



Research Article

A Review: *Bacillus velezensis* as Plant Growth Promoting Bacteria for a Sustainable Biocontrol Agent

Nuratiqah Ismail^a, Abd Rahman Jabir Mohd Din^b, Chew Swee King^c, Solleh Ramli^d, Nor Zalina Othman^{a,b,*}

^a Department of Biosciences, Universiti Teknologi Malaysia, 81310, Skudai, Johor, Malaysia

^b Innovation Centre in Agritechology, Universiti Teknologi Malaysia, 84600, Pagoh, Johor, Malaysia

^c Forest Fine Foods (M) Sdn Bhd, Lot 15947, Jalan Loji Penapisan Air Grisek, Mukim Gerisek, 84700, Tangkak, Johor, Malaysia

^d Institute of Bioproduct Development, Universiti Teknologi Malaysia, 81310, Skudai, Johor, Malaysia

ARTICLE INFO

Article History:

Received 15 April 2026

Received in revised form 08 June 2026

Accepted 08 June 2026

Available online 30 June 2026

Keywords:

Biocontrol,
Antifungal,
Bacillus velezensis,
Endospore,
Sustainable agriculture

ABSTRACT

Bacillus velezensis has gained increasing attention as a sustainable biocontrol agent due to its multifaceted mechanisms against phytopathogens and its capacity to endure harsh environmental conditions through endospore formation. This review critically examines the biological attributes and functional mechanisms that position *B. velezensis* as a viable alternative to chemical fungicides in modern agriculture. Central to its efficacy is the development of the functional endospore, a highly specialized dormant structure that serves as a critical delivery vehicle, ensuring the bacterium's survival during industrial processing and environmental stress. Particular emphasis is placed on its dual-action strategy: direct mechanisms involving the production of diverse antifungal secondary metabolites such as cyclic lipopeptides, polyketides, and volatile organic compounds (VCOs) which physically disrupt pathogenic fungi, and indirect mechanisms that activate plant immune responses through Induced Systemic Resistance (ISR). The bacterium's capacity to colonize the rhizosphere through chemotaxis, biofilm formation, and root adhesion further enhances its competitiveness and persistence. Additionally, the structural and biochemical resilience of its endospores enables high shelf stability and consistent efficacy in field applications. Collectively, this synthesis underscores *B. velezensis* as a biologically robust, environmentally safe, and agronomically promising solution for sustainable crop protection.

©UTM Penerbit Press. All rights reserved

INTRODUCTION

Fungal plant pathogens are a major cause of crop yield losses worldwide, threatening food security and sustainable agricultural production. Although chemical fungicides remain widely used due to their rapid disease control, their intensive and prolonged application has led to environmental contamination, disruption of soil microbiota, pathogen resistance, and potential risks to human health (Gikas et al., 2022). These limitations have driven increasing interest in environmentally sustainable alternatives for plant disease management. Therefore, the use of beneficial microorganisms in green technology is becoming

increasingly popular. *Bacillus* sp. are Gram-positive, endospore-forming bacteria commonly found in diverse environments such as soil, aquatic systems, and the gastrointestinal tracts of mammals (Saxena et al., 2020). Their widespread occurrence is attributed to their adaptability and ability to produce a variety of bioactive substances. These include enzymes, antimicrobial compounds, and insecticidal proteins, which make them valuable in multiple sectors including agriculture, environmental remediation, and others industrial biotechnology applications such as enzymes production (Saxena et al., 2020).

* Corresponding Author

E-mail address: norzalina@utm.my

DOI address: 10.11113/bioprocessing.v5n1.96

ISBN/©UTM Penerbit Press. All rights reserved

Within agriculture, *Bacillus* species are frequently employed as biopesticides due to their effectiveness in controlling plant pathogens and nematodes. A large number of *Bacillus* sp. have an ability to produce endospores, this trait is one of the defining characteristics of the genus. Endospore formation is a survival strategy that allows *Bacillus* sp. to withstand harsh environmental conditions such as extreme temperatures, desiccation, radiation ultraviolet radiation, and nutrient limitation and chemical exposure (Ahmed et al., 2024; Russi et al., 2024). Through this endospores formation, it shows the ability of *Bacillus* sp. to act as antifungal. The most extensively studied and utilized species for biological control are *B. velezensis*, *Bacillus subtilis*, *Bacillus thuringiensis*, *Bacillus amyloliquefaciens*, as well as *Bacillus firmus* and *Bacillus pumilus*. Among biological control agents, the spore-forming bacterium such as *Bacillus velezensis* has emerged as a highly effective and eco-friendly option. This species exhibits strong antagonistic activity against diverse phytopathogens through the production of antimicrobial secondary metabolites, including cyclic lipopeptides and polyketides, as well as through the induction of plant systemic resistance (Kim et al., 2021). This review explores the increasing use of beneficial microorganisms in green technologies for plant disease management. It specifically highlights the applications of endospore forming *Bacillus velezensis*. and their contribution to environmental sustainability in agriculture.

Bacillus velezensis

B. velezensis has attracted considerable attention as a highly effective biocontrol agent due to its remarkable capacity for endospore formation and its ability to synthesize a wide array of antifungal secondary metabolites such as lipopeptides, polyketides and VOCs (Baptista et al., 2022). This species was originally isolated from the rhizosphere of crops in Velez-Málaga, Spain, and was later taxonomically clarified as a distinct species closely related to *B. subtilis* and *B. amyloliquefaciens* (Balderas-Ruiz et al., 2021). Subsequent genomic and phylogenetic analyses revealed that *B. velezensis* is particularly enriched in biosynthetic gene clusters responsible for antimicrobial compound production, which underpins its strong antagonistic activity against plant pathogens (Fazle Rabbee & Baek, 2020). By the presence of biosynthetic gene clusters (BGCs) for lipopeptides, hydrolytic enzymes, and VOCs, all of which contribute to its broad-spectrum activity. Importantly, these BGCs offer molecular targets for future strain engineering (Markelova & Chumak, 2025).

In comparison to conventional chemical fungicides, *B. velezensis* offers several advantages, including lower environmental toxicity, reduced risk of pathogen resistance development, biodegradability, and compatibility with integrated pest management strategies (Kenfaoui et al., 2024). While chemical fungicides often provide rapid and broad-spectrum disease suppression, their prolonged use can lead to environmental contamination and resistance in target pathogens (Gikas et al., 2022). In contrast, *B. velezensis* exerts multifaceted and sustained disease suppression through antimicrobial metabolite production, niche competition, and host-mediated defence activation, making it a more sustainable alternative for long-term crop protection (Karačić et al., 2024).

