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Research progress of *Bacillus velezensis* in plant disease resistance and growth promotion

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Bacillus velezensis has a wide range of beneficial activities, such as fighting plant diseases, promoting growth, improving crops' ability to handle stress, and boosting plant defenses. These traits make it a strong candidate for agricultural use, especially as a biocontrol agent and growth-promoting bacteria. This review takes a close look at the origins, working mechanisms, and potential agricultural benefits of *B. velezensis*. Both lab and field studies have shown its success in reducing plant diseases and supporting crop growth by producing helpful compounds, taking up space in the environment, and strengthening plant defenses. Although *B. velezensis* is already used in some fertilizers and biopesticides, there are still challenges in scaling up production, selecting the right strains, and ensuring product stability. This review points out current research gaps and suggests future directions, such as improving strain selection, developing better biofertilizers, and advancing production techniques to make the most of *B. velezensis* in agriculture. These findings aim to guide further research and improve its use in sustainable farming.

KEYWORDS

B. velezensis, disease resistance, promoting effect, mechanism, application

1 Introduction

Bacillus velezensis is a functional bacterium (a class of beneficial microorganisms that exert one or more physiological effects, directly or indirectly influencing the health of the host.) with a broad range of biological activities. It is found in various habitats (including

soil, plant rhizosphere, and even aquatic environments) and was first isolated and identified in 1999, although its taxonomic classification remained unresolved until 2005 (Ruiz-Garcia et al., 2005). *B. velezensis* is characterized by its strong enzyme production capacity, abundant secondary metabolites, robust stress resistance, broad-spectrum antibacterial activity, and high efficacy against pathogens (Masmoudi et al., 2019; Zhang et al., 2019; Keshmirshakan et al., 2024; Xu P.D. et al., 2024). It can inhibit pathogenic infections and promote plant growth under both biotic (fungi, bacteria, and insects) and abiotic (temperature, water, and saline-alkaline) stress conditions. Due to these attributes, *B. velezensis* is widely applied in agricultural production and holds significant value in practical applications (Ye et al., 2018; Zhang et al., 2020; Chen et al., 2022; Cao et al., 2024; Su et al., 2024).

In light of the rapid growth of the global population, ensuring the production and safety of key agricultural products, including food, has become increasingly vital. While chemical pesticides and fertilizers have been widely used to boost agricultural output, their excessive and improper application has led to various issues such as soil degradation, pest resistance, reduced crop yields, and increased pesticide residues in the environment (Khan et al., 2022). In this context, microbial-based approaches are gaining attention as sustainable alternatives. Among these, *Bacillus velezensis* has emerged as a promising candidate due to its ability to antagonize plant pathogens, promote plant growth, and improve crop resilience to environmental stresses (Singh et al., 2021). Unlike traditional chemical inputs, *B. velezensis* offers a broad spectrum of benefits, including enhancing nutrient absorption, improving soil structure, and inducing plant systemic resistance (Singh and Trivedi, 2017). Therefore, its application as a biocontrol agent and plant growth-promoting bacterium holds great potential for achieving environmentally friendly agricultural practices that support food security and crop health. This review focuses on the biological properties and agricultural potential of *B. velezensis*, highlighting its role in disease resistance and growth promotion, and addressing current challenges in its commercial application.

Given its wide range of beneficial activities, *Bacillus velezensis* has attracted increasing attention as a promising candidate for agricultural applications. This review provides a comprehensive overview of the latest research on *B. velezensis*, focusing on its origin, disease resistance mechanisms, and growth-promoting effects. In addition, we analyze its potential applications in biopesticides and biofertilizers. The manuscript covers both laboratory and field studies, highlighting the ability of *B. velezensis* to reduce plant diseases, promote crop growth, and enhance stress resistance. Finally, we discuss the current challenges related to strain selection, large-scale production, and product stability, while offering suggestions for future research to fully unlock the agricultural potential of *B. velezensis*. By addressing these challenges, this review aims to provide valuable insights that will support the development of more sustainable and effective agricultural practices.

2 Isolation source of *B. velezensis*

B.velezensis is a Gram-positive, aerobic, endospore-forming bacterium; it is widely present in various habitats (Kim et al., 2021; Zhang H. et al., 2022). A search of the *B. velezensis* genome in the NCBI database (as of September 2023) identified 625 strains; they are mainly sourced from soil (24.32%) and plant rhizosphere and phyllosphere (19.84%). The sources of *B. velezensis* from rivers and sediments, food, animal gastrointestinal tract and contents, and animal feces accounted for 5.28%, 9.12%, 3.52%, and 1.92%, respectively; 14.56% of strains were sourced from other environments, while 21.44% had unknown origins (Figure 1). In summary, while *B. velezensis* is found in diverse ecological environments, its primary sources are the rhizosphere soil and root tissue of plants.

