



Biocontrol of *Sclerotinia sclerotiorum* and plant growth promotion in common bean (*Phaseolus vulgaris* L.) by *Bacillus* spp.

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Received: 25 October 2025 / Accepted: 14 May 2026 / Published online: 23 May 2026
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Abstract White mold, caused by *Sclerotinia sclerotiorum*, is one of the most important diseases affecting common bean crops. Due to its global distribution and wide host range, the persistence of *S. sclerotiorum* in the environment is favored by the formation of survival structures, which complicates control measures. In this context, biological control emerges as a sustainable strategy for pathogen suppression and plant growth promotion. To explore this approach, nine strains of *Bacillus* spp. were screened for their ability to control *S. sclerotiorum* strain SSF and promote growth of common bean (*Phaseolus vulgaris* L.) plants. All strains exhibited antagonistic activity against *S. sclerotiorum* strain SSF, demonstrated through in vitro antagonism assays, including dual culture and cell-free supernatant (CFS) tests, and

volatile organic compounds (VOCs) exposure, indicating the involvement of multiple antagonistic mechanisms. In addition, the strains displayed key in vitro biocontrol traits, such as the production of cell wall-degrading enzymes and siderophores. Greenhouse trials confirmed the efficacy of selected strains in controlling white mold and promoting bean plant growth. Isolates EVSA, BERA II, and BEFA I stood out by enabling the survival of plants inoculated with *S. sclerotiorum* while not impairing seed germination. Both bacterial co-inoculation (EVSA, BERA II, and BEFA I) and the EVSA strain alone promoted shoot and root development in bean plants. EVSA demonstrated multifunctional activity, combining effective suppression of *S. sclerotiorum* strain SSF with plant growth promotion, positioning it as a promising candidate for bioinoculant development in the sustainable management of white mold.

Handling Editor: James Tambong.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s10526-026-10409-6>.

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Keywords Biological control · Phytopathogen · Sustainable agriculture · Bio-inputs · White mold

Introduction

Phytopathogenic fungi are among the most destructive microbial agents in agriculture (Almeida et al. 2019). Fungal diseases affect crops at all stages of production, resulting in significant yield losses and posing serious threats to food security and ecosystem stability (Savary et al. 2019). Various strategies

are employed to control phytopathogens, including cultural, chemical, physical, and genetic approaches. Chemical control, particularly the use of fungicides, remains the most widely adopted method. However, it is associated with multiple environmental concerns, such as pollution, the selection of resistant microorganisms, and negative impacts on non-target biota (Pandit et al. 2022; Vero et al. 2023).

In recent years, Brazil has ranked among the world's largest producers and consumers of common beans (*Phaseolus vulgaris* L.) (FAO 2024). This crop is susceptible to several pathogens, among which white mold is one of the most damaging diseases. Its high virulence, combined with favorable climatic conditions, can result in severe yield losses or even total crop failure (Singh and Schwartz 2010; Miklas et al. 2013; Lehner et al. 2019). White mold is caused by the fungus *Sclerotinia sclerotiorum* (Lib.) de Bary, whose symptom is characterized by the presence of cotton-like white mycelium on stems, leaves, flowers, pods, and grains of the common bean plant (Miklas et al. 2013).

S. sclerotiorum is a necrotrophic fungus with a global distribution and the ability to infect more than 500 plant species, thereby complicating disease management in areas with a history of infestation (Saharan and Mehta 2008). In addition to these management challenges, effective control of *S. sclerotiorum* in commercial fields is further limited by the formation of sclerotia, which are resistant survival structures that allow the phytopathogen to persist in the soil for extended periods (Guilger-Casagrande et al. 2019; Villarreal-Delgado et al. 2021; Aulakh et al. 2025). As a result, chemical fungicides remain the most widely used strategy for managing white mold in agricultural systems (Han et al. 2023).

Therefore, the development of more efficient and environmentally sustainable methods for controlling white mold in common beans is urgently needed. In this context, the use of antagonistic microorganisms, known as biological control agents (BCAs), represents a promising alternative to conventional agrochemical fungicides (Triantafyllou et al. 2023). Several microbial taxa, including fungi (Montalvão et al. 2023; Abdelrhim et al. 2024), bacteria (Villarreal-Delgado et al. 2021; Triantafyllou et al. 2023; Ma et al. 2024; Aulakh et al. 2025), actinomycetes (Gebily et al. 2021), and viruses (Zhang et al. 2020;

Fu et al. 2023), have demonstrated effectiveness as BCAs in the management of white mold.

Among BCAs, *Bacillus* spp. are widely studied and applied due to their broad-spectrum antagonistic activity, ease of cultivation, tolerance to environmental stress, and long-term storage capacity (Cheng et al. 2024). Biological control mediated by *Bacillus* spp. involves multiple activities, including the production of secondary metabolites (e.g., antibiotics and siderophores), hydrolytic enzymes, volatile compounds, hydrogen cyanide, and competition for nutrients (Maral-Gül and Eltem 2024). In addition, *Bacillus* spp. are well-known for their ability to promote plant growth and induce systemic resistance in host plants (Sabaté et al. 2018; Cao et al. 2023; Dutilloy et al. 2024).

Considering these multifunctional traits, *Bacillus* spp. represent suitable candidates for the sustainable management of white mold. Accordingly, this study aimed to identify and evaluate *Bacillus* spp. strains exhibiting dual functionality, acting as both BCA against *S. sclerotiorum* strain SSF and as plant growth promoters for common bean (*P. vulgaris* L.) cv. Rajado.

Materials and methods

Isolation, identification and phytopathogenicity of the SSF isolate

The *S. sclerotiorum* isolate SSF was obtained from bean plants exhibiting white mold symptoms in the municipality of Lucas do Rio Verde (Mato Grosso, Brazil) in 2021. The isolate was purified on PDA culture medium (potato, dextrose, agar) and exhibited morphocultural characteristics consistent with those described for this species. Colonies grown on PDA showed abundant white, cottony mycelium with radial growth and the formation of black, irregularly shaped sclerotia distributed across the colony surface. These phenotypic features were later confirmed by molecular identification based on sequence analysis. Genomic DNA was extracted using a commercial kit (Norgen Biotek Corp., Canada), which was used as a template for amplification of the ITS region, and was amplified using the universal primers ITS1 and ITS4 (White et al. 1990).

PCR reactions were prepared in a final volume of 25 µl, containing 2.5 µl of 10×PCR buffer (without MgCl₂), 0.75 µl of MgCl₂ (50 mM), 1.0 µl of dNTP mix (10 mM), 1.0 µl of each primer, 0.5 µl of Taq DNA polymerase (Invitrogen), 4.0 µl of genomic DNA, and Milli-Q water to complete the volume. The resulting ITS sequences were then analyzed using BLAST, aligned with MUSCLE, and used to construct a phylogenetic tree using the Neighbor-Joining method with 1,000 bootstrap replicates in MEGA v11.

The phytopathogenicity of the isolate was subsequently evaluated by inoculating ten sclerotia into 2 l pots containing a sand/vermiculite mixture (1:1, v/v) adjusted to 70% field capacity. After one week, surface-disinfested common bean seeds cv. Rajado (*P. vulgaris* L.) were sown. Soil moisture was maintained daily, and Hoagland's nutrient solution was applied weekly. Plants were grown under controlled conditions until the appearance of typical white mold symptoms.

