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RESEARCH ARTICLE

Identification of novel *Bacillus velezensis* zm026 in corn diseases control and fumonisin inhibition

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Highlights

- *Bacillus velezensis* zm026 functions as an effective *in-situ* management strain for regulating the microbial community structure within maize kernels.
- *Bacillus velezensis* zm026 colonizes the surfaces of maize roots and activates the plant's immune system.
- Bacillomycin D disrupts the integrity of the fungal cell membrane and inhibits spore germination.

Abstract

Fungal diseases affecting maize not only reduce maize yields but also generate fungal toxins that pose risks to both human and animal health, particularly when the straw is returned to the field. Microbial *in-situ* control is considered an environmentally friendly method that effectively addresses the limitations of unstable effects. In this study, we isolated *Bacillus velezensis* zm026 from rhizosphere soil for *in-situ* restoration, based on the soil community structure, which exhibits high antagonistic activity against *Fusarium verticillioides* and *Exserohilum turcicum*. Zm026 effectively colonized the surface of maize roots within 5 days and activated the plant immune system, significantly increasing the expression of defense genes such as *ZmGST*, *ZmZHD*, *ZmPR*-1, *ZmPR*-2, and *ZmPR*-3. The efficient anti-fungal substance of zm026 was identified by HPLC-MS and determined to be bacillomycin D. Further observations using trypan blue staining, along with DAPI (4′,6-diamidino-2-phenylindole) and PI (propidium iodide) fluorescent staining, revealed that bacillomycin D could inhibit fungal spore germination, disrupt the integrity of fungal cell membranes, induce apoptosis, and cause spore tips to protrude, swell, or rupture. Ultimately, indoor pot experiments demonstrated that the application of zm026 fermentation broth significantly promoted growth, inhibited the onset of fungal diseases in maize, and effectively reduced the abundance of *Fusarium* spp. in maize grains. This research provides a beneficial *in-situ* restoration strain for the high-quality development of maize.

Keywords: rhizosphere microbiome, bacillomycin D, fumonisin B1, biological control

1. Introduction

Maize is a vital food source globally, ranking as the third largest crop behind wheat and rice (Zhao *et al.* 2017). It is susceptible to infections from fungi such as *Fusarium verticillioides* and *Exserohilum turcicum*, which can cause corn ear rots (CER) and northern corn leaf blight (NCLB) throughout the supply chain (De Rossi *et al.* 2022; Torrijos *et al.* 2022). Fusarium is also capable of synthesizing mycotoxins that possess strong toxicity and pose a serious threat to food security (Alshannaq and Yu 2017). It is extensively grown in tropical and temperate regions. Currently, the surplus of maize straw poses a significant challenge, with returning straw to the field being identified as the most direct, effective, and environmentally friendly

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disposal method. Research indicates that reintroducing maize stover into the soil can enhance soil organic carbon and its active components (Ndzelu *et al.* 2021). The Food and Agriculture Organization (FAO) of the United Nations estimates that maize production decreases annually by 7% due to various biological and abiotic factors. When combined with the impact of maize straw returning to the field, the global objective of increasing maize production by 2.4% per year becomes unattainable (Ray *et al.* 2013). In recent years, the adoption of straw returning to the field technology and crop rotation systems in China has led to the accumulation and survival of pathogens causing maize ear rot in the soil, resulting in a yearly increase in maize ear rot occurrences (Wang *et al.* 2023; Xu *et al.* 2024).

The prolonged use of chemical pesticides for maize disease control can lead to significant mortality of beneficial microorganisms, disrupting native community structures and impacting soil health (Zhang *et al.* 2023). The widespread application of some fungicides may also adversely affect beneficial microorganisms, such as arbuscular mycorrhizal fungi, which have a symbiotic relationship with host plants. This symbiosis can enhance the absorption of phosphorus (P) by plants during their early vegetative development stages, thereby exerting a profound influence on plant health and yield over the long term (Cameron *et al.* 2017). As a result, there is a growing interest in finding environmentally friendly and sustainable alternatives for managing maize diseases (Anwar *et al.* 2016). One such approach involves the use of biological control agents (BCAs) for post-harvest fruit disease management, which have been proposed as eco-friendly and low health risk solutions (Bhatta 2022; Du *et al.* 2023). Notably, *Paenibacillus* isolates have emerged as promising BCAs for plant disease management (Lal and Tabacchioni 2009; Rybakova *et al.* 2015). These strains have demonstrated effectiveness in reducing disease incidence in various crops, such as field potatoes and olive trees, both in greenhouse and field settings (Tjamos *et al.* 2004; Markakis *et al.* 2015). For example, *Pseudomonas chlororaphis* subsp. *aurantiaca* SPR19 isolated from sugarcane rhizosphere soil effectively inhibited the growth of *F. sacchari* and exhibited plant growth-promoting activity (Chetan *et al.* 2024). The selection of *B. cereus* B25 in greenhouse pot experiments showed a reduction in the severity of *F. verticillioides* disease and plant incidence, confirming its potential for controlling *F. verticillioides* in maize (Figueroa-Lopez *et al.* 2016). Additionally, after the application of *B. subtilis* R31, the yield of sweet corn was significantly increased, and it also had a positive effect on disease resistance. BCAs have been found to promote plant growth (Souza *et al.* 2015; Shao *et al.* 2023). Studies have highlighted the importance of diverse microorganisms in plants and their rhizosphere soil for overall plant health and disease control, offering new insights into microbial resources (Cordovez *et al.* 2019). The use of microbial agents has shown positive effects on soil health, influencing soil microorganism functions and ecosystem health, ultimately impacting aboveground plant health (Li *et al.* 2012).

Previous studies have conclusively demonstrated that the inoculation of rhizosphere microorganisms effectively modulates plant restoration processes by altering the intricate microecology of rhizosphere soil (Zhang *et al.* 2021). This modulation encompasses a broad range of aspects, such as the enhancement of carbon utilization efficiency, carbon metabolic potential, and the improvement of soil physicochemical properties (Xing *et al.* 2022). Notably, this process can significantly augment decomposer efficiency, thereby accelerating carbon cycling over a specific duration. Moreover, soil microorganisms actively engage in a myriad of biochemical reactions, including the decomposition of organic residues, the synthesis of humus, and the transformation of various inorganic compounds (Bi *et al.* 2022). The high frequency of nutrient flow among microorganisms in rhizosphere soil results in elevated microbial activity, ultimately rendering native microorganisms more advantageous in facilitating soil restoration efforts (Kuzyakov *et al.* 2006; Hamdi *et al.* 2007). Bioaugmentation is considered a valuable tool to enhance the rate and extent of biodegradation of target toxic molecules (Lv *et al.* 2024). Some studies indicate that bioremediation efforts utilizing exogenous microbial populations often fail. This is primarily due to the inability of these foreign microorganisms to compete with native species. Additionally, the survival conditions of these microorganisms significantly impact their remediation capabilities (Hosokawa *et al.* 2009). Furthermore, when employing bioaugmentation, the use of native (indigenous to the site) microorganisms appears more practical, as environmental factors can influence the effectiveness of bioaugmentation (Madueño *et al.* 2011). Therefore, if these native microorganisms are isolated, cultured, and introduced into the soil, they can effectively remove harmful substances without the need to apply any exotic strains (Fernández-Luqueño *et al.* 2010).

