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Rhizobacteria as Biofungicides: Mechanisms and Applications

Ade-Ogunnowo, F. E.

Department of Biological Sciences, Tai Solarin Federal University of Education, Ijagun, Nigeria.

Corresponding Author: adeogunnowo@tasued.edu.ng

Abstract

Plant pathogenic fungi are a major cause of agricultural losses worldwide, stressing the need to transition toward biologically derived fungicide alternatives that pose less risk to environmental and human health. Rhizobacteria are beneficial root-associated microbes with strong biocontrol capacity, acting against fungal pathogens via competition, antibiosis, parasitism, and triggering systemic resistance in plants. This review consolidates current insights into the mechanisms underlying rhizobacterial biofungicides and explores their practical applications in crop protection. It discusses notable successes in field trials, key obstacles to commercialisation, and emerging strategies such as genetic engineering and nano-formulation technologies to enhance efficacy and scalability.

Keywords: Rhizobacteria, Biofungicides, Antifungal mechanisms, Biocontrol, Sustainable agriculture

INTRODUCTION

The widespread impact of fungal plant pathogens continues to result in severe agricultural losses, posing a serious risk to global food supply chains. Although conventional chemical fungicides have proven effective, their widespread use has been linked to environmental degradation, adverse health effects, and the emergence of resistant pathogen strains. In response, rhizobacteria, which are beneficial microbes inhabiting the rhizosphere (an ecological niche), have garnered increasing attention as sustainable biofungicidal agents. These microorganisms suppress fungal pathogens through a range of mechanisms, including competition, antibiosis, parasitism, and the induction of systemic resistance in host plants (Nehra *et al.*, 2022).

The rhizosphere, defined as the soil microenvironment affected by root secretions (exudates) and microbial activity, is a highly dynamic environment characterised by intricate interactions among plant roots, soil constituents, and diverse microbial communities. Within this niche, rhizobacteria, particularly plant growth-promoting rhizobacteria (PGPR), play a central role in shaping rhizosphere structure and function. PGPR are a functionally diverse group of root-associated bacteria that colonise the rhizosphere and/or root surfaces and enhance plant performance through multiple interacting mechanisms. Their ecological significance lies not only in their ability to directly stimulate plant growth via nutrient mobilisation (e.g., nitrogen fixation and phosphate solubilisation) and phytohormone production, but also in their capacity to influence rhizosphere microbial community dynamics and suppress soil-borne pathogens (Vocciante *et al.*, 2022). PGPR are key mediators of plant–microbe interactions within the rhizosphere, responding to root exudates and, in turn, modifying the chemical and biological environment surrounding the root (Zhalnina *et al.*, 2018). This bidirectional interaction enables PGPR to contribute to plant resilience under both biotic and abiotic stress conditions, including pathogen pressure,

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drought, and nutrient limitation (Yang *et al.*, 2009). As a result, PGPR function not merely as individual beneficial microbes but as integral components of the rhizosphere microbiome that link microbial activity to plant health and soil ecosystem processes (Berendsen *et al.*, 2012). The ability of PGPR to synthesise a wide range of bioactive compounds, including antibiotics, siderophores, and hydrolytic enzymes, equips them to inhibit the growth of fungal pathogens effectively (Chowdhury *et al.*, 2020). *Bacillus* and *Pseudomonas* which are among PGPR have emerged as model genera given their antifungal properties, producing metabolites such as iturins, fengycins, and phenazines, which disrupt fungal cell membranes and prevent spore germination (Sofija, 2022).

Rhizobacteria also play a crucial role in activating induced systemic resistance (ISR), a physiological state that strengthens the plant's ability to fend off future pathogen invasions (Rabar *et al.,* 2023). This form of resistance is mediated via intricate signaling networks involving phytohormones such as jasmonic acid and ethylene, which subsequently activate defence-related gene expression and the synthesis of pathogenesis-related proteins (Rabar *et al.,* 2023). Importantly, the activation of ISR occurs independently of direct pathogen challenge thereby preparing the plant to respond more effectively upon later infection. Studies have shown the capacity of rhizobacteria-induced ISR to reduce disease incidence and severity across various crops, underscoring its potential as a cornerstone of sustainable plant disease management (Meena *et al.*, 2020; Rabar *et al.*, 2023). Thus, the use of rhizobacterial biofungicides in agriculture offers several notable advantages, including environmental compatibility, specificity towards target pathogens, and the potential for integration into existing crop management practices (Palmieri *et al.,* 2022). Nonetheless, their widespread adoption remains constrained by factors such as inconsistent performance under field conditions, limited formulation stability, and regulatory barriers (Ghorui *et al*., 2025). Interestingly, recent advancements, particularly in genetic engineering and nano-formulation technologies, offer promise in addressing these limitations and enhancing the efficacy and scalability of rhizobacteria-based solutions.

This review synthesises the current knowledge regarding the mechanisms through which rhizobacteria act as biofungicides and to evaluate their practical utility in crop protection. It highlights significant findings from laboratory and field studies, examines key challenges impeding commercialisation, and explores emerging strategies designed to optimise their performance. By consolidating recent research, this review seeks to provide a thorough understanding of the role of rhizobacteria in sustainable plant disease management and to identify directions for future investigation and innovation.

THE RHIZOSPHERE

The rhizosphere, the biologically active zone surrounding plant roots, is frequently described as a hotspot of microbial activity, a complex microenvironment characterized by intense interactions among plant roots, beneficial microorganisms, and pathogenic agents. Rich in organic compounds such as amino acids, sugars, and organic acids secreted by plant roots (collectively referred to as root exudates), the rhizosphere represents an attractive ecological niche for a wide array of microbial communities (Berendsen *et al.*, 2012). These exudates function not only as nutrient sources but also as chemical signals that influence microbial behaviour, colonisation dynamics, and competitive interactions (Chen & Liu, 2024).

Rhizobacteria, particularly PGPR, are especially well-adapted to thrive in the rhizosphere. They demonstrate a remarkable capacity to colonise root surfaces rapidly, often reaching densities of up to 10^9 colony-forming units (CFU) per gram of root tissue (Lugtenberg & Kamilova, 2009). This rapid colonisation is facilitated by chemotaxis, a movement in response to chemical gradients, which enables rhizobacteria to efficiently navigate towards root exudates (Feng *et al.*, 2021). Upon reaching the root zone, these bacteria exhibit strong adherence abilities, allowing them to establish themselves along the rhizoplane (root surface) and on adjacent soil particles. Various adaptive traits further enhance the success of rhizobacteria in the rhizosphere. Many strains possess flagella and pili that confer motility, facilitating movement towards favourable root-associated niches and escape from adverse microenvironments.

Additionally, rhizobacteria frequently form robust biofilms which are multicellular

structures embedded within a self-produced extracellular matrix and can enhance survival and persistence under stress conditions (Bhattacharyya *et al.*, 2023). Biofilm formation not only increases colonisation efficiency but also provides a protective barrier against predation and environmental fluctuations such as changes in moisture levels and pH (Bhattacharyya *et al.*, 2023).

The rhizosphere is an ecosystem of active microbial antagonism, where beneficial rhizobacteria suppress plant pathogens through competitive exclusion and the production of inhibitory compounds (Santoyo *et al.*, 2021). By rapidly utilizing available nutrients, they limit pathogenic fungi and bacteria's access to essential resources. Additionally, many rhizobacteria synthesize antimicrobial metabolites, including antibiotics, siderophores, and lytic enzymes, which directly inhibit or kill competing pathogens (Weller, 2007; Santoyo *et al.*, 2021). Such multifaceted antagonism enables rhizobacterial dominance and contributes to disease-suppressive soils. Within this competitive niche, plants and rhizobacteria engage in mutualism: plants provide carbon-rich exudates, while rhizobacteria enhance plant health through pathogen suppression, nutrient solubilisation, and phytohormone-mediated growth promotion (Li *et al.*, 2021). This synergy underscores the rhizosphere's role in sustainable disease management and positions rhizobacteria as key agents in natural pathogen biocontrol.