Antagonistic bacteria

The antagonistic bacterial strains were selected from the collection of microorganisms of the Federal Institute of Education, Science and Technology of Mato Grosso (IFMT), Advanced Campus of Lucas do Rio Verde, Brazil. PCR reactions were prepared in a final volume of 25 µl, containing 2.5 µl of 10×PCR buffer (without MgCl₂), 0.75 µl of MgCl₂ (50 mM), 1.0 µl of dNTP mix (10 mM), 1.0 µl of each primer, 0.5 µl of Taq DNA

polymerase (Invitrogen), 3.0 µl of genomic DNA, and 15.25 µl of Milli-Q water to complete the final volume. PCR cycling conditions consisted of an initial denaturation at 94 °C for 5 min, followed by 35 cycles of 94 °C for 40 s, 58 °C for 35 s, and 72 °C for 80 s, with a final extension at 72 °C for 10 min.

The amplicons (ITS and 16S) were purified (ExoSap-it, GE Healthcare) and sequenced by the Sanger method (BigDye Terminator Cycle Sequencing). The sequences were edited using the Chromas software (version 2.6.6) and compared to the sequences deposited in GenBank, using the nBLAST tool (<http://www.ncbi.nlm.nih.gov/>). Finally, the nucleotide sequences were deposited in GenBank under accession numbers listed in Table 1.

In vitro antibiosis using dual culture (DC) assay

A seven-day-old (5 mm in diameter) *Sclerotinia sclerotiorum* strain SSF mycelial disc was placed on PDA plates approximately 2 cm from the edge of the Petri dish in the dual-culture treatments. Bacterial isolates were inoculated on the opposite side of the plate at 2 cm from the edge, after adjustment to an optical density of OD₆₃₀=0.1. For the control treatment, a mycelial disc of *S. sclerotiorum* was placed at the center of the PDA plate. Plates were incubated at 25 °C for seven days, and the experiment was conducted in triplicate. After incubation, the diameter of the fungal colony was measured, and the percentage of mycelial growth inhibition was calculated in comparison with the control group (Ma et al. 2024).

Table 1 Antagonistic bacterial strains selected for biological control assays and evaluation of plant growth-promoting traits

Strain	Environmental niche	Host plant	Molecular identification	16S rRNA length (bp)	GenBank
BACI-A	Soil	–	<i>Bacillus</i> sp.	1366	ON998495.1
BEFA-I	Endophytic (leaf)	<i>Arachis hypogaea</i>	<i>Bacillus</i> sp.	1413	ON997085
BEFA-II	Endophytic (leaf)	<i>Arachis hypogaea</i>	<i>Bacillus</i> sp.	1383	ON997087
BERA-I	Endophytic (root)	<i>Arachis hypogaea</i>	<i>Bacillus</i> sp.	1395	ON997088
BERA-II	Endophytic (root)	<i>Arachis hypogaea</i>	<i>Bacillus</i> sp.	1243	ON997086.1
EVSA	Rhizosphere	<i>Phaseolus vulgaris</i>	<i>Bacillus</i> sp.	1370	ON997081.1
RIZO-A	Rhizosphere	<i>Phaseolus vulgaris</i>	<i>Bacillus</i> sp.	1407	ON997082
RIZO-C	Rhizosphere	<i>Phaseolus vulgaris</i>	<i>Bacillus</i> sp.	1357	ON997080
RIZO-H	Rhizosphere	<i>Phaseolus vulgaris</i>	<i>Bacillus</i> sp.*	–	–

*Strain identified by ERIC-PCR fingerprinting

Preparation and antifungal activity of cell-free supernatant (CFS)

The bacteria were cultured in Luria–Bertani (LB) broth at 150 rpm and 30 °C for five days. After incubation, the fermented culture broth was centrifuged (4000 rpm for 10 min) and filtered through a 0.22 µm membrane, thus obtaining the CFS of each culture. PDA medium was prepared and supplemented with CFS at a 3:1 ratio before solidification. Mycelium discs of *S. sclerotiorum* strain SSF were deposited in the center of the Petri dish with PDA medium supplemented with CFS. The experiment was conducted in triplicate and incubated for seven days. Mycelial growth was measured, and the percentage of inhibition was calculated (Ma et al. 2024).

Production and evaluation of volatile organic compounds (VOCs)

VOCs produced by *Bacillus* spp. were evaluated using the double-sealed plate method (Fiddaman et al. 2000). Petri dishes containing PDA medium were inoculated separately with *Bacillus* spp. ($OD_{630}=0.1$) and with a mycelial disc (5 mm in diameter) of *Sclerotinia sclerotiorum* strain SSF. Plates inoculated with the bacteria and the phytopathogen were paired face-to-face, overlaid, and sealed with Parafilm®. The plates were incubated at 25 °C for seven days. The experiment was conducted in triplicate, and the percentage of growth inhibition was determined (Ma et al. 2024).

In vitro inhibition of the germination of phytopathogen sclerotia

The antagonistic potential of bacterial strains to inhibit sclerotial germination of *S. sclerotiorum* strain SSF was evaluated following Zazzerini et al. (1987), with modifications. Ten-day-old sclerotia produced on PDA medium were used, surface-disinfested with 2% sodium hypochlorite, and rinsed three times with sterile distilled water.

Bacterial cell suspensions were grown in 10 ml of LB broth at 30 °C for 48 h. The experiment was conducted with three biological replicates per treatment, and each consisting of nine sclerotia. Sclerotia were transferred to flasks containing bacterial suspensions and incubated for 72 h at 25 °C under constant

agitation (175 rpm). In the control treatment, sclerotia were incubated under the same conditions in sterile LB broth only.

After incubation, the sclerotia were removed from the flasks and transferred to PDA plates (three sclerotia per plate) and incubated at 25 °C for five days. Sclerotial germination was then evaluated and expressed in comparison with the control treatment.

Preliminary screening of *Bacillus* spp. compatibility with bean seed germination

To ensure that the candidate *Bacillus* strains selected for greenhouse assays would not adversely affect bean seed germination, a preliminary compatibility screening was performed under in vitro conditions. Surface-disinfested common bean seeds cv. Rajado (*P. vulgaris* L.) were incubated in bacterial suspensions adjusted to $OD_{630}=0.1$ for 30 min. Five seeds per replicate (three replicates per treatment) were placed in Petri dishes containing 0.8% agar and incubated at 28 °C for ten days. Germination was recorded at the end of the incubation period. This assay was used only as an initial screening step to exclude strains with potential negative effects on germination prior to greenhouse experiments.

Evaluation of plant growth-promoting traits

The production of indoleacetic acid (IAA) was quantified using colorimetric method according to Gordon and Weber (1951). The medium employed was LB, enriched with tryptophan (150 mg l^{-1}). The supernatant of each sample was mixed with Salkowski's reagent (1:1), incubated for 30 min. in the dark and analyzed in a spectrophotometer ($\lambda=530 \text{ nm}$). The indole compounds concentration was estimated based on an IAA standard curve ($7.8\text{--}500 \text{ µg ml}^{-1}$).

Siderophore production was assessed using the chrome azurol S (CAS) assay. Bacterial isolates were grown in King's B broth, and siderophore production was estimated by measuring the absorbance of the culture supernatant of treated samples (As) and the reference control (Ar) using a spectrophotometer ($\lambda=630 \text{ nm}$). Siderophore production was expressed as a percentage relative to the control treatment.