According to the results of literature research (Rabbee et al., 2022; Jia et al., 2023), *B. velezensis* used for disease resistance and growth promotion is mainly isolated from plant rhizosphere and

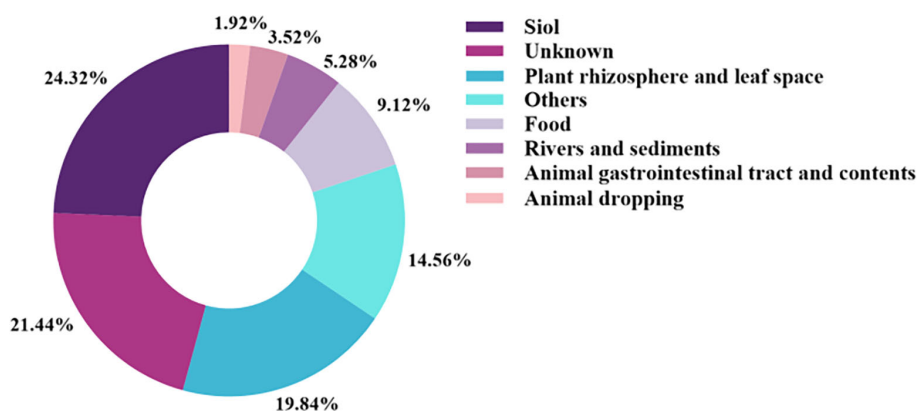


FIGURE 1

Source of *B. velezensis*. The sources of *B. velezensis* from soil, plant rhizosphere and leaf space, rivers and sediments, food, animal gastrointestinal tract and contents, and animal feces accounted for 24.32%, 19.84%, 5.28%, 9.12%, 3.52%, and 1.92%, respectively. Other and unknown sources accounted for 14.56% and 21.44%, respectively.

soil and some from plant tissue sites, such as leaf surface and fruit surface. In addition to plant sources, some special habitat-derived strains, such as *B. velezensis*, exhibit antibacterial and growth promoting biological characteristics. For example, Barman et al. isolated *B. velezensis* from coal mining areas, which can not only tolerate various heavy metals, but also produce auxin, iron carrier, and various plant-promoting biomass, as well as dissolve phosphate (Barman et al., 2022). Alvarez et al. isolated *B. velezensis* MEP218 from saline soil, thereby producing lipopeptide antibacterial compounds, such as surfactin, iturin, and fengycin, and can significantly inhibit soybean stem rot caused by *Sclerotinia sclerotiorum* (Alvarez et al., 2012). Wekesa et al. isolated two strains of *Bacillus velezensis* from Lake Bogoria, a region known for its hot springs. Their study demonstrated that these strains could grow in a wide pH range, tolerate varying salinity conditions, and thrive at diverse temperatures. Additionally, both strains exhibited the ability to produce IAA and solubilize phosphorus (Wekesa et al., 2022). In summary, *B. velezensis* is widely distributed and has strong stress resistance. *B. velezensis* from different habitats also exhibit strong foundation for screening excellent strains with special requirements, thereby expanding their potential application and prospects.

3 Disease resistance and growth-promoting effects of *B. velezensis*

3.1 Disease resistance effect of *B. velezensis*

As a newly identified biocontrol bacterium, *B. velezensis* is synonymous with *Bacillus methylotrophicus* and *Bacillus amyloliquefaciens* subsp. *Plantarum* (Dunlap et al., 2016). Recently, these bacteria have been reclassified under *B. velezensis*. Some of the *B. velezensis* identified so far have broad-spectrum antibacterial activity, effectively inhibiting various plant pathogens (fungi, bacteria, viruses, and nematodes) in agricultural production and efficiently controlling various plant diseases, especially those caused by plant pathogenic fungi (Medhioub et al., 2022; Yin et al., 2022). Partial results are summarized in Table 1.

B. velezensis can significantly inhibit fungal diseases caused by pathogens, such as *Fusarium oxysporum*, *Phytophthora capsici*, and *Botrytis cinerea*. For example, Hong et al. isolated a strain of *B. velezensis* CE100 from tomato planting soil that can produce chitinase and β -Dextranase. This strain degrades fungal cell walls and effectively inhibits the growth of *F. oxysporum* mycelium. In addition, under co-inoculation with *B. velezensis*, CE 100 and plant pathogenic fungi can effectively inhibit strawberry wilt disease (Hong et al., 2022). Rahman et al. used silica gel thin-layer chromatography to isolate the antibacterial substance of *B. velezensis* UQ156. The results indicate that the metabolites of UQ156 contain 2,5-diketopiperazine compounds with broad-spectrum antibacterial and antiviral activities, which can effectively inhibit *P. capsici* (Syed-Ab-Rahman et al., 2021). Navarro et al. found that the volatile compounds produced by *B. velezensis* XT1 greatly inhibit the growth of *B. cinerea*. When

exposed to these volatile compounds, the mycelial membrane and cell wall of *B. cinerea* underwent thinning and degradation. This process led to the complete coagulation of cytoplasmic contents and the loss of identifiable organelles, ultimately resulting in cell death. As a consequence, the growth and development of pathogenic fungi were inhibited (Toral et al., 2021).