Microbial regulation is essential for sustainable agricultural development and environmental protection, with significant potential for prevention and control (Lv *et al.* 2024). This study aimed to isolate efficient antagonistic bacterial strains based on *Bacillus* from the rhizosphere soil with straw returned of maize. The research focused on investigating their colonization effects, ability to promote maize growth and disease resistance, and uncovering the molecular mechanisms underlying the interaction between antagonistic bacteria and pathogens. These findings establish a foundation for the precise control of maize ear rot and facilitate efficient and environmentally friendly *in-situ* restoration of the micro-ecological environment in maize rhizosphere soil.

2. Materials and methods

2.1. Microbiome analysis of soil and grain samples

Rhizosphere soil samples of maize plants grown in straw-returned soil were collected from 12 maize-producing areas in China, yielding 137 soil samples. To determine the microbial community structure in soil, we employed amplification of the 16S rDNA for bacteria and the ITS for fungi. Bacterial communities were analyzed by amplifying the V5–V7 hypervariable regions of the 16S rDNA gene using primers 799F and 1193R (Zhang *et al.* 2019). Fungal communities

were assessed by amplifying the ITS1 region with primers ITS1F and ITS2R, known for their comprehensive coverage and taxonomic resolution of fungal sequences (Schmidt *et al.* 2019). Subsequently, the data obtained were analyzed using the Majorbio Cloud platform (https://cloud.majorbio.com).

2.2. Preparation of fungal spore suspensions

Add 5–6 fresh *F. verticillioides* dishes into the CMC medium, incubate at 180 r min^{-1} for 3–5 d in the dark at 25°C, centrifuge for 5 min at 4,000 r min^{-1}, discard the supernatant, and add it dropwise onto a hemocytometer after filtration with Miracloth, then dilute the *F. verticillioides* spore suspension concentration to 1×10^6 cfu mL^{-1} with sterile water.

2.3. Isolation of bacteria from maize rhizosphere soils

A total of 5 g of inter-root soil were shock-mixed with 50 mL of sterile water and spread on LB solid Petri dishes after being diluted into five concentration gradients with a tenfold dilution factor (Li *et al.* 2022). Single colonies were separated based on different colors and shapes once formed. Plate confrontation assays were conducted to assess antagonism following the method outlined by Duan *et al.* (2024) with minor adjustments.

2.4. Screening and identification of highly effective antagonistic strains

The screened biocontrol bacteria were identified using 16S rDNA sequence comparisons. *Fusarium oxysporum*, *F. verticillioides*, *F. graminearum*, and *E. turcicum* were selected for incubation with antagonistic bacteria using the dual plate confrontation assay method. The incubation period lasted 7–10 days in a dark inverted incubator at 28°C (Shen *et al.* 2024).

2.5. Promote growth and prevent diseases in greenhouse

Several rows of mature maize kernels were randomly selected and injected with 2 μL of a *F. verticillioides* spore suspension. The treatment group received zm026 fermentation broth, while the control group was injected with an equal volume of water. The blank group was injected with 4 μL of fresh water per kernel, with each group replicated three times. The development of ear rot in maize was then observed. Uniform and intact maize leaves were rinsed with sterile water at least three times, after which a small hole was punctured using a syringe. The zm026 fermentation solution was evenly applied to the surface of the leaves, with sterile water serving as a control. The leaves were subsequently placed in a fresh-keeping box lined with filter paper, with two leaves in each box. Bacterial trays of *E. turcicum* were inoculated onto the leaf surface, and the area of the lesions was measured.

2.6. Field activity of the antagonistic strain

The samples were collected at maturity, and the collected maize kernels were ground into powder and processed according to the method for the determination of major seed mycotoxins as specified in the Chinese Food Industry Standard. A total of 5 g of the crushed maize samples were weighed and added into 20 mL of acetonitrile:ultrapure water: glacial acetic acid (70:29:1, v/v). After vortexing for 30 min, the sample was centrifuged at 4,000 r min^{-1} for 5 min, and the supernatant was mixed 1:1 with ultrapure water and filtered through a 0.22 μm PTFE membrane, then detected by UPLC-MS/MS. The standard curve was constructed by preparing seven calibration points at 5, 10, 20, 50, 100, and 200 μg kg^{-1} with the blank sample extract. The concentration of fumonisin B1 was used as the horizontal coordinate, and the peak area was used as the vertical coordinate to plot the standard curve, with the addition and recovery method according to a previous reference (Cheng *et al.* 2022).

2.7. Symbiotic relationship between strains and corn

Strain zm026 was labeled with GFP tags. A single colony of zm026 was selected and incubated in LB liquid medium at 37°C with shaking for 12 h. Bacterial cells were then collected by centrifugation at 5,000×g for 5 min at 4°C and transferred to 1 mL of electrotransformation buffer. A pre-cooled 2 mm electrotransformation cup was placed on ice. After adding 100 μL of competent cells and 50 ng of plasmid to the cup, a 2.0 kV, 1 mm electric shock was applied once. The mixture was quickly moved to LB medium containing 0.5 mol L^{-1} sorbitol and 0.38 mol L^{-1} mannitol. After incubating at 37°C in a shaking incubator at 200 r min^{-1} for 3 h, 100 μL of the sample was spread onto an LB solid plate with ampicillin resistance and incubated upside down at 37°C for 12 h (Olubajo and Bacon 2008). The labeled strain was then applied to the soil, and its integration into the maize root system was observed using laser confocal microscopy after 7 d.