Table 1 summarizes several important *Bacillus* species commonly used as biological control agents against fungal plant pathogens. The table highlights the target pathogens, including *Fusarium oxysporum*, *Rhizoctonia solani*, *Botrytis cinerea*, and *Phytophthora infestans*, as well as the primary mechanism include the production of antimicrobial compounds such as lipopeptides and antibiotics, secretion of lytic enzymes, competition for nutrients, induction of plant systemic resistance, and endospore-mediated survival. Among the listed species, *Bacillus velezensis* demonstrates broad-spectrum antifungal activity through both direct antagonistic effects and indirect activation of plant defense responses, highlighting its strong potential as a sustainable biocontrol agent in agriculture.

Importantly, *B. velezensis* also functions as a plant growth-promoting rhizobacterium (PGPR). It enhances plant growth through multiple direct and indirect mechanisms, including the production of phytohormones such as indole-3-acetic acid (IAA), solubilization of insoluble phosphate, and secretion of siderophores that improve iron acquisition by plants (Suárez-Bautista et al., 2024). Additionally, *B. velezensis* produces VOCs that stimulate root elongation and biomass accumulation (Ling et al., 2022). They solubilise essential nutrients such as phosphorus and potassium, improving nutrient availability and uptake by plants. Furthermore, these cells synthesise phytohormones, particularly IAA, which enhances root development, nutrient absorption, and overall plant vigour (Balderas-Ruiz et al., 2021). Indirectly, it promotes plant health by inducing systemic resistance (ISR), thereby priming plant immune responses against a broad spectrum of pathogens. These combined PGPR traits not only improve nutrient uptake and plant vigor but also contribute to enhanced stress tolerance and yield stability under field conditions (Etesami et al., 2023; Xiong et al., 2024).

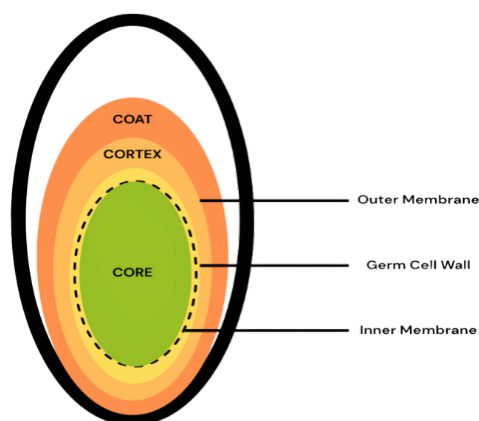
One of the defining features contributing to the ecological success and agricultural relevance of *B. velezensis* is, its ability to form highly resilient endospores (Wang et al., 2025). These dormant structures allow *B. velezensis* to persist in soil environments for extended periods, maintaining viability until favourable conditions are restored (Etesami et al., 2023). This characteristic is particularly advantageous in agricultural systems, where fluctuating environmental conditions often limit the efficacy and consistency of biological control agents. Upon improvement of environmental conditions, the endospores rapidly germinate into metabolically active vegetative cells capable of colonizing plant roots and aerial surfaces (Xiong et al., 2024). The multifunctional attributes of *B. velezensis*, including robust endospore formation, potent antifungal activity, plant growth-promoting capabilities, and environmental resilience, underscore its significance as a sustainable tool in modern agriculture and biotechnology.

Table 1 Antifungal activities and mechanisms of selected *Bacillus* species against major phytopathogenic fungi

Strain	Target Fungal Pathogens	Mode of Action	References
<i>Bacillus velezensis</i>	<i>Botrytis cinerea</i> <i>Sclerotinia sclerotiorum</i> <i>Fusarium sp.</i>	Produces lipopeptides, induced systemic resistance, proteases	Su et al., 2023; Zhong et al., 2024
<i>Bacillus subtilis</i>	<i>Fusarium oxysporum</i> <i>Rhizoctonia solani</i> <i>Alternaria solani</i>	Produces lipopeptides and chitinases that competes for nutrients	Hashem et al., 2019
<i>Bacillus amyloliquefaciens</i>	<i>Phytophthora infestans</i> <i>Fusarium oxysporum</i> <i>Colletotrichum gloeosporioides</i>	Antibiotics, cell wall degradation enzymes	Zalila-Kolsi et al., 2023
<i>Bacillus thuringiensis</i>	<i>Sclerotium rolfsii</i> <i>Fusarium sp.</i>	Antifungal toxins, endospore-mediated biocontrol	Belousova et al., 2021
<i>Bacillus pumilus</i>	<i>Aspergillus flavus</i> <i>Fusarium graminearum</i>	Lytic enzymes, oxidative stress induction in fungi	Dobrzyński et al., 2023
<i>Bacillus firmus</i>	<i>Phytium sp.</i> Nematodes (indirect fungal benefits)	Induces plant resistance, produces metabolites with antifungal and nematocidal effects	Ghahremani et al., 2020

Endospore Structure and Function of *Bacillus velezensis*

Bacterial endospores are resistant structures formed by stressed vegetative cells. Structurally complex and biologically inert, the endospore is designed to ensure long-term survival and rapid reactivation under favourable conditions (Gikas et al., 2022). Its architecture is conserved among *Bacillus* species and comprises multiple specialised layers that contribute to its exceptional resistance and functional versatility. **Figure 1** shows the structure of endospore. The core of the endospore contains the cell's genetic material (DNA), ribosomes, and essential enzymes, but exists in a metabolically dormant state. The core is dehydrated, with water content reduced to approximately 10–25% of the levels found in vegetative cells, which contributes to its enzymatic dormancy and thermal stability. A high concentration of dipicolinic acid (DPA) complexed with calcium ions (Ca-DPA) is present in the core and plays a crucial role in DNA stabilization, dehydration, and resistance to wet heat and oxidizing agents (Mugadza 2018; McKenney et al., 2012).

