsis versicolor*, and *Fusarium solani*, primarily through antibiotic production.

In a recent study in stored ginger seeds, the lowest disease index for rhizome rot (27.33%) was observed in the treatment with a consortium of *Bacillus* isolates, which was comparable to the chemical control with 2% copper oxychloride (Nandana and Anith, 2024). In another recent study, the rhizobacterial strain *B. subtilis* UD1022 was shown to inhibit the growth of *Listeria monocytogenes*, a human pathogen, particularly during its logarithmic growth phase. When applied as a dip treatment to cantaloupes, the strain significantly reduced *Listeria* levels on the rind after 8 hours of incubation at 37 °C, indicating its potential use in food safety applications beyond plant disease control (Swain et al., 2008). These findings collectively support the versatility of *Bacillus* spp. as biocontrol agents across both agricultural and food safety domains.

Bacillus species are widely recognized as effective biocontrol agents against a broad spectrum of plant pathogens, including bacterial, fungal, viral and nematode diseases (Table 1). These beneficial microbes exert their antagonistic effects through multiple mechanisms such as the production of antibiotics, lytic enzymes, and siderophores, as well as by inducing systemic resistance in host plants. For bacterial diseases, strains like *B. amyloliquefaciens* and *B. subtilis* have demonstrated control over pathogens such as *Streptomyces scabies*, *Clavibacter michiganensis*, and *Xanthomonas axonopodis*. In fungal disease management, *Bacillus* spp. effectively suppress biotrophic, hemibiotrophic, and necrotrophic fungi, including *Fusarium oxysporum*, *Botrytis cinerea*, and *Plasmopara viticola*, by disrupting their growth and infection cycles. Additionally, *Bacillus* strains have shown promise in managing plant viral infections such

as Tomato yellow leaf curl virus (TYLCV) and Cucumber mosaic virus (CMV) by priming plant immune responses and limiting viral spread. Their ability to colonize plant surfaces and rhizospheres, along with their environmental safety and ease of formulation, makes *Bacillus* an ideal candidate for sustainable disease management in agriculture.

5. ABIOTIC STRESS MITIGATION

Bacillus species are widely acknowledged for their ability to mitigate abiotic stresses such as drought, salinity, and heavy metal toxicity, all of which can severely affect crop performance. They employ multiple mechanisms to reduce the negative effects of these stresses.

5.1 Stress Due to Salinity and Heavy Metal Toxicity

Marulanda et al. (2009) reported that *Bacillus* colonization enhances root function, particularly by improving water absorption and maintaining ion balance under drought and saline conditions. *Bacillus* spp. play a significant role in regulating ion homeostasis in plants under salinity stress by influencing the expression of the high-affinity potassium transporter 1 (HKT1), which is essential for maintaining the sodium-potassium balance (Viera-Pires et al., 2013). Under saline conditions, where sodium levels in the soil are elevated, *Bacillus*-produced exopolysaccharides help reduce sodium uptake by forming a protective barrier at the root surface. This action supports ion regulation in the plant, enhancing stress tolerance and promoting growth (Radhakrishnan et al., 2017).

The role of *Bacillus subtilis* in alleviating salinity stress has been highlighted by Abeer et al (2015), who reported that the bacterium enhances lipid synthesis, thereby helping to maintain membrane integrity and reduce oxidative damage caused by lipid peroxidation. Oxidative stress, commonly triggered by salinity and heavy metals such as cadmium, copper, zinc, chromium, and nickel, leads to cellular damage in plants. *Bacillus* spp. mitigates this stress by boosting the plant's antioxidant defence system, including the activation of catalase and peroxidase enzymes that neutralize reactive oxygen species (ROS). In addition, they enhance protease activity, which may assist in detoxifying metal-binding proteins or degrading damaged proteins under metal stress (Pandey et al., 2013).

