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REVIEW ARTICLE

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Bacillus spp. as Bioagents- Applications and Effective Strategies in Plant Bacterial Disease Management: A Review

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ABSTRACT

Phytopathogenic bacteria (PPB) cause plant diseases, resulting in significant global economic losses. Over 200 bacterial species across 25 genera damage various plant species, predominantly from the Pseudomonadaceae, Xanthomonadaceae and Enterobacteriaceae families. These bacteria invade plant tissues and surfaces to live and obtain nourishment, often in collaboration with fungi and viruses, along with the impact of abiotic stress factors like chemical pollution, climate change, biodiversity loss, post-harvest loss, food waste and environmental degradation. These challenges collectively pose a substantial threat to global agricultural food production. Achieving global food security, sustainability in agriculture and enhancing the yield of high-quality healthy crops require effective control of plant bacterial diseases. Traditional chemical control methods have led to bacterial resistance, environmental pollution, high costs and negative impacts on human and ecological health. To address these issues, attention has shifted towards the alternatives of synthetic agrochemicals, with a focus on biopesticides. This paper comprehensively analyzes using *Bacillus* species as bioagents and investigating their mechanisms of action, including competition, antibiosis and induced plant resistance and evaluating their effectiveness in managing bacterial plant diseases. The findings suggest that *Bacillus* spp. offer a promising solution to sustainable agricultural practices, providing a safer and more eco-friendly approach to plant disease management.

Key words: *Bacillus* spp., Biocontrol agent, Biopesticides, Mechanisms, Phytopathogenic bacteria.

Plant pathogenic bacteria (PPB) cause diseases that result in significant economic losses, with crop damage estimated at 30-40%, amounting to between one billion dollars and five billion euros annually, particularly affecting pears, vineyards and apple orchards (Kannan *et al.*, 2015; Khan *et al.*, 2023; Mansfýeld *et al.*, 2012; Verhaegen *et al.*, 2023). More than 200 bacterial species from 25 genera cause significant damage to diverse plant species(Buttimer C *et al.*, 2017). Most of these bacteria belong to the families Pseudomonadaceae, Xanthomonadaceae and Enterobacteriaceae, targeting both plant surface structures and internal tissues where they can obtain nutrients and establish habitats. These families include *Acidovorax, Agrobacterium* (some strains), *Pectobacterium, Xanthomonas, Clavibacter, Burkholderia, Pseudomonas* (some strains), *Streptomyces, Spiroplasma, Erwinia, Pantoea, Ralstonia* and *Xylella,* which are a significant number of highly destructive phytopathogenic bacteria (Kannan *et al.*, 2015; Sharma *et al.*, 2023). The interaction of these bacteria with other pathogens such as fungi and viruses, alongside abiotic stressors like climate change, pollution and biodiversity loss, presents a substantial challenge to global agricultural food production (Martins *et al.*, 2018). Therefore, maintaining global food security requires the application of management strategies to eradicate plant pathogenic bacteria by reducing their survival chances (Rizzo *et al.*, 2021; Strange *et al.*, 2005). Farmers often depend extensively on chemical fertilizers and pesticides (Satyadev Prajapati and Maurya, 2020). While chemical pesticides have proven effective in eradicating plant diseases in agriculture, the unfortunate consequence is that the misuse of certain chemicals, coupled with prolonged and excessive use, causes numerous environmental problems, the rapid emergence of resistance in phytopathogenic bacteria and pests and can be costly. Furthermore, when these chemicals accumulate in soil or plants, they can be harmful to humans and affect non-target animals, microbial communities and non-target plants (Said, 2023; Tudi *et al.*, 2021). Consequently, scientists turned their attention to natural alternatives to artificial agrochemicals, leading to the improvement of biopesticides for controlling diseases and pests.