In addition to effectively preventing and treating fungal diseases, *B. velezensis* exhibits strong inhibitory effects against plant diseases caused by bacteria, viruses, and nematodes. *B. velezensis* SC60 with strong colonization ability from sesbania was screened by Dong et al (Dong et al., 2022). This bacterium can significantly inhibit not only plant pathogens, such as *P. capsici*, *F. oxysporum*, *Fusarium graminearum*, and *B. cinerea*, but also the growth of various *Bacillus subtilis*, *Bacillus megaterium*, and *B. amyloliquefaciens*. A biocontrol strain *B. velezensis* SYL-3 that can colonize tobacco leaves was isolated by Liu et al (Liu et al., 2022). The bacterial suspension has a significant inhibitory effect on tobacco mosaic virus. With research confirming that the bacterium can alter soil microbial community structure and dynamics, thereby suppressing tobacco mosaic virus-induced diseases. *B. velezensis* Bv-25, isolated by Tian et al., can effectively kill most southern root knot nematodes (Tian et al., 2022). This strain readily colonizes crop roots, inhibiting the *in vitro* hatching of insect eggs. Furthermore, it can activate the defense signaling pathways of salicylic acid (SA) and jasmonic acid (JA) in crop roots, leading to the upregulation of plant defense genes. As a result, it induces enhanced crop resistance to southern root knot nematode infection.

3.2 Promoting effect of *B. velezensis*

In addition to the advantages in inhibiting plant pathogens, *B. velezensis* significantly promotes plant yield, root length, and fruiting rate, thereby effectively enhancing plant growth. Hasan et al. isolated a strain of *B. velezensis* HNH9 that can produce siderophores. In greenhouse cultivation experiments, plants treated with HNH9 showed an increase in their photosynthetic rate and stomatal conductance. The expression of genes involved in ethylene (ET) biosynthesis was down-regulated, whereas that of growth-related genes was up-regulated, promoting the growth of upland cotton plants (Hasan et al., 2022). Choub et al. isolated a strain of *B. velezensis* CE100 from the pot soil of tomato plants. This bacterium produces indole-3-acetic acid (up to 1.4 $\mu\text{g/mL}$) and shows potential for ammonia production and phosphate solubilization. The field test results showed that after inoculation with this bacterium, the chlorophyll content, total nitrogen, and total phosphorus content of walnut trees increased by 1.3, 1.5, and 1.6 times compared with the control group, respectively. Additionally, branch length, rhizome diameter, and biomass of walnut trees were significantly enhanced (Choub et al., 2021).

Plants are subjected to various abiotic or biological stresses during their growth process, including salt alkali stress, heavy metal stress, and drought stress. The application of *B. velezensis* as plant growth-promoting rhizobacteria (PGPR) has been shown to enhance resistance to abiotic stress in plants (Ayaz et al., 2021),

TABLE 1 Control of diseases by *B. velezensis* and its effect.

Categories of control plants	Plants	Antagonistic bacteria	Diseases	No. of strains	Effects	References
Fruit	Citrus	<i>Xanthomonas citri subsp. citri</i>	Citrus canker	Bv-21	Exhibiting the highest antibacterial activity against wild type and streptomycin resistant <i>Xcc</i> .	(Rabbee et al., 2022)
	Pear	<i>Erwinia amylovora</i> .	Fire blight	OEE1	Inhibiting the growth of <i>E. amylovora</i> ; high levels of multi-resistance to diverse antibiotics; improving the collar diameter and the number of leaves.	(Medhioub et al., 2022)
	Grape	<i>Coniella vitis</i> .	Grape white rot	GSBZ09	Presenting broad spectrum antifungal activity and produce extracellular enzymes; high capacity for IAA production, siderophore production and mineral phosphate solubilization.	(Yin et al., 2022)
	Apple	<i>Valsa mali</i> .	Valsa canker	D4	Inhibiting <i>V. mali</i> and <i>V. pyri</i> mycelia; high capacity for siderophores production and solubilize phosphorus; upregulating the brassinosteroid synthesis pathway and the JA-, SA-signaling pathways.	(Liu et al., 2021)
	Banana	<i>Fusarium oxysporum f.sp.</i>	Fusarium wilt	YE6BR6	Inhibiting <i>Fusarium oxysporum</i> ; increasing the expression of transcription factors and defense genes WRKY, MAPK, CERK 1, LOX, and PAL.	(Saravanan et al., 2022)
Vegetable	Spinach	<i>Fusarium oxysporum f.sp.</i>	Fusarium wilt	AD-3	Inhibiting <i>Fusarium oxysporum</i> ; reducing the severity of Fusarium wilt disease.	(Sugiyama et al., 2022)
	Tomato	<i>Fusarium oxysporum f.sp.</i>	Fusarium wilt	Bs006	Inhibiting <i>Fusarium oxysporum</i> ; changing the rhizosphere microbial behavior for carbon sources consumption.	(Másmela-Mendoza and Moreno-Velandia, 2022)
	Eggplant	<i>Fusarium oxysporum f.sp.</i>	Fusarium wilt	KY568715	Producing lytic enzymes, indole acetic acid (IAA) and ammonia; suppressing Fusarium wilt symptoms and enhance plant growth.	(Chakraborty et al., 2021)
	Capsicum	<i>Phytophthora capsica</i> .	Stem canker	UQ154	Exhibiting high <i>P. capsici</i> growth inhibition; producing pyrrolopyrazine and various phenolic compounds.	(Syed-Ab-Rahman et al., 2021)
Grain	Rice	<i>Dickeya zeae</i> .	<i>Dickeya zeae</i>	J17-4	Inhibiting <i>Dickeya zeae</i> ; containing nine gene clusters involved in the production of secondary metabolites.	(Shi et al., 2022)
	Wheat	<i>Fusarium oxysporum f.sp.</i>	Fusarium wilt	BA	Decreasing in disease severity caused by <i>Fusarium oxysporum</i> ; producing indole acetic acid (IAA), hydrogen cyanide (HCN) cellulase enzymes; plant growth-promoting.	(Abassum et al., 2022)
	Maize	<i>Fusarium verticillioides</i> .	Stalk rot	CT02	Inhibiting <i>Fusarium verticillioides</i> ; producing enzyme (cellulase, pectinase, protease, lipase, and chitinase).	(De Fátima Dias Diniz et al., 2022)