MECHANISMS OF FUNGAL SUPPRESSION

The mechanisms of fungal suppression by plant-growth-promoting rhizobacteria (PGPR) can be broadly classified into direct and indirect pathways. Direct mechanisms include iron scavenging, carbon competition, antibiosis, and parasitism, which directly inhibit pathogen growth or establishment. In contrast, indirect mechanisms, such as induced systemic resistance (ISR), operate through activation of plant defence systems, thereby enhancing host resistance to fungal infection.

Iron Scavenging

One of the principal competitive strategies employed by rhizobacteria in the suppression of fungal pathogens is their ability to sequester essential micronutrients, most notably, iron (Lemanceau *et al.*, 2009). Within the rhizosphere, iron is typically present at very low bioavailable concentrations due to its propensity to form insoluble ferric hydroxides under aerobic and near-neutral pH conditions (Du Laing *et al.*, 2009). As iron is vital for numerous cellular processes in both plants and microbes, it becomes a highly contested resource in the soil environment. To address iron limitation, rhizobacteria produce siderophores which are high-affinity compounds that sequester Fe^{3+} from the environment and transport it into cells via receptor-mediated uptake (Saha *et al.*, 2016).

Among the most extensively studied siderophores are the pyoverdines produced by *Pseudomonas* spp., which possess particularly strong iron-binding affinities (Ghssein & Ezzeddine, 2022). Through the production of these molecules, rhizobacteria can monopolise the limited available iron, thereby gaining a competitive advantage over fungal pathogens, many of which lack equivalent high-affinity iron acquisition systems. This results in an iron-depleted microenvironment that restricts fungal metabolism, growth, and sporulation (Lemanceau *et al.*, 2009). Notably, this mechanism operates via nutrient competition rather than direct antagonism, subtly shifting the ecological balance in favour of beneficial microbes (Loper & Henkels, 1999).

In addition to pyoverdines, other siderophores such as pyochelin, ornibactin, and enterobactin have been identified in various rhizobacterial taxa, each possessing distinct chemical structures and metal-binding properties (Ghssein & Ezzeddine, 2022). This diversity contributes to the ecological versatility of rhizobacteria, allowing them to adapt to different soil types and varying iron availability conditions (Kraepiel *et al.*, 2021). Notably, certain siderophores also exhibit direct antimicrobial activity by disrupting fungal cell membranes or promoting the generation of reactive oxygen species under iron-limiting conditions, thereby enhancing their antifungal effectiveness (Balhara *et al.*, 2016). Siderophore production thus, represents a sophisticated and highly effective mechanism by which rhizobacteria suppress fungal pathogens within the rhizosphere. This strategy exemplifies the broader concept of resource competition as a mode of biocontrol and highlights the potential of siderophore-

producing strains as promising candidates for development into biofungicides in sustainable agricultural systems.

Carbon Competition

In the nutrient-limited environment of the rhizosphere, carbon represents one of the most intensely contested resources (Prescott *et al.*, 2020). Plants secrete a diverse array of carbon-rich compounds via root exudation, including simple sugars (e.g. glucose, fructose), amino acids, and organic acids. These secretions not only sustain plant-associated microbial communities but also attract a variety of pathogenic fungi that exploit these substrates to colonise and infect host plants (Badri & Vivanco, 2009). Beneficial rhizobacteria, however, have evolved highly efficient metabolic systems that enable them to rapidly assimilate these carbon sources, thereby restricting their availability to potential pathogens (Oleńska *et al.*, 2020).

Rhizobacteria such as *Pseudomonas* and *Bacillus* species possess high-affinity uptake mechanisms and versatile enzymatic toolkits, which allow them to out-compete fungal pathogens for access to these valuable carbon substrates (Haas & Défago, 2005). This form of resource exclusion, commonly referred to as "carbon competition", constitutes a fundamental mechanism of rhizobacterial biocontrol. By depleting the pool of root-derived exudates, these bacteria effectively deprive pathogens of the nutrients required for establishment and proliferation in the rhizosphere (Yuan *et al.*, 2018). Beyond resource depletion, rhizobacteria frequently alter the chemical composition of the rhizosphere to create conditions less conducive to fungal growth. Certain strains can, for example, modify local pH levels or release secondary metabolites that disrupt fungal enzymatic activity, thereby impairing nutrient acquisition by pathogens (Vacheron *et al.*, 2013). Moreover, some PGPR display notable metabolic plasticity, enabling them to utilise a broad range of substrates, including those inaccessible to fungi, thus maintaining a competitive advantage even under variable environmental conditions (Pattnaik *et al.*, 2021). Of note, carbon competition not only limits pathogen development but also facilitates the early colonization of root zones by beneficial microbes (Jones *et al.*, 2009). This phenomenon results in the establishment of a microbial community structure that is more resistant to invasion by opportunistic pathogens (Wei *et al.*, 2015). Taken together, carbon competition represents a subtle yet highly effective form of pathogen suppression, where long-term biocontrol is sustained without repeated applications of microbial inoculants (O'Callaghan *et al.*, 2022).

Antibiosis

Antibiosis involves the synthesis and secretion of antimicrobial substances by rhizobacteria that directly inhibit or kill phytopathogenic fungi. This mode of action is among the most extensively studied and well-characterised mechanisms of rhizobacterial biocontrol. Unlike competitive exclusion, which restricts pathogen access to nutrients, antibiosis involves the active suppression of fungal growth via biochemical antagonism. Rhizobacteria synthesise a wide spectrum of secondary metabolites, including antibiotics such as phenazines, lipopeptides, pyrrolnitrin, 2,4-diacetylphloroglucinol (2,4-DAPG), and hydrogen cyanide (HCN), that disrupt various physiological processes within fungal pathogens (Raaijmakers & Mazzola, 2012).

Phenazines, for instance, are nitrogen-containing heterocyclic compounds commonly produced by *Pseudomonas* spp (Serafim *et al.*, 2023). These redox-active molecules trigger the formation of reactive oxygen species (ROS) within fungal cells ultimately causing oxidative stress and cellular damage. A well-characterised strain, *Pseudomonas fluorescens strain 2-79* produces phenazine-1-carboxylic acid (PCA), a compound shown to effectively suppress *Gaeumannomyces graminis var. tritici*, the fungal pathogen causing wheat take-all disease (Mavrodi *et al.*, 2006). Similarly, lipopeptides such as iturins, fengycins, and surfactins, primarily synthesised by *Bacillus* spp., compromise fungal cell membranes by integrating into the lipid bilayer, thereby increasing membrane permeability and resulting in cellular leakage and death (Ongena & Jacques, 2008).

The ecological success of these antibiotics is largely attributable to their structural diversity and multi-functionality. Many exhibit broad-spectrum antimicrobial activity, affecting not only fungi but also oomycetes and, in some cases, bacterial competitors. Furthermore, several of these compounds possess surfactant properties that enhance

bacterial motility and root colonisation, thereby providing additional competitive advantages in the rhizosphere (Raaijmakers *et al.*, 2010). Notably, the production of such antibiotics is tightly regulated by environmental stimuli, quorum sensing, and global transcriptional regulators, ensuring their production is both energy-efficient and context-specific (de Oliveira Pereira, 2024).