Phosphate solubilization was assessed by cultivating isolates on solid SRSM1 medium (1.6% agar) (Shi et al. 2017). Similarly, the production of

hydrolytic enzymes (protease, glucanase, cellulase, and chitinase) was evaluated qualitatively on specific assay media. Isolates were first grown in a nutrient broth before being spot-inoculated onto the respective agar plates. Based on the size of the hydrolysis or solubilization halo formed, bacterial activity was categorized as low (+), medium (++), high (+++), or absent (-) (Nagpure et al. 2014; Zia et al. 2021).

Greenhouse test

Three *Bacillus* spp. isolates (EVSA, BERA-II and BEFA-I), capable of inhibiting the growth of *S. sclerotiorum* strain SSF in the dual-culture tests and not affecting the germination of bean seeds, were selected for both biocontrol and plant growth promotion experiment. The experiment was conducted in December 2022 through a completely randomized design, considering the phytopathogen presence (+SSF) and absence (-SSF). Therefore, the treatments were distributed as follows: EVSA + SSF, EVSA-SSF, BERA-II + SSF, BERA-II-SSF, BEFA-I + SSF, BEFA-I-SSF, Co-inoculation + SSF, Co-inoculation-SSF, Control + SSF, and Control-SSF. Three strains were simultaneously used in the co-inoculation.

Bean seeds were disinfested with 70% alcohol (30 s), 1% sodium hypochlorite (1 min) and rinsed three times in sterile distilled water. The inoculation of the seeds with the phytopathogen was performed by the direct contact method in culture medium under water restriction. Mycelial discs (5 mm in diameter) from the phytopathogen inoculum were transferred to Petri dishes containing PDA medium supplemented with sucrose and a water potential of -0.6 MPa (Rey et al. 2009).

The plates were incubated in a growth chamber at 25 °C with a L:D 12:12 photoperiod during seven days. After this period, 30 surface-disinfested common bean seeds were placed onto each plate, which was fully colonized by the fungus. For the control group, seeds were placed onto plates containing only the culture medium (without the fungus). After 48 h of contact, the seeds were removed and dried on sterile filter paper at room temperature.

After inoculation with the phytopathogen, the seeds were soaked in bacterial suspension for 30 min ($OD_{630}=0.1$) to evaluate the protective effect of the bacterial isolates under controlled conditions. Subsequently, the seeds were sown in plastic pots (18 cm

in width, 12 cm at the base, and 16 cm in height) containing a sand/vermiculite mixture (1:1, v/v) and fertilized with 5 g of 9:25:25 (N:P:K), following a completely randomized design with four replicates per treatment.

The study was conducted in a greenhouse under natural environmental conditions, with natural light and no control of temperature or photoperiod. Substrate moisture was maintained at approximately 80% of field capacity, estimated using a gravimetric method based on pot weighing, with irrigation adjusted as needed to maintain the target moisture level. After 30 days, the following parameters were evaluated: plant survival, plant height (cm), root length (cm), and shoot and root dry biomass (g).

Statistical analysis

Experimental data were analyzed using R software version 4.5.2 (R Core Team 2025). Data normality was assessed using the Shapiro–Wilk test. ANOVA were performed using base R functions, and mean comparisons were conducted using Duncan's multiple range test implemented in the agricolae package, at a significance level of $p < 0.05$.

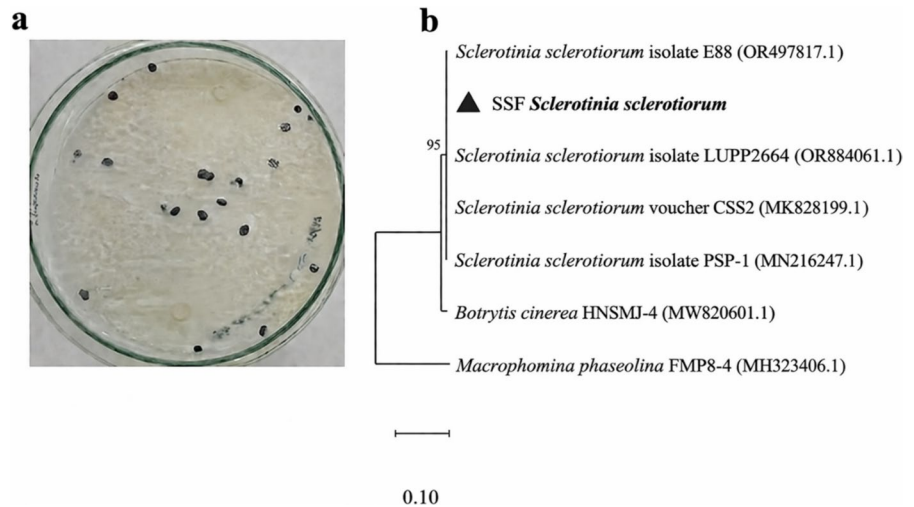
Results

Identification, molecular characterization of isolates, and phytopathogenicity

The SSF isolate obtained from common bean tissues was identified as *Sclerotinia sclerotiorum* based on ITS rDNA sequencing (482 bp) (GenBank accession number OR238909.1). In culture, the isolate exhibited morphological characteristics consistent with *S. sclerotiorum*, including fast-growing white mycelium with a cottony texture and the formation of dark, irregularly shaped sclerotia distributed over the colony surface (Fig. 1a).

Phylogenetic analysis of the ITS region, based on comparisons with reference sequences available in the NCBI database, showed that the SSF isolate clustered with other *S. sclerotiorum* sequences, further supporting its taxonomic identification (Fig. 1b). Phytopathogenicity was confirmed by sclerotial inoculation of healthy plants, which subsequently developed typical white mold symptoms, including chlorosis,

Fig. 1 Molecular and morphological characterization of the SSF isolate. **a** Colony morphology of *Sclerotinia sclerotiorum* isolate SSF on PDA. **b** Neighbor-joining phylogenetic tree based on ITS rDNA sequences. Bootstrap values (%) are shown at the nodes (1000 replicates). The triangle indicates the SSF isolate. Scale bar: substitutions per site



leaf lesions, and premature plant death (Supplementary Fig. S1). The bacterial isolates evaluated in this study were identified at the genus level as *Bacillus* spp. based on 16S rRNA gene sequence analysis (Table 1).

In vitro sclerotial germination and mycelial inhibition of *S. sclerotiorum* strain SSF

The *Bacillus* spp. strains showed significant antagonistic activity against *S. sclerotiorum* strain SSF across the in vitro assays performed (Table 2; Supplementary Table S1). In the dual-culture test, the reduction in mycelial growth of the phytopathogen ranged from 24.2% to 65.9%, with the highest inhibition observed for the BERA-I, RIZO-A, EVSA, and BEFA-II strains (Table 2; Supplementary Fig. S2).

The cell-free supernatant (CFS) of the bacterial cultures exhibited strong antifungal activity. Complete inhibition of mycelial growth was observed when *S. sclerotiorum* was inoculated onto media supplemented with CFS from strains BERA-I, RIZO-A, BERA-II, and RIZO-C.

In addition, bacterial isolates produced VOCs that inhibited phytopathogen growth by more than 40.2%, while VOCs emitted by BERA-I, RIZO-A, EVSA, and RIZO-H resulted in complete inhibition. Sclerotia exposed to *Bacillus* strains failed to germinate under the experimental conditions evaluated (Supplementary Fig. S3, Table 2).

Bean seeds germination enhancement, plant growth-promoting traits and hydrolytic enzymes production demonstrated by *Bacillus* spp.