(Continued)

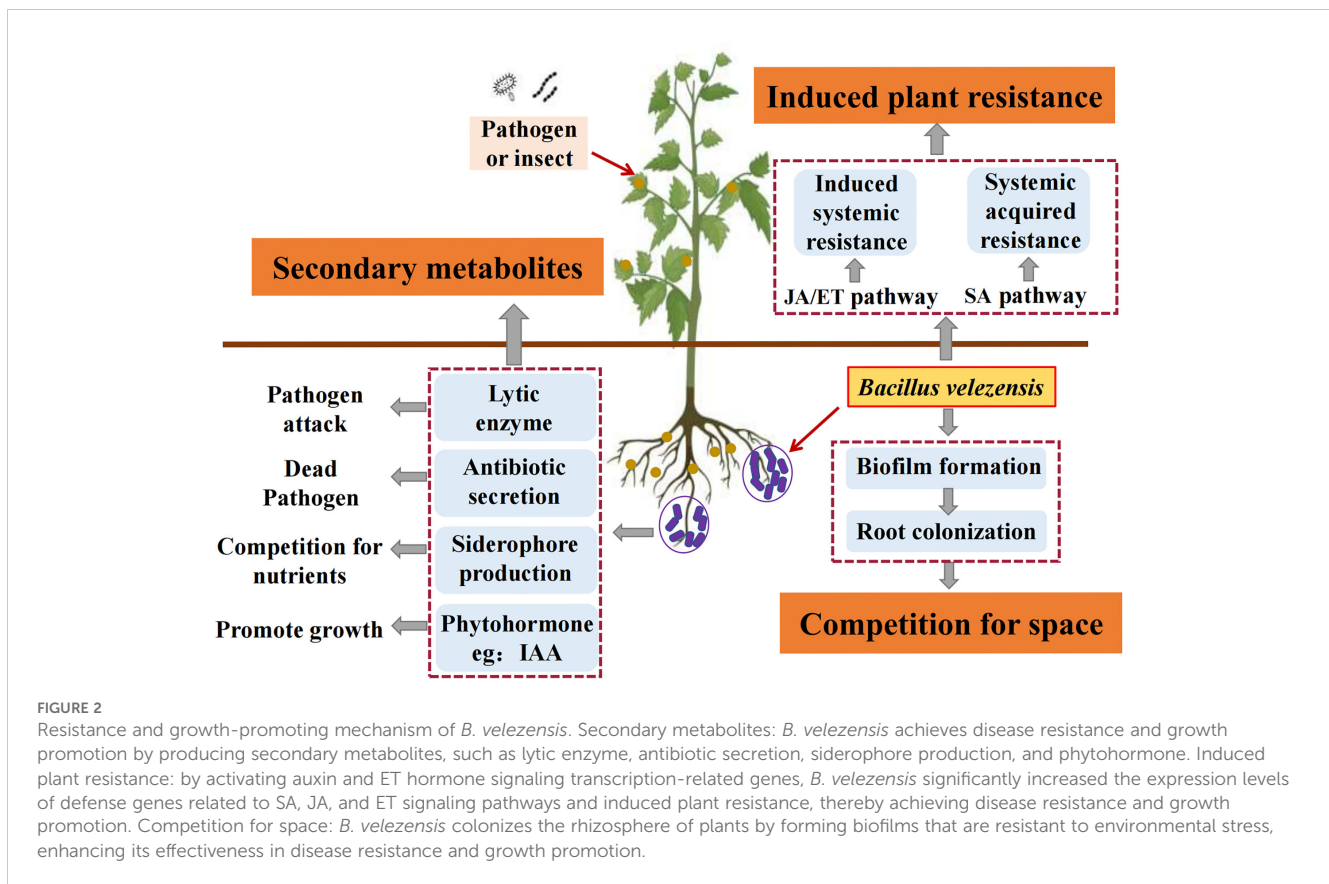
TABLE 1 Continued

Categories of control plants	Plants	Antagonistic bacteria	Diseases	No. of strains	Effects	References
	Soybean	<i>Phytophthora sojae</i> .	Root rot	FZB42	inhibiting the expression of <i>P. sojae</i> genes related to growth, macromolecule biosynthesis, pathogenicity, and ribosomes.	(Han et al., 2021)
	Potato	<i>Phytophthora infestans</i> .	Late blight	AFB2-2	Harboring the biosynthetic genes for bacillomycin D, iturin, and surfactin; inhibiting <i>Phytophthora infestans</i> .	(Naseem et al., 2022)
Medicinal materials	Ginger	<i>Bacillus pumilus</i> .	Stem rot disease	IUB-3	Plant growth promotion; zinc solubilization; producing exopolysaccharides, siderophore, HCN, catalase, protease.	(He et al., 2022)
	Honeysuckle flower	<i>Erysiphe lonicerae</i> var.	Powdery mildew	HC-8	Suppressing the conidia germination of <i>E. lonicerae</i> ; inducing defense-related enzyme activities in the leaves of honeysuckle.	(Ding et al., 2021)
	Tobacco	<i>Phytophthora nicotianae</i> .	Black shank disease	GUMT319	Inhibiting the growth of <i>P. nicotianae</i> ; forming biofilm	(Lilai et al., 2022)
Nuts	Cashew nut	<i>Fusarium oxysporum</i> f.sp.	Fusarium wilt	/	Inhibiting <i>Fusarium oxysporum</i> ; developing significantly lower cashew wilt disease severity.	(Moradi Pour et al., 2022)
	Pistachio	<i>Phytophthora drechsleri</i> .	Pistachio gummosis	/	Controlling pistachio gummosis; having growth-promoting effects on pistachios.	(Choub et al., 2021)
	Walnut	<i>Colletotrichum gloeosporioides</i> .	Anthraco-nose disease	CE100	Exhibiting chitinase, protease, and β -1,3-glucanase activity; degrading the cell wall of <i>C. gloeosporioides</i> ; improving walnut root development, nutrient uptake and chlorophyll content.	(Hong et al., 2022)

demonstrating its strong stress resistance. It not only adapts to growth under non-stress conditions but also promotes plant growth under stress. Wang Ru et al. isolated a salt-tolerant *B. velezensis* A-1 from saline soil; it could grow stably under 0%–10% NaCl stress. It could also improve the germination rate of wheat seeds under different salt concentrations and promote the growth of seedlings (Wang et al., 2021). *B. velezensis* DD10 isolated from the coal dumping area by Barman et al. can not only tolerate various heavy metals, but also produce auxin and siderophore, showing 1-aminocyclopropane-1-carboxylic acid (ACC) deaminase activity and the ability to dissolve phosphate (Barman et al., 2022). Nadeem et al. isolated and screened *B. velezensis* D3 from the rhizosphere soil of corn in water-deficient areas, which have ACC deaminase activity and extracellular polysaccharide production activity. In the drought resistance test, this strain showed significant effects in improving physiological parameters, such as photosynthetic rate, stomatal conductance, steam pressure, water use efficiency, and transpiration rate of maize plants. At the same time, it can significantly increase the stem length, root length, and dry and fresh weights of maize seedlings, effectively promoting plant growth (Nadeem et al., 2021).