2.8. Host plant resistance analysis

Maize leaves were treated with antagonistic strains for 7 days, and control samples were collected for RNA extraction following the protocol provided by the E.Z.N.A.® Plant RNA Kit (Omega Bio-tek, Inc., Norcross, USA). The extracted RNA was then reverse transcribed using Hifair® III 1st Strand cDNA Synthesis Super Mix from Yeasen Biotechnology Co., Ltd. in Shanghai, China. RT-qPCR assays were analyzed using the $2^{-\Delta\Delta Ct}$ method, and the primers used for RT-qPCR are shown in Appendix A.

2.9. Identification of antifungal substances from zm026

Transfer 1 L of fermentation broth into a 50 mL centrifuge tube, separate the bacterial precipitate by centrifuging at 12,000 r min^{-1} for 10 min at 4°C, and retain the supernatant. Adjust the pH to 2.0 using 6 mol L^{-1} HCl, then refrigerate at 4°C overnight. The following day, discard the supernatant, collect the precipitate, add methanol for extraction for 4–6 h, and centrifuge at 8,000 r min^{-1} for 10 min at 4°C. Evaporate the supernatant using a rotary evaporator at 45°C to obtain a solid. Measure the mass of the solid for yield calculation. For further analysis, dissolve 10 mg of the extract in 1 mL of methanol, sonicate for 30 min, and centrifuge at 13,000 r min^{-1} for 10 min. Mix 0.5 mL of the supernatant with water and filter. The samples were analyzed on a C18 column with

a flow rate of 0.3 mL min^{-1} and an injection volume of 10 μL. The mobile phases were 0.1% formic acid in acetonitrile and 0.1% formic acid in ultrapure water; the samples were subjected to data-dependent scanning analysis (DDA) with the loop count set at 10, and the HCD energy was step-wise normalized to the collision energy with values of 10, 28, and 35 eV. The primary mass spectrometry (MS) scanning range was 80–1,200 m/z, the resolution was set to 70,000, the AGC target was set to 3E6, and the injection time was set to 200 ms. The resolution of the secondary mass spectrum was set to 17,500, the AGC target was set to 1E5, and the injection time was set to 50 ms. Utilize Compound Discover software to identify bacteriostatic components.

2.10. Mechanism of active ingredients inhibiting the development of pathogens

The impact of bacteriostatic active substances from zm026 on fungal growth was investigated following established protocols. A spore suspension of pathogenic fungus was prepared and added to PDA medium to create a medium with fungal spores. Petri dishes were filled with the medium to a 5 mm thickness, and six holes were punched in the agar. PDA medium was placed at the bottom of each hole, followed by 1, 2, or 3 drops of the antifungal active ingredient from zm026 in three holes. The remaining three holes were used as negative controls. The inoculated plates were then incubated at 28°C for 3–5 days until zones of inhibition were clearly visible. Additionally, the effect of antifungal compounds from zm026 on pathogenic fungal spores was investigated. Following the methodology outlined by Schmidt and French (1979), fungal spore suspensions were added to sterilized slides. Treatment groups received a methanol solution of bacteriostatic active substances, and a control group was established. The slides were cultured at 28°C in a humid environment for 0, 6, 12, 24, and 36 h and then observed by microscope. Furthermore, apoptosis and necrosis were examined by treating fungal spore suspensions with an inhibitory crude extract at 28°C overnight. Staining kits such as DAPI and PI were used to stain and observe spores in the treated and control groups after 24 h of treatment.

3. Results

3.1. Maize straw incorporation affects microbial community composition

Relative abundance of bacterial communities at the genus level was determined using 16S rRNA amplicon sequences (Fig. 1-A). A total of six dominant bacterial genera were identified, namely *Bacillus* spp., *Sphingomonas* spp., *Streptomyces* spp., *Chaetomium* spp., *Nocardia* spp., and *Rhizobium* spp. Among these, all genera except *Bacillus* spp. exhibited higher relative abundance in soils where straw was returned compared to non-returned soils. Notably, only *Bacillus* spp. showed a significant change in relative abundance between the two conditions. It showed a 0.5% decrease in abundance of soil populations after straw return compared to soil populations without straw return. The analysis of fungal communities at the genus level was based on ITS amplicon sequences (Fig. 1-B), revealing significant differences in the relative abundance of dominant species before and after straw return. A total of nine fungal taxa with relative abundance exceeding 1% were identified, including *Mortierella Coemans* spp., *Chaetomium* spp., *Talaromyces* spp., *Aspergillus* spp., *Exophiala* spp., *Gibberella* spp., *Papulospora* spp., *Cercophora* spp., and *Stachybotrys* spp. The relative abundance of *Gibberella* spp., *Trichoderma* spp., and *Talaromyces* spp. was notably different in soils where straw was returned compared to non-returned soils. *Gibberella* spp. showed a 1.2% increase in abundance in soil populations after straw return compared to soil populations without straw return, indicating an impact of straw return on the microbial community structure.

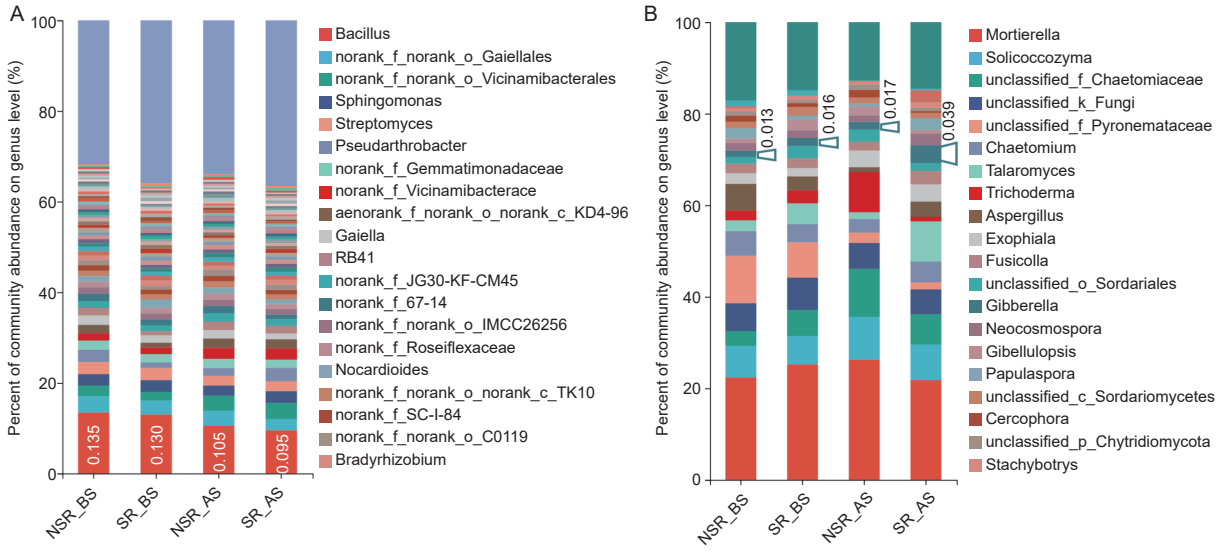


Fig. 1 Microbial ecological balance was broken by straw returning. A, community barplot analysis of bacteria. B, community barplot analysis of fungi. NSR for non-straw-returned, SR for straw-returned, AS for before straw-returned, BS for after straw-returned.