Bean seed inoculation with the bacterial strains influenced germination rates, which ranged from 6.7 to 60%. This assay was conducted as an initial screening step to identify bacterial strains that could negatively affect seed germination prior to greenhouse experiments. The BEFA-I, BERA-II, and EVSA strains did not differ from the control, whereas the other strains significantly reduced germination, particularly BERA-I, which exhibited only 6.7% germinated seeds (Table 2). Based on this screening, BEFA-I, BERA-II, and EVSA were selected for subsequent greenhouse trials to avoid potential adverse effects on seed germination.

Five out of the nine isolates produced IAA, with isolates RIZO-A, EVSA, BERA-I, BEFA-II, and RIZO-H showing significantly higher values (Table 2, Supplementary Table S1). All isolates showed the capacity for siderophore synthesis, with values ranging from 27.5% (RIZO-H) to 70.5% (RIZO-C). Phosphate solubilization ability was confirmed in isolates BEFA-I, BEFA-II, BERA-II, RIZO-C, BACI-A, and RIZO-H, based on the formation of solubilization halos. All strains were positive for protease production, and seven showed cellulolytic activity. Similarly, isolates BEFA-I, BEFA-II, and BERA-II were positive for the production of both chitinase and glucanase on selective culture media (Table 2).

Table 2 Plant growth-promoting traits and hydrolytic enzymes produced by antagonistic bacterial strains of *Bacillus* spp., as well as the effects of inoculation of these isolates on the inhibition of mycelial growth of *S. sclerotiorum* strain SSF and on the germination of bean seeds

Strains	Plant growth promotion traits			Extracellular enzyme				% inhibition of mycelium growth			% Seed germination
	IAA (µg ml ⁻¹)	Sid	P solub	Cel	Prot	Chit	Gluc	DC	CFSs	VOCs	
RIZO-A	147.0±0.9 ^a	25.0±1.9 ^e	–	++	+++	–	–	56.3±1.1 ^b	100.0±0.0 ^a	100.0±0.0 ^a	26.7±6.7 ^{bc}
EVSA	128.2±8.5 ^b	35.0±3.3 ^{cd}	–	++	+++	–	–	53.2±1.3 ^{bc}	78.5±1.1 ^b	100.0±0.0 ^a	60.0±0.0 ^a
BERA-I	107.5±1.4 ^c	36.3±2.8 ^c	–	+++	+++	–	–	65.9±1.7 ^a	100.0±0.0 ^a	100.0±0.0 ^a	6.7±6.7 ^c
BEFA-II	93.9±0.9 ^d	31.9±3.6 ^{cde}	++	–	+++	+	++	49.0±1.8 ^c	43.2±1.5 ^c	60.1±4.0 ^c	13.3±6.7 ^c
RIZO-H	82.2±0.3 ^e	27.5±3.3 ^{de}	+++	+++	+++	–	–	25.0±2.4 ^e	27.1±1.3 ^d	100.0±0.0 ^a	46.7±6.7 ^{ab}
BEFA-I	0.0±0.0 ^f	49.1±2.8 ^b	+	–	++	++	+++	33.0±1.9 ^d	43.9±0.6 ^c	48.8±3.1 ^d	53.3±6.7 ^a
BERA-II	0.0±0.0 ^f	67.2±0.8 ^a	++	+	++	++	++	26.7±1.7 ^e	100.0±0.0 ^a	40.2±2.8 ^e	60.0±11.5 ^a
BACI-A	0.0±0.0 ^f	34.4±2.3 ^{cd}	+++	+++	+++	–	–	25.7±1.7 ^e	0.0±0.0 ^e	66.0±3.4 ^b	20.0±11.5 ^c
RIZO-C	0.0±0.0 ^f	70.5±1.3 ^a	+	+	+++	–	–	24.2±2.0 ^e	100.0±0.0 ^a	64.4±2.6 ^b	13.3±6.7 ^c
Control	–	–	–	–	–	–	–	–	–	–	53.3±6.7 ^a
ANOVA	F _{8,18} = 437.6, p < 0.001	F _{8,18} = 39.8, p < 0.001						F _{8,18} = 82.4, p < 0.001	F _{8,18} = 2352.5, p < 0.001	F _{8,18} = 608.2, p < 0.001	F _{9,20} = 7.9, p < 0.001

Means $\pm$ SE followed by different letters within the same column indicate significant differences according to Duncan's multiple range test ($p < 0.05$). IAA, indole-3-acetic acid; Sid, siderophore production; P solub, phosphate solubilization; Cel, cellulase; Prot, protease; Chit, chitinase; Gluc, glucanase; DC, dual culture; CFSs, cell-free supernatants; VOCs, volatile organic compounds. The symbols –, +, ++, and +

In vivo evaluation under greenhouse conditions

Across in vivo assays, no strain affected the germination of bean seeds. Plant survival was 100% in treatments in which the phytopathogen was absent. In contrast, inoculation with *S. sclerotiorum* and absence of bacterial isolates (Control+SSF) severely compromised the development of bean plants, resulting in high plant mortality until the end of the experiment (Supplementary Table S2). The presence of *Bacillus* spp. strains conferred protection, evidencing their ability to attenuate the effects of the phytopathogen.

Co-inoculation of all strains (co-culture) increased plant height and shoot dry weight under both conditions, compared to the control without the

phytopathogen (Control-SSF). The EVSA strain also enhanced plant growth by increasing both plant height and shoot dry weight, indicating that, in addition to its biocontrol activity, it functions as a plant growth promoter even in the absence of biotic stress (Fig. 2a, c).

In root tissues, the effects were even more significant (Fig. 2b and d). The EVSA strain increased root length by more than 61% and root dry weight by 7% relative to the negative control, maintaining this growth-promoting effect under both conditions. These results highlight the multifunctional role of EVSA, combining plant growth promotion with suppression of white mold. Co-inoculation treatments also enhanced root development. Although BEFA-I

