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The Role of *Paenibacillus* in the Plant Pathogen Biological Control Strategies: A Literature Review

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Abstract

Modern agriculture has faced many serious challenges due to the increasing attack of plant pathogens, that resulted in the decline in productivity and quality of agricultural products. Over-reliance on chemical pesticides often poses many problems in pathogen resistance, environmental pollution, and health risks, so more sustainable alternative strategies are needed. Paenibacillus is a genus of endospore-forming gram-positive soil bacteria that has been widely studied for its potential as a biocontrol agent. Its biocontrol mechanisms include the production of antimicrobial compounds (lipopeptides, antibiotics, secondary metabolites), the activity of hydrolytic enzymes (chitinase, β-glucanase, cellulase), and inhibition through volatile compounds (VOCs) that play a role in suppressing pathogens remotely. In addition to the direct mechanism, Paenibacillus also supports plant health indirectly through the induction of systemic resistance (ISR), which activates the plant's hormonal pathways and defense genes, as well as its role as a plant growth-promoting rhizobacteria (PGPR) through nitrogen fixation, phosphate and potassium dissolution, siderophore production, and phytohormone synthesis. Recent studies have shown the effectiveness of species such as P. polymyxa, P. terrae, P. peoriae, and P. elgii in suppressing important pathogens, including Meloidogyne incognita, Fusarium proliferatum, Coniella vitis, Pectobacterium brasiliense, and Ralstonia solanacearum. This literature review confirms that Paenibacillus has great potential as a multifunctional biocontrol agent that not only suppresses the development of plant diseases but also increases plant growth and resilience, making it feasible to develop as an environmentally friendly biological control strategy that supports sustainable agriculture.

Keywords: biocontrol agent, induced systemic resistance (ISR), *Paenibacillus*, phytopathogens, volatile compounds (VOCs)

Introduction

Modern agriculture is facing serious challenges due to the attack of various plant pathogens that contribute to a significant decrease in crop yields and production quality. Infections caused by fungi, bacteria, and nematodes have been shown to reduce the productivity of food crops and horticulture, posing a threat to world food security. The most common control effort so far is the use of chemical pesticides. However, high dependence on these chemicals has negative consequences, including the development of pathogen resistance, environmental degradation, and potential risks to human health and ecosystems [1].

The limited effectiveness and adverse impact of chemical pesticides encourage the need for more environmentally friendly control alternatives. One of the approaches that is getting more attention is the use of microorganism-based biological agents. Biocontrol agents have advantages, such as the ability to suppress pathogens more specifically, suppress the accumulation of chemical residues in agricultural products, as well as contribute to the sustainability of agricultural ecosyst [3]. Among the promising candidates, soil bacteria of the genus *Paenibacillus* are the focus of research because of their great potential in plant disease control.

Paenibacillus is a soil bacterium that lives in symbiosis with plants and has various antagonistic mechanisms against pathogens. These bacteria are able to produce antimicrobial compounds, such as lipopeptides (fusaricidin, paenimyxin, pelgipeptin), hydrolytic enzymes, and volatile compounds that can inhibit the development of fungal pathogens, bacteria, and nematodes [3,4]. Moreover, *Paenibacillus* can induce plant systemic resistance as well as support growth through nitrogen fixation activity, phytohormone production, and phosphate dissolution [5,6,7]. Effectiveness of some species, such as *P. polymyxa*, *P. elgii*and *P. peoriae*, has been widely proven in suppressing diseases in cultivated crops [1,2,8].

Strategic value of *Paenibacillus*. As a biocontrol agent, it not only comes from its ability to suppress pathogens, but also its contribution to improving plant health and productivity. Some commercial formulations based on *Paenibacillus* have been developed and widely used, although the majority still rely on *P. polymyxa* [1]. Recent research shows that other species in this genus also hold great potential for future application as biological agents. This review article aims to present a comprehensive understanding of the roles, working mechanisms, and prospects of applications of *Paenibacillus* in the control of plant pathogens. Through this understanding, it is hoped that it can support the formulation of effective, safe, and sustainable biological control strategies to answer challenges in modern agricultural systems.