3.2. Isolation and identification of zm026

A total of 2,700 bacterial strains were isolated from 137 rhizosphere soil samples of maize grown in soil with straw returning, using a high-throughput isolation method. Among these strains, one with the most potent antifungal activity and stable subculture was identified. This particular strain exhibited significant antifungal activity against *F. verticillioides*, *F. graminearum*, *F. oxysporum*, and *E. turcicum* on PDA for 3 days (Fig. 2-A), forming a clear inhibition ring after incubation. The entire genome has been sequenced and assembled into a complete circular chromosome with a length of 3,869,997 bp. The average GC content across the entire genome is 46.43%, and it comprises a total of 3,685 genes. Genomic identification has confirmed it to be *Bacillus velezensis* (Fig. 2-B).

3.3. Zm026 colonizes maize

To investigate the colonization of the zm026 strain in the maize root system, the zm026 strain was transformed with GFP. The stability of the zm026-GFP strain was confirmed through multiple cultures. Comparison between the zm026 and zm026-GFP strains demonstrated that the introduction of the exogenous plasmid did not impact the growth and metabolic function of the zm026 strain. The GFP-tagged zm026 transformant was then inoculated into the soil, and after 7 days, bright green fluorescence was observed on the root tips of maize under a laser scanning confocal microscope (Fig. 3-A). The fluorescence was densely distributed on the root tip and its sides, indicating successful colonization of the biocontrol zm026 strain in the soil.

3.4. Zm026 exhibits prevention and control of corn diseases indoors

In the pot experiments, strain zm026 exhibited growth-promoting effects. The fresh weight of the whole maize plant, root length, plant height, and stem thickness increased by 63.95%, 30.36%, 21.43%, and 22.83%, respectively (Fig. 3-B and E). In the study of corn northern leaf blight, it was observed that treating maize leaves with zm026 fermentation broth resulted in less severe disease and significantly reduced lesion areas (Fig. 3-C). This suggests that the zm026 strain effectively controlled corn northern leaf blight in indoor conditions. Additionally, in indoor pot tests for maize ear and kernel rots, it was found that the application of zm026 significantly reduced maize kernel rot (Fig. 3-D) and decreased the number of diseased kernels, achieving an inhibition rate of about 64.53%. This demonstrates the effectiveness of zm026 fermentation solution in controlling maize ear and kernel rots indoors.

3.5. Corn disease control and fumonisin inhibition by zm026 in the field

Zm026 effectively promoted maize growth at the seedling stage. After 15 days of applying zm026 fermentation broth, maize growth in the treatment group was significantly higher compared to the control group (Fig. 4-A). Plant height, leaf length, and stem thickness increased by 20.52%, 15.32%, and 20.09%, respectively. Field application of zm026 fermentation solution also led to a smaller maize cob spot area and a higher percentage of healthy kernels in the treatment group (Fig. 4-A). Statistical analysis of disease levels in maize samples (Table 1) revealed an ear rot disease index of 17.14% in the treated group compared to 28.28% in the control group, resulting in a preventive efficacy of 39.39%; the corn northern leaf blight disease index of 34.30% in the treated group compared to 54.59% in the control group, resulting in a preventive efficacy of 37.17%. These findings indicate that field application of zm026 had a superior effect on controlling maize ear rot and corn northern leaf blight. Analysis of fumonisin B_1 content in maize kernels from the treatment and control groups revealed a significant difference

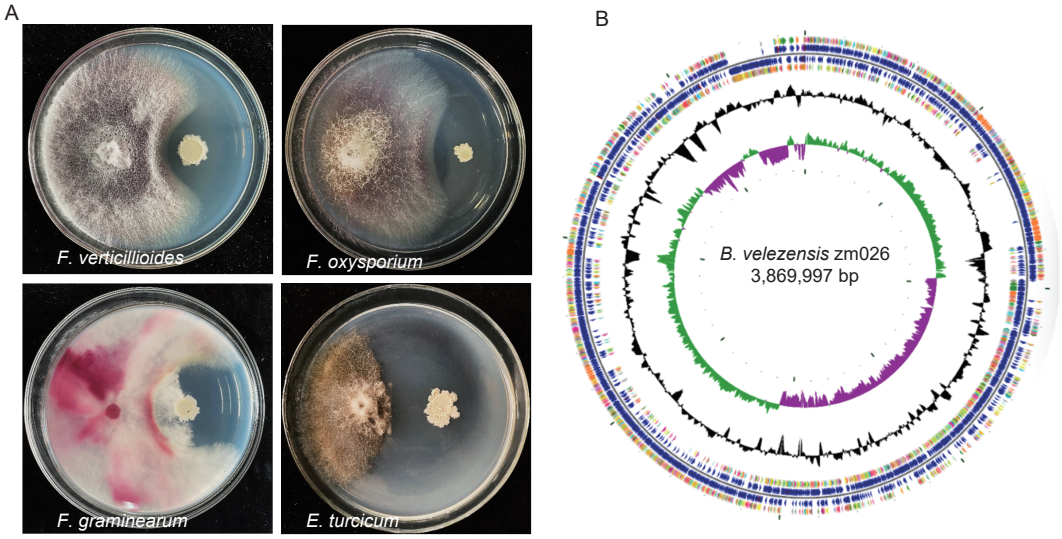


Fig. 2 *Bacillus velezensis* zm026 was screened for *in-situ* remediation of corn disease ecological control in straw returning modes. A, the inhibitory effect of zm026 on corn pathogenic fungi *Fusarium verticilliodes*, *F. oxysporum*, *F. graminearum*, and *Exserohilum turcicum*. B, circular genome map of *Bacillus velezensis* zm026.