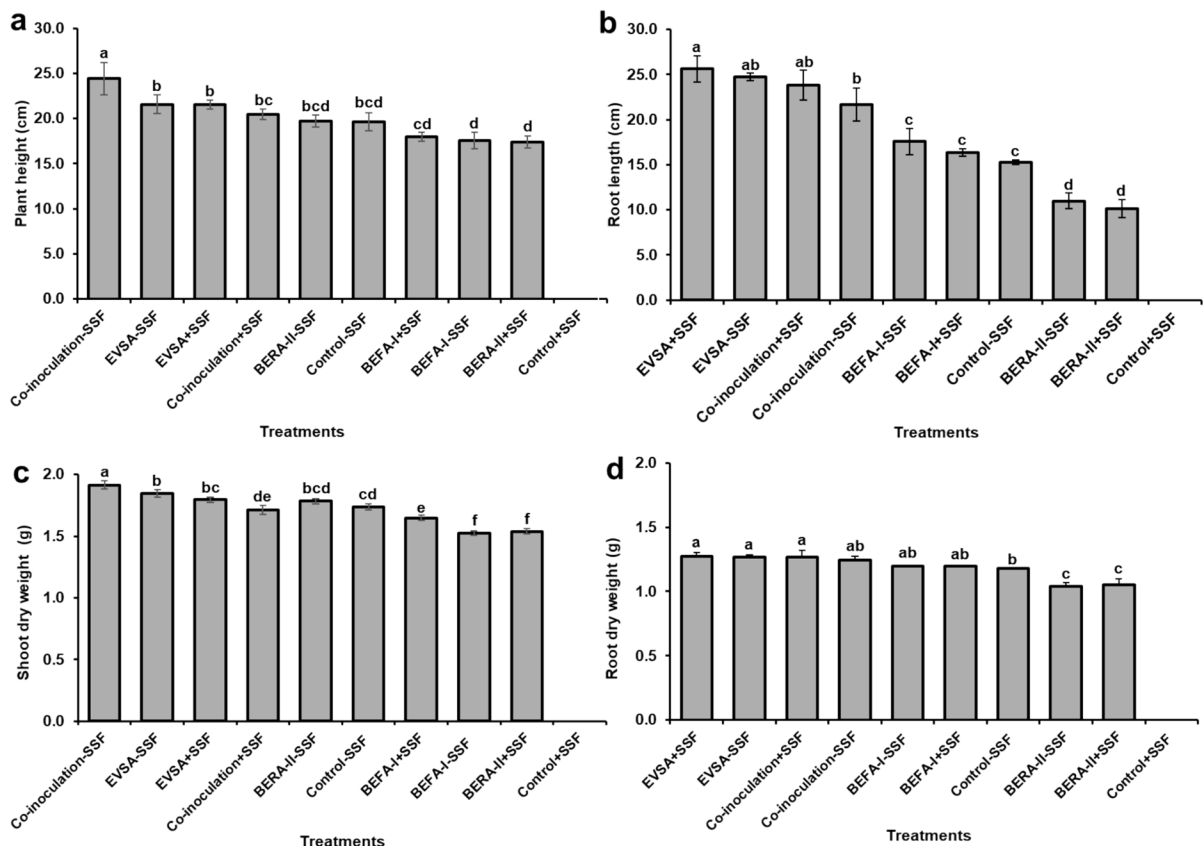


Fig. 2 Effect of inoculation with *Bacillus* spp. isolates on the growth of common bean plants derived from seeds grown in the presence (+SSF) and absence (-SSF) of *Sclerotinia sclerotiorum*. **a, c** Plant height and shoot dry weight; **b, d** root length and root dry weight. Values are expressed as mean $\pm$ SE. Means followed by different letters differ significantly according to Duncan's multiple range test ($p < 0.05$).

ANOVA results: plant height, $F_{9,30} = 55.63$, $p < 0.001$; shoot dry weight, $F_{9,30} = 526.74$, $p < 0.001$; root length, $F_{9,30} = 51.10$, $p < 0.001$; root dry weight, $F_{9,30} = 195.81$, $p < 0.001$. The Control + SSF treatment is shown on the horizontal axis but has no bar because all plants in this treatment died before the end of the experiment. Therefore, no growth measurements were obtained

and BERA-II did not significantly increase shoot or root growth, they effectively suppressed the disease, allowing plant development even in the presence of *S. sclerotiorum* strain SSF (Fig. 2a–d).

Discussion

White mold is a difficult-to-control disease due to the survival strategy of the phytopathogen. It forms a resting structure known as sclerotia, which can survive in the soil for up to ten years (Guilger-Casagrande et al. 2019). Conventional management relies on the use of chemical fungicides, which can lead to environmental pollution, human health risks, and selection of resistant pathogens (Maral-Gül and Eltem 2024).

A major challenge for modern and sustainable agriculture is to reduce or replace the use of chemical pesticides as the primary means of disease control. In this context, the interaction between microorganisms and plants is recognized as playing an important role in promoting plant growth and inhibiting the development of phytopathogenic microorganisms (Maral-Gül and Eltem 2024).

The *Bacillus* spp. strains evaluated in this study exhibited significant antifungal activity against *Sclerotinia sclerotiorum* strain SSF, as demonstrated across different in vitro antagonism assays. Mycelial growth inhibition of up to 65.9% was observed in dual-culture tests, indicating a strong antagonistic potential. In addition, assays using CFSs and VOCs revealed complete fungal growth inhibition for some strains, highlighting the diversity of antagonistic effects expressed by these bacteria. Additionally, all sclerotia exposed to *Bacillus* strains lost their germination capacity, reinforcing the potential of these bacteria to interfere with the survival and persistence of the phytopathogen. Similar inhibition levels against *S. sclerotiorum* have been reported for *Bacillus* spp. in previous studies, with rates ranging from 17.6 to 100.0% depending on the strains and experimental conditions (Sabaté et al. 2018; Ribeiro et al. 2021; Yaderets et al. 2021; Santos et al. 2023). Nevertheless, the specific molecular or biochemical mechanisms underlying these effects were not addressed in the present study and warrant further investigation.

Among the antagonistic activities evaluated, VOCs produced by the EVSA, RIZO-A, BERA-I, and RIZO-H strains were particularly effective,

resulting in complete suppression of *S. sclerotiorum* mycelial growth. VOCs represent a promising strategy for the biological control of white mold, as they can act at a distance and reach infection sites that are often inaccessible to conventional chemical treatments. Previous studies have shown that bacterial VOCs may exert distinct levels of antifungal activity, ranging from partial growth reduction to near-complete inhibition, and can induce morphological alterations in fungal hyphae and reproductive structures (Chaurasia et al. 2005; Chacón-Orozco et al. 2020).

We suggest that RIZO-A, BERA-I, RIZO-C, and BERA-II secrete high-efficiency antifungal metabolites in the culture medium. Through in vitro tests, CFS from bacterial cultures totally inhibited the development of *S. sclerotiorum*. These metabolites have not been characterized. However, it is known that members of the Bacillaceae produce several biologically active compounds, including cyclic lipopeptides, such as surfactin, iturin, and fengycin (Harwood et al. 2018; Kaspar et al. 2019; Villarreal-Delgado et al. 2021; Cheng et al. 2024; Ma et al. 2024) as well as polyene antibiotics (Yaderets et al. 2021). These substances have often been indicated as efficient broad-spectrum antibiotic compounds with antagonistic activity against different plant pathogens. Previous studies have indicated that the suppression of *S. sclerotiorum* by *Bacillus* species is mainly due to the production of pumilacidin, bacillibactin, bacillisin, and other antifungal compounds (Ribeiro et al. 2021; Santos et al. 2023).

Our strains secreted hydrolytic enzymes, especially BERA-II (cellulase, chitinase, glucanase, and protease). These enzymes participate in the degradation of the fungal cell wall. Proteases and cellulases have been related to the hydrolysis of glycosidic bonds in the polysaccharide cell wall of phytopathogens (Steindorff et al. 2014). Bacterial chitinases cause damage to the mycelium of fungal pathogens since they are involved in the fungal cell wall degradation (Steindorff et al. 2014).

Additionally, bacterial chitinases cause damage to the mycelium of fungal pathogens (Zalila-Kolsi et al. 2016) and inhibit spore germination and germ tube elongation, demonstrating antagonistic effects on fungi (Li et al. 2016). All evaluated strains synthesized siderophores that are compounds capable of inhibiting competing microbial pathogens. The

siderophore production is also considered a direct promoter of plant growth (Kumar et al. 2022).

It was found that suppression of sclerotia germination of *S. sclerotiorum* is associated with bacterial growth in the treated sclerotia, causing inhibition of mycelial growth of the fungus. A similar result was obtained by Abdeljalil et al. (2016), in which, bacterial strains absolutely inhibited the development of sclerotia of *S. sclerotiorum*. The results corroborate those of Gebily et al. (2021) that confirmed the reduction of viability and germination of sclerotia when immersed in *Streptomyces* spp. suspension.