Field applications of antibiotic-producing rhizobacteria have yielded promising results. For example, *Pseudomonas fluorescens* Q2-87, which produces 2,4-DAPG, has been successfully employed to mitigate root rot and wilt disease outbreaks in various cereals and legumes. These antibiotics not only diminish pathogen populations but also contribute to the development of suppressive soils, in which disease incidence remains consistently low across multiple growing seasons without the need for repeated bacterial applications (Weller *et al.*, 2007). An emerging approach involves formulating microbial consortia comprising strains that produce complementary antibiotics, thereby enhancing biocontrol efficacy and broadening the spectrum of pathogen suppression.

Parasitism

Parasitism, as a mechanism of biocontrol, entails the direct attack and degradation of fungal pathogens by rhizobacteria. In contrast to antibiosis, parasitism requires the physical colonization and enzymatic breakdown of fungal structures. The mode of action shows particular efficacy against fungal pathogens characterized by resilient mycelial networks or the production of resistant propagules such as sclerotia and chlamydospores. Parasitic rhizobacteria commonly employ a synergistic combination of enzymatic activity, spatial competition, and tissue penetration to incapacitate fungal pathogens (Duhan *et al.*, 2022).

A prominent example of parasitic biocontrol involves *Serratia marcescens*, a Gram-negative bacterium known for its antagonistic activity against *Sclerotinia* spp., which are major causal agents of plant diseases such as white mould. *S. marcescens* produces a suite of extracellular enzymes, notably chitinases, which hydrolyse chitin, a key structural polysaccharide in fungal cell walls. This enzymatic action enables *S. marcescens* to degrade the hyphal networks of *Sclerotinia* spp., thereby obstructing their ability to colonise host tissue or propagate (Someya *et al.*, 2000). By depolymerising chitin, the fungal cell wall becomes destabilised and structurally compromised, limiting pathogen viability and spread. Moreover, *S. marcescens* may secrete secondary metabolites that exacerbate cellular disruption, further amplifying its parasitic effectiveness (Timmusk & Wagner, 2018). Beyond direct fungal degradation, *S. marcescens* exhibits additional traits that reinforce its biocontrol potential. Through siderophore production, *S. marcescens* competes for iron availability, limiting pathogen access to this vital element. Furthermore, this species can elicit ISR in the host plant, priming the plant's immune system for a heightened response to subsequent pathogenic encounters (Köhl *et al.*, 2019). This multifaceted interaction positions *S. marcescens* as a versatile agent in integrated disease management.

Other rhizobacterial taxa also exhibit parasitic activity through the secretion of hydrolytic enzymes. For instance, *Bacillus* spp. are known to combat fungal pathogens such as *Rhizoctonia solani* and *Fusarium oxysporum* via the production of chitinases, glucanases, and cellulases. These lytic enzymes degrade key polymers in fungal cell walls, namely chitin, glucans, and cellulose and thus lead to the collapse of hyphal integrity and facilitating microbial colonisation of the pathogen (Larkin & Fravel, 1998). This enzymatic arsenal allows *Bacillus* species to effectively parasitise and neutralise a broad spectrum of phytopathogens. Thus, parasitism as a biocontrol strategy offers several distinct advantages that include reducing dependence on synthetic fungicides, thereby mitigating associated environmental and health concerns, and

then fostering natural pathogen suppression, particularly in soils where chemical control methods are inadequate or unsustainable.

Induced Systemic Resistance (ISR)

ISR is a well-characterized plant defence mechanism mediated by PGPR, which enhances plant's innate immune capacity against a diverse range of phytopathogens. Unlike Systemic Acquired Resistance (SAR), that is generally mediated by pathogen invasion and largely reliant on salicylic acid (SA) signaling, ISR is predominantly activated by beneficial rhizosphere microbes and is modulated through the jasmonic acid (JA) and ethylene (ET) signalling pathways (Pieterse *et al.*, 2014). Following the colonisation of root tissues, PGPR including *Pseudomonas fluorescens* and *Bacillus subtilis* release a suite of elicitors such as microbe-associated molecular patterns (MAMPs), siderophores, lipopolysaccharides, and volatile organic compounds (VOCs). These microbial signals are recognised by host plants, initiating a physiological state of priming—an enhanced readiness for defence activation without the substantial metabolic costs associated with constitutive defence expression (Tiwari & Singh, 2021).

The induction of ISR results in systemic upregulation of plant defence mechanisms, including the transcriptional activation of defence-related genes and enhanced activity of key enzymes such as peroxidases and phenylalanine ammonia-lyase (PAL). Additionally, ISR enhances the synthesis of pathogenesis-related (PR) proteins, notably chitinases and β-1,3-glucanases, which strengthen the plant cell wall matrix and suppress pathogen ingress and proliferation (Pieterse *et al.*, 2014). Interestingly, ISR functions independently of direct pathogen suppression and enhances the plant's capacity to detect and respond more rapidly and robustly to subsequent biotic challenges (Heil & Bostock, 2002). This form of induced resistance offers broad-spectrum protection, conferring resilience not only against bacterial and fungal pathogens but also certain viral agents and insect herbivores (Shoresh *et al.*, 2010). Given that ISR harnesses endogenous plant defence pathways rather than relying on exogenous biocidal inputs, it represents a sustainable and environmentally compatible strategy for crop protection in modern agriculture.

PRACTICAL APPLICATIONS IN CROP PROTECTION: CASE STUDIES

Wheat (Fusarium Head Blight)

Fusarium head blight (FHB), chiefly attributed to *Fusarium graminearum* and related species, is a devastating fungal disease that affects wheat and other cereal crops (Alisaac & Mahlein, 2023). It leads to substantial reductions in grain yield and contamination of the harvested grain with harmful mycotoxins like deoxynivalenol (DON), which present serious health risks to both humans and livestock. The disease is characterised by blighting of the wheat head, resulting in premature floret death and marked declines in both grain quality and quantity. Management of FHB using traditional chemical fungicides has been limited, particularly in mitigating mycotoxin accumulation, due to the complex epidemiology of the disease and the critical timing of pathogen infection. This has driven increasing interest in sustainable control measures, notably the use of biocontrol agents such as rhizobacteria.

Among promising biocontrol candidates is *Bacillus velezensis* FZB42, a beneficial rhizobacterial strain recognised for its potent antifungal activity and plant growth-promoting attributes. Field experiments conducted by Palazzini *et al.* (2016) confirmed that treatment with *B. velezensis* FZB42 reduced FHB severity in wheat by approximately 60%. The underlying biocontrol mechanism is considered multifactorial, encompassing both direct antagonism of the pathogen and indirect induction of systemic resistance in the host plant. *B. velezensis* FZB42 synthesises a suite of bioactive molecules, including lipopeptides, which have been shown to disrupt the growth of *Fusarium* species (Chowdhury *et al.*, 2015). These compounds compromise fungal cell

membrane integrity and inhibit mycelial development, thereby limiting pathogen proliferation on wheat heads.

In addition to direct antifungal effects, *B. velezensis* FZB42 stimulates plant immune responses. Inoculation of wheat plants with this strain activates defence pathways, leading to enhanced production of phytoalexins, fungal cell wall–lysing enzymes like chitinases and glucanases and reinforcement of cell walls. Such responses not only mitigate *Fusarium* infection but also strengthen plant defences against environmental stressors (Zhao *et al.*, 2014). Moreover, *B. velezensis* FZB42 has been observed to promote overall plant growth, contributing to increased crop yield even under pathogen pressure—an important advantage for agricultural productivity.