Materials and Methods

The method used in this study is a literature review by collecting several research results that have been verified as credible. The literature study approach was carried out by examining various relevant scientific publications from the Scopus, Springer, Web of Science, PubMed, Google Scholar, and Elsevier databases. The literature reviewed was selected based on the 2020-2025 publication year range to ensure that the discussion includes the latest developments related to the role of *Paenibacillus* in plant pathogen biocontrol. Keywords used in searches include "*Paenibacillus*", "*biocontrol*", and "*plant pathogen*". The criteria used are inclusion criteria, including articles that discuss the mechanism, effectiveness, and application of *Paenibacillus* as a biocontrol agent in plants. All selected literature was critically analyzed and synthesized to gain a comprehensive understanding of the mechanisms, potentials, and challenges of the implementation of *Paenibacillus* sp. in the biological control of plant pathogens.

Results and Discussion

Paenibacillus is a genus of rod-shaped gram-positive bacteria that belongs to the endospore-forming group. Its ability to form endospores is like a "sleep capsule" that allows it to remain in the soil even in the face of extreme conditions such as drought, high temperatures, or nutrient scarcity. Its natural habitat is mostly in the root area (rhizosphere), and several species can be found from the seed germination phase, so they are often considered part of the plant's core microbiome from the beginning of growth. Uniquely, the colony *Paenibacillus* often exhibits intricate branching patterns when grown in dense mediums—forming tree-branch-like structures or fine webs—that are not only visually appealing, but also reflect adaptive strategies for exploring, expanding contact surfaces, and efficiently searching for nutrients [9]. In the context of biocontrol, *Paenibacillus* can be seen as a "versatile fighter" that blends various mechanics. One of its main weapons is the production of antimicrobial metabolites, such as the lipopeptides fusaricidin, paenimyxin, and pelgipeptin, which work against pathogenic cell membranes. In addition, these bacteria also produce hydrolytic enzymes—such as chitinase, β-glucanase, and cellulase—which play a role in degrading the cell walls of fungi and pathogenic bacteria [2] . Some strains are known to produce volatile compounds (VOCs) with antimicrobial effects, which can suppress pathogen growth remotely [10].

Paenibacillus is reported that it not only functions as a pathogen control agent, but also acts as a plant growth-promoting rhizobacteria (PGPR). Its functions include fixing nitrogen, dissolving phosphate, producing siderophores that help iron absorption, and synthesizing phytohormones such as indole-3-acetic acid (IAA), which can increase root growth and plant vigor [11]. Some studies have also mentioned its potential in triggering plant resistance mechanisms through systemic resistance induction (ISR), which strengthens the plant's natural defense system against various types of pathogens [12]. This combination of direct antagonistic properties and indirect physiological support is what makes *Paenibacillus* as a multifunctional biocontrol agent that is very promising in modern sustainable farming systems. Therefore, this review aims to summarize the current knowledge about the application of *Paenibacillus* spp. in the biological control of phytopathogens and outlines new research aimed at improving antagonistic properties of *Paenibacillus* (Table 1).

Research conducted by Shi et al. [8] succeeded in finding out the mechanism of effectiveness of the P strain. *Polymyxa* J2-4 in against *Meloidogyne incognita* (root-destroying nematodes) in cucumber plants is supported by various tests showing nematical activity and induction of plant resistance. In vitro testing showed that J2-4 was able to kill the J2 nematode significantly, with mortality rates reaching 86.58% and 97.47% after 24 and 48 hours, which is comparable to the effects of abamectin. In addition, field testing showed that plants treated with J2-4 experienced a significant decrease in galls and egg mass, by 65.94% and 51.64%, respectively, as well as smaller gall sizes compared to controls. The study also revealed that J2-4 is able to induce plant defense mechanisms through increased salicylic acid (SA) levels and decreased jasmonic acid (JA), which plays a role in local and systemic resistance to nematodes. In addition, genome analysis showed that J2-4 has biosynthesis genes for antimicrobial compounds such as polymyxin and fusaricidin, in the absence of virulence genes, making it safe to use as a biocontrol agent. With a combination of direct nematikidal activity and the ability to activate plant defense pathways, J2-4 has been shown to be effective as a natural biocontrol agent against M. *incognita* on cucumber plants.