The inhibition of sclerotia germination promoted by bacterial action means less source of disease inoculum and consequently less aggressiveness of white mold at field levels, which can interrupt the reproductive cycle of white mold (Chacón-Orozco et al. 2020; Gebily et al. 2021). Destroying sclerotia, preventing germination or limiting the formation of this resistance structure, represents the basis for successful control of *S. sclerotiorum*, especially considering that the chemical fungicides often used to control white mold (e.g., fluazinam fungicide) have become ineffective due to circumstances associated with the production of sclerotia in the fields (Sabaté et al. 2018).

The antagonistic activity observed in vitro by the EVSA, BEFA-I and BERA-II strains against *S. sclerotiorum* strain SSF was also corroborated by the assays performed in the greenhouse. Inoculation of *S. sclerotiorum* strain SSF caused the death of all control plants of common bean (Fig. 2). On the other hand, plants that simultaneously received phytopathogen and *Bacillus* isolates (EVSA, BEFA-I and BERA-II) did not show symptoms of white mold. These results support the ability of the strains to inhibit the growth and infection of *S. sclerotiorum* strain SSF in vivo, preventing white mold symptoms in plants co-inoculated with both the phytopathogen and *Bacillus* strains. This protective effect may be related to the production capacity of hydrolytic enzymes, siderophores, and antifungal metabolic compounds produced by the *Bacillus* under study, which promoted a greater capacity to withstand adversity and combat the pathogen.

The increase in dry matter observed in the roots and aerial parts of the plants in the experiments with or without the phytopathogen suggests that EVSA can act as a growth-promoting agent. The strain was isolated from the rhizosphere of bean plants (Table 1).

It is widely recognized that diverse rhizosphere bacteria can improve plant growth and health, acting as plant growth-promoting rhizobacteria (PGPR) (Haas and Défago 2005). These bacteria promote plant growth directly by producing IAA (Patten and Glick 2002), root hormone levels regulation (Glick 2014), improved nutrient acquisition, e.g., through phosphate solubilization and nitrogen fixation (Souza et al. 2015). In addition, other processes such as ACC deaminase activity, induction of systemic resistance, modulation of plant gene expression, emission of volatile organic compounds (VOCs), and the suppression of phytopathogens mediated by the production of antimicrobial compounds also contribute to plant growth promotion and disease control (Mhlongo et al. 2022; Zhu et al. 2022; Dutilloy et al. 2024; Alonazi et al. 2025; Gayithri et al. 2026).

The use of *Bacillus* strains as BCAs to inhibit *S. sclerotiorum* has been extensively studied in other crops. For example, Zhang and Xue (2010) observed a reduction in the severity of Sclerotinia stem rot by 60 to 90% when soybean plants were treated with different concentrations of *Bacillus subtilis* SB24 cell suspension. Ma et al. (2024) showed that *B. cereus* HF10 significantly reduced the incidence of Sclerotinia disease in treated rapeseed. Fernando et al. (2007) showed that *B. amyloliquefaciens* reduced the incidence of *S. sclerotiorum* by 10 and 30% in pulverized canola petals.

Most studies have evaluated the antagonistic potential of *Bacillus* species against *Sclerotinia sclerotiorum* primarily through in vitro antibiosis assays (Torres et al. 2017; Sabaté et al. 2018; Villarreal-Delgado et al. 2021). In contrast, the present study shows that the EVSA strain displays dual-functional performance, combining effective suppression of white mold with the promotion of common bean plant growth. The plant growth-promoting effect may result from both indirect benefits associated with pathogen suppression and from traits commonly attributed to *Bacillus* spp., such as phytohormone production and improved nutrient availability. Accordingly, EVSA represents a promising candidate for the biological control of *S. sclerotiorum*.

Although previous studies have demonstrated that the combined application of multiple biological control agents (BCAs) can enhance disease suppression (Guetsky et al. 2001; Jetiyanon and Kloepper 2002). Our results indicate that EVSA alone was sufficient to

prevent infection and promote plant growth, particularly in root tissues (Fig. 2).

Based on 16S rRNA gene sequencing, the EVSA isolate was identified at the genus level as *Bacillus* sp. (Table 1). Because the 16S rRNA gene does not provide sufficient resolution for reliable species-level discrimination within the genus *Bacillus*, species assignment was not attempted in this study, and additional molecular approaches would be required for precise taxonomic identification. Nevertheless, members of the genus *Bacillus* have been extensively reported as effective biological control agents and plant growth-promoting bacteria in agricultural systems, including against phytopathogenic fungi such as *S. sclerotiorum* (Chowdhury et al. 2015; Torres et al. 2017; Yang et al. 2024). In this context, the functional performance exhibited by the EVSA isolate is consistent with the well-documented biocontrol and plant growth-promoting potential of *Bacillus* spp., irrespective of its precise taxonomic position.

Therefore, the use of biological products for pest and disease control and as growth promoters is one of the fastest growing segments in modern agriculture. However, their effective use requires adequate crop monitoring and ideal application conditions, thereby allowing producers to combine control efficiency, pest selectivity, and absence of toxic effects on the environment. Likewise, this approach enables more sustainable agriculture (Shiomi et al. 2017). The use of microorganisms that can provide beneficial effects on plant growth, as well as assist in the control of phytopathogens is an excellent strategy for a more sustainable agriculture. The tested *Bacillus* spp. exhibited promising antifungal and plant growth-promoting traits, supporting their potential for biotechnological applications in sustainable agriculture.

The *Bacillus* strains tested showed satisfactory results for the in vitro control of *S. sclerotiorum* strain SSF, the causal agent of white mold in common beans. The combination of pathogen suppression and growth promotion highlights EVSA as a promising candidate for the development of bioinoculants in the sustainable management of white mold in common bean. Future evaluations under field conditions and the characterization of the bioactive compounds will be essential to confirm their efficacy and stability.

Acknowledgements The authors would like to thank the Federal Institute of Education, Science and Technology of

Mato Grosso (IFMT – Lucas do Rio Verde Campus), Brazil, for its technical support, infrastructure and funding through its own institutional resources for the execution of this study.

Funding The Article Processing Charge (APC) for the publication of this research was funded by the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior - Brasil (CAPES) (ROR identifier: 00x0ma614).

Declarations

Conflict of interest The authors declare that they have no conflicts of interest regarding the publication of this article.

Research involving human and animal participants This study did not involve human participants or vertebrate animals. All experimental procedures involving microorganisms and plants were conducted in accordance with institutional biosafety and research ethics guidelines. The assays were performed under controlled laboratory and greenhouse conditions at the Federal Institute of Education, Science and Technology of Mato Grosso – Advanced Campus Lucas do Rio Verde (IFMT – Advanced Campus Lucas do Rio Verde), Brazil, following the standards established by the Brazilian National Technical Commission on Biosafety (CTNBio, Resolution No. 32/2013).

