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Antifungal activity of *Streptomyces* sp. CACIS-2.15CA, as a potential biocontrol agent, against some soil-borne fungi

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Abstract

Background: Soil biocontrol streptomycetes are considered as ecofriendly agents, which inhibit the growth of multiple fungal pathogens. In addition, the majority of species are considered non-plant pathogenic, and they are beneficial to plant growth and soil salinity because they produce broad bioactive secondary metabolites, i.e., polyenes, volatile organic compounds, fatty acids, plant growth regulators, and diversity of extracellular hydrolytic enzymes. Therefore, this study aimed to select, characterize, and perform the molecular identification of a streptomycete isolate by in vitro antagonistic activity against some soil-borne fungi.

Results: Twenty-five isolates obtained from the Germplasm Bank of Actinomycetes were tested in dual confrontation assay to determine their inhibitory activity against the growth of *Colletotrichum musae*. In addition, 22 isolates (88%) inhibited the mycelial growth of *C. musae*, particularly the isolate CACIS-2.15CA, which showed the highest antagonistic activity. Furthermore, an antifungal evaluation using additional fungal species was performed. The CACIS-2.15CA isolate exhibited a high inhibitory activity against *Phytophthora capsici*, *C. musae*, *Botrytis cinerea*, *Lasiodiplodia* sp., *Sclerotinia* sp., *Fusarium oxysporum*, *F. oxysporum* f sp. *lycopersici Fusarium* sp., and *Aspergillus* sp. at percentages ranging from 7.3 to 61.2%. The isolate was characterized by its morphology and physiology and by the presence of genetic biosynthetic clusters for non-ribosomal polyketide synthases and polyketide synthases type I and II using polymerase chain reaction assays; the selected strain harbored genes for NRPS and PKS type I clusters. Moreover, the isolate was molecularly identified as a member of *Streptomyces* genus based on the partial sequence of the 16S rRNA gene. Based on its morphological and physiological characteristics, the CACIS-2.15CA isolate belongs to *Streptomyces* genus.

Conclusion: Given the aforementioned characteristics, *Streptomyces* sp. CACIS-2.15CA can be a potential biocontrol agent against various fungal strains.

Keywords: *Streptomyces*, Phytopathogenic fungi, Biocontrol agent, Antagonistic activity

Background

Globally, the production of field crops was affected by plant diseases, in which fungi and oomycetes attribute to 70 to 80% of product losses and reduced quality of food products (Yang et al. 2019).

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The fungal group is a diverse group of microorganisms in nature, and it is a principal group with more than 8000 plant pathogenic species (Shuping and Eloff 2017). A diversity of fungal species is responsible for diseases on roots, stems, leaves, flowers, fruits, and seeds. *Fusarium oxysporum* is an important phytopathogen, and it is the causal agent of plant wilt diseases (Dean et al. 2012). Anthracnose disease caused by the genus *Colletotrichum* is affecting the leaves, flowers, and fruits of plants. In addition, *Colletotrichum musae* is the causal agent of anthracnose in banana fruit (de Silva et al. 2017). *Botrytis*

cinerea is a fungal pathogen responsible for gray mold disease that has a broad host plant range, including many important crop species (De Angelis et al. 2022). *Lasiodiplodia theobromae* is the causal agent associated with dieback and fruit rot in mango, grapes, papaya, and citrus fruits (Picos-Muñoz et al. 2015). *Aspergillus* species are responsible for various plant diseases, which primarily cause postharvest diseases on fruits, thereby affecting quality and nutrient content; some other species are producers of aflatoxins (Perrone et al. 2007).

Traditionally, the control of fungal phytopathogens is carried out with chemical pesticides, which could represent serious risks to the environment and human health (Law et al. 2017). Thus, the use of biocontrol agents (BCAs) has emerged as a safe alternative to chemical pesticides (Evangelista-Martinez 2014). BCAs are antagonistic microorganisms than can inhibit or regulate the population of pathogens by using some mechanisms, including the competition for nutrients or space, parasitism, production of secondary metabolites (SeM), secretion of lytic enzymes, or induction of a resistance mechanism in host plants (Thambugala et al. 2020). *Trichoderma*, Actinobacteria, *Pseudomonas*, and *Bacillus* species have been extensively investigated as potential BCAs to control plant diseases (Thambugala et al. 2020). Among these antagonists in particular, *Streptomyces* species could be used as potential biopesticides to control phytopathogenic fungi and plant growth-promoting activity (Nonthakaew et al. 2022).