Table 1. Mechanism of *Paenibacillus* in controlling phytopathogens

Biocontrol Agent	Phytopathogens	Host	Mechanism	Reference
Paenibacillus polymyxa	*Meloidogyne incognita*	Cucumber (*Cucumis sativus*)	Production of antibacterial substances such as antibiotics and lipopeptides, competition for space and nutrients, and systemic induction of plant resistance	(Shi et al., 2024)
Paenibacillus terrae B6a	*Fusarium proliferatum*	Corn (*Zea mays*)	Competition of space and nutrients and production of antimicrobial compounds (VOCs and non-VOCs)	(Smith et al., 2025)
Paenibacillus peoriae ZBFS16	*Coniella vitis*	Grapes (*Vitis vinifera*)	Production of antimicrobial metabolites (fusaricidin, polymyxin, tridecaptin) and hydrolytic enzymes, PGPR, root colonization and biofilm	(Yuan et al., 2022)
Paenibacillus peoriae ZF390	*Pectobacterium brasiliense*	Cucumber (*Cucumis sativus*)	Production of antimicrobial metabolites (fusaricidin, polymyxin, tridecaptin) and hydrolytic enzymes, PGPR, root colonization, and biofilm	(Zhao et al., 2022)
Paenibacilllus elgii JCK-5075	*Ralstonia solanacearum, Pectobacterium carotovorum subsp. Carotovorum, Xanthomonas axonopodis* pv. *Vesicatoria*	Tomatoes (*Solanum lycopersicum*), kimchi mustard (*Brassica rapa* subsp. *pekinensis*), and red chili peppers (*Capsicum annuum)*	Competition space and nutrition, antibiotic/lipopeptide production with direct antibacterial activity	(Le et al., 2020)

Research by Smith et al., [13] that conducted in vitro and in plant tests demonstrating the effectiveness of strains *Paenibacillus terrae* B6a in inhibiting *Fusarium proliferatum* which causes corn cob rot. In vitro test results showed that the intracellular metabolite (ICM) P. *Terrae* B6a is effective in inhibiting the growth *F. proliferatum,* significantly reaching 71.64% and resulted in structural disruption in fungal hyphae. Meanwhile, the volatile compound test showed an inhibition of fungal mycelia growth with a percentage of 35.66% and chemical analysis showed a significant decrease in the percentage of extracellular polysaccharide content of 48.99% which indicates a weakening of the pathogen's defense structure. In addition, biopriming treatment with P. *Terrae* B6a stimulates the defense mechanism of maize with a 44.99% increase in root length, accompanied by increased activity of key antioxidant enzymes (SOD and APX) and decreased pathogen-induced oxidative stress accumulation (ROS) and reduced cell membrane damage (MDA). With a combination of direct antifungal activity and the continued ability to modulate the plant's defense response, P. *Terrae* B6a is effective as a biocontrol agent that has the potential to be developed in the world of agriculture in a sustainable manner.

The research of Yuan et al., [14] conducted a comparative analysis of the ZBSF16 genome compared to three strains of *Paenibacillus peoriae* others, namely ZF390, HS311, and HJ-2. Based on the results of the Dual-Culture Assay test, ZBSF16 formed a clear zone around the ZBSF16 colony and was proven to be able to inhibit the growth of 12 plant pathogens, including fungi *Coniella vitis,* which is the causative agent of white rot in wine. In plants, ZBSF16 has been proven to be able to significantly increase root length, bud length, and biomass by potting test method and then given ZBSF16 treatment and then measured growth parameters. In addition, OrthoANI and GGDC confirmed a kinship relationship between ZBSF16 and three P strains. *peoriae* others (ZF390, HS311, and HJ-2). Then, a pan-genome analysis revealed 357 unique genes that are thought to contribute to its functional excellence in maintaining plant viability. The data obtained indicated that the percentage of preventive effect of ZBSF16 was 90.59% and the percentage of curative effect was 94.52%. This high level of efficacy proves that ZBSF16 is able to suppress the development of pathogenic infections and suppress the severity of diseases that have already occurred.