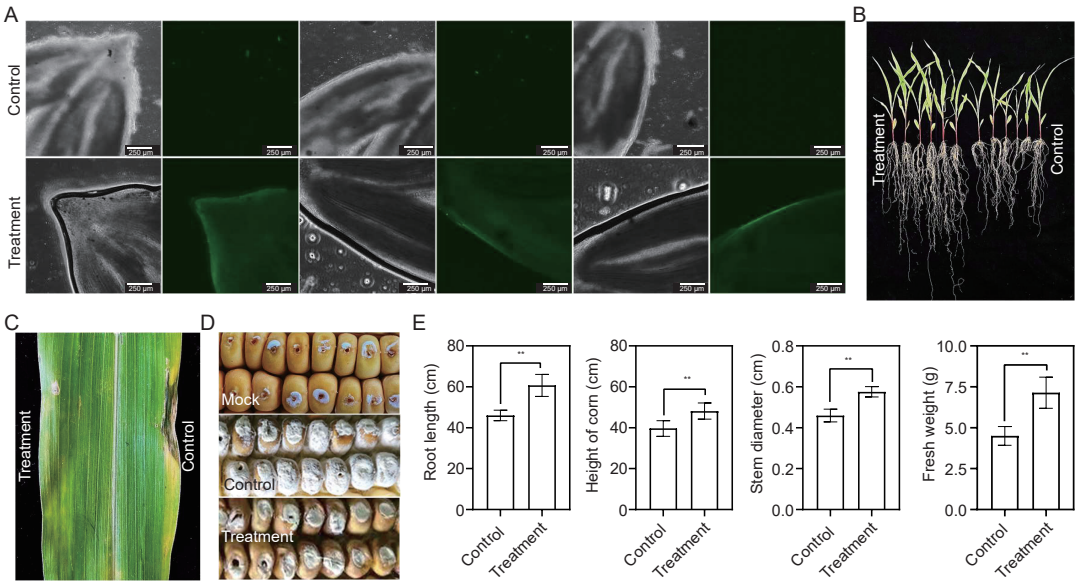


Fig. 3 Rhizosphere colonization and growth-promoting disease control efficacy of zm026. A, laser confocal image of root tip of maize colonized by zm026 GFP strain. B, corn growth-promoting effect diagram, with the left side showing the treatment group and the right side showing the control group. C, visual effect diagram of *Exserohilum turcicum*-treated corn leaves, with the left side showing the treatment group that has been applied with zm026 and the right side representing the control group. D, the top of the image is a blank control; the middle of the image depicts puncture inoculation with *Fusarium verticilliodes*; the bottom of the image depicts puncture inoculation with *F. verticilliodes*+zm026. E, comparison and statistical chart of maize growth indicators. Different asterisks indicate significant differences at ns, $P>0.05$; **, $P<0.01$.

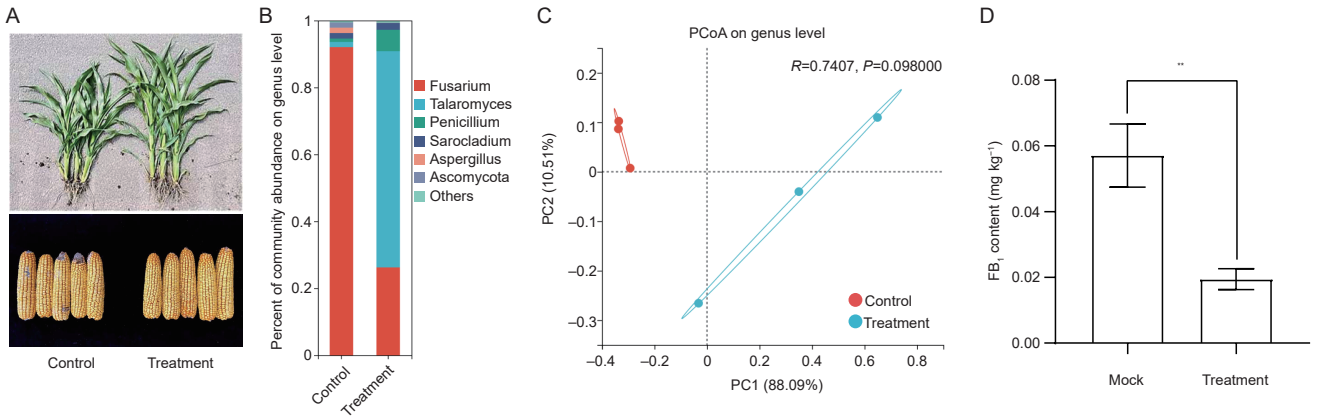


Fig. 4 The effect of zm026 application in field trials. A, the above figure shows the growth-promoting effect of zm026, while the below figure demonstrates its effectiveness in preventing ear rot. B, the relative abundance of different genera across various treatments. C, principal coordinate analysis (PCoA) using the abundance-based Jaccard distance matrix. D, changes in fumonisin B1 (FB_1) levels after treatment with zm026. Different asterisks indicate significant differences at ns, $P>0.05$; **, $P<0.01$.

(Fig. 4-D). Maize kernels treated with zm026 fermentation broth showed a significantly lower concentration of fumonisin B1 compared to the control group, with an inhibition rate of 65.91%. These results indicate that strain zm026 not only enhances maize yield but also inhibits toxin production by the pathogen, leading to a reduction in fumonisin B1 content in maize.

Subsequently, microbial content in corn kernels was analyzed through metagenomic sequencing. The principal component analysis (PCA) obtained from the anion model indicated significant differences in microbial composition between the control group and the treatment group exposed to zm026 fermentation broth (Fig. 4-C). In the control group, *Fusarium* genus was the dominant species. However, the dominant species in the treatment group treated with zm026

Table 1 Control effect of zm026 on corn ear rots and northern corn leaf blight

Group	Disease index (%)		Control effect (%)
	Control	Treatment	
Corn ear rots	28.28	17.14	39.39
Northern corn leaf blight	54.59	34.30	37.17

fermentation broth had been replaced by *Talaromyces* genus. These results demonstrate that zm026 treatment can significantly inhibit *F. verticillioides* growth and have a pronounced effect on the prevention and control of maize ear rot (Fig. 4-B).

3.6. Antifungal substances exhibit bacteriostatic effect

The antifungal substances derived from the fermentation broth of zm026 were obtained as a brownish viscous solid with a yield of 0.15 g L^{-1}. This substance was then formulated into a 10 mg mL^{-1} concentration methanol solution for subsequent experiments. The antifungal activity of these substances was assessed using an agar punch method (Fig. 5-A), which revealed significant inhibition of *F. verticillioides* and *E. turcicum* around the designated areas, while normal growth was observed in the control groups. The inhibition rates were approximately 67.30% against *F. verticillioides* and 77.97% against *E. turcicum*.