5.2 Drought and Oxidative Stress

Several studies have demonstrated the effectiveness of endophytic *Bacillus* strains in enhancing plant tolerance to drought and oxidative stress. Kuramshina and Khairullin (2023) reported that biopriming wheat, pea, and maize seeds with *Bacillus subtilis* strains enhanced resistance to drought and oxidative stress by activating the plant antioxidant defence system. Similarly, *B. licheniformis* K11, known to produce ACC deaminase, was shown to improve drought tolerance in pepper plants (Lim and Kim, 2013). Eke et al. (2019) isolated endophytic *Bacillus* from cactus and used it for tomato seed biopriming, which led to changes in stomatal behaviour, photosystem activity, oxidative response, and internal leaf temperature through the action of enzymes such as guaiacol peroxidase and catalase. In another study, *Bacillus subtilis* was found to enhance drought tolerance in wheat seedlings by reducing lipid peroxidation and proline content, while also preventing electrolyte leakage from plant tissues under stress conditions (Lastochkina et al., 2020).

5.3 Stress Due to Submergence and Flooding

Endospore-producing endophytes, particularly those belonging to the phylum Firmicutes such as *Bacillus* and *Paenibacillus*, play a pivotal role in mitigating flooding and submergence stress in plants. Their ability to form resilient endospores allows them to survive and remain functionally active under oxygen-deprived, waterlogged conditions. Under flooding stress, rice culms exhibit a marked decline in aerobic bacterial groups like Gammaproteobacteria, while members of Firmicutes, especially *Bacillus* species, become more dominant due to their adaptability (Cui et al., 2019). In addition, the application of endospore-forming bacteria such as *Bacillus*, *Paenibacillus*, *Microbacterium*, and *Methylophaga* has been shown to alleviate flooding stress in rice by significantly reducing ethylene levels, a stress hormone that accumulates under submergence (Bal & Adhya, 2021). Flooding also causes a shift in the soil microbial community, favouring the proliferation of bacterial taxa capable of anaerobic respiration, including those within Firmicutes and Desulfobacterota, while reducing the abundance of Actinobacteria and Proteobacteria. Moreover, genera such as *Geobacter* and *Clostridium*, known for their strict anaerobic metabolism and

Table 1. Endospore producing endophytes used as biocontrol agents against various pathogen groups

Pathogen group	Pathogen species	Disease	Biocontrol *Bacillus* species	Crop(s)	Experimental set-up	Reference
Bacteria	*Streptomyces scabies*	Common scab	*B. amyloliquefaciens*	Potato	*In vitro*, Pot assays, Field	Lin et al., 2018
	Clavibacter michiganensis subsp. *michiganensis*	Bacterial canker	*B. amyloliquefaciens*	Tomato	*In vitro*, Pot assays	Gautam et al., 2019
	Rhizobium radiobacter	Crown gall	*B. subtilis/B. amyloliquefaciens*	Tomato	*In vitro*, *In vivo*	Frikha-Gargouri et al., 2017
	Erwinia amylovora	Fire blight	*B. amyloliquefaciens*	Pear/Apple	*In vitro*, Field	Ait Bahadou et al., 2018
	Pseudomonas syringae	Leaf spot	*B. amyloliquefaciens/B. pumilus*	Sugar beet	*In vitro*, *In vivo*	Nikolić et al., 2019
	Xanthomonas axonopodis pv. *vesicatoria*	Bacterial leaf spot	*B. amyloliquefaciens*	Tomato/Pepper	*In vitro*, *In vivo*	Medoet et al., 2020
Fungi	*Cladosporium fulvum*	Tomato leaf mold	*B. subtilis*	Tomato	*In vitro*, Pot assays	Wang et al., 2018
	Blumeria graminis	Powdery mildew	*B. velezensis*	Winter wheat/Spring barley/Oats/Triticale	Field, Greenhouse	Matzen et al., 2019
	Plasmopara halstedii	Downy mildew	*Bacillus* spp.	Sunflower	Field, Greenhouse	Nandeeshkumar et al., 2008
	Plasmopara viticola	Downy mildew	*B. subtilis/B. pumilus*	Grapevine	*In vitro*, Field	Zhang et al., 2017
	Mycosphaerella graminicola (*Zymoseptoria tritici*)	Leaf blotch	*B. megaterium*	Winter wheat	*In vitro*, *In vivo*	Kildea et al., 2008
	Pyricularia oryzae	Rice blast	*Bacillus* spp.	Rice	*In vitro*, Greenhouse	Rais et al., 2016
	Bipolaris sorokiniana	Wheat spot blotch	*B. subtilis*	Wheat	*In vitro*, *In vivo*	Villa-Rodríguez et al., 2019
	Colletotrichum acutatum	Anthracnose	*B. amyloliquefaciens*	Loquats	*In vitro*, *In vivo*	Wang et al., 2020
	Botrytis cinerea	Gray mold	*B. velezensis*	Pepper	*In vitro*, Greenhouse	Jiang et al., 2018
	Fusarium oxysporum	Wilt	*B. velezensis*	Tomato	Greenhouse, Field	Elanchezhiyan et al., 2018
	Rhizoctonia solani	Damping-off	*B. subtilis/B. amyloliquefaciens*	Tomato	*In vitro*, Greenhouse, Field	Solanki et al., 2015
	Sclerotinia sclerotiorum	White mold	*B. velezensis*	Tomato	*In vivo*, Greenhouse	Farzand et al., 2019
	Pythium aphanidermatum	Damping-off	*B. amyloliquefaciens*	Tomato	*In vivo*, Greenhouse	Zouari et al., 2016
	Phytophthora infestans	Late blight	*B. subtilis*	Potato	*In vitro*, Pilot field	Caulier et al., 2018
Virus	Tomato yellow leaf curl virus (TYLCV)	-	*B. velezensis/B. amyloliquefaciens*	Tomato	*In vitro*, Pot assays	Guo et al., 2019
	Cucumber mosaic virus (CMV)	-	*B. amyloliquefaciens*	Pepper/*Nicotiana benthamiana*	*In vivo*, Field	Lee and Ryu, 2016
Nematodes	*Meloidogyne incognita*	-	*B. subtilis*	Sugarcane	*Field*	Morgado et al., 2015
	M. javanica	-	*B. subtilis*	Egg plant	*Field*	Abbasi et al., 2014