The research conducted by Zhao et al., [15, 16] in various tests were carried out to assess the potential and characteristics of the strain *Paenibacillus peoriae* ZF390 as a biocontrol and plant growth-promoting agent. Testing of the effectiveness of biocontrol is carried out through in vitro assays and in the field against key pathogens such as *Pectobacterium brasiliense* which causes soft rot on cucumber plants. The results showed that the ZF390 strain was able to inhibit the growth of the pathogen with a control rate of 77.47%, even higher than the antibiotic zhongshengmycin. In addition, enzyme activity testing showed that ZF390 is capable of producing enzymes such as cellulase, protease, and phosphatase that play a role in antagonism to pathogens and aid in the decomposition process of organic matter. Tolerance to heavy metals was tested by growing this strain on metal-containing media such as Cd, Co, Mn, Pb, and Zn, and the results showed that ZF390 was able to grow and survive in these conditions, signaling potential as a bioremediation agent. Morphological and physiological tests show that ZF390 is a Gram-positive bacterium that is rod-shaped, motil, and is capable of utilizing a variety of carbon sources. Genomic testing and biosynthesis analysis showed that ZF390 has a large number of genes associated with the production of secondary metabolites such as antibiotics and other antimicrobial compounds, which support its antagonistic activity. Overall, these tests show that the ZF390 strain has strong antagonistic capabilities against plant pathogens, is able to produce important enzymes, is tolerant of harsh environmental conditions, and has great potential as a biocontrol agent and plant growth enhancer.

Le et al. [3] research carried out various methods used to evaluate the antibacterial activity and mechanism of action of *Paenibacillus elgii* JCK-5075 and its metabolites, PGPs against three important diseases of horticultural plants, namely tomato bacterial wilting, soft rot in kimchi mustard greens, and leaf spots in red chilies. The researcher performed isolation and culture of the JCK-5075 strain, followed by in vitro antagonistic assays against the target pathogen (*Ralstonia solanacearum*, *Pectobacterium carotovorum* subsp. *carotovorum*, and *Xanthomonas axonopodis* pv. *vesicatoria*) to test antibacterial activity. The pyang method used was an in vitro antibacterial test using the broth dilution method on a 96-well plate, in which the culture filtrate, coarse material, and PGPs were tested against various plant pathogens with different concentrations, and bacterial growth was measured via optical density (OD) at 600 nm after 1-2 days of incubation at 28-30°C. The results showed that culture filtrates and PGPs had strong antibacterial activity, with MICs ranging from 0.31% to 10% for filtrates and 0.31–100 μg/ml for PGPs, with *Xanthomonas arboricola* pv. pruni as the most sensitive pathogen. Results of chemical analysis of secondary metabolites through high-performance liquid chromatography (HPLC) and mass spectrometry (LC-MS) showed that these strains produce several bioactive lipopeptides, including fengisin, iturin, and elgiicin, which are known to play a role in the cell membrane breakdown of pathogenic bacteria. In addition, *in vivo testing* was carried out in the field and pots to assess the effectiveness of disease control by inoculating tomato, kimchi mustard greens, and red pepper plants using pathogen suspensions (*Ralstonia solanacearum*, *Pectobacterium carotovorum* subsp. *carotovorum*, and *Xanthomonas axonopodis* pv. *vesicatoria*), in which culture fermentation and PGPs were able to significantly suppress disease progression, the results being comparable to positive controls using the chemical pesticide oxolinic acid. To understand the mechanism of action, membrane assays were performed using SYTOX Green fluorescence and membrane depolarization measurements, which showed that PGP-C damages the bacterial membrane by causing depolarization and increased permeability, thereby inhibiting bacterial growth. This test as a whole shows that P. *elgii* JCK-5075 and its metabolites have strong antibacterial activity and a mechanism of action involving membrane damage, supporting its potential as an effective and environmentally friendly plant biocontrol agent.