Field trials further highlight the potential of *B. velezensis* FZB42 within integrated disease management (IDM) frameworks. When combined with agronomic practices such as crop rotation and deployment of resistant wheat cultivars, the effectiveness of FHB control is enhanced. As a non-toxic and environmentally sustainable alternative to chemical fungicides, *B. velezensis* FZB42 offers a promising strategy to reduce pesticide dependency, with beneficial implications for environmental and human health (Palazzini *et al.*, 2016).

Despite encouraging results, challenges remain in scaling the practical application of *B. velezensis* FZB42 across diverse agroecosystems. Variability in field performance under differing environmental conditions and integration into existing farming systems require further research. Nonetheless, the demonstrated efficacy of this biocontrol agent in field settings underscores its potential as a valuable tool in sustainable wheat production, supporting both disease suppression and crop health improvement.

Tomatoes (Fusarium Wilt)

Fusarium wilt, induced by *Fusarium oxysporum* f. sp. *lycopersici*, is a widespread soil-borne pathogen affecting tomato crops worldwide. The pathogen invades the vascular tissues, impairing xylem function resulting in wilting, leaf yellowing, and ultimately plant death (Hassan, 2020). Fusarium wilt is difficult to manage because the pathogen persists in soil for extended periods, particularly in the form of resistant conidia and chlamydospores. Conventional chemical fungicides often prove ineffective, while the deployment of resistant tomato cultivars is hampered by the pathogen's evolving virulence. Consequently, biocontrol approaches, notably those involving rhizobacteria, have gained prominence within integrated disease management (IDM) strategies for tomato production.

A promising biocontrol agent against Fusarium wilt is *Pseudomonas fluorescens* strain CHA0. This rhizobacterium synthesises a diverse spectrum of antimicrobial metabolites, including the antibiotic 2,4-diacetylphloroglucinol (2,4-DAPG), which has demonstrated efficacy in reducing the growth of *Fusarium oxysporum* (De Meyer *et al.*, 1998). Trials under both greenhouse and field conditions reveal that *P. fluorescens* CHA0 not only reduces Fusarium wilt incidence by up to 40% but also fosters improved plant growth. The reduction in disease severity is largely attributed to the direct antifungal activity of 2,4-DAPG, which disrupts the pathogen's cellular functions and inhibits its proliferation (Mavrodi *et al.*, 2001).

Beyond its antifungal properties, *P. fluorescens* CHA0 enhances plant growth by synthesising plant growth-promoting substances such as indole-3-acetic acid (IAA) and siderophores. These compounds improve nutrient availability, stimulate root development, and enhance overall plant vigour, which are critical factors when combating soil-borne pathogens. Furthermore, *P. fluorescens* CHA0 induces systemic resistance in tomato plants, priming the host's defence responses through activation of defence-related gene expression and accumulation of phytoalexins, thereby bolstering resistance against Fusarium wilt (Bakker *et al.*, 2007). The demonstrated success of *P. fluorescens* CHA0 in mitigating Fusarium wilt highlights its potential as a potent biocontrol agent. However, challenges persist in achieving consistent performance under variable environmental conditions such as fluctuating soil moisture and temperature, which can impact the efficacy of rhizobacterial treatments. Additionally, issues related to formulation stability, shelf-life, and large-scale production remain to be addressed for widespread commercial adoption (Bakker *et al.*, 2007).

Grapevines (Downy Mildew)

Downy mildew, induced by *Plasmopara viticola*, is a serious disease affecting grapevines, particularly in humid climates. The pathogen infects leaves, stems, and grape clusters, causing lesions, necrosis, and defoliation, which result in reduced yield and poor fruit quality (Koledenkova *et al.*, 2022). Additionally, infection predisposes plants to secondary pathogens, further complicating disease management. Conventional control strategies rely heavily on chemical fungicides; however, these often have limited effectiveness, contribute to environmental pollution, encourage pathogen resistance, and disrupt beneficial microbial communities (Islam *et al.*, 2024). Consequently, biological control strategies involving rhizobacteria have gained considerable interest as environmentally sustainable alternatives.

One of the most extensively studied biocontrol agents for downy mildew is *Bacillus subtilis* strain QST 713. This rhizobacterium exhibits broad-spectrum antifungal activity alongside plant growth-promoting properties. Field trials have demonstrated that application of *B. subtilis* QST 713 can reduce downy mildew incidence in grapevines by up to 50%, while also enhancing grape yield and quality. The efficacy of this biocontrol agent is primarily attributed to its production of antifungal metabolites such as lipopeptides—including surfactin, which disrupts fungal cell membranes, and iturin, which inhibits fungal spore germination (Ongena *et al.*, 2007). These bioactive compounds act directly on *P. viticola*, preventing establishment and infection of grapevine tissues.

In addition to direct antifungal effects, *B. subtilis* QST 713 induces systemic resistance in grapevines. Applications to soil or foliage prime the plant's defence responses, leading to enhanced resistance against downy mildew and other diseases. This priming involves activation of defence pathways, including the generation of ROS and upregulation of defence-related genes, enhancing the plant's capacity to respond robustly to pathogen invasion (Mousa *et al.*, 2012). The systemic nature of this induced resistance renders *B. subtilis* QST 713 effective in protecting grapevines against both local and systemic infections by *P. viticola*.

B. subtilis QST 713 also promotes plant growth by producing substances such as indole-3-acetic acid (IAA) and gibberellins, which stimulate root development and overall plant vigour, helping grapevines to thrive despite pathogen pressure. The bacterium also synthesises siderophores that sequester essential nutrients like iron, outcompeting the pathogen and further limiting its capacity to colonise plant tissues (Chowdhury *et al.*, 2015). Thus, the utilisation of *B. subtilis* QST 713 offers several advantages over conventional chemical fungicides such as provision of effective disease control while reducing environmental impacts associated with synthetic chemicals.

Sweet Potato (Soilborne Fungal Diseases)

Sweet potato (*Ipomoea batatas*) is a vital staple crop globally, especially in developing nations where it serves as a primary source of carbohydrates and essential vitamins. However, sweet potato production is severely constrained by soilborne fungal pathogens, including those causing Fusarium wilt and Rhizoctonia root rot. These pathogens result in significant yield losses, diminished tuber quality, and harvesting difficulties. The extensive reliance on chemical fungicides for disease control has raised concerns regarding environmental pollution, the emergence of pesticide resistance, and food safety issues. Consequently, the use of biological control agents, including rhizobacteria, has emerged as a promising and sustainable approach for managing soilborne fungal diseases in sweet potato cultivation.

In Nigeria, where sweet potato is a critical staple food, dry rot caused by *Fusarium solani* represents a major production threat. The potential of utilizing rhizospheric microorganisms for environmentally friendly disease management was investigated and Rhizospheric isolates, such as *Bacillus* spp., inhibited *F. solani* mycelial growth by over 51% in dual-culture assays, while combined applications with *Trichoderma* spp. significantly enhanced tuber survival during storage (Ade-Ogunnowo, 2023). These findings suggest a viable alternative to conventional chemical fungicides.

Among biocontrol agents, *Trichoderma harzianum* is one of the most extensively studied for the management of soilborne fungal diseases in sweet potato. This well-known soil fungus acts as a natural antagonist against a wide range of plant pathogens, including *Fusarium* spp. and *Rhizoctonia solani* (Ade-Ogunnowo, 2023; Abbas *et al.*, 2017). In a

study by Wang *et al.* (2011), application of *T. harzianum* significantly reduced the incidence of Fusarium wilt and Rhizoctonia root rot in sweet potato. The biocontrol efficacy is attributed to multiple mechanisms, including competition for nutrients and space, secretion of lytic enzymes such as chitinases and glucanases that degrade fungal cell walls, and production of antifungal secondary metabolites. Notably, *Trichoderma* produces compounds such as trichodermol that inhibit the growth of pathogenic fungi, enhancing its effectiveness as a biocontrol agent (Harman *et al.*, 2004).