Streptomyces is the largest genus of Actinobacteria with more than 700 species of Gram-positive, spore-producing, and filamentous bacteria (Law et al. 2017). The genus has been recognized by the production of a wide variety of SeM, many of which have an inhibitory activity against bacteria, fungi, parasites, and virus, and some of which are recognized as antitumor and cytotoxic metabolites (Qi et al. 2019). Moreover, the members of this genus have an exceptional repertoire of extracellular enzymes, including lipases, proteases, amylases, chitinases, and β-1,3-glucanases, which play an important role in inhibiting the growth of phytopathogenic fungi (Pérez-Rojas et al. 2015). This study aimed to evaluate the antagonistic activity of streptomycetes obtained from the Germplasm Bank of Actinomycetes against some fungal strains.

Methods

Microorganisms used and culture conditions

Twenty-five streptomycetes preserved at the Actinomycetes Germplasm Bank from CIATEJ, which were originally isolated from bulk and rhizosphere samples of soils from natural protected areas in México, were selected. The commercial strain *Streptomyces lydicus* WYEC108 was used as a positive control. All the strains were cultured on International *Streptomyces* Project media No. 2 (ISP-2) at 29 °C for 14 to 21 days. Streptomycete spore suspensions (SS) were adjusted at 0.5 McFarland standard (10^6 spores/ml).

Phytopathogenic fungi

The following fungal strains were used for confrontation assays: *Colletotrichum musae* N1 and *C. musae* C6, both isolated from banana fruit; *Lasiodiplodia* sp. LA isolated from coconut palm; *Phytophthora capsici* isolated from serrano chili plant; *Sclerotinia* sp. S1 isolated from *Aloe vera*; *Fusarium oxysporum* F4 isolated from *Agave tequilana*; *F. oxysporum* f sp. *lycopersici* F6, isolated from tomato plant; *Fusarium oxysporum* F7 isolated from gladiolus corms; *Botrytis cinerea* B1 isolated from tomato fruit; *Lasiodiplodia theobromae* Rh2 isolated from Ataulfo mango fruit; *Aspergillus* sp. A3 isolated from sweet-orange fruit (Evangelista-Martínez et al. 2022). The strains were cultured on potato dextrose agar (PDA) at 29 °C for 10 days.

Primary screening for antagonistic streptomycetes

The selection of streptomycete strain with antagonistic activity against fungi was evaluated by dual confrontation assays from twenty-five streptomycetes (Evangelista-Martínez 2014). *S. lydicus* WYEC 108, the strain of the biological fungicide product Actinovate®, was used to compare the antagonism potential of the streptomycete strains. In brief, the confrontation assay consisted in the simultaneous inoculation at opposite sites onto ISP2 agar media of 2 µl of a streptomycete SS and 2 µl of the SS of *S. lydicus*. This process was repeated with all streptomycete strains. Thereafter, Petri plates were kept at 29 °C for 3 days. Then, agar plugs (9 mm in diameter) with mycelium of *C. musae* C6 from a recent PDA Petri plate culture were placed at the center of each plate. All the plates were maintained at 29 °C for additional 10 days. All experiments were performed in duplicate using plates inoculated only with *C. musae* as growth control. Fungal growth was measured using a caliper. The percentage of inhibition (PI) was calculated using the following formula: $\mathrm{PI}\ (\%) = \mathrm{FR} - \mathrm{AR}/\mathrm{FR} \times 100$, where FR represents the radial growth (mm) of fungi of a control culture and AR represents the radial growth (mm) of fungi in the direction of the tested streptomycete (Evangelista-Martínez et al. 2020). The isolate with the highest PI value was selected for further evaluation.

Antifungal activity of the CACIS-2.15CA isolate

The antifungal activity of the CACIS-2.15CA isolate was evaluated on PDA plates by dual confrontation assay against 10 fungal strains. An aliquot (3 µl) of SS isolates was deposited 1.0 cm from the edge of the plate. On the

opposite side of the same plate, 3 µl of SS of *S. lydicus* was inoculated. The Petri plates were maintained at 29 °C for 3 days. Thereafter, agar plugs of 9 mm diameter covered with actively growing fungal mycelium of the pathogens were transferred onto the center of each plate and incubated at 29 °C for additional 7–10 days, until the fungal control cultures reach the border of the control plate. Control cultures containing the fungus alone were used to compare the inhibition of fungal growth. All tests were conducted in triplicate. The PI was determined as previously described (Evangelista-Martínez et al. 2020).

Morphological and physiological characterization of CACIS-2.15CA

The isolate was grown on different culture media for 14 days to characterize its morphology such as aerial and substrate mycelia, soluble pigment, and spore production (Shirling and Gottlieb 1966). The morphology of the spore mass was observed by scanning electron microscopy (Evangelista-Martínez et al. 2020). Moreover, the samples were analyzed by using an electronic microscope EVO-50 (Carl Zeiss) at the Science Faculty from the Autonomous University of Querétaro, México.