4 Resistance and growth-promoting mechanism of *B. velezensis*

Bacteria used for plant disease resistance and growth promotion have many direct or indirect mechanisms of action. These mechanisms enhance plant resistance to diseases and promote growth in different agricultural environments. The currently recognized mechanisms include metabolic regulation, control of plant hormone levels, and root colonization (Ali et al., 2017; Ismail et al., 2021; Khan et al., 2021), as well as stimulation of plant resistance to various biotic and abiotic stresses (such as pathogen attacks and heavy metal pollution) to indirectly improve plant growth (Mustafa et al., 2019). At present, the research on the mechanism of disease resistance and growth promotion of *B. velezensis* mainly includes the following points (Figure 2): nutrition and ecological site competition, production of secondary metabolites, and stimulation of plant system resistance. Moreover, *B. velezensis* can exert synergistic effects on disease resistance and growth promotion through one or more of these mechanisms.



4.1 Nutrition and ecological site competition

Soil microorganisms are widely distributed in plant roots; the integration of beneficial bacterial communities into host plants contributes to soil nutrient cycling and enhances nutrient use efficiency (Nwachukwu et al., 2021). Many studies have shown that microbial inoculants can induce changes in plant rhizosphere microbial communities and improve soil fertility, soil environment, and crop growth (Huang et al., 2022). *B. velezensis* interacts with plants through colonization and competes with pathogenic microorganisms for limited nutrient elements and spatial sites, preventing pathogenic bacteria from obtaining the necessary nutrients and living space for growth, thereby exerting their disease resistance and growth promoting effects. The competition primarily centers on critical nutrients such as iron, potassium, and phosphorus, with iron being particularly essential for biological growth. The primary metabolite siderophore produced by *B. velezensis* has a very high affinity for trivalent iron, thereby forming an iron-siderophore complex to promote the absorption of iron by microorganisms. At the same time, plants can use the complex to increase the iron content in plant tissues and promote plant growth (Chuljerm et al., 2020).