Additionally, *Pseudomonas fluorescens*, a rhizobacterium with broad-spectrum antimicrobial activity, has been investigated for its potential in controlling soil-borne pathogens in sweet potato. Application of *P. fluorescens* markedly reduced the severity of *Rhizoctonia solani* infection in sweet potato plants (Kadhum *et al.*, 2020). This bacterium synthesises antimicrobial compounds including phenazines and 2,4-diacetylphloroglucinol (2,4-DAPG), which are toxic to numerous plant pathogens. The biocontrol efficacy of *Pseudomonas fluorescens* is further improved when combined with other agents. For example, co-application of *P. fluorescens* and *Trichoderma harzianum* has demonstrated synergistic effects, resulting in reduced pathogen populations and improved plant growth. Greenhouse and field trials revealed that sweet potato plants treated with this combination exhibited enhanced resistance to soilborne diseases, increased tuber yield, and lower infection levels compared with untreated controls (Naylor *et al.*, 2008). This strategy highlights the potential of deploying multiple biocontrol agents that target diverse aspects of pathogen biology.

The application of rhizobacteria-based biocontrol agents offers multiple advantages to sweet potato farmers. These agents reduce reliance on chemical pesticides and promote sustainable agricultural practices by improving soil health and supporting beneficial microbial communities. Moreover, biocontrol agents such as *Trichoderma harzianum* and *Pseudomonas fluorescens* can be applied flexibly through seed treatments, soil inoculations, or foliar sprays, providing cost-effective options. Nevertheless, challenges remain regarding the development of stable, efficacious commercial formulations capable of withstanding environmental stresses and suitable for large-scale application across diverse agricultural systems (Harman *et al.*, 2004).

KEY BARRIERS TO BIOFUNGICIDE COMMERCIALISATION

Despite the growing interest in microbial biofungicides as sustainable alternatives to chemical fungicides, several critical barriers continue to impede their widespread adoption and commercial success. Chief among these is their vulnerability to fluctuating environmental conditions. In contrast to synthetic fungicides, which are chemically stable and relatively unaffected by environmental variability, microbial biofungicides depend on the viability and metabolic activity of living organisms. Environmental stressors such as temperature extremes, irregular soil moisture, pH fluctuations, and ultraviolet (UV) radiation can severely impair microbial survival and biocontrol efficacy (Compant *et al.*, 2005). For instance, although *Pseudomonas fluorescens* is renowned for its antifungal activity under laboratory conditions, it often fails to establish effective rhizosphere colonisation under field conditions characterised by drought or elevated temperatures (Mavrodi *et al.*, 2012). Such inconsistencies in performance erode farmer confidence and present a significant obstacle to commercial deployment.

The ecological complexity of the rhizosphere presents an additional challenge. It is a highly competitive environment where introduced plant growth-promoting rhizobacteria (PGPR) must vie with indigenous microbial communities for nutrients and colonisation niches. While strains such as *Bacillus subtilis* have demonstrated strong biocontrol capabilities under sterile or low-microbial-load conditions, they often fail to persist or function effectively in diverse and microbially rich soil systems (Lugtenberg & Kamilova, 2009). Furthermore, soil management practices, including intensive fertiliser and pesticide use, can disrupt native microbial assemblages, thereby altering the ecological dynamics of the rhizosphere and potentially diminishing the efficacy of introduced biofungicides (Berg *et al.*, 2017).

Another major constraint lies in the formulation and shelf-life of microbial products. Ensuring microbial viability during storage and application remains a technical

bottleneck. Biofungicides based on *Trichoderma spp.* or *Bacillus spp.* often require specialised preservation methods such as lyophilisation or refrigeration to retain viability and efficacy (Harman *et al.*, 2010). Although liquid formulations offer ease of application, they are frequently associated with reduced shelf-lives, owing to microbial senescence or cell death during storage under ambient or suboptimal conditions (Harman *et al.*, 2010). These technical challenges contribute to increased production costs and create logistical difficulties in distribution and storage, especially in low-resource agricultural settings.

Finally, regulatory and sociocultural barriers must be addressed to facilitate broader adoption. The registration process for biofungicides is often protracted and complex, requiring comprehensive datasets on microbial safety, environmental impact, and efficacy (McSpadden Gardener & Fravel, 2002). Unlike synthetic agrochemicals, which benefit from well-established and standardised testing frameworks, biofungicides are subject to heightened scrutiny. Moreover, widespread farmer scepticism, often rooted in perceptions of lower efficacy compared to conventional chemical fungicides, continues to impede market uptake. In the absence of robust policy incentives, demonstration programmes, or economic subsidies, adoption remains limited, despite the well-documented environmental advantages of microbial alternatives.

ENHANCING BIOFUNGICIDE EFFICACY

A suite of emerging technologies and scientific advancements is paving the way for a new generation of biofungicides with enhanced efficacy, stability, and environmental resilience. First, advances in genetic engineering present promising avenues for improving the functional performance of PGPR. One key strategy involves the manipulation of microbial genomes to overproduce antifungal secondary metabolites, such as phenazines and lipopeptides, which enhance pathogen suppression (Ongena & Jacques, 2008). For instance, *Pseudomonas* strains genetically modified to boost the synthesis of 2,4-diacetylphloroglucinol (DAPG) have demonstrated increased antifungal activity against *Fusarium* species (Mavrodi *et al.*, 2006). Moreover, contemporary gene-editing approaches, particularly CRISPR–Cas systems, enable precise modification of microbial genomes to enhance traits such as heat tolerance, desiccation resistance, and root colonisation efficiency, thereby potentially improving persistence and functional performance under field conditions (Arif *et al.*, 2020).

Second, nanotechnology is increasingly being harnessed to improve the formulation and delivery of biofungicides. Encapsulation of microbial agents in biodegradable polymers such as chitosan or alginate can shield cells from abiotic stressors and facilitate controlled release in the rhizosphere (Khan & Rizvi, 2014). Nano-coatings can provide protection against ultraviolet radiation and oxidative damage, while functionalised nanoparticles may enhance root adhesion and colonisation efficiency (Kah *et al.*, 2018). Furthermore, combining microbial biofungicides with metal nanoparticles, such as silver or zinc oxide, has been shown to amplify antimicrobial activity, offering a synergistic defence against a broad spectrum of pathogens (Prasad *et al.*, 2017).

Third, there is growing recognition that multi-strain or multi-species microbial consortia may more effectively mimic the complexity and functionality of natural soil microbiomes. Such consortia can provide complementary biocontrol mechanisms, enhance ecological stability, and improve plant health. For example, formulations combining *Pseudomonas* (noted for antibiosis), *Bacillus* (with parasitic action), and arbuscular mycorrhizal fungi (facilitating nutrient uptake) can generate robust and synergistic disease suppression outcomes (Hu *et al.*, 2016). This ecological approach aligns with holistic soil health management and is particularly well-suited for sustainable farming systems.

Finally, emerging digital technologies offer significant potential to optimize the application of biofungicides in real time. Drone-assisted spraying systems provide efficient and uniform distribution of microbial agents, especially in large or difficult-to-access fields. Additionally, artificial intelligence (AI) and machine learning are being leveraged to develop predictive models that integrate real-time soil health metrics, weather conditions, and pathogen surveillance data to determine the optimal timing and dosage of biofungicide applications (Kamilaris *et al.*, 2017). Such precision

agriculture tools can significantly reduce variability in field performance and contribute to the reliability and scalability of microbial biocontrol strategies.