Carbon utilization was determined using the Biolog FF Microplate™ (Biolog Inc., USA) system, following the manufacturer's instructions. In addition, antibiotic susceptibility testing was performed by the disk diffusion assay using the commercial multidisc PT-34 Multibac I.D. (Investigación Diagnostica), as described by the Clinical and Laboratory Standards Institute (CLSI 2011). All tests were performed in triplicate.

Molecular identification and phylogenetic analysis of the CACIS-2.15CA isolate

DNA purification was performed as described by Evangelista-Martínez (2014) using the GenElute Bacteria genomic DNA kit (Invitrogen). Purified DNA was used as a template to amplify the 16S rRNA gene by polymerase chain reaction (PCR). The amplification was performed using GoTaq DNA polymerase (Promega) and universal primers fD1 (5′-CCGAATTCGTCGACAACAGAG TTTGATCCTGGCTCAG-3′) and rD1 (5′-CCCGGG ATCCAAGCTTAAGGAGGTGATCCAGCC-3′) (Weisburg et al. 1991). The amplified PCR product was purified using the PureLink kit (Invitrogen) and sequenced at Macrogen Inc., Seoul, Korea. The sequence was compared in BLASTn (https://blast.ncbi.nlm.nih.gov/Blast.cgi) against the nr database available on the NCBI Web site. Homologous sequences were retrieved and used for multiple alignments with Clustal. A phylogenetic tree was constructed using the neighbor-joining algorithm approach in MEGAX (Kumar et al. 2018).

Screening of SeM genes

The identified *Streptomyces* sp. CACIS-2.15CA was screened to detect gene clusters encoding for non-ribosomal peptide synthetases (NRPS) and polyketide synthase (PKS) types I and II. Detection was performed by PCR using GoTaq DNA polymerase (Promega) and degenerate primers K1F (5′-TSAAGTCSAACATCCGBCA-3′) and M6R (5′-CGCAGGTTSCSG TACCAGTA-3′) for the detection of NRPS genes and A3F (5′-GCSTACSYSAT-STACACSTCSGG-3′) and A7R (5′-SASGTCVCCS-GTSCGGTAS-3′) for the detection of PKS-type cluster genes (Ayuso-Sacido and Genilloud, 2005). In addition, the detection of the PKS II gene was performed using the primers KSα (5′-TSGRCTACRTCAACGGSCACGG-3′) and KSβ (5′-TACSAGTCSWTCGCCTGGTTC-3′) (González et al. 2005). Moreover, amplified loci were analyzed by 1.5% agarose gel electrophoresis and stained with SyBR safe (Invitrogen) using a GelDoc EZ analyzer (Bio-Rad, CA, USA).

Statistical analysis

Antifungal activity was expressed as mean ± standard deviation. Means were compared using a one-way analysis of variance, followed by Tukey's test ($P = 0.05$). Statistical analysis was performed using the GraphPad Prism 8 program (GraphPad Software Inc., La Jolla, CA, USA).

Results

Preliminary selection of actinomycetes with antagonistic activity

The antagonistic activity of isolates against *C. musae* C6 is presented in Table 1. Data showed the PI of isolates over fungal growth, wherein 22 isolates inhibited the mycelial growth and 5 isolates (Y21, AGS-4, CACIS-2.15CA, CACIS-2.16CA, and CACIS-2.17CA) exhibited a superior value of PIs to *S. lydicus* WYEC108 (48.0 ± 0.07%). Considering its high PI (58.6 ± 2.1%), the CACIS-2.15CA isolate was selected for further evaluation.

Antifungal activity of CACIS-2.15CA

The in vitro confrontation assay revealed that CACIS-2.15CA inhibited the mycelial growth of the tested fungi at least by 30%, except for *F. oxysporum* (F6), *L. theobromae* (Rh2), and *Aspergillus* sp. (A3). It also showed a high inhibitory activity compared with the commercial strain WYEC108. Comparative analysis of the antagonism of CACIS-2.15CA versus *S. lydicus* showed high PIs against *C. musae* N1, *Lasiodiplodia* sp., *F. oxysporum* F4, and *B. cinerea* ($P < 0.05$). However, statistical differences were observed when *S. lydicus* inhibited the growth of *P. capsici* and *Sclerotinia* sp. ($P < 0.05$). Neither of the two

Table 1 Preliminary selection of antagonistic streptomycetes from various soil samples