The competition for ecological sites is an important factor that enables *B. velezensis* to contribute to disease resistance, growth promotion, and the development of microbial control agents. The formation of biofilm is conducive to the colonization of microorganisms. *B. velezensis* with its biofilm-forming capability

holds a distinct advantage in competing for ecological sites (Flemming et al., 2016). Even under the presence of pathogens, *B. velezensis* NKG-2 forms a biofilm that is resistant to environmental pressure and interacts symbiotically with tomato plants, thereby protecting them from the harmful effects of *F. oxysporum* (Myo et al., 2021). Numerous studies have shown that *B. subtilis* can colonize the rhizosphere of crops, such as corn, cucumber, and tomato, and have significant control effects on plant diseases, such as corn stem rot and tomato gray mold (De Fátima Dias Diniz et al., 2022; Másmela-Mendoza and Moreno-Velandia, 2022). For example, Jin et al. found that *B. velezensis* S3-1 can effectively colonize maize rhizosphere soil and root tissue. The collected corn root exudates significantly induced the chemotaxis, cluster movement, and biofilm formation of strain S3-1. These results indicate that maize root exudates play an important role in the colonization of S3-1 (Jin et al., 2019). Agarwal et al. isolated a growth-promoting *B. velezensis* strain from medicinal plants and found that it can colonize the roots of tomato seedlings, promoting growth and effectively controlling bacterial wilt disease (Agarwal et al., 2020).

4.2 Producing bioactive substances

B. velezensis can produce various broad-spectrum antimicrobial substances to contribute to disease resistance. The main antimicrobial substances are antimicrobial proteins, lipopeptides, polyketides, and volatile compounds. Among them, antibacterial

proteins mainly include proteases, chitinases, and β -Dextranase (Li et al., 2020). Lipopeptide substances mainly include surfactins, bacillomycin-D, and fengycins (Ongena and Jacques, 2008). Polyketone compounds mainly include bacillaene, difficidin, and macroactin (Tan et al., 2020). Volatile compounds mainly include acetylurea, isoamyl alcohol, and 2,3-butanediol (Liu et al., 2020; Toral et al., 2021). Reports showed that lipopeptide compounds are the main contributors to the biocontrol activity of *B. velezensis*. Notably, *B. velezensis* possesses genetic characteristics related to the synthesis of cyclic lipopeptides (Rabbee et al., 2019).

In addition to abundant antibacterial substances, *B. velezensis* produces various growth promoting substances, such as auxin, iron carrier, and 1-aminocyclopropane-1-carboxylate deaminase, to promote plant growth. Pacifico et al. isolated three strains of *B. velezensis* from the cotton rhizosphere, producing auxin and iron carriers and possessing phosphorus and nitrogen fixing effects. These strains of *B. velezensis* may be promoters of plant growth (Pacifico et al., 2021). Chebotar et al. isolated the plant growth-promoting bacterium *B. velezensis* BS89 from the rhizosphere of winter wheat. Genome-wide sequencing revealed that the genome of BS89 contains a synthetic gene cluster of indole-3-acetic acid and volatile metabolites that promote plant growth (Chebotar et al., 2021). Wang et al. isolated 3S, 3R, and 4R-acetylbutanediol, which is obtained from the fermentation broth of *B. velezensis* WRN031. The fungus secreted two non-active compounds in a ratio of 1:2 into the soil when it was inoculated into the rhizosphere soil of corn seedlings. After seven days of treatment with the two compounds, the roots of corn seedlings were significantly longer than those of the control plant (Wang et al., 2020).

In recent years, many studies have shown that *B. velezensis* contains a large number of gene clusters encoding secondary metabolites, mainly including polyketide synthases (PKS) and non-ribosomal peptide synthetases (NRPS) (Xu P. et al., 2024). Different *Bacillus velezensis* contain different gene clusters. Nine gene clusters (srf, bmy, fen, dhh, bac, min, bae, dfn and nrs) were found in this genome (Fan et al., 2019a). Among them, surfactins (srf), bacillomycin-D (bmy) and fengycins (fen) are non-ribosomal lipopeptides (LPS). Macrolactin (mln), bacillaene (bae) and difficidin (dfn) are polyketides synthesized under the guidance of polyketide synthase. In addition, the siderophore bacillibactin (dhh) plays a role in protecting plants by competing with pathogenic microorganisms for nutrients such as iron.

The genome of *Bacillus velezensis* GQJK49 annotated by Ma et al. There were 12 gene clusters related to antimicrobial activity. Six of them presented high similarity with the biosynthesis gene clusters of relevant secondary metabolism. Two transAT polyketide synthase-nonribosomal peptide synthetase (TATPKS-NRPS)-type clusters showed similarity with the biosynthetic gene clusters of macrolactin and difficidin, respectively. Two gene clusters, which belonged to the transAT TATPKS-NRPS type, were related to bacillaene and fengycin, respectively. One gene cluster belonged to NRPS-bacteriocin, which was similar to the biosynthetic gene cluster of bacteriocin. One gene cluster was related to bacilysin biosynthesis. The other gene clusters may be related to the production of new antimicrobial substances. The complete genome sequence of *B. velezensis* will be helpful in the study of its

mechanisms for biocontrol and plant growth promotion and will facilitate the expansion of the scope of application of this strain in agriculture (Ma et al., 2017).

4.3 Inducing plant resistance

B. velezensis can induce plant resistance to protect plants from pathogen infection, including systemic acquired resistance (SAR) and induced systemic resistance (ISR). SA, JA, and ET play crucial roles in plant defense. SA-dependent signaling pathways are involved in SAR, whereas JA- and ET-dependent signaling pathways are involved in ISR. Jasmonic acid (JA) are involved in a variety of plant physiological processes, and salicylic acid (SA) plays an important role in stomatal behavior and respiration, among other functional roles. SA also functions in immune response by activating signaling pathways at the molecular level that lead to the induction of systemic disease resistance (Zou et al., 2024).