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References

- Abdeljalil N, Vallance J, Rey P, Daami-Remadi M (2016) Bio-suppression of *Sclerotinia* stem rot of tomato and biostimulation of plant growth using tomato-associated rhizobacteria. *J Plant Pathol Microbiol* 7:214
- Abdelrhim AS, Hemeda NF, Mwaheb MA, Omar MOA, Dawood MFA (2024) The role of *Trichoderma koningii* and *Trichoderma harzianum* in mitigating the combined stresses motivated by *Sclerotinia sclerotiorum* and salinity in common bean (*Phaseolus vulgaris*). *Plant Stress* 11:1010–1016
- Almeida F, Rodrigues ML, Coelho C (2019) The still underestimated problem of fungal diseases worldwide. *Front Microbiol* 10:214
- Alonazi MA, Alwathnani HA, AL-Barakah FNI, Alotaibi F (2025) Native plant growth-promoting rhizobacteria

- containing acc deaminase promote plant growth and alleviate salinity and heat stress in maize (*Zea mays* L.) plants in Saudi Arabia. *Plants* 14:1107
- Aulakh SK, Buttar DS, Choudhary AA, Brar GS (2025) *Bacillus siamensis* strain B9 suppresses *Sclerotinia* stem rot in Egyptian clover. *BioControl* 70:391–404
- Cao S, Jiang B, Yang G, Pan G, Pan Y, Chen F, Gao Z, Dai Y (2023) Isolation and evaluation of *Bacillus subtilis* RSS-1 as a potential biocontrol agent against *Sclerotinia sclerotiorum* on oilseed rape. *Eur J Plant Pathol* 166:9–25
- Chacón-Orozco JG, Bueno CJ, Shapiro-Ilan DI, Hazir S, Leite LG, Harakava R (2020) Antifungal activity of *Xenorhabdus* spp. and *Photorhabdus* spp. against the soybean pathogen *Sclerotinia sclerotiorum*. *Sci Rep* 10:20649
- Chaurasia B, Pandey A, Palni LMS, Trivedi P, Kumar B, Colvin N (2005) Diffusible and volatile compounds produced by an antagonistic *Bacillus subtilis* strain cause structural deformations in pathogenic fungi in vitro. *Microbiol Res* 160:75–81
- Cheng Y, Lou H, He H, He X, Wang Z, Gao X, Liu J (2024) Genomic and biological control of *Sclerotinia sclerotiorum* using an extracellular extract from *Bacillus velezensis* 20507. *Front Microbiol* 15:1385067
- Chowdhury SP, Hartmann A, Gao X, Borriss R (2015) Biocontrol mechanism by root-associated *Bacillus amyloliquefaciens* FZB42—a review. *Front Microbiol* 6:780
- Dutilloy E, Arias AA, Richet N, Guise JF, Duban M, Leclerc V, Selim S, Jacques P, Jacquard C, Clément C, Ait Barka E, Esmael Q (2024) *Bacillus velezensis* BE2 controls wheat and barley diseases by direct antagonism and induced systemic resistance. *Appl Microbiol Biotechnol* 108:64
- FAO (2024) FAOSTAT – Food and agriculture data. Food and Agriculture Organization of the United Nations. <https://www.fao.org/faostat>
- Fernando WGD, Nakkeeran S, Zhang Y, Savchuk S (2007) Biological control of *Sclerotinia sclerotiorum* (Lib.) de Bary by *Pseudomonas* and *Bacillus* species on canola petals. *Crop Prot* 26:100–107
- Fiddaman PJ, O'Neill TM, Rossall S (2000) Screening of bacteria for suppression of *Botrytis cinerea* and *Rhizoctonia solani* on lettuce (*Lactuca sativa*) using leaf-disc bioassays. *Ann Appl Biol* 137:223–235
- Fu M, Qu Z, Pierre-Pierre N, Jiang D, Souza FL, Miklas PN, Porter LD, Vandemark GJ, Chen W (2023) Exploring the mycovirus *Sclerotinia sclerotiorum* hypovirulence-associated DNA virus 1 as a biocontrol agent of white mold caused by *Sclerotinia sclerotiorum*. *Plant Dis* 108:624–634
- Gayithri M, Singh S, Pradhan B, Boorla V, Chand S (2026) Multifunctional roles of *Bacillus* spp. in sustainable agriculture: advances in biocontrol, omics, and ecological applications. *Microb Ecol* 89:55
- Gebily DAS, Ghanem GAM, Ragab MM, Ali AM, Soliman NEK, Abd El-Moity TH (2021) Characterization and potential antifungal activities of three *Streptomyces* spp. as biocontrol agents against *Sclerotinia sclerotiorum* (Lib.) de Bary infecting green bean. *Egypt J Biol Pest Control* 31:1–15
- Glick BR (2014) Bacteria with ACC deaminase can promote plant growth and help to feed the world. *Microbiol Res* 169:30–39
- Gordon SA, Weber RP (1951) Colorimetric estimation of indoleacetic acid. *Plant Physiol* 26:192–195
- Guetsky R, Shtienberg D, Elad Y, Dinor A (2001) Combining biocontrol agents to reduce the variability of biological control. *Phytopathology* 91:621–627
- Guilger-Casagrande M, Germano-Costa T, Pasquoto-Stigliani T, Fraceto LF, Lima R (2019) Biosynthesis of silver nanoparticles employing *Trichoderma harzianum* with enzymatic stimulation for control of *Sclerotinia sclerotiorum*. *Sci Rep* 9:14351
- Haas D, Défago G (2005) Biological control of soil-borne pathogens by fluorescent pseudomonads. *Nat Rev Microbiol* 3:307–319
- Han VC, Michael PJ, Swift B, Bennett SJ (2023) Biological control of *Sclerotinia sclerotiorum*: modes of action of biocontrol agents, soil organic amendments, and soil microbiome manipulation. *Biol Control* 186:105346
- Harwood CR, Mouillon JM, Pohl S, Arnau J (2018) Secondary metabolite production and safety of industrially important members of the *Bacillus subtilis* group. *FEMS Microbiol Rev* 42:721–738
- Jetiyanon K, Kloepper JW (2002) Mixtures of plant growth-promoting rhizobacteria for induction of systemic resistance against multiple plant diseases. *Biol Control* 24:285–291
- Kaspar F, Neubauer P, Gimpel M (2019) Bioactive secondary metabolites from *Bacillus subtilis*: a comprehensive review. *J Nat Prod* 82:2038–2053
- Kumar S, Diksha SSS, Kumar R (2022) Biofertilizers: an ecofriendly technology for nutrient recycling and environmental sustainability. *Curr Res Microb Sci* 3:100094
- Lehner MS, Silva RA, Paula Júnior TJ, Carneiro JES, Mizubuti ESG (2019) The population of *Sclerotinia sclerotiorum* affecting common bean in Brazil is structured by mycelial compatibility groups. *Trop Plant Pathol* 44:41–52
- Li X, Zhang Y, Wei Z, Guan Z, Cai Y, Liao X (2016) Antifungal activity of isolated *Bacillus amyloliquefaciens* SYBC H47 for the biocontrol of peach gummosis. *PLoS ONE* 11(9):e0162125
- Ma W, Ding J, Jia Q, Li Q, Jiao S, Guo X, Fan C, Chen Y, Hu Z (2024) A novel strain of *Bacillus cereus* with strong antagonistic effect specific to *Sclerotinia* and its genomic and transcriptomic analysis. *Microorganisms* 12:611
- Maral-Gül D, Eltem R (2024) Evaluation of *Bacillus* isolates as biological control agents against soilborne phytopathogenic fungi. *Int Microbiol* 28:75–89
- Mhlongo MI, Piater LA, Dubery IA (2022) Profiling of volatile organic compounds from four plant growth-promoting rhizobacteria by SPME–GC–MS: a metabolomics study. *Metabolites* 12:763
- Miklas PN, Porter LD, Kelly JD, Myers JR (2013) Characterization of white mold disease avoidance in common bean. *Eur J Plant Pathol* 135:525–543
- Montalvão SCL, Marques E, Martins I, da Silva JP, de Mello SCM (2023) Suppression of the phytopathogens *Sclerotinia sclerotiorum* and *Sclerotium rolfsii* by *Trichoderma* spp. *Biologia* 78:2941–2952
- Nagpure A, Choudhary B, Gupta RK (2014) Mycolytic enzymes produced by *Streptomyces violaceusniger* and