**Figure 1** Structure of the *B. velezensis* endospore

The surrounding of the core is the inner membrane, which is impermeable to many toxic molecules and contributes significantly to the spore's resistance to harmful chemicals. Outside this is the germ cell wall, which will eventually become the cell wall of the germinated vegetative cell (Cho et al., 2020). Enclosing the germ cell wall is the cortex, a thick layer of loosely cross-linked peptidoglycan. The cortex is critical in maintaining the core's dehydrated state and provides mechanical support against osmotic pressure. External to the cortex is the spore coat, made up of multiple protein layers that protect the spore from UV radiation, enzymes, and antimicrobial compounds (Russi et al., 2024). In some strains, including environmental isolates of *B. velezensis*, an additional exosporium layer may be present, although it is less defined than in other spore-forming bacteria such as *B. anthracis*. The function of the endospore in *B. velezensis* extend beyond mere survival. These structures enable the bacterium to persist in soil ecosystems for extended periods, making them especially valuable in agricultural applications where long-term shelf life and environmental stability are crucial (Zhong et al., 2024). Upon encountering favourable conditions, such as in the rhizosphere of a plant, *B. velezensis* endospores germinate into metabolically active vegetative cells capable of colonizing plant roots, producing antimicrobial compounds, and promoting plant growth. This transition is rapid and efficient, allowing the bacterium to respond swiftly to environmental opportunities (Etesami et al., 2023; Jang et al., 2023). Moreover, the robustness of *B. velezensis* endospores is central to its use in biocontrol formulations.

Recent proteomic and transcriptomic analyses further elucidate the molecular basis of endospore structure. Chen et al. (2022) showed that the sporulation process in *B. velezensis* is accompanied by the upregulation of genes encoding structural proteins such as SpoIVA, CotA, CotE, and enzymes involved in DPA synthesis. These proteins are essential for proper coat assembly and spore maturation. Interestingly, the study also found that environmental stressors such as pH variation or iron limitation not only

induced sporulation but altered the composition of spore coat proteins, potentially enhancing their environmental adaptability. According to [Zhong et al. \(2024\)](#), formulations containing *B. velezensis* spores demonstrated superior shelf stability and maintained viability for over six months under ambient conditions, making them more effective than vegetative cell-based products. The resistance traits of the spores ensure that they can survive industrial processing, such as spray-drying or granulation, without significant loss of function.

Moreover, spore-based formulations are compatible with integrated pest management strategies and can be applied across diverse climatic conditions, soil types, and cropping systems ([Chen et al., 2022](#)). *B. velezensis* endospores do not directly produce bioactive compounds in their dormant state, they play a pivotal role as robust, long-lasting carriers that ensure rapid establishment of metabolically active populations capable of producing a broad spectrum of antimicrobial and plant growth-promoting compounds ([Jin et al., 2024](#)). This unique combination of durability, efficacy, and multifunctionality underscores the significant potential of *B. velezensis* endospores as a cornerstone of next-generation biological control products in agriculture ([Fazle Rabbee & Baek, 2020](#)).

In conclusion the endospore structure of *B. velezensis* reflects a highly evolved survival mechanism that integrates physical protection, chemical resistance, and functional readiness for reactivation. The unique structural integrity of its endospore ensures both longevity and immediate functional activation upon application in soil or plant-associated environments.

***B. velezensis* AS A BIOCONTROL AGENT IN AGRICULTURE**

B. velezensis has been extensively studied for its potential in suppressing a wide range of plant pathogens, particularly those responsible for soil-borne diseases. Its efficacy as a biocontrol agent in agriculture is attributed to its dual mechanism of action: direct antagonism of pathogens and indirect stimulation of plant defense responses ([Yao et al., 2025](#)). Numerous studies have demonstrated its successful application in controlling diseases across diverse crops and agroecosystems.

A prominent example is the use of *B. velezensis* strain EB1 in managing *Fusarium oxysporum* wilt in banana. [Liu et al. \(2025\)](#) reported that the co-application of *B. velezensis* strain EB1 with potassium sorbate resulted in complete disease suppression, outperforming conventional fungicides even at tenfold higher concentrations. Notably, this synergy also enhanced the production of antifungal lipopeptides, emphasizing the metabolic plasticity of *B. velezensis* under combinatory treatments. This finding underscores the importance of formulation synergy in maximizing biocontrol potential. Similarly, [Jiang et al. \(2024\)](#) evaluated *B. velezensis* strain Bv S3 in controlling *F. oxysporum* in rice seedlings. The treatment significantly reduced disease severity by over 65% and simultaneously improved soil enzymatic activity, indicating a dual function of disease suppression and rhizosphere health promotion. This illustrates the added value of *B. velezensis*-based biocontrol in enhancing soil microbiome function, a trait lacking in chemical fungicides.

In vegetable production, [Kuo et al. \(2023\)](#) developed a fermentation-based formulation of *B. velezensis* Tcb43 for controlling powdery mildew in greenhouse-grown

cucumber. The results demonstrated efficacy comparable to commercial chemical sprays, with added benefits of increased plant vigor and chlorophyll content. However, challenges in formulation stability and field-scale delivery remain significant barriers to commercial scalability.

[Figueiredo et al. \(2025\)](#) highlighted the performance of *B. velezensis* CNPMS-22 in mitigating maize root rot caused by *Fusarium verticillioides*. The strain not only reduced disease incidence under both greenhouse and field conditions but also showed high endospore viability post-application. In solanaceous crops, [Yan et al. \(2021\)](#) demonstrated that *B. velezensis* SDTB038 produced surfactin that effectively suppressed late blight in potato, with comparable efficacy to fluopimomide, a synthetic fungicide. Surfactin's stability across a wide pH and temperature range makes it particularly suitable for fluctuating field conditions, a limitation often encountered with synthetic chemical agents.

Direct Antagonism Mechanism of *B. velezensis* Against Plant Pathogens

Direct biocontrol mechanisms are primarily mediated through the biosynthesis of a diverse array of antimicrobial secondary metabolites, including cyclic lipopeptides (iturins, fengycins, and surfactins), polyketides, bacteriocins, and VOCs ([Su et al., 2024](#)). Among the most important antimicrobial compounds produced by *B. velezensis* are cyclic lipopeptides (CLPs), which are synthesised by non-ribosomal peptide synthetases (NRPSs) ([Fazle Rabbee & Baek, 2020](#)). These CLPs are classified into three major families: surfactins, fengycins, and iturins. Fengycins and iturins exhibit strong antifungal activity by disrupting fungal membrane integrity and inhibiting spore germination and mycelial growth, whereas surfactins display potent antibacterial, antiviral, and biosurfactant properties that facilitate pathogen suppression and root colonisation ([Xiao et al., 2021](#)). Numerous *B. velezensis* strains have been reported to possess multiple NRPS gene clusters, enabling the simultaneous production of diverse lipopeptides and thereby enhancing their biocontrol efficacy ([Balleux et al., 2025](#)).