Biopesticides derive from various sources, including microorganisms, natural compounds and pesticidal substances with additional genetic material (Kumar *et al.*, 2021). They offer safe, environmentally acceptable solutions for hazardous pesticides when used in agricultural and horticultural applications. This paper comprehensively analyzes the potential of *Bacillus* species as biocontrol agents, exploring their mechanisms of action and the advantages they provide in managing plant bacterial diseases.

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Characteristics of the bacillus genus

Bacillus subtilis, the first identified Bacillus species, was discovered by Christian Gottfried Ehrenberg in 1835. He named the bacterium *Vibrio subtilis* because of its rod-shaped appearance (Jörg Stülke *et al.*, 2023; Sella *et al.*, 2014). In 1872, Cohn renamed the bacterium to *Bacillus subtilis* (Harirchi *et al.*, 2022). Since then, *Bacillus* has been discovered in a variety of environments, including ponds, air, soil, fresh and saline water and food as contaminants. It can also be present in the digestive tracts of animals like pigs (Haque *et al.*, 2022; Wei *et al.*, 2015). *Bacillus* species are rod-shaped, facultatively anaerobic, endospore-forming and catalase-positive bacteria with flagellar motility and variable sizes (0.5 to 10 µm*)* bacteria that grow best in a neutral pH (Márquez *et al.*, 2011; Radhakrishnan *et al.*, 2017; Zhou *et al.*, 2022). These species are frequently employed as bioagents for plant diseases because of their capability to form spores, which enable them to live in harsh environments. They release extracellular proteins, exhibit rapid growth and possess efficient biosynthetic pathways (Liu *et al.*, 2020). Additionally, numerous organic and inorganic substances can be used by *Bacillus* species for growth and energy. Moreover, there are significant differences in nutritional needs among species. Certain strains, classified as prototrophs rely solely on an organic carbon source, while others, categorized as auxotrophs depend on the substrate for essential organic compounds (Logan NA and P, 2009). Certain *Bacillus* species, such as *B. licheniformis, B. anthracis and B. cereus*, can infect humans and animals, whereas *B. thuringiensis* is harmful to invertebrates (Pinos *et al.*, 2021; Ramirez-Olea *et al.*, 2022).

Use of the *Bacillus* genus as a bioagent

Using *Bacillus* species for biological control is a practical, eco-friendly approach to managing plant diseases. Studies on employing *Bacillus* species as biological agents to manage plant diseases have been ongoing for a long time. *Bacillus* spp., particularly *B. subtilis*, are widely recognized as plant growth-promoting rhizobacteria that live in soil. They are crucial in giving plants resistance against abiotic and biotic stresses, as shown in Fig 1, through the formation of biofilms, induced systemic resistance and lipopeptide production. These species, at controlled concentrations, boost carbon sequestration, denitrify soils and aid in metal-contaminated soil bioremediation (Mahapatra *et al.*, 2022). They release antimicrobial metabolites that can supplement or replace synthetic chemicals in biofertilizers and biopesticides to prevent plant diseases. They also produce endospores to survive adverse conditions, along with phytohormones, siderophores and the ability to solubilize potassium and phosphorus, enhancing plant growth and nutrient uptake (Collins and Jacobsen, 2003; Fan *et al.*, 2019; Ongena *et al.*, 2005).

Many *Bacillus* species have antagonistic activity against a variety of phytopathogenic bacteria found in field crops including fruit trees, rice, corn and others (Li *et al.*, 2015).

The mode of action of *Bacillus* biological control for phytopathogenic bacteria is as follows:

Direct mode of action

Antibiosis

Antibiotics are small, low molecular-weight molecules produced mainly by soil-dwelling microbes as secondary metabolites. It is known that some *Bacillus* species, like *B. amyloliquefaciens, B. mycoides, B. megaterium, B. subtilis, B. cereus and B. licheniformis*, can generate strong antibiotic substances that prevent phytopathogenic growth. These include both non-ribosomal and ribosomal cyclic peptides, which researchers have extensively studied (Cawoy *et al.*, 2011; Li *et al.*, 2015). A study by Bottone *et al.* (2003) stated that the Bacilli class produces about 167 different antibiotics. Of these, 23 are obtained from *Bacillus subtilis* and 66 from *Bacillus brevis*, with other *Bacillus* species contributing the remaining antibiotic peptides (Bottone and Peluso, 2003). Different *Bacillus* strains produce antimicrobial peptides that vary significantly and this variation impacts their effectiveness in inhibiting plant pathogenic bacteria (Basi-Chipalu *et al.*, 2022; Cladera-Olivera *et al.*, 2004).