CHALLENGES AND FUTURE PROSPECTS

Although rhizobacteria-based biocontrol agents have demonstrated considerable promise in managing fungal diseases and promoting sustainable agriculture, several limitations and challenges must be addressed to maximize their efficacy and commercial viability. A primary challenge is their environmental sensitivity. Rhizobacteria are highly susceptible to fluctuating environmental conditions, including temperature, soil moisture, pH, and the presence of competing microbial communities, all of which can significantly influence their survival and effectiveness (Compant *et al.*, 2005). For example, biocontrol agents such as *Pseudomonas fluorescens* and *Bacillus subtilis* may perform well under controlled greenhouse conditions but often exhibit reduced efficacy in field environments where abiotic factors are more variable.

Furthermore, application in regions experiencing extreme weather events, such as drought or elevated temperatures, may further diminish their capacity to suppress pathogens effectively.

Rhizobacteria require specific environmental conditions to thrive and exert their protective effects. High soil salinity or drought stress, for instance, can impair microbial activity and colonisation abilities. Moreover, certain soil borne diseases are more prevalent under particular environmental conditions, complicating the use of rhizobacteria as a universally applicable solution for fungal control (Abdelaziz *et al.*, 2023). In areas with unpredictable weather patterns, the inconsistent performance of biocontrol agents may lead to reduced confidence among farmers and stakeholders.

Microbial competition within the rhizosphere represents another significant obstacle to the successful implementation of biocontrol agents. The rhizosphere is a complex and competitive microbial habitat where beneficial and harmful microorganisms coexist. Although rhizobacteria such as *Pseudomonas* and *Bacillus* can suppress specific pathogens, their ability to outcompete well-established native microbial communities for nutrients and niche space is not guaranteed (Compant *et al.*, 2005). This challenge is particularly pronounced in soils with rich microbial diversity or those previously subjected to intensive chemical fertiliser and pesticide use, which may disrupt microbial equilibrium.

Stability and shelf-life also limit the widespread use of biocontrol agents. Many rhizobacteria are sensitive to environmental stressors such as ultraviolet radiation, desiccation, and temperature extremes, which degrade viability and reduce efficacy over time (Harman *et al.*, 2004). Liquid formulations, though effective immediately post-application, may lose potency if improperly stored or exposed to adverse conditions. Similarly, dry or granular formulations face stability challenges that necessitate advanced packaging or storage solutions to maintain long-term effectiveness.

Cost-effectiveness and scalability remain additional hurdles. While biocontrol agents may be economical at a small scale, commercial production and large-scale deployment often incur substantial costs. The development, formulation, and application of these agents require specialized infrastructure and expertise, potentially limiting accessibility, particularly for smallholder farmers in developing regions. Production costs escalate further due to the need for high-quality, contaminant-free cultures and appropriate delivery systems that ensure viable colonisation of target pathogens (Van Der Hoeven *et al.*, 2017).

Despite these challenges, the increasing demand for sustainable agriculture offers avenues to overcome such limitations. Advances in genetic engineering, nano-formulation technologies, and microbial ecology hold promise for enhancing the stability, efficacy, and environmental adaptability of rhizobacteria-based biocontrol agents. Furthermore, integrated pest management (IPM) approaches that incorporate biocontrol agents with complementary measures that include crop rotation, resistant cultivars, and soil health enhancement can mitigate environmental variability and improve the overall success of biocontrol applications.

CONCLUSION

Rhizobacteria-based biocontrol agents provide a sustainable alternative to chemical fungicides, suppressing fungal pathogens through nutrient competition, antimicrobial production, and the activation of systemic plant defences. Strains like *Pseudomonas fluorescens* and *Bacillus subtilis* have demonstrated efficacy across diverse crops. However, challenges such as environmental sensitivity, inconsistent field performance, and formulation stability limit widespread adoption.

Scalable production and cost-effective delivery remain critical barriers, particularly for smallholder farmers. Innovations in nano encapsulation, genetic engineering, and integration with IPM systems could enhance agent resilience and efficacy. With targeted research, rhizobacteria-based solutions may reduce reliance on synthetic fungicides, promoting sustainable agriculture and global food security.

REFERENCES

Abbas, A., Jiang, D., & Fu, Y. (2017). Trichoderma spp. as antagonist of Rhizoctonia solani. *Journal of Plant Pathology and Microbiol*ogy *8*(3), 1-9.

Ade-Ogunnowo, F. E. (2023). *Selected antagonistic microorganisms and botanicals in the management of Fusarium solani Sacc. associated with dry rot disease of Ipomea batatas in Ogun State* [Doctoral dissertation, University of Ibadan].

Alisaac, E., & Mahlein, A. K. (2023). Fusarium head blight on wheat: Biology, modern detection and diagnosis and integrated disease management. *Toxins*, *15*(3), 192.

Arif, I., Batool, M., & Schenk, P. M. (2020). Plant microbiome engineering: expected benefits for improved crop growth and resilience. *Trends in Biotechnology*, *38*(12), 1385-1396.

Bakker, P. A. H. M., Pieterse, C. M. J., & van Loon, L. C. (2007). Induced systemic resistance by fluorescent Pseudomonas spp. Phytopathology, 97(2), 239–243.

Berendsen, R. L., Pieterse, C. M. J., & Bakker, P. A. H. M. (2012). The rhizosphere microbiome and plant health. Trends in Plant Science, 17(8), 478–486.

Berg, G., Köberl, M., Rybakova, D., Müller, H., Grosch, R., & Smalla, K. (2017). Plant microbial diversity is suggested as the key to future biocontrol and health trends. *FEMS Microbiology Ecology*, *93*(5), fix050.

Balhara, M., Chaudhary, R., Ruhil, S., Singh, B., Dahiya, N., Parmar, V. S., ... & Chhillar, A. K. (2016). Siderophores; iron scavengers: the novel & promising targets for pathogen specific antifungal therapy. *Expert Opinion on Therapeutic Targets*, *20*(12), 1477-1489.

Berendsen, R. L., Pieterse, C. M., & Bakker, P. A. (2012). The rhizosphere microbiome and plant health. *Trends in Plant Science*, *17*(8), 478-486.

Bhattacharyya, A., Mavrodi, O., Bhowmik, N., Weller, D., Thomashow, L., & Mavrodi, D. (2023). Bacterial biofilms as an essential component of rhizosphere plant-microbe interactions. In *Methods in microbiology* (Vol. 53, pp. 3-48). Academic Press

Chen, L., & Liu, Y. (2024). The function of root exudates in the root colonization by beneficial soil rhizobacteria. *Biology*, *13*(2), 95.

Chowdhury, F. T., Zaman, N. R., Islam, M. R., & Khan, H. (2020). Anti-fungal secondary metabolites and hydrolytic enzymes from rhizospheric bacteria in crop protection: A review. *Journal of Bangladesh Academy of Sciences*, *44*(2), 69-84.

Chowdhury, S. P., Hartmann, A., Gao, X., & Borriss, R. (2015). Biocontrol mechanism by root-associated Bacillus amyloliquefaciens FZB42 – A review. *Frontiers in Microbiology*, *6*, 780.

Compant, S., Duffy, B., Nowak, J., Clément, C., & Barka, E. A. (2005). Use of plant growth-promoting bacteria for biocontrol of plant diseases: Principles, mechanisms of action, and future prospects. Applied and Environmental Microbiology, 71(9), 4951–4959.

De Meyer, G., Capieau, K., Audenaert, K., Buchala, A., Métraux, J. P., & Höfte, M. (1998). Nanogram amounts of salicylic acid produced by the rhizobacterium Pseudomonas aeruginosa 7NSK2 activate the systemic acquired resistance pathway in bean. *Molecular Plant-Microbe Interactions*, *12* (5), 450–458.

de Oliveira Pereira, T. (2024). *Influence of Environmental Cues into the Quorum Sensing Regulatory Network in the Opportunistic Pathogen Pseudomonas aeruginosa* (Doctoral dissertation, Université du Québec, Institut national de la recherche scientifique).