Cyclic lipopeptides exert strong antifungal activity by inserting into fungal cell membranes, leading to pore formation, membrane destabilisation, ion leakage, and ultimately cell lysis ([Jiang et al., 2024](#); [Liu et al., 2025](#)). Fengycins are particularly effective against filamentous fungi by inhibiting spore germination and hyphal elongation, while iturins display broad-spectrum antifungal activity through sterol-binding interactions that disrupt membrane integrity ([Figueiredo et al., 2025](#)). In addition to lipopeptides, *B. velezensis* synthesizes polyketide antibiotics such as bacillaene, difficidin, and macrolactin, which exhibit potent antibacterial and antifungal activities by inhibiting protein synthesis, DNA replication, and key metabolic pathways in competing microorganisms ([Fazle Rabbee & Baek, 2020](#)). Bacteriocins further enhance competitive exclusion by targeting closely related bacterial pathogens within the rhizosphere. These antimicrobial compounds act synergistically, creating a chemically hostile microenvironment that suppresses pathogen establishment and proliferation ([Sharma & Yadav, 2023](#)). *B. velezensis* also produces an array of hydrolytic enzymes, including chitinases, β -1,3-glucanases, proteases, and cellulases, which degrade the structural components of fungal cell walls ([Chen et al., 2022](#)). This enzymatic degradation

weakens pathogen integrity and enhances the efficacy of antimicrobial metabolites. The coordinated action of enzymatic lysis and chemical inhibition significantly reduces fungal viability and infectivity (Liu et al., 2025).

Indirect Mechanism of *B. velezensis*

Beyond direct antagonism, germinated spores activate plant innate immune responses by inducing systemic resistance pathways, such as induced systemic resistance (ISR) and, in some cases, systemic acquired resistance (SAR), thereby increasing plant tolerance to both biotic and abiotic stresses (Yao et al., 2025). Indirectly, *B. velezensis* activates ISR in host plants, a defence mechanism mediated primarily through jasmonic acid (JA) and ethylene signalling pathways. ISR primes the plant immune system, enabling faster and stronger defence responses upon pathogen attack without incurring the metabolic costs associated with constitutive defence activation. This systemic protection extends to a broad spectrum of fungal and bacterial pathogens, even in tissues not directly colonized by the bacterium.

Figure 2 shows *B. velezensis* utilizes chemotaxis to move toward root exudates, where chemoreceptors detect specific chemical signals and direct flagellar motility toward the rhizosphere, enhancing colonization efficiency and competitive establishment (Chen et al., 2022). Upon reaching the root surface, the bacterium adheres through surface proteins, adhesins, and extracellular polymeric substances (EPS), enabling stable root attachment and beneficial plant association. Xiong et al. (2024) reported that *B. velezensis* WRN014 highly expressed TasA and PS operons, which are essential for root adhesion and EPS production. The bacterium subsequently forms biofilms that protect both bacterial cells and plant roots from environmental stress while suppressing pathogens through nutrient and space competition. Enhanced biofilm formation was shown to improve rhizosphere persistence and disease suppression against *Phytophthora capsica* in pepper plants (Zhong et al., 2024).

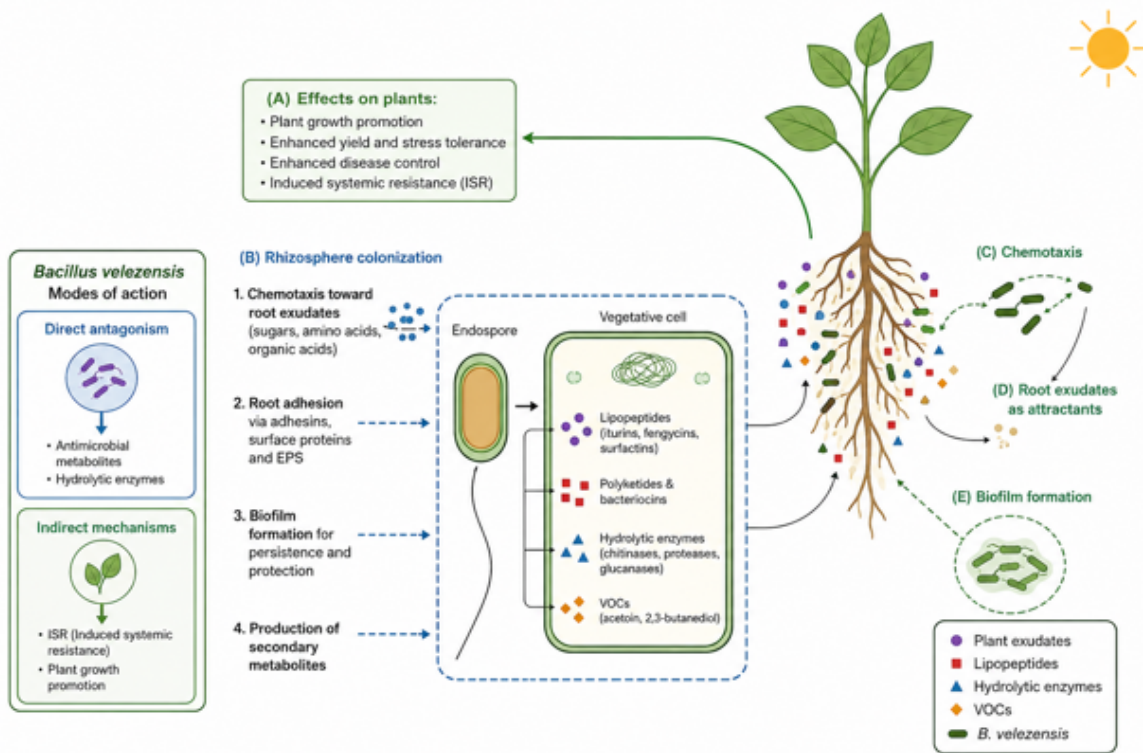


Figure 2 Antagonism mechanism of *Bacillus velezensis* (Adapted and modified from Kenfaoui et al., 2024)

In addition to rhizosphere colonization, *B. velezensis* produces diverse antimicrobial secondary metabolites that contribute to its strong biocontrol activity. Cyclic lipopeptides such as iturins, fengycins, and surfactins disrupt fungal membranes, inhibit filamentous fungi, promote biofilm formation, and stimulate plant immune responses through ISR activation (Fan et al., 2018). The bacterium also synthesizes polyketides including bacillaene, difficidin, and macrolactin, which inhibit microbial protein synthesis, as well as VOCs such as acetoin and 2,3-butanediol that suppress pathogens and promote plant growth (Tu et al., 2024). Production of these metabolites is regulated by two-component signal transduction systems that respond to

environmental and rhizosphere cues (Chen et al., 2022). Furthermore, interaction with plant roots activates ISR, where microbial-associated molecular patterns such as flagellin and lipopeptides trigger reactive oxygen species production, defense gene expression, and enhanced resistance against biotic and abiotic stresses.