Bacillus species produce various bacteriocins with antimicrobial properties, including subtilin, thuricin, amylolysin, amylocyclicin, subtilosin A, subtilosin B and amysin (Abriouel *et al.*, 2011). Some of these are trained in the biological management of phytopathogens. As an example, *B. clausii* GM17 produces Bac GM17, which is active in combating *Agrobacterium tumefaciens*, or *B. thuringiensis* subsp. *kurstaki* Bn1's thuricin Bn1 inhibits *Pseudomonas syringae* and *Pseudomonas savastanoi* (Mouloud *et al.*, 2013; Ugras *et al.*, 2013). Furthermore, several antimicrobial substances, like bacillomycin D, zwittermicin A, fengycins, iturins and surfactins, are formed by *Bacillus* strains. These substances, which are referred to as cyclic lipopeptides (CLPs), have potent pathogen-inhibiting properties (Farace *et al.*, 2014; Li *et al.*, 2019). Several *Bacillus* variants, including *Bacillus amyloliquefaciens*

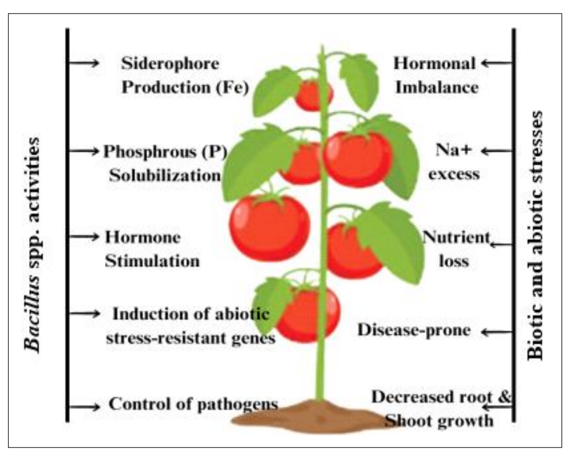

Fig 1: Roles of *Bacillus* spp. in managing abiotic and biotic stresses in crops.

A17 (currently *B. velezensis*) and *B. amyloliquefaciens* KPS46, have been shown to produce CLPs, with antibacterial activity (Chaisit Preecha *et al.*, 2010; Mora *et al.*, 2011, 2015; Saha *et al.*, 2016).

Siderophore production

Soil organisms frequently face competition for vital resources including nutrients, oxygen and space. Competition for space and nutrients around host plants between pathogenic and non-pathogenic microorganisms can result in biological control (Pal and McSpadden Gardener, 2006). The most common nutrient element over which beneficial microbes, such as *Bacillus* spp. and pathogenic microorganisms compete is Iron (Fe). There is intense competition because there is a shortage of bioavailable iron in the soil environment. The process responsible for this competition is known as Siderophore. Its primary function is to chelate iron, allowing it to be soluble and extracted from organic materials and minerals (Miljakoviæ *et al.*, 2020). It is essential to biological control because it combats infectious agents for iron, limiting their accessibility (Beneduzi *et al.*, 2012). A variety of bacteria, including *Azospirillum*, *Azotobacter*, *Bacillus*, *Dickeya*, *Enterobacter*, *Kosakonia*, *Klebsiella*, *Methylobacterium*, *Nocardia*, *Pantoea*, *Paenibacillus*, *Pseudomonas*, *Serratia*, *Streptomyces* and others, can produce siderophore.