Du Laing, G., Rinklebe, J., Vandecasteele, B., Meers, E., & Tack, F. M. (2009). Trace metal behaviour in estuarine and riverine floodplain soils and sediments: a review. Science of the total environment, 407(13), 3972-3985.

Duhan, L., Kumari, D., Verma, R., & Pasrija, R. (2022). Fungal hydrolytic enzymes produced by plant growth-promoting rhizobacteria (PGPR). In Secondary metabolites and volatiles of PGPR in plant-growth promotion (pp. 313-333). Cham: Springer International Publishing.

Feng, H., Fu, R., Hou, X., Lv, Y., Zhang, N., Liu, Y., ... & Zhang, R. (2021). Chemotaxis of beneficial rhizobacteria to root exudates: the first step towards root–microbe rhizosphere interactions. International Journal of Molecular Sciences, 22(13), 6655.

Ghorui, M., Chowdhury, S., & Burla, S. (2025). Recent advances in the commercial formulation of arbuscular mycorrhizal inoculants. *Frontiers in Industrial Microbiology*, *3*, 1553472.

Ghssein, G., & Ezzeddine, Z. (2022). A review of Pseudomonas aeruginosa metallophores: Pyoverdine, pyochelin and pseudopaline. Biology, 11(12), 1711.

Haas, D., & Défago, G. (2005). Biological control of soil-borne pathogens by fluorescent pseudomonads. Nature Reviews Microbiology, 3(4), 307–319.

Harman, G. E., Howell, C. R., Viterbo, A., Chet, I., & Lorito, M. (2004). Trichoderma species— Opportunistic, avirulent plant symbionts. Nature Reviews Microbiology, 2(1), 43–56.

Harman, G. E., Howell, C. R., Viterbo, A., Chet, I., & Lorito, M. (2010). *Trichoderma* species - opportunistic, avirulent plant symbionts. *Nature Reviews Microbiology, 2*(1), 43-56.

Hassan, H. A. (2020). Biology and Integrated Control of Tomato Wilt Caused by Fusarium oxysporum lycopersici: A Com-prehensive Review under the Light of Recent Advancements. J Bot Res, 3(1), 84-99.

Heil, M., & Bostock, R. M. (2002). Induced systemic resistance (ISR) against pathogens in the context of induced plant defences. *Annals of botany*, *89*(5), 503-512.

Hu, J., Wei, Z., Friman, V.-P., Gu, S.-H., Wang, X.-F., Eisenhauer, N., Yang, T.-J., Ma, J., Shen, Q.-R., Xu, Y.-C., & Jousset, A. (2016). Probiotic diversity enhances rhizosphere microbiome function and plant disease suppression. *mBio, 7*(6), e01790-16.

Islam, T., Danishuddin, Tamanna, N. T., Matin, M. N., Barai, H. R., & Haque, M. A. (2024). Resistance mechanisms of plant pathogenic fungi to fungicide, environmental impacts of fungicides, and sustainable solutions. *Plants*, *13*(19), 2737.

Jones, D. L., Nguyen, C., & Finlay, R. D. (2009). Carbon flow in the rhizosphere: carbon trading at the soil–root interface. 5-33

Kadhum, A. A., Abed, J. M., & Farhan, T. A. (2020). Role of Pseudomonas Fluorescens and Organic Matter in Controlling of Potato Black Scurf Disease Caused by Rhizoctonia Solani. *Systematic Reviews in Pharmacy*, *11*(11).

Kah, M., Kookana, R. S., Gogos, A., & Bucheli, T. D. (2018). A critical evaluation of nanopesticides and nanofertilisers against their conventional analogues. *Nature Nanotechnology*, *13*, 677–684.

Kamilaris, A., Kartakoullis, A., & Prenafeta-Boldú, F. X. (2017). A review on the practice of big data analysis in agriculture. *Computers and Electronics in Agriculture, 143*, 23-37.

Khan, M. S., & Rizvi, T. F. (2014). Nanotechnology: Scope and application in plant disease management. *Plant Pathology Journal, 13*(3), 214-231.

Koledenkova, K., Esmaeel, Q., Jacquard, C., Nowak, J., Clément, C., & Ait Barka, E. (2022). Plasmopara viticola the causal agent of downy mildew of grapevine: from its taxonomy to disease management. *Frontiers in Microbiology*, *13*, 889472.

Köhl, J., Kolnaar, R., & Ravensberg, W. J. (2019). Mode of action of microbial biological control agents against plant diseases: Relevance beyond efficacy. *Frontiers in Plant Science*, *10*, 845.

Kraepiel, A. M. L., Bellenger, J. P., Wichard, T., & Morel, F. M. M. (2021). Multiple roles of siderophores in free-living nitrogen-fixing bacteria. *Biometals*, *22*(4), 573–581.

Larkin, R. P., & Fravel, D. R. (1998). Efficacy of various fungal and bacterial biocontrol organisms for control of Fusarium wilt of tomato. *Plant Disease*, *82*(9), 1022–1028.

Lemanceau, P., Bakker, P. A. H. M., De Kogel, W. J., Alabouvette, C., & Schippers, B. (1992). Effect of pseudobactin 358 production by Pseudomonas putida WCS358 on suppression of Fusarium wilt of carnations by nonpathogenic Fusarium oxysporum Fo47. Applied and Environmental *Microbiology*, *58*(9), 2978–2982.

Lemanceau, P., Expert, D., Gaymard, F., Bakker, P. A. H. M., & Briat, J. F. (2009). Role of iron in plant–microbe interactions. *Advances in Botanical Research, 51*, 491-549.

Li, E., de Jonge, R., Liu, C., Jiang, H., Friman, V. P., Pieterse, C. M., ... & Jousset, A. (2021). Rapid evolution of bacterial mutualism in the plant rhizosphere. *Nature Communications*, *12*(1), 3829.

Loper, J. E., & Henkels, M. D. (1999). Utilization of heterologous siderophores enhances levels of iron available to Pseudomonas putida in the rhizosphere. *Applied and Environmental Microbiology*, *65*(12), 5357–5363.

Lugtenberg, B., & Kamilova, F. (2009). Plant-growth-promoting rhizobacteria. *Annual Review of Microbiology, 63*, 541–556.

Mavrodi, D. V., Blankenfeldt, W., & Thomashow, L. S. (2006). Phenazine compounds in fluorescent Pseudomonas spp. biosynthesis and regulation. *Annual Review of Phytopathology, 44*, 417–445.

Mavrodi, O. V., Gardener, B. B. M., Mavrodi, D. V., Bonsall, R. F., Weller, D. M., & Thomashow, L. S. (2001). Genetic diversity of phlD from 2,4-diacetylphloroglucinol-producing fluorescent Pseudomonas spp. *Phytopathology*, *91*(1), 35–43.

McSpadden Gardener, B. B., & Fravel, D. R. (2002). Biological control of plant pathogens: Research, commercialisation, and application in the USA. *Plant Health Progress, 3*(1), 17.

Meena, M., Swapnil, P., Divyanshu, K., Kumar, S., Harish, Tripathi, Y. N., ... & Upadhyay, R. S. (2020). PGPR-mediated induction of systemic resistance and physiochemical alterations in plants against the pathogens: Current perspectives. *Journal of Basic Microbiology*, *60*(10), 828-861.