Effective rhizosphere colonisation is a critical prerequisite for sustained biocontrol activity. *B. velezensis* exhibits strong chemotactic responses toward root exudates rich in sugars, amino acids, and organic acids, mediated by methyl-accepting chemotaxis proteins (Fazle Rabbee & Baek, 2020). Upon reaching the root surface, the bacterium adheres via cell surface adhesins and secretes extracellular

polymeric substances that facilitate robust biofilm formation (Fazle Rabbee & Baek, 2020). These biofilms act as a physical barrier, limiting pathogen access to root tissues while simultaneously enhancing nutrient acquisition and microbial persistence. Biofilm formation also improves tolerance to environmental stresses such as desiccation, oxidative stress, and fluctuating pH, thereby stabilising *B. velezensis* populations in the rhizosphere (Sharma et al., 2023).

Biofilm-associated cells display enhanced resistance to abiotic stresses and exhibit increased production of antimicrobial metabolites (Singh et al., 2025). This has been demonstrated in pathosystems such as *Phytophthora capsici*-infected pepper plants, where biofilm-forming *B. velezensis* strains provided superior disease suppression compared to planktonic cells. Furthermore, surfactin plays a dual role by facilitating biofilm architecture and acting as a signalling molecule that modulates plant defence responses (Chen et al., 2025).

VOCs produced by *B. velezensis*, including acetoin and 2,3-butanediol, contribute to both pathogen suppression and plant growth promotion (Srikamwang et al., 2023). These VOCs inhibit pathogen development at low concentrations while simultaneously enhancing plant stress tolerance by modulating antioxidant enzyme activity and hormonal balance (Ling et al., 2022). VOC-mediated signalling also promotes systemic resistance and improves plant resilience under drought and salinity stress conditions.

At the regulatory level, the biosynthesis of antimicrobial compounds and stress-response factors is tightly controlled by complex regulatory networks, including two-component signal transduction systems and global regulators such as Spo0A and ComA (Yu et al., 2023). These systems sense environmental cues, root exudates, and microbial competition, enabling dynamic modulation of gene expression in response to changing rhizosphere conditions (Rabbee et al., 2023). Transcriptomic and metabolomic studies have demonstrated that rhizosphere colonisation significantly upregulates genes associated with non-ribosomal peptide synthetase (NRPS) and polyketide synthase (PKS) pathways, leading to enhanced production of antifungal and antibacterial metabolites (Amutuhaire et al., 2025). Collectively, the integration of antimicrobial metabolite production, enzymatic pathogen degradation, biofilm-mediated root protection, induction of plant systemic resistance, and resilience to abiotic stresses underscores the exceptional versatility of *B. velezensis* as a biocontrol agent. These adaptive and multifunctional defence mechanisms reinforce its potential as a sustainable and environmentally friendly alternative to chemical pesticides in modern agriculture.

Induced Systemic Resistance Mediated by *Bacillus velezensis*

Induced systemic resistance (ISR) is a plant-mediated defence strategy activated by beneficial rhizobacteria, including *Bacillus velezensis*, that enhances the plant's ability to resist a broad spectrum of pathogens without directly inhibiting them at the site of infection (Yu et al., 2022). Unlike systemic acquired resistance (SAR), which is typically triggered by pathogen invasion and associated with salicylic acid (SA) accumulation, ISR is predominantly regulated through JA and ethylene (ET) signalling pathways and does not involve constitutive expression of defence genes (Wilson et al., 2023).

Root colonisation by *B. velezensis* is the initial step in ISR activation. Upon establishing stable populations on the root surface and in the rhizosphere, *B. velezensis* releases microbial-associated molecular patterns (MAMPs) and bioactive metabolites that are perceived by plant pattern recognition receptors (Kenfaoui et al., 2024). Key ISR-eliciting signals produced by *B. velezensis* include cyclic lipopeptides such as surfactin, fengycin, and iturin, as well as VOCs like acetoin and 2,3-butanediol. Among these, surfactin plays a central role by acting as both a biosurfactant and a signalling molecule that primes plant immune responses (Sun et al., 2021).

ISR enables faster and stronger activation of defence mechanisms upon pathogen challenge. This primed state is characterised by enhanced accumulation of defence-related enzymes such as phenylalanine ammonia-lyase, peroxidases, polyphenol oxidases, and β -1,3-glucanases following pathogen attack (Yu et al., 2022). Additionally, ISR leads to increased production of phytoalexins, lignin deposition, and callose formation, which collectively strengthen cell walls and limit pathogen penetration and spread (Zhong et al., 2024).

ISR induced by *B. velezensis* provides broad-spectrum protection against diverse fungal and bacterial pathogens, including *Fusarium*, *Rhizoctonia*, *Phytophthora*, and *Pseudomonas* species (Figueiredo et al., 2025). Because ISR relies on host-mediated defence activation rather than direct antimicrobial toxicity, it imposes lower selection pressure on pathogens and reduces the likelihood of resistance development. This makes ISR a particularly valuable component of long-term disease management strategies (Zhong et al., 2024).

Transcriptomic studies have shown that *B. velezensis*-induced ISR results in the upregulation of JA/ET-responsive genes, including those encoding transcription factors, defence-related enzymes, and signalling components involved in oxidative burst regulation (Wu et al., 2023). Cross-talk between JA, ET, and SA pathways allows plants to fine-tune their immune responses depending on the nature of the invading pathogen, thereby enhancing defence efficiency without compromising plant growth (Mo et al., 2025).