B. velezensis activates defense enzymes, such as phenylalanine ammonia lyase, ascorbic acid peroxidase, peroxidase, and catalase, in plants through its primary and secondary metabolites, such as volatile organic compounds, surface active- proteins, proteases, and acetylureas, thereby inducing plant resistance and improving plant disease resistance. Zhang et al. applied *B. velezensis* BY6 to the roots of poplar with root rot through pot experiments, and the plant growth indices (dry weight, fresh weight, and plant height) increased significantly. Auxin hormone signaling transcription-related genes were activated, and the expression levels of defense genes related to SA and JA signaling pathways were significantly increased, indicating that BY6 activated ISR and SAR was induced by diseased poplar seedlings to enhance their disease resistance (Zhang P. et al., 2022). Acetylurea produced by *B. velezensis* GJ1 causes callose deposition and enhances the activity of peroxidase, polyphenol oxidase, and phenylalanine ammonia lyase, thereby triggering ISR in plants. In addition, studies have found that reactive oxygen species play a crucial role in pathogen-plant interactions and play a crucial role in plant ISR (Peng et al., 2019). The subtilisin produced by *B. velezensis* LJ02 has no direct inhibitory effect on *B. cinerea*, but induced the outbreak of reactive oxygen species. This condition triggers SAR and enhances the plant's resistance to *B. cinerea* (Hu et al., 2022).

5 Applications of *B. velezensis* in the plant field

5.1 *B. velezensis* as biological control agents

Bacillus is one of the most common endophytes in plants. Spores are resistant to adverse environmental conditions and can easily be developed and preserved due to their unique properties. They have unique advantages in the commercial production and application of microbial preparations (Aloo et al., 2019). The main *Bacillus* strains that have been developed as biological control

agents include *B. amyloliquefaciens*, *Bacillus licheniformis*, *B. subtilis*, and *Bacillus cereus* (Fan et al., 2019b). *B. velezensis* is considered a potential biocontrol agent for plant disease prevention and control given its ability to stably colonize the rhizosphere or soil environment of plants, secrete various antibacterial active substances, and activate the host's defense mechanisms against pathogens to inhibit harmful microorganisms (Hong et al., 2022). Research on the development of *B. velezensis*-based biological agents has been underway internationally for quite some time. *B. velezensis* FZB42 is a model strain of rhizosphere bacteria for plant biocontrol. It was isolated in 1998 and sequenced in 2007, and it is widely used in agriculture as a biological fertilizer and biocontrol agent (Fan et al., 2019b). However, the research and development of biopesticides based on *B. velezensis* in China are still in their infancy. As of September 2023, among the pesticide registration data available on the China Pesticide Information Network, two *B. velezensis* and five *Bacillus methylotrophicus* (currently classified as *B. velezensis*) have been registered; the results are shown in Table 2.

5.2 *B. velezensis* as bio-fertilizer

Biological fertilizer is a promising alternative to chemical fertilizer, which is greatly important for sustainable agriculture. At present, *Bacillus velezensis* is gradually being developed into commercial products internationally. Recognized as a model plant growth-promoting rhizobacterium, GB03 has exhibited outstanding performance in enhancing the growth and protection of many crop plants including cucumber, pepper, wheat, barley, soybean, and cotton (Jang et al., 2023). *B. velezensis* GB03 is commercially registered in the USA as a biocontrol and growth-promoting product, named Kodiak[®] (Gustafson, Inc., Plano, TX, USA), which is considered as one of the most effective biological control products currently available in the market. The use of Kodiak[®] is widespread and versatile. Like Kodiak[®], Companion[®] (Advance Grass Solution Ltd., UK) is a commercial plant health product formulated from *B. velezensis* strain GB03, and is widely used in horticultural and agricultural production (Klopper et al., 2004; Anckaert et al., 2021). Companion[®] application facilitates the rapid colonization of plant roots by GB03, leading to enhanced growth

and effective pathogen inhibition across a variety of plant species. Although the number of *Bacillus velezensis* microbial fertilizers is increasing year by year, most products are still primarily microbial inoculants[®] to improve noun agreement and clarity. Commercial products such as bio-organic fertilizer, soil remediation agent, compound microbial fertilizer, microbial concentrate, and organic material decomposing agent are relatively scarce. This indicates that the types of *Bacillus velezensis* microbial fertilizers are not well-balanced, which means that the development and commercial application prospects of its product resources are broad.

5.3 *B. velezensis* as soil amendment

Soil is a dynamic and living resource. With the extensive use of pesticides and fertilizers, the discharge of industrial waste gases and wastewater, and the smelting of metal ores, the global soil environment has deteriorated. At present, many physical, chemical and biological improvement measures for soil remediation have been proposed by scientists. Plant-microorganism combined remediation technology has become the main research direction of soil remediation due to its advantages of *in-situ* remediation, low cost, environmental friendliness and high remediation efficiency (Chen et al., 2020; Chen et al., 2023).