3.7. RT-qPCR of maize systemic acquired resistance genes by zm026

To further investigate the impact of zm026 on maize systemic acquired resistance post successful root system colonization, various genes including phenylalanine ammonia lyase (*ZmPAL*), alternative oxidase (*ZmAO*), zinc finger homeo domain protein (*ZmZHD*), peroxidase (*ZmPOD*), glutathione transferase (*ZmGST*), pathogenesis-related protein (*ZmPR-1*), pathogenesis-related protein (*ZmPR-2*), pathogenesis-related protein (*ZmPR-3*), and elongation factor 1 (*ZmEF1a*) were quantified in maize plant leaves inoculated with zm026 fermentation broth up to the 3-leaf stage. The expression levels of these genes showed varying degrees of increase post-treatment (Fig. 5-B). Particularly noteworthy was the significant increase in expression of genes associated with glutathione S-transferase (*ZmGST*) and zinc finger protein (*ZmZHD*), known for their crucial roles in plant growth, development, and responses to biotic and abiotic stresses. This suggests that zm026 not only triggers effector-triggered immunity but also enhances plant growth and stress resistance.

3.8. Identification of bacteriostatic active substances from zm026

HPLC-MS analysis (Fig. 6-A) identified 18 active ingredients in the bacteriostatic substances of zm026, with the primary active compounds being the antifungal lipopeptide bacillomycin D and its congeners D1, D2, D3, and D4, accounting for 18.16% of the total composition. Additionally, nutrients such as leucine (13.56%), L-tyrosine, L-valine, and vitamins like pantothenic acid and pyridoxamine dihydrochloride were also present. Genome sequencing was conducted to identify the biosynthetic gene cluster for bacillomycin D in zm026. The multiple secondary metabolite synthesis gene clusters in zm026 were predicted by antiSMASH. Cluster 3 displayed 100% homology with the bacillomycin biosynthesis gene cluster, indicating it as the biosynthesis gene cluster of bacillomycin D. The NRPS gene cluster for bacillomycin D biosynthesis in zm026 spanned approximately 44 kb, comprising three open reading frames named bmyA, bmyB, and bmyC (Fig. 6-B).

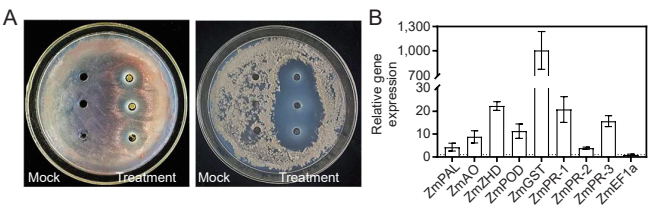


Fig. 5 Analysis of the antibacterial activity of zm026. A, the left shows the antibacterial activity of the extract against *Fusarium verticillioides*; the right figure shows the antibacterial activity of the extract against *Bacillus cinerea*. B, analysis of zm026-induced disease resistance.

3.9. Bacteriostatic active substances from zm026 inhibitory effects on fungi

Following treatment with bacteriostatic active substances, microscopic observation revealed distinct germination patterns among spores of *F. verticillioides* and *E. turcicum*. Untreated spores of the two fungi exhibited gradual germination stages, from initial germination at 6 h to full mycelium development at 36 h. Conversely, treated spores of *E. turcicum* and *F. verticillioides* displayed immediate distortion and swelling at 6 h, leading to rupture and release of inclusions by 12 h, followed by complete spore disruption at 36 h (Fig. 6-C).

To determine whether the inhibitory crude extract of strain zm026 induces apoptosis or necrosis in pathogenic fungi, two fluorescent staining tests were conducted. Initially, DAPI staining was performed, revealing diffuse but intense blue fluorescence in *E. turcicum* and *F. verticillioides* treated with the bacteriostat, compared to the compact weak blue fluorescence in untreated spores of the same species (Fig. 6-D). This suggests chromatin breakage in the treated fungi, leading to apoptotic changes. Lastly, PI staining revealed both green and red fluorescence in the treated spores, signifying damage to the cell membrane integrity and apoptosis induction by the bacteriostatic activity of zm026 (Fig. 6-D).

4. Discussion

In our study, it was first found by microbiome sequencing that straw return had a great impact on the structure of the microbial community in the soil, with a significant decrease in the percentage of *Bacillus* spp. and a significant increase in *Fusarium* spp. as a pathogenic fungus. This change could be attributed to the change in cropping pattern (Sun *et al.* 2015), and previous studies have suggested that straw farming can lead to significant changes in the number of microorganisms in the soil and the structure of the community (Bennett *et al.* 2015). Microbial communities in nature have a wide range of applications and make beneficial contributions to human health (Gargari *et al.* 2020; Idicula *et al.* 2023). In recent years, the important role of soil microbial community composition in maintaining soil health has been increasingly emphasised. The roles of soil