In agricultural systems, ISR triggered by *B. velezensis* contributes not only to disease suppression but also to improved plant fitness and stress tolerance. ISR-primed plants often exhibit enhanced resistance to abiotic stresses such as drought, salinity, and temperature fluctuations due to strengthened antioxidant systems and improved hormonal balance (Jang et al., 2023). Consequently, *B. velezensis* functions not only as a biocontrol agent but also as a biological elicitor of plant immunity, providing durable and environmentally sustainable protection against plant pathogens.

CHALLENGES, ADVANCEMENTS AND FUTURE OUTLOOK OF *Bacillus velezensis*

Despite the promising potential of *B. velezensis* as a plant growth-promoting and biocontrol bacterium, several challenges still limit its large-scale agricultural application (Jang et al., 2023). Its biocontrol efficacy often varies under field conditions due to environmental factors such as soil pH, temperature, moisture, nutrient availability, and microbial competition, which can affect rhizosphere colonization, metabolite production, and long-term

persistence (Kenfaoui et al., 2024). To overcome these limitations, future studies should focus on strain optimization and advanced formulation technologies, including encapsulation systems, nanoformulations, and carrier-based biofertilizers to improve spore stability, shelf life, and controlled release. Omics-based approaches, genetic engineering, and adaptive evolution studies may further enhance stress tolerance, colonization efficiency, and antimicrobial metabolite production while maintaining environmental safety.

Commercialization also remains challenging due to inconsistent field performance, shorter residual activity compared to chemical fungicides, costly large-scale spore production, and complex regulatory approval processes (Zhong et al., 2024). Therefore, commercial strategies should emphasize cost-effective fermentation optimization, scalable downstream processing, and formulation standardization to ensure consistent product quality. Collaboration between research institutions, biotechnology industries, and agricultural sectors could accelerate technology transfer and field validation. Integrating *B. velezensis* into Integrated Pest Management (IPM) systems, alongside farmer education and demonstration trials, may further improve market acceptance and adoption.

Despite these limitations, *B. velezensis* offers substantial opportunities due to increasing global demand for sustainable agriculture and environmentally friendly crop protection (Rabbee et al., 2023). Its multifunctional properties, including pathogen suppression, plant growth promotion, biofilm formation, ISR induction, and durable endospore formation, make it a promising microbial biopesticide. Future research should also explore synergistic microbial consortia, long-term ecological impacts on soil microbiomes, crop-specific applications, precision agriculture integration, and climate-resilient formulations to strengthen its reliability and sustainability in modern agriculture.

CONCLUSION

In conclusion, *Bacillus velezensis* represents a next-generation biocontrol agent with significant potential to reshape sustainable crop protection strategies. Its multifunctional mechanisms, integrating direct antimicrobial activity, plant immune stimulation, and environmental persistence, provide a resilient and holistic approach to disease management. As global agriculture faces increasing pressure to reduce chemical inputs while maintaining productivity, biologically based solutions such as *B. velezensis* offer a viable pathway toward environmentally responsible intensification. However, despite these promising outcomes, several limitations persist in the translation of *B. velezensis* from lab to field. Formulation consistency, spore recovery rates post-drying, and colonization efficiency under abiotic stress conditions remain key research priorities. Ultimately, the deployment of *B. velezensis* within integrated pest management systems may contribute substantially to long-term food security, ecosystem stability, and the transition toward climate-smart and sustainable farming practices.

Acknowledgement

The authors acknowledge Universiti Teknologi Malaysia for giving cooperation and full of support in this research activity. The authors would like to acknowledge Forest Fine

Foods (M) Sdn Bhd, Tangkak, Johor for funding this research (R.J130000.7654.4C782).

Conflicts of Interest

The author declares that there is no conflict of interest regarding the publication of this paper.

References

- Ahmed, Faraz, Dingwu Zhang, Xiaoyang Tang, and Pradeep K. Malakar. 2024. "Targeting Spore-Forming Bacteria: A Review on the Antimicrobial Potential of Selenium Nanoparticles." *Foods* 13 (24): 4026. <https://doi.org/10.3390/foods13244026>.
- Amutuhaire, H., Faigenboim-Doron, A., Kraut-Cohen, J., Friedman, J., & Cytryn, E. (2025). Identifying rhizosphere bacteria and potential mechanisms linked to compost suppressiveness towards *Fusarium oxysporum*. *Environmental Microbiome*, 20(1), 52.
- Balderas-Ruiz, K. A., Gómez-Guerrero, C. I., Trujillo-Roldán, M. A., Valdez-Cruz, N. A., Aranda-Ocampo, S., Juárez, A. M., ... & Serrano-Carreón, L. (2021). *Bacillus velezensis* 83 increases productivity and quality of tomato (*Solanum lycopersicum* L.): Pre and postharvest assessment. *Current Research in Microbial Sciences*, 2, 100076.
- Balleux, G., Höfte, M., Arguelles-Arias, A., Deleu, M., & Ongena, M. (2025). *Bacillus lipopeptides* as key players in rhizosphere chemical ecology. *Trends in Microbiology*, 33(1), 80-95.
- Baptista, J. P., Teixeira, G. M., de Jesus, M. L. A., Bertê, R., Higashi, A., Mosela, M., ... & de Oliveira, A. G. (2022). Antifungal activity and genomic characterization of the biocontrol agent *Bacillus velezensis* CMRP 4489. *Scientific Reports*, 12(1), 17401.
- Belousova, M. E., Malovichko, Y. V., Shikov, A. E., Nizhnikov, A. A., & Antonets, K. S. (2021). Dissecting the environmental consequences of *Bacillus thuringiensis* application for natural ecosystems. *Toxins*, 13(5), 355.
- Chen, H. J., Liu, Y., Zhong, Y. S., Li, M. Z., Lai, J. J., Luo, Y. Y., ... & Shao, M. W. (2025). Modulating surfactin biosynthesis in *Bacillus subtilis* R31 enhances behavioural traits and biocontrol efficacy against *Banana fusarium* Wilt. *Microbial Biotechnology*, 18(11), e70261.
- Chen, Q., Qiu, Y., Yuan, Y., Wang, K., & Wang, H. (2022). Biocontrol activity and action mechanism of *Bacillus velezensis* strain SDTB038 against *Fusarium crown* and root rot of tomato. *Frontiers in Microbiology*, 13, 994716.
- Cho, W. I., & Chung, M. S. (2020). *Bacillus* spores: A review of their properties and inactivation processing technologies. *Food Science and Biotechnology*, 29(11), 1447.
- Dobrzyński, J., Jakubowska, Z., Kulkova, I., Kowalczyk, P., & Kramkowski, K. (2023). Biocontrol of fungal phytopathogens by *Bacillus pumilus*. *Frontiers in Microbiology*, 14, 1194606.
- Etesami, H., Jeong, B. R., & Glick, B. R. (2023). *Potential Use of Bacillus Spp. as an Effective Biostimulant Against Abiotic Stresses in Crops—A Review*. *Current Research in Biotechnology*, 5: 100128.