According to the literature, *Bacillus velezensis* mainly focuses on the remediation of heavy metal contaminated land in soil remediation. The mechanisms by which *Bacillus velezensis* decontaminates heavy metals involves various methods, including siderophore chelation, biological adsorption, and biodegradation. *Bacillus velezensis* secrete metabolites that can release iron carriers and organic acids, which aid in the chelation of soil toxic metal ions and contribute to the adsorption of heavy metals (Li et al., 2022). The exopolysaccharides (EPS) produced by *Bacillus velezensis* can adsorb some metal ions such as Cd²⁺, Pb²⁺, Cu²⁺, etc (Abd-El-Haleem, 2023). When used as a soil remediation agent, *Bacillus velezensis* is often combined with *Paenibacillus polymyxa*, *Paenibacillus mucilaginosus*, *Bacillus subtilis*, *Bacillus licheniformis*, etc. to achieve better remediation effects. Combine *Bacillus velezensis* with *Pseudomonas azotoformans*, *Serratia rubidaea*, *Paenibacillus pabuli*. by Saadony et al. Compared to no or single PGPR treatment, the consortia increased the photosynthetic pigment contents, relative

TABLE 2 Pesticide registration records of *B. velezensis*.

Registration certificate number	Nomenclature of pesticides	Pesticide category	Formulation	Registration certificate holders
PD20211360	<i>B.velezensis</i> CGMCC	Fungicide	Water dispersible granule	Sichuan Pepsi Dongwang Biotechnology Co., Ltd.
PD20211348	<i>B.velezensis</i> CGMCC	Fungicide	Technical concentrate	
PD20211957	<i>B.methylotrophic</i> LW-6	Fungicide	Wettable powder	Shanxi Hengtian Biological Agriculture Co., Ltd.
PD20181620	<i>B.methylotrophic</i> LW-6	Fungicide	Technical concentrate	
PD20181621	<i>B.methylotrophic</i> LW-6	Fungicide	Wettable powder	
PD20181602	<i>B.methylotrophic</i> 9912	Fungicide	Wettable powder	North China Pharmaceutical Group Aino Co., Ltd.
PD20181603	<i>B.methylotrophic</i> 9912	Fungicide	Technical concentrate	

water content, and membrane stability index but lowered the electrolyte leakage and contents of malondialdehyde and hydrogen peroxide by suppressing the (non) enzymatic antioxidants in plant tissues. The contents of Cd, Cu, Pb and Ni in pepper were significantly decreased (El-Saadony et al., 2024). At present, the soil remediation agent on the market is also dominated by multi-strain combined bacteria. The commercial microbial fertilizer of *Bacillus velezensis* single bacteria as soil remediation agent has not been reported. It can be seen that the application of *Bacillus velezensis* in soil remediation has great development value.

6 Conclusion and future perspectives

After the taxonomic status of *Bacillus velezensis* was determined, it has attracted extensive attention from researchers. In recent years, the research on the application of *Bacillus velezensis* in agriculture has become increasingly popular. The related research mainly focuses on plant growth promotion and disease prevention and control, animal feed, aquaculture and other aspects. More and more studies have shown that *Bacillus velezensis* has broad application prospects as a biocontrol bacterium: (1) It produces abundant secondary metabolites, induces plant systemic resistance, promotes plant growth, and reduces the use of chemical fertilizers; (2) Competitive ecological sites, reduce the abundance of pathogenic bacteria in the environment, inhibit the infection of pathogenic bacteria, and reduce the use of chemical drugs.

Laboratory and field experiments have proven that *B. velezensis* has excellent disease resistance and growth promoting effect on plants. At present, biological fungicides based on *B. velezensis* have been registered as pesticides and successfully applied to microbial fertilizers. However, the current research on the growth-promoting and disease-resistant aspects of the bacteria mainly focuses on theoretical aspects, such as its effectiveness and mechanism. Moreover, the industrial scale of using the bacteria for microbial preparations is small. Although *B. velezensis* has great potential, it has not been fully utilized in the agricultural field. On the one hand, highly active bacterial resources are limited, and on the other hand, the preparation technology of bacterial agents is insufficient to ensure the stability of product quality, resulting in a short shelf life of the product. Therefore, in the future, the development and utilization of *B. velezensis* for growth promotion and disease resistance for *B. velezensis* can be strengthened through the following aspects:

(1) exploration of highly active bacterial resources, improve the screening system, and selectively screen highly active agricultural strains; (2) develop bio fertilizers with minimal environmental impact and strengthen research on their biosafety assessment; (3)

strain improvement through appropriate physical, chemical, biological, and other technological approaches to enhance the growth-promoting and disease-resistance performance of *B. velezensis*.

Author contributions

XZ: Funding acquisition, Writing – original draft. YJ: Writing – original draft. HR: Writing – original draft. TH: Supervision, Writing – review & editing. JZ: Data curation, Writing – review & editing. WF: Conceptualization, Writing – review & editing. JH: Formal analysis, Writing – review & editing. ZC: Formal analysis, Writing – review & editing. AW: Formal analysis, Writing – review & editing. HL: Formal analysis, Writing – review & editing. KZ: Visualization, Writing – review & editing. GH: Writing – review & editing.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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