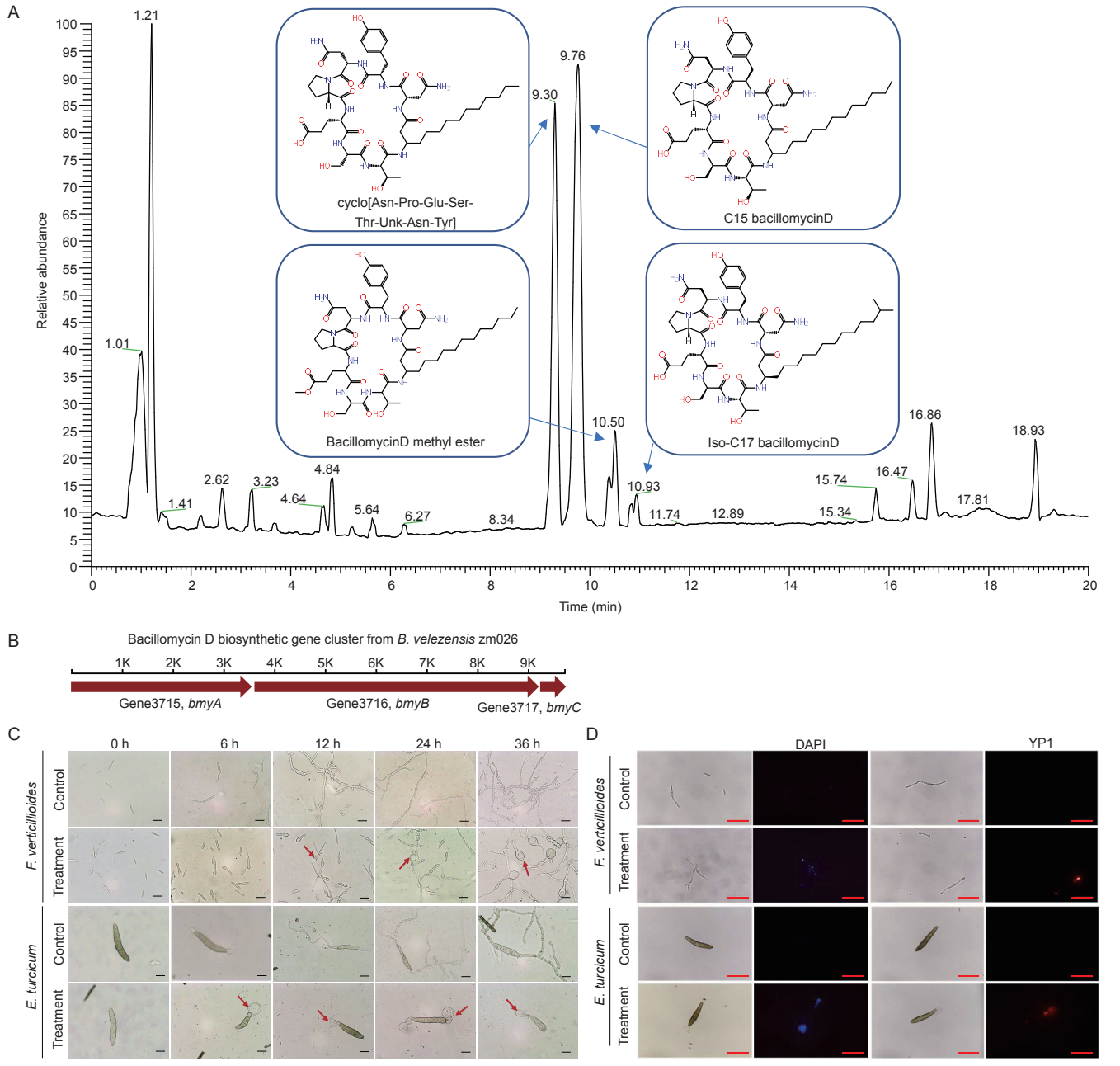


Fig. 6 Analysis of the composition of antibacterial active substances in zm026 and its antibacterial mechanism. A, chromatogram of base peak of bacteriostatic substance in single -component anion mode. B, bacitracin D gene cluster. C, micrograph of spore germination of *Fusarium verticillioides* and *Exserohilum turcicum*. Bar=20 μm. D, micrographs of DAPI and PI staining of *F. verticillioides* and *E. turcicum*. Bar=40 μm.

microorganisms in soil ecosystems are mainly to maintain soil nutrient cycling, biocontrol soil-borne pests and diseases, and induce plant disease resistance, etc. Their abundance and diversity are highly related to plant species, soil types, and cultivation techniques (Berg and Smalla 2009). For example, investigations conducted by Zhao *et al.* (2019) and Yu *et al.* (2024) showed that the abundance of Ascomycota increased significantly due to straw return practices. Studies have shown that bacteria favour the use of easily decomposed plant residues, and that fungi, which grow more slowly than bacteria, favour the decomposition of compounds that are difficult to break down (Paterson *et al.* 2008; Poll *et al.* 2008; Bastian *et al.* 2009). In contrast, the results of this study determined the microbial composition of maize soil with and without straw return by 16S rRNA amplicon sequencing and found that the relative abundance of *Gibberella* spp. in the fungal microbial community of soil with straw in the field was significantly different compared with that without straw in the field. The relative abundance of *Bacillus* spp. in the bacterial community was significantly different compared with other strains, indicating that stover-returning had a significant effect on the microbiome of the soil, which is consistent with previous studies.

Modulation of soil microbial communities not only improves soil health but also effectively prevents and controls plant diseases by suppressing plant pathogens. Currently,

microbial transplantation engineering has been successfully applied to alter the composition of plant microflora (Williams *et al.* 2014), thereby improving soil health and promoting the role of sustainable defence and control of plant diseases. When beneficial microorganisms colonise crops, they usually show high affinity for the root system of plants (Ali *et al.* 2020). Beneficial microorganisms compete with plant pathogens for ecological niches, occupy invasion sites of pathogens, and aggregate on the plant surface in multicellular aggregates to form biofilms (Flemming *et al.* 2016). This biofilm prevents pathogenic bacteria from entering the plant surface and protects the plant from infection by pathogenic bacteria. When biocontrol agents fail to achieve the desired control effect, it may be due to the poor colonisation ability of probiotics (Balsanelli *et al.* 2010; Kandel *et al.* 2017). Therefore, whether probiotics can successfully colonise plant roots is the key to measuring whether biocontrol fungicides can play a role in promoting and preventing disease, and the fluorescent gene marker method is currently the most widely used research method because it is convenient to detect and is not limited by the genus of the receptor (Wang *et al.* 2020). In this experiment, the plasmid with green fluorescent protein gene was transferred into zm026 by electrotransformation using gene marker tracer technology, and in general, the effective expression of GFP in the bacterium burdens it with additional metabolism, which affects its physiological and metabolic activities and biological functions (Zhang *et al.* 2014). In this experiment, however, there was no significant difference in the growth characteristics and antagonistic activity between the GFP-labelled bacteria and the original bacteria zm026, indicating that GFP protein expression did not adversely affect the physiological metabolism and bacteriostatic function of zm026. The colonisation of zm026-GFP in the inter-root zone of maize was observed by laser scanning confocal microscopy, and it was observed that zm026-GFP was able to stably and intensively colonise the root tip and both sides of the maize root after 5 d of application of the bacterial solution. This provides a theoretical basis for the practical application of zm026-GFP as a biocontrol agent.