Most studies documented the significance of siderophores in inhibiting plant bacterial diseases. In 2004, Kloepper *et al.* (1989) investigated the importance of siderophores in suppressing pathogens like *Pectobacterium carotovorum*, showcasing the potential of PGPR in managing plant diseases biologically (Kloepper *et al.*, 2004). The effectiveness of *Bacillus amyloliquefaciens* strain S1 against *C. michiganensis* spp. *Michiganensis*, which causes canker disease in tomatoes, was reported. The effectiveness of strain S1 was linked to the synthesis of siderophores, antibacterial metabolites and lytic enzymes *in vitro* conditions (Gautam *et al.*, 2019).

Production of hydrolytic and lytic enzymes

Bacillus Species are known as valuable reservoirs for a broad range of enzymes. *B. licheniformis*, *B. subtilis and* other microorganisms produce Keratinases which are widely used in animal feed, leather industries, detergent and feed, as well as in biomedical and healthcare applications (Gupta and Ramnani, 2006; Silva *et al.*, 2014). The hydrolytic enzymes found in *Bacillus* species, such as glucanases, cellulases, lipases, proteases, chitinases and chitosanases, contribute to the effective degradation of essential elements of bacterial and fungal cell walls (Miljaković *et al.*, 2020). Bacteria predominantly produce chitinases to break down chitin for energy consumption. Moreover, particular bacterial chitinases are utilized as potent bioagents for combating a range of plant diseases induced by fungal pathogens (Kumar *et al.*, 2018; Saber *et al.*, 2015). The breakdown of cell walls that results from interactions between *Bacillus* species and pathogens may be facilitated by the action of bacterial cellulases, lipases and proteases (Guleria *et al.*, 2016). Previous research has been published on isolating these enzymes from *Bacillus brevis, Bacillus subtilis, Bacillus halodurans, Bacillus circulans and Bacillus licheniformis* (Planas, 2000). Recent studies have extensively examined the production of lytic and hydrolytic enzymes by *Bacillus* species, emphasizing their promising role as biocontrol agents in managing plant diseases. The ability of *B. amyloliquefaciens* to form lytic enzymes like cellulase, protease, lipase and chitinase is associated with its potential to function as a bioagent against *Clavibacter michiganensis* ssp. *Michiganensis* (Gautam *et al.*, 2019).

Indirect mode of action

Plant growth-promoting rhizobacteria (PGPR)

Plant growth-promoting rhizobacteria (PGPR) are beneficial living soil bacteria that colonize plant roots and promote plant growth (Kloepper *et al.*, 1989). PGPRs improve plant growth directly by supplying compounds like phytohormones or aiding nutrient absorption and indirectly by limiting phytopathogens or inducing plant resistance (Glick, 1995). Some PGPRs form biofilms, which are structures made of bacteria encased in organic and inorganic compounds. Biofilms help PGPRs colonize plant roots, promoting a stable and sustained interaction with the host plant. Consequently, this may improve PGPR's capacity to encourage plant development and offer pathogen protection (Haque *et al.*, 2020; Karimi *et al.*, 2022). Toxins such as bacillomycin, fengycin, iturin, surfactin and macrolactin, are released by *Bacillus* species when they form a biofilm on the root surface. By doing this activity, harmful bacterial populations are eliminated and the frequency of plant diseases is reduced (Elshakh *et al.*, 2016; Huang *et al.*, 2014).

The *Bacillus* genus, broadly studied and utilized in agriculture for its practical potential as PGPB, includes species like *Priestia megaterium* (formerly *Bacillus megaterium*), *B. circulans*, *B. coagulans*, *B. subtilis*, *B. azotofixans*, *B. macerans* and *B. velezensis* (Blake *et al.*, 2021; Etesami *et al.*, 2023; Fan *et al.*, 2018).