prevalence in waterlogged soils, increase in diversity and abundance, further emphasizing the importance of anaerobic and endospore-forming microbes in stress adaptation (Cui et al*.,* 2019). These findings highlight the essential role of endospore-producing endophytes in enhancing plant resilience to flooding through both microbial community restructuring and physiological regulation.

While significant progress has been made in understanding the plant growth-promoting and protective roles of *Bacillus* spp., several avenues remain open for future exploration. More detailed genomic and metabolomic studies are needed to unravel the molecular basis of their interactions with different plant species. Field-level evaluations under diverse agroclimatic conditions will be crucial to validate their consistency and efficacy. Furthermore, the development of stable, cost-effective, and crop-specific bioformulations using indigenous *Bacillus* strains could revolutionize eco-friendly farming. Integrating these microbes into precision agriculture and smart delivery systems (e.g., seed coating, soil capsules) may enhance their practical utility. Overall, leveraging the full potential of endophytic *Bacillus* spp. requires interdisciplinary research bridging microbiology, plant physiology, and biotechnology to meet the global demand for sustainable crop production.

6. CONCLUSION

Endospore-forming *Bacillus* species represent a versatile and resilient group of endophytic bacteria with tremendous potential in sustainable agriculture. Their multifaceted role in promoting plant growth is evident through mechanisms such as nutrient solubilization, nitrogen fixation, phytohormone production, and improvement of root architecture. Moreover, *Bacillus* spp. offer robust biocontrol capabilities by producing a wide array of antimicrobial compounds, including bacteriocins, lipopeptides, and cell-wall degrading enzymes, while also inducing systemic resistance in plants. Importantly, their ability to withstand extreme environmental conditions through endospore formation makes them ideal candidates for bioformulation and field application. Additionally, their role in enhancing plant tolerance to abiotic stresses such as drought, salinity, and heavy metal toxicity further underscores their agricultural value, particularly in the context of changing climate and declining soil health.

DISCLAIMER (ARTIFICIAL INTELLIGENCE)

The authors declare that generative AI tools (e.g., ChatGPT) were used solely for grammar correction and sentence restructuring. No conceptual or content-level edits were made.

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COMPETING INTERESTS

Authors have declared that they have no known competing financial interests or non-financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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