Based on various studies, the biocontrol mechanisms possessed by the genus *Paenibacillus* It is very diverse and works through a combination of direct and indirect activity against pathogens. P. *Polymyxa* J2-4 exhibits nematisidal activity by killing juvenile nematodes *Meloidogyne incognita* significantly and induce plant resistance through increased salicylic acid (SA) and decreased jasmonic acid (JA) [8]. P. *terrae* B6a plays a role in inhibiting *Fusarium proliferatum* through intracellular metabolites that damage HYPHA, volatile compounds that inhibit the growth of mycelia, as well as stimulate corn defenses by increasing antioxidant enzyme activity and root growth [13]. P. *peoriae* ZBSF16 exhibits broad ability to suppress a wide range of pathogens, in particular *Coniella vitis*, with a high level of preventive and curative efficacy supported by the presence of unique genes from pan-genome analysis [14]. *P. peoriae* ZF390 pressing *Pectobacterium brasiliense* Causes of soft rot in cucumbers through the production of hydrolytic enzymes (cellulase, protease, phosphatase), harsh environmental tolerance, and biosynthesis of antimicrobial metabolites from secondary gene clusters [15, 16] Meanwhile, P. *Elgii* JCK-5075 effectively controls various horticultural bacterial diseases such as tomato bacterial wilting, soft rot of mustard kimchi, and chili leaf spot through the production of bioactive lipopeptides (fengicin, iturin, elgiicin) that damage pathogen membranes, with in vivo test results comparable to chemical pesticides oxolinic acid [3].

Overall, based on the above research, the mechanism as a biocontrol agent is *Paenibacillus* able to produce antimicrobial compounds such as antibiotic lipopeptides. Lipopeptides are chemical compounds consisting of peptide chains and hydrdrophobic lipid chains. This compound is the main determinant of antifungal properties *Paenibacillus* Because it exhibits a broad spectrum of antibacterial and antifungal activity through various mechanisms such as disrupting pathogenic cell membranes, inhibiting cell wall biosynthesis, and inducing apoptosis or death [16, 17]. The most widely known antibiotics are produced by *Paenibacillus* mainly non-ribosomal synthesized peptides, such as fusaridin, pelgipeptin, polymyxin B, tridecaptin, and colistin (polymycin E). In addition, there are also peptides that are synthesized ribosomal such as paenibacillin, paenilan, and panisidin [18, 19]. The activity of hydrolytic enzymes is owned by *Paenibacillus*, plays an important role in the biological control of phytopathogens, especially fungi by degrading the structural components of fungal cells. These enzymes include chitinase, glucanase (hydrolysing ÿ-1,3- and ÿ-1,6-glucan), and cellulase [20, 21]. This is because chitin is the most abundant and main cell wall component in most fungi, chitinase is the most important enzyme possessed by *Paenibacillus* potentially involved in the biological control of fungal phytopathogens [22,23,24]. In addition to producing compounds that can inhibit directly to pathogens, there are other mechanisms that have *Paenibacillus* as a biocontrol agent, namely the inhibition of kakamolae CVOCs that serve as "long-range weapons" so that they can travel through the air or soil.

Conclusion

Paenibacillus It is considered a potential biocontrol agent because it has been widely used to protect plants from various diseases caused by phytopathogenic bacteria and fungi. Genus *Paenibacillus* has the ability of direct and indirect biocontrol mechanisms against pathogens. From the results of article reviews as many as five journals that are used as the main source, it is stated that several types of *Paenibacillus* can inhibit various types of pathogens such as *Meloidogyne incognita, Fusarium proliferatum, Coniella vitis, Pectobacterium brasiliense, Ralstonia solanacearum, Pectobacterium carotovorum subsp. Carotovorum, Xanthomonas axonopodis pv. Vesicatory*. Resulting interactions *Paenibacillus* There are also various that produce antimicrobial compounds such as antibiotic lipopeptides, have hydrolytic enzyme activity, produce volatile organic compounds (VOCs), and induce systemic resistance of plants, as well as *plant growth-promoting rhizobacteria* (PGPR) which increases plant resistance in inhibiting pathogens from entering indirectly.

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