Biocontrol agents derived from the *Bacillus* genus are frequently more potent compared to other PGPB species such as *Pseudomonas* spp., because These species have the superior capability to produce metabolites and form spores, thereby enhancing cell viability in commercially viable products (Haas and Défago, 2005). Three *Bacillus* strains isolated from the pepper rhizosphere in Turkey significantly reduced bacterial spot disease severity, achieving reductions ranging from 11% to 62% in field conditions and 38% to 67% in greenhouse experiments. Additionally, these strains enhanced plant growth and increased yield (Mirik *et al.*, 2008).

Induction of systemic resistance (ISR) and SAR

Plants have evolved defenses against abiotic and biotic stresses, including threats from herbivores, pests and phytopathogens. Their defense mechanisms, known as systemic acquired resistance (SAR), remain dormant until activated by pathogens, triggering a widespread response throughout the plant (Pandey *et al.*, 2016; Pieterse *et al.*, 2014). Two types of plant systemic resistance are: induced systemic resistance (ISR) and systemic acquired resistance (SAR). ISR refers to resistance activated by beneficial microbes and is typically independent of salicylic acid (SA), while, SAR is termed when induced resistance is initiated by pathogens and is closely associated with the salicylic acid signaling pathway (Pieterse *et al.*, 2014; Yu *et al.*, 2022). Beneficial microorganisms can activate defense mechanisms in the host through various pathways, providing plants resistance against several pathogens. *B. cereus, B. atrophaeus, Bacillus amyloliquefaciens, Bacillus megaterium, Bacillus subtilis* and similar microbes have been indicated to be effective against bacterial, viral and fungal invasions through ISR (Yu *et al.*, 2022). Various studies investigated the impact of ISR-producing *Bacillus* spp. and SAR on phytopathogenic bacteria including *Erwinia carotovora* subsp. *Carotovora*, *Pseudomonas syringae* pv. *tomato*, *Pectobacterium carotovorum*, *Xanthomonas citri* subsp. *Citri* and *Clavibacter michiganensis* subsp. *Michiganensis* (Dadaşoğlu *et al.*, 2020; Jang *et al.*, 2022).

CONCLUSION

This review discusses the challenges posed by agrochemicals and explores viable alternatives, focusing on employing *Bacillus* species to biologically control plant-pathogenic bacteria (PPB). It also delves deeply into its mechanisms including antibiosis, the production of siderophores, lytic and hydrolytic, as well as ISR and SAR. Members of multiple *Bacillus* species, such as *Bacillus subtilis, Bacillus licheniformis, Bacillus megaterium, Bacillus cereus, Bacillus mycoides, Bacillus amyloliquefaciens* and *Bacillus pumilus*, are recognized as prolific producers of highly effective antibiotic molecules. These antibiotics, encompassing ribosomal (bacteriocins) and non-ribosomal cyclic peptides, inhibit the growth of phytopathogenic agents. Siderophore production is one of the main properties of *Bacillus* spp. enabling them to chelate iron and reduce its availability, thereby succeeding in competition with pathogens. *Bacillus* Species are recognized as valuable reservoirs for a wide range of enzymes. The hydrolytic enzymes found in *Bacillus* species, such as glucanases, cellulases, lipases, proteases, chitinases and chitosanases, may facilitate the effective degradation of key elements of bacterial and fungal cell walls. *Bacillus* spp. also create biofilm surrounding the root surface and releases toxic substances, including surfactin, macrolactin, bacillomycin, iturin and fengycin. This action results in the elimination of harmful bacterial populations and a decrease in disease incidence in plants. *Bacillus amyloliquefaciens,* B. atrophaeus*,* B. cereus*, Bacillus megaterium, Bacillus subtilis and* similar microbes have demonstrated efficacy against fungal, bacteria and viral invasions through induced systemic resistance. Finally, we recommend further in-depth research on beneficial bacteria such as *Bacillus* species and their genetic interactions with pathogens and plants to maintain biodiversity balance and mitigate the environmental challenges posed by pesticides.

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Conflict of interest

The author confirms the absence of any conflicts of interest related to the publication of this paper.

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