- their role in antagonism towards wood-rotting fungi. *J Basic Microbiol* 54:397–407
- Pandit MA, Kumar J, Gulati S, Bhandari N, Mehta P, Katyal R, Rawat CD, Mishra V, Kaur J (2022) Major biological control strategies for plant pathogens. *Pathogens* 11:273
- Patten CL, Glick BR (2002) Role of *Pseudomonasputida* indoleacetic acid in development of host plant root system. *Appl Environ Microbiol* 68:3795–3801
- R Core Team (2025) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <https://www.r-project.org/>
- Rey MS, Limairo NB, Santos J, Pierobom CR (2009) Seed-to-seedling transmission of *Colletotrichum lindemuthianum* in common bean (*Phaseolus vulgaris*). *Arq Inst Biol* 76:465–470
- Ribeiro IDA, Bach E, da Silva Moreira F, Müller AR, Rangel CP, Wilhelm CM, Barth AL, Passaglia LMP (2021) Antifungal potential against *Sclerotinia sclerotiorum* and plant growth-promoting abilities of *Bacillus* isolates from canola roots. *Microbiol Res* 248:126754
- Sabaté DC, Brandan CP, Petroselli G, Erra-Balsells R, Audisio MC (2018) Biocontrol of *Sclerotinia sclerotiorum* (Lib.) de Bary on common bean by native lipopeptide-producer *Bacillus* strains. *Microbiol Res* 211:21–30
- Saharan GS, Mehta N (2008) *Sclerotinia* diseases of crop plants: biology, ecology and disease management. Springer, Berlin
- Santos JB, Cruz JO, Geraldo LC, Dias EG, Queiroz PRM, Monnerat RG, Borges M, Blassioli-Moraes MC, Blum LEB (2023) Detection and evaluation of volatile and non-volatile antifungal compounds produced by *Bacillus* spp. strains. *Microbiol Res* 275:127465
- Savary S, Willocquet L, Pethybridge SJ, Esker P, McRoberts N, Nelson A (2019) The global burden of pathogens and pests on major food crops. *Nat Ecol Evol* 3:430–439
- Shi Y, Xie H, Cao L, Zhang R, Xu Z, Wang Z, Deng Z (2017) Effects of Cd- and Pb-resistant endophytic fungi on growth and phytoextraction of *Brassica napus* in metal-contaminated soils. *Environ Sci Pollut Res Int* 24:417–426
- Shiomi HF, Ferreira MVR, Melo IS (2017) Bioprospecting of bacterial isolates for the biological control of white mold in soybean. *Sci Electron Arch* 10:56–63
- Singh SP, Schwartz HF (2010) Breeding common bean for resistance to diseases: a review. *Crop Sci* 50:2199–2223
- Souza R, Ambrosini A, Passaglia LMP (2015) Plant growth-promoting bacteria as inoculants in agricultural soils. *Genet Mol Biol* 38:401–419
- Steindorff AS, Ramada MH, Coelho AS, Miller RN, Pappas GJ, Ulhoa CJ, Noronha EF (2014) Identification of mycoparasitism-related genes against the phytopathogen *Sclerotinia sclerotiorum* through transcriptome and expression profile analysis in *Trichoderma harzianum*. *BMC Genomics* 15:204
- Torres MJ, Pérez Brandan C, Sabaté DC, Petroselli G, Erra-Balsells R, Audisio MC (2017) Biological activity of the lipopeptide-producing *Bacillus amyloliquefaciens* PGPBacCA1 on common bean *Phaseolus vulgaris* L. pathogens. *Biol Control* 105:93–99
- Triantafyllou A, Kamou N, Papadopoulou A, Leontidou K, Melidou I, Karamanoli K (2023) Evaluation of the biocontrol potential of PGPB strains isolated from drought-tolerant tomatoes against fungal pathogens. *J Plant Pathol* 105:1013–1029
- Vero S, Garmendia G, Allori E, Sanz JM, Gonda M, Alconada T, Cavello I, Dib JR, Diaz MA, Nally C, Pimenta RS, da Silva JFM, Vargas M, Zaccari F, Wisniewski M (2023) Microbial biopesticides: diversity, scope, and mechanisms involved in plant disease control. *Diversity* 15:457
- Villarreal-Delgado MF, Parra-Cota FI, Cira-Chávez LA, Estrada-Alvarado MI, de los Santos-Villalobos S (2021) *Bacillus* sp. FSQ1: a promising biological control agent against *Sclerotinia sclerotiorum*, the causal agent of white mold in common bean (*Phaseolus vulgaris* L.). *Biol Bull* 48:729–739
- Wattiau P, Renard ME, Ledent P, Debois V, Blackman G, Agathos S (2001) A PCR test to identify *Bacillus subtilis* and closely related species and its application to monitoring wastewater biotreatment. *Appl Microbiol Biotechnol* 56:816–819
- White TJ, Bruns T, Lee S, Taylor J (1990) Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenetics. In: Innis MA, Gelfand DH, Sninsky JJ, White TJ (eds) PCR protocols. Academic Press, New York, pp 315–322
- Yaderets VV, Karpova NV, Glagoleva EV, Ovchinnikov AI, Petrova KS, Dzhavakhiya VV (2021) Inhibition of growth and development of *Sclerotinia sclerotiorum* (Lib.) de Bary by combining azoxystrobin, *Penicillium chrysogenum* VKM F-4876D, and *Bacillus* strains. *Agronomy* 11:2520
- Yang K, Dai X, Maitikadir Z, Zhang H, Hao H, Yan C (2024) Comparative genome analysis of endophytic *Bacillus amyloliquefaciens* MR4: a potential biocontrol agent isolated from wild medicinal plant root tissue. *J Appl Genet* 65:907–923
- Zalila-Kolsi I, Ben Mahmoud A, Ali H, Sellami S, Nasfi Z, Tounsi S, Jamoussi K (2016) Antagonistic effects of *Bacillus* spp. strains against *Fusarium graminearum* for protection of durum wheat (*Triticum turgidum* L. subsp. *durum*). *Microbiol Res* 192:148–158
- Zizzerini A, Tosi L, Rossi J (1987) Antagonistic effects of *Bacillus* spp. on *Sclerotinia sclerotiorum* sclerotia. *Phytopathol Mediterr* 26:185–187
- Zhang X, Xue AG (2010) Biological control of *Sclerotinia sclerotiorum* on soybean by *Bacillus subtilis* SB24. *Crop Prot* 29:1220–1225
- Zhang H, Xie J, Fu Y, Cheng J, Qu Z, Zhao Z, Cheng S, Chen T, Li B, Wang Q, Liu X, Tian B, Collinge DB, Jiang D (2020) A 2-kb mycovirus converts a pathogenic fungus into a beneficial endophyte for *Brassica* protection and yield enhancement. *Mol Plant* 13:1420–1433
- Zhu L, Huang J, Lu X, Zhou C (2022) Development of plant systemic resistance by beneficial rhizobacteria: recognition, initiation, elicitation and regulation. *Front Plant Sci* 13:952397
- Zia MA, Riaz R, Batool A, Yasmin H, Nosheen A, Naz R, Hassan MN (2021) Glucanolytic rhizobacteria associated with wheat–maize cropping system suppress *Fusarium* wilt of tomato (*Lycopersicon esculentum* L.). *Sci Hortic* 287:110275

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