- Fan, B., Wang, C., Song, X., Ding, X., Wu, L., Wu, H., ... & Borriss, R. (2018). *Bacillus velezensis* FZB42 in 2018: the gram-positive model strain for plant growth promotion and biocontrol. *Frontiers in Microbiology*, *9*, 2491.
- Fazle Rabbee, M., & Baek, K. H. (2020). Antimicrobial activities of lipopeptides and polyketides of *Bacillus velezensis* for agricultural applications. *Molecules*, *25*(21), 4973.
- Figueiredo, J. E. F., Diniz, G. D. F. D., Marins, M. S., Silva, F. C., Ribeiro, V. P., Lanza, F. E., ... & Cruz-Magalhães, V. (2025). *Bacillus velezensis* CNPMS-22 as biocontrol agent of pathogenic fungi and plant growth promoter. *Frontiers in Microbiology*, *16*, 1522136.
- Ghahremani, Z., Escudero, N., Beltrán-Anadón, D., Saus, E., Cunqueiro, M., Andilla, J., ... & Sorribas, F. J. (2020). *Bacillus firmus* strain I-1582, a nematode antagonist by itself and through the plant. *Frontiers in Plant Science*, *11*, 796.
- Gikas, G. D., Parlakidis, P., Mavropoulos, T., & Vryzas, Z. (2022). Particularities of fungicides and factors affecting their fate and removal efficacy: A review. *Sustainability*, *14*(7), 4056.
- Hashem, A., Tabassum, B., & Fathi Abd Allah, E. (2019). *Bacillus subtilis*: A plant-growth promoting rhizobacterium that also impacts biotic stress. *Saudi Journal of Biological Sciences*, *26*: 1291–1297.
- Jang, S., Choi, S. K., Zhang, H., Zhang, S., Ryu, C. M., & Kloepper, J. W. (2023). History of a model plant growth-promoting rhizobacterium, *Bacillus velezensis* GB03: from isolation to commercialization. *Frontiers in Plant Science*, *14*, 1279896.
- Jiang, W., Liu, J., He, Y., Payizila, A., & Li, Y. (2024). Biological control ability and antifungal activities of *Bacillus velezensis* Bv S3 against *Fusarium oxysporum* that causes rice seedling blight. *Agronomy*, *14*(1), 167.
- Jin, P., Chu, L., Xuan, Z., Lin, Z., Fang, Y., Pan, X., ... & Miao, W. (2024). *Bacillus velezensis*, a new valuable source of bioactive molecules within plant microbiomes and natural weapons for the biocontrol of plant pathogens. *Tropical Plants*, *4*(1).
- Karacic, V., Miljakovic, D., Marinkovic, J., Ignjatov, M., Milošević, D., Tamindzic, G., & Ivanovic, M. (2024). *Bacillus* species: excellent biocontrol agents against tomato diseases. *Microorganisms*, *12*, 457.
- Kenfaoui, J., Dutilloy, E., Benchli, S., Lahlali, R., Ait-Barka, E., & Esmaeel, Q. (2024). *Bacillus velezensis*: a versatile ally in the battle against phytopathogens—insights and prospects. *Applied Microbiology and Biotechnology*, *108*(1), 439.
- Kim, Young Soo, Younmi Lee, Wonsu Cheon, Jungwook Park, Hyeok-Tae Kwon, Kotnala Balaraju, Jungyeon Kim, Yeo Jun Yoon, and Yongho Jeon. 2021. "Characterization of *Bacillus Velezensis* AK-0 as a Biocontrol Agent Against Apple Bitter Rot Caused by *Colletotrichum Gloeosporioides*." *Scientific Reports* *11* (1): 626. <https://doi.org/10.1038/s41598-020-80231-2>.
- Kuo, C. C., Huang, Y. C., & Deng, W. L. (2023). Evaluating the efficacy of the fermentation formula of *Bacillus velezensis* strain tcb43 in controlling cucumber powdery mildew. *Agriculture*, *13*(8), 1558.
- Ling, L., Luo, H., Yang, C., Wang, Y., Cheng, W., Pang, M., & Jiang, K. (2022). Volatile organic compounds produced by *Bacillus velezensis* L1 as a potential biocontrol agent against postharvest diseases of wolfberry. *Frontiers in Microbiology*, *13*, 987844.
- Liu, T., Zheng, Y., Wang, L., Wang, X., Wang, H., & Tian, Y. (2025). Optimizing surfactin yield in *Bacillus velezensis* BN to enhance biocontrol efficacy and rhizosphere colonization. *Frontiers in Microbiology*, *16*, 1551436.
- Markelova, N., & Chumak, A. (2025). Antimicrobial activity of *Bacillus* cyclic lipopeptides and their role in the host adaptive response to changes in environmental conditions. *International Journal of Molecular Sciences*, *26*(1), 336.
- McKenney, P. T., Driks, A., & Eichenberger, P. (2013). The *Bacillus subtilis* endospore: Assembly and functions of the multilayered coat. *Nature Reviews Microbiology*, *11*(1), 33-44.
- Mo, S., Zhao, W., Wei, Y., Su, Z., Li, S., Lu, X., ... & Ma, P. (2025). Defense responses stimulated by *Bacillus subtilis* NCD-2 through salicylate- and jasmonate-dependent signaling pathways protect cotton against verticillium wilt. *International Journal of Molecular Sciences*, *26*(7), 2987.
- Mugadza, Desmond T. 2018. *Bacillus* and *Paenibacillus* spp. associated with extended shelf life milk. UpSpace Institutional Repository (University of Pretoria). <http://hdl.handle.net/2263/65919>.
- Rabbee, M. F., Hwang, B. S., & Baek, K. H. (2023). *Bacillus velezensis*: a beneficial biocontrol agent or facultative phytopathogen for sustainable agriculture. *Agronomy*, *13*(3), 840.
- Russi, A., Granada, C. E., & Schwambach, J. (2024). Optimization of *Bacillus velezensis* S26 sporulation for enhanced biocontrol of gray mold and anthracnose in postharvest strawberries. *Postharvest Biology and Technology*, *210*, 112737.
- Saxena, A. K., Kumar, M., Chakdar, H., Anuroopa, N., & Bagyaraj, D. J. (2020). *Bacillus* species in soil as a natural resource for plant health and nutrition. *Journal of Applied Microbiology*, *128*(6), 1583-1594.
- Sharma, P., & Yadav, M. (2023). Enhancing antibacterial properties of bacteriocins using combination therapy. *Journal of Applied Biology and Biotechnology*, *11*(1), 232-243.
- Sharma, S., Mohler, J., Mahajan, S. D., Schwartz, S. A., Bruggemann, L., & Aalinkel, R. (2023). Microbial biofilm: A review on formation, infection, antibiotic resistance, control measures, and innovative treatment. *Microorganisms*, *11*(6), 1614.
- Singh, B., Dahiya, M., Kumar, V., Ayyagari, A., Chaudhari, D. N., & Ahire, J. J. (2025). Biofilm and antimicrobial resistance: mechanisms, implications, and emerging solutions. *Microbiology Research*, *16*(8), 183.
- Srikamwang, C., Onsa, N. E., Sunanta, P., Sangta, J., Chanway, C. P., Thanakkasaranee, S., & Sommano,