Probiotics secrete bacteriostatic substances that exhibit inhibitory effects on fungi (Zhang *et al.* 2024). It has been demonstrated that the bacteriostatic effect of *B. amyloliquefaciens* is that its bacteriostatic substances can form pores in the cell membrane of *Rhizoctonia* solani Kühn, resulting in the leakage of intracellular substances and causing cell apoptosis (Zhang *et al.* 2013). In this study, the bacteriostatic substances in zm026 fermentation broth were preliminarily extracted by acid precipitation method, and its bacteriostatic active substances were identified mainly as bacillomycin D, which belongs to the family of iturin in the lipopeptide antibiotics of *Bacillus* (She *et al.* 2024). Earlier studies have found that antimicrobial analogues produced by metabolism of *Bacillus* are able to effectively inhibit the normal growth and reproduction of some pathogenic bacteria (Cavazzoni *et al.* 1998); for example, *Bacillus* 151B1 causes morphological abnormalities in conidia and loss of cell membrane integrity (Chen *et al.* 2021). In the present study, the inhibitory mechanism of zm026 was further confirmed to cause apoptosis by observation of Trypan blue staining, DAPI, and YPI fluorescence staining. This is almost consistent with the findings of previous studies. In a number of studies, bacillus-containing bioproducts significantly promoted sweet pepper root growth and yield increases, while increasing nitrogen fertiliser efficiency (Huang *et al.* 2019). Our finding that Zm026 promotes plant growth is also consistent with the previous finding that *B. velezensis* BAC03 produces IAA, ammonia, and 1-aminocyclopropane-1-carboxylic acid deaminase, which promotes the growth of plants such as sugar beet, carrot, and cucumber (Meng *et al.* 2016). We observed a significant increase in the expression of defense enzyme genes in maize following the application of the zm026 solution, suggesting that zm026 may enhance disease resistance. Similarly, the application of BVE7 fermentation solution effectively promoted soybean growth and enhanced the activities of defense enzymes, including catalase (CAT), polyphenol oxidase (PPO), and superoxide dismutase (SOD) in soybeans (Sun *et al.* 2023). Following the colonization of biocontrol bacteria in the crop rhizosphere, root commensals assist plants in resisting pathogen invasion through various mechanisms, including Induced Systemic Resistance (ISR). Certain microorganisms can induce ISR directly or indirectly by producing antibacterial substances that inhibit pathogens. For example, the tomato pathogenic bacterium *Pseudomonas syringae* (PST) infects tomato leaves, prompting infected plants to increase the secretion of malic acid in their roots and recruit *B. subtilis* to elicit a stronger immune response to PST (Rudrappa *et al.* 2008; Bai *et al.* 2022).

A large number of traditional physical and chemical methods for the elimination or inactivation of mycotoxins have been reported in the literature (Stoev 2013). However, these methods have limitations in terms of safety and nutritional value of feeds, as well as limited efficiency and cost. Therefore, the search for an effective, specific, and environmentally feasible decontamination technology has become imperative. Mycotoxin biodetoxification technology, which uses microorganisms to degrade mycotoxins into non-toxic or less toxic compounds, could be an option for such technology (Taylor and Draughon 2001). It has been proved that *Actinomycetales* could degrade aflatoxins. For example, *Nocardia corynebacteroides* (NC) was tested for its capability of aflatoxin detoxification in Ross 308 chicks, which showed a 60% reduction rate after 24 h (Tejada-Castaneda *et al.* 2008). Pseudomonas aeruginosa N17-1 has been reported to degrade 82.8%, 46.8%, and 31.9% of AFB_1, AFB_2, and AFM_1, respectively, after 72 h of incubation in Nutrient Broth medium at 37°C (Sangare *et al.* 2014). Some *Bacillus* sp. also have aflatoxin reducing activity, such as *B. subtilis* (Farzaneh *et al.* 2012), *B. licheniformis* (Petchkongkaew *et al.* 2008), and so on. *Nocardioides* WSN05-2 isolated from soil samples collected from wheat fields degrades DON to a novel intermediate 3-epi-DON (Ikunaga *et al.* 2011). It is worth noting that the application of zm026 found in this study can directly reduce the content of fumonisin in corn kernels. More importantly, zm026 is found in rhizosphere soil, which is more suitable for the living environment.

5. Conclusion

In summary, we screened bacteria with efficient inhibitory effects on *F. verticillioides*, identified as *B. velezensis* and named zm026, possessing broad-spectrum antimicrobial activity. It not only has a significant growth-promoting effect on maize but also exhibits efficacy against maize leaf blight and maize ear rot. Using GFP to label zm026, we observed that it colonized the root tip and both sides of the maize root. It was detected that zm026 enhance plant disease resistance. The bacteriostatic active substances of zm026 were coarsely extracted, and the effective bacteriostatic component was identified as bacteriocin D. The zm026 genome and the bacteriocin biosynthesis gene cluster were also identified. The antagonist strain was found to inhibit fungal spore germination, disrupt fungal spore cell membranes, and induce apoptosis (Fig. 7).

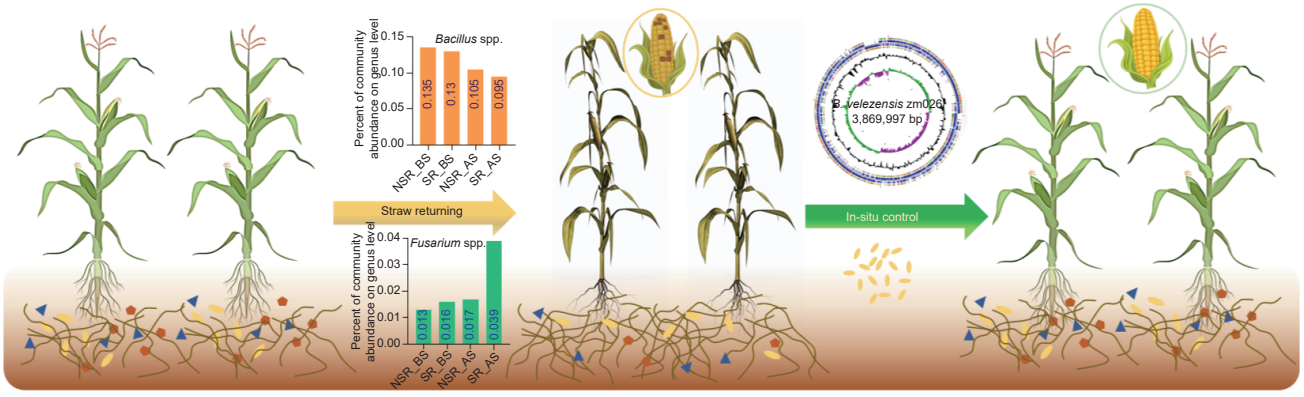


Fig. 7 Zm026 *in-situ* remediation of straw-returned soil alters microbial community structure and effectively reduces maize ear rot.

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Declaration of competing interest

The authors declare that they have no conflict of interest.

Declaration of generative AI and AI-assisted technologies in the writing process

The authors declare that they did not use AI in the preparation and writing of this manuscrlpt.

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