Mousa, W. K., Shearer, C. R., Limay-Rios, V., Ettinger, C. L., Eisen, J. A., & Raizada, M. N. (2012). Root-hair endophyte stacking in finger millet creates a physicochemical barrier to trap the fungal pathogen Fusarium graminearum. *Nature Microbiology, 1*(12), 16167.

Nehra, S., Gothwal, R. K., Dhingra, S., Varshney, A. K., Solanki, P. S., Meena, P., ... & Ghosh, P. (2022). Mechanism of antagonism: hyperparasitism and antibiosis. In *Microbial Biocontrol:*

Sustainable Agriculture and Phytopathogen Management: Volume 1 (pp. 257-277). Cham: Springer International Publishing.

Oleńska, E., Małek, W., Wójcik, M., Swiecicka, I., Thijs, S., & Vangronsveld, J. (2020). Beneficial features of plant growth-promoting rhizobacteria for improving plant growth and health in challenging conditions: A methodical review. Science of the Total Environment, 743, 140682.

Ongena, M., & Jacques, P. (2008). Bacillus lipopeptides: Versatile weapons for plant disease biocontrol. *Trends in Microbiology*, *16*(3), 115–125.

Palazzini, J. M., Dunlap, C. A., Bowman, M. J., & Chulze, S. N. (2016). Bacillus velezensis RC 218 as a biocontrol agent against Fusarium graminearum: Effect on disease severity and deoxynivalenol accumulation in wheat. *Plant Pathology*, *65*(5), 859–866.

Palmieri, D., Ianiri, G., Del Grosso, C., Barone, G., De Curtis, F., Castoria, R., & Lima, G. (2022). Advances and perspectives in the use of biocontrol agents against fungal plant diseases. *Horticulturae*, *8*(7), 577.

Pattnaik, S., Mohapatra, B., & Gupta, A. (2021). Plant growth-promoting microbe mediated uptake of essential nutrients (Fe, P, K) for crop stress management: Microbe–soil–plant continuum. *Frontiers in Agronomy*, *3*, 689972.

Pieterse, C. M. J., Zamioudis, C., Berendsen, R. L., Weller, D. M., Van Wees, S. C. M., & Bakker, P. A. H. M. (2014). Induced systemic resistance by beneficial microbes. *Annual Review of Phytopathology*, *52*, 347–375.

Prasad, R., Bhattacharyya, A., & Nguyen, Q. D. (2017). Nanotechnology in sustainable agriculture: Recent developments, challenges, and perspectives. *Frontiers in Microbiology*, *8*, 1014.

Prescott, C. E., Grayston, S. J., Helmisaari, H. S., Kaštovská, E., Körner, C., Lambers, H., ... & Ostonen, I. (2020). Surplus carbon drives allocation and plant–soil interactions. *Trends in Ecology & Evolution*, *35*(12), 1110-1118.

Raaijmakers, J. M., De Bruijn, I., Nybroe, O., & Ongena, M. (2010). Natural functions of lipopeptides from Bacillus and Pseudomonas: more than surfactants and antibiotics. *FEMS microbiology reviews*, *34*(6), 1037-1062.

Raaijmakers, J. M., & Mazzola, M. (2012). Diversity and natural functions of antibiotics produced by beneficial and plant pathogenic bacteria. *Annual Review of Phytopathology*, *50*, 403–424.

Saha, M., Sarkar, S., Sarkar, B., Sharma, B. K., Bhattacharjee, S., & Tribedi, P. (2016). Microbial siderophores and their potential applications: A review. *Environmental Science and Pollution Research*, *23*(5), 3984–3999.

Santoyo, G., Urtis-Flores, C. A., Loeza-Lara, P. D., Orozco-Mosqueda, M. D. C., & Glick, B. R. (2021). Rhizosphere colonization determinants by plant growth-promoting rhizobacteria (PGPR). *Biology*, *10*(6), 475.

Serafim, B., Bernardino, A. R., Freitas, F., & Torres, C. A. (2023). Recent developments in the biological activities, bioproduction, and applications of Pseudomonas spp. phenazines. *Molecules*, *28*(3), 1368.

Shoresh, M., Harman, G. E., & Mastouri, F. (2010). Induced systemic resistance and plant responses to fungal biocontrol agents. *Annual Review of Phytopathology*, *48*, 21–43.

Sofija, A. (2022). *Featuring Secondary Metabolites in Bacillus-Pseudomonas Molecular Interactions: Roles in Signaling and Defense Response* (Doctoral dissertation, Universite de Liege (Belgium)).

Someya, N., Nakajima, M., Hirayae, K., Hibi, T., & Akutsu, K. (2000). Synergistic antifungal activity of chitinolytic enzymes and prodigiosin produced by

biocontrol bacterium Serratia marcescens strain B2 against gray mold pathogen, Botrytis cinerea. *Journal of General Plant Pathology*, *67*(4), 312–317.

Timmusk, S., & Wagner, E. G. H. (2018). The plant-growth-promoting rhizobacterium Paenibacillus polymyxa induces changes in Arabidopsis thaliana gene expression: A possible connection between biotic and abiotic stress responses. *Molecular Plant-Microbe Interactions, 12(11), 951–959.

Tiwari, M., & Singh, P. (2021). Plant defense priming: a new tool for sustainable global food security. *Agricultural Innovations and Sustainability*, 133-153.

Vacheron, J., Desbrosses, G., Bouffaud, M. L., Touraine, B., Moënne-Loccoz, Y., Muller, D., Legendre, L., Wisniewski-Dyé, F., & Prigent-Combaret, C. (2013). Plant growth-promoting rhizobacteria and root system functioning. *Frontiers in Plant Science*, *4*, 356.

Van Wees, S. C. M., Van der Ent, S., & Pieterse, C. M. J. (2008). Plant immune responses triggered by beneficial microbes. *Current Opinion in Plant Biology*, *11*(4), 443–448.

Vocciante, M., Grifoni, M., Fusini, D., Petruzzelli, G., & Franchi, E. (2022). The role of plant growth-promoting rhizobacteria (PGPR) in mitigating plant's environmental stresses. *Applied sciences*, *12*(3), 1231.

Wang, S. L., Liang, T. W., & Yen, Y. H. (2011). Bioconversion of chitin-containing wastes for the production of enzymes and bioactive materials. *Carbohydrate Polymers*, *84*(2), 732–742.

Wei, Z., Yang, T., Friman, V. P., Xu, Y., Shen, Q., & Jousset, A. (2015). Trophic network architecture of root-associated bacterial communities determines pathogen invasion and plant health. *Nature Communications*, *6*, 8413.

Weller, D. M. (2007). Pseudomonas biocontrol agents of soilborne pathogens: Looking back over 30 years. *Phytopathology*, *97*(2), 250–256.

Yang, J., Kloepper, J. W., & Ryu, C. M. (2009). Rhizosphere bacteria help plants tolerate abiotic stress. *Trends in plant science*, *14*(1), 1-4.

Yuan, J., Raza, W., & Shen, Q. (2018). Root exudates dominate the colonization of pathogen and plant growth-promoting rhizobacteria. Root biology, 167-180.

Zhalnina, K., Louie, K. B., Hao, Z., Mansoori, N., Da Rocha, U. N., Shi, S., ... & Brodie, E. L. (2018). Dynamic root exudate chemistry and microbial substrate preferences drive patterns in rhizosphere microbial community assembly. *Nature microbiology*, *3*(4), 470-480.

Zhao, Y., Selvaraj, J. N., Xing, F., Zhou, L., Wang, Y., Song, H., Tan, X., Sun, L., Sangare, L., Folly, Y. M. E., & Liu, Y. (2014). Antagonistic action of Bacillus subtilis strain SG6 on Fusarium graminearum. PLOS ONE, 9(3), e92486.