- S. R. (2023). Role of microbial volatile organic compounds in promoting plant growth and disease resistance in horticultural production. *Plant Signaling & Behavior*, 18(1), 2227440.
- Su, T., Shen, B., Hu, X., Teng, Y., Weng, P., Wu, Z., & Liu, L. (2024). Research advance of *Bacillus velezensis*: bioinformatics, characteristics, and applications. *Food Science and Human Wellness*, 13(4), 1756-1766.
- Suárez-Bautista, J. D., Manotas-Viloria, H. S., Leal-Mejía, L., Boyacá-Vásquez, J., Pineros-Castro, Y., Corrales, L. C., ... & Vanegas, J. (2024). Agricultural Biotechnological Potential of *Bacillus velezensis* C3-3 and *Cytobacillus* sp. T106 from Resource Islands of a Semi-arid Zone of La Guajira-Colombia: Agricultural Biotechnological Potential of *Bacillus velezensis* C3-3 and *Cytobacillus*.... *Current Microbiology*, 81(10), 341.
- Sun, X., Xu, Z., Xie, J., Hesselberg-Thomsen, V., Tan, T., Zheng, D., ... & Kovács, Á. T. (2022). *Bacillus velezensis* stimulates resident rhizosphere *Pseudomonas stutzeri* for plant health through metabolic interactions. *The ISME Journal*, 16(3), 774-787.
- Tu, M., Zhu, Z., Zhao, X., Cai, H., Zhang, Y., Yan, Y., ... & Zou, L. (2025). The versatile plant probiotic bacterium *Bacillus velezensis* SF305 reduces red root rot disease severity in the rubber tree by degrading the mycelia of *Ganoderma pseudoferreum*. *Journal of Integrative Agriculture*, 24(8), 3112-3126.
- Wang, Y., Chen, L., Wu, X., Gong, B., Lv, G., Zhang, J., ... & Gao, H. (2025). *Bacillus velezensis* SF-10 modulates the rhizosphere core microbiome by stimulating the probiotic community to control tomato wilt disease. *Pesticide Biochemistry and Physiology*, 106805.
- Wilson, S. K., Pretorius, T., & Naidoo, S. (2023). Mechanisms of systemic resistance to pathogen infection in plants and their potential application in forestry. *BMC Plant Biology*, 23(1), 404.
- Wu, W., Wang, J., Wang, Z., Yan, X., Wang, Y., & He, X. (2023). Comparative transcriptome analysis reveals the molecular mechanism of *Bacillus velezensis* GJ-7 assisting *Panax notoginseng* against *Meloidogyne hapla*. *International Journal of Molecular Sciences*, 24(24), 17581.
- Xiao, J., Guo, X., Qiao, X., Zhang, X., Chen, X., & Zhang, D. (2021). Activity of fengycin and iturin A isolated from *Bacillus subtilis* Z-14 on *Gaeumannomyces graminis* var. *tritici* and soil microbial diversity. *Frontiers in Microbiology*, 12, 682437.
- Xiong, Q., Zhang, H., Shu, X., Sun, X., Feng, H., Xu, Z., ... & Liu, Y. (2024). Autoinducer-2 relieves soil stress-induced dormancy of *Bacillus velezensis* by modulating sporulation signaling. *npj Biofilms and Microbiomes*, 10(1), 117.
- Yan, H., Qiu, Y., Yang, S., Wang, Y., Wang, K., Jiang, L., & Wang, H. (2021). Antagonistic activity of *Bacillus velezensis* SDTB038 against *Phytophthora infestans* in potato. *Plant Disease*, 105(6), 1738-1747.
- Yao, Y., Wang, L., Zhai, H., Dong, H., Wang, J., Zhao, Z., & Xu, Y. (2025). *Bacillus velezensis* A-27 as a potential biocontrol agent against *Meloidogyne incognita* and effects on rhizosphere communities of celery in field. *Scientific Reports*, 15(1), 1057.
- Yu, C., Qiao, J., Ali, Q., Jiang, Q., Song, Y., Zhu, L., ... & Wu, H. (2023). degQ associated with the degS/degU two-component system regulates biofilm formation, antimicrobial metabolite production, and biocontrol activity in *Bacillus velezensis* DMW1. *Molecular Plant Pathology*, 24(12), 1510-1521.
- Yu, Y., Gui, Y., Li, Z., Jiang, C., Guo, J., & Niu, D. (2022). Induced systemic resistance for improving plant immunity by beneficial microbes. *Plants*, 11(3), 386.
- Zalila-Kolsi, I., Ben-Mahmoud, A., & Al-Barazie, R. (2023). *Bacillus amyloliquefaciens*: Harnessing its potential for industrial, medical, and agricultural applications—A comprehensive review. *Microorganisms*, 11(9), 2215.
- Zhong, X., Jin, Y., Ren, H., Hong, T., Zheng, J., Fan, W., ... & Huang, G. (2024). Research progress of *Bacillus velezensis* in plant disease resistance and growth promotion. *Frontiers in Industrial Microbiology*, 2, 1442980.