Isolates from Oxkutzcab, Yucatán. México (Rejón-Martínez et al. 2022)					
ID	Y7	Y18	Y21	Y31	Y36
PI	9.1 ± 2.5	8.6 ± 2.2	50.0 ± 2.5	46.6 ± 3.0	36.8 ± 3.6
Isolates from Aguascalientes, México (Evangelista-Martínez et al. 2022)					
ID	AGS4	AGS6	AGS12	AGS13	AGS32
PI	56.3 ± 0.1	1.5 ± 0.7	37.8 ± 3.0	38.7 ± 0.7	33.0 ± 0.1
Isolates from Los Petenes Biosphere Reserve, Campeche. México (Evangelista-Martínez 2014)					
ID	CACIS-2.3CA	CACIS-2.67CA	CACIS-2.15CA	CACIS-2.16CA	CACIS-2.17CA
PI	19.5 ± 0.9	15.5 ± 3.0	58.6 ± 2.1	49.4 ± 0.9	53.3 ± 0.7
Isolates from Calcehtok Cave, Yucatán. México					
ID	GCAL3	GCAL7	GCAL17	GCAL19	GCAL33
PI	0.0 ± 0.0	6.9 ± 1.6	8.8 ± 0.5	0.0 ± 0.0	5.2 ± 0.1
Isolates from Nacional Park "El Chico," Hidalgo. México (Evangelista-Martínez 2014)					
ID	1.3H	1.44H	1.47H	1.54H	1.7H
PI	45.2 ± 0.6	23.0 ± 1.5	16.2 ± 0.8	3.9 ± 1.5	10.2 ± 0.4

Percentage of inhibition: *Streptomyces lydicus* WYEC108 48.0 ± 0.07

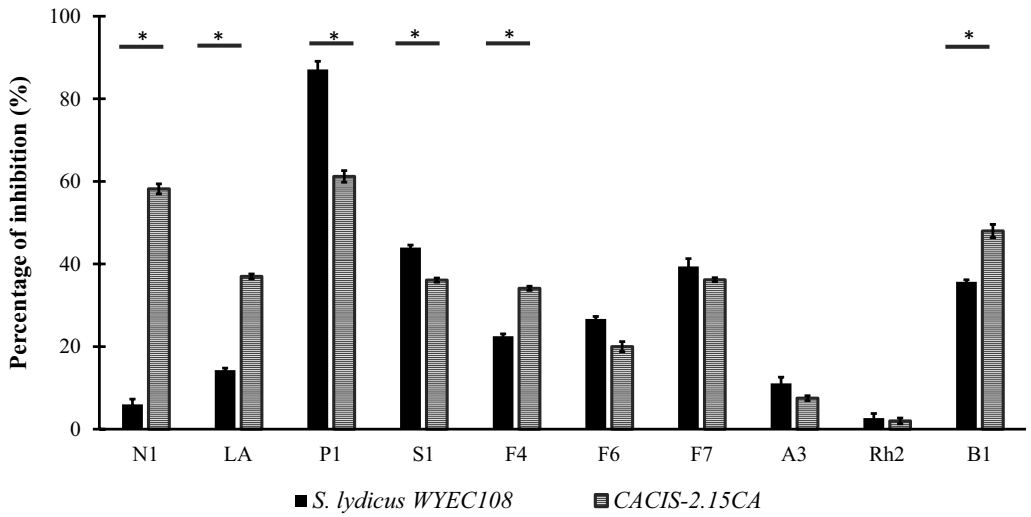

Fig. 1 In vitro antagonistic activity of isolate CACIS-2.15CA against different phytopathogenic fungi. Means of PI over fungal species: N1, *Colletotrichum musae* N1; LA, *Lasiodiplodia* sp.; P1, *Phytophthora capsica*; S1, *Sclerotinia* sp.; F4, *F. oxysporum*; F6, *F. oxysporum* f sp. *lycopersici*; F7, *Fusarium oxysporum*; B1, *Botrytis cinerea*; Rh2, *Lasiodiplodia theobromae*; and A3, *Aspergillus* sp. In the assay, *S. lydicus* WYEC108 was included as control. The error bar represents one standard deviation. *Significant differences ($P < 0.05$)

streptomycetes inhibited the growth of *L. theobromae* (Fig. 1).

Molecular identification and phenotypic characterization of CACIS-2. 15CA

The partial sequence of the rRNA 16S gene (1432 nucleotides) of the isolate CACIS-2.15CA was deposited in the Gen Bank database (OP313935). The sequence showed a 99.72% similarity to 16S rRNA gene sequences of *S. angustmyceticus* (OK335988.1) and *S. nigrescens* (FJ532430.1), 99.65% similarity to the sequences of *S. libani* (JN180219.1), and 99.58% similarity to the sequences of *S. lydicus* WYEC108 (MH894216.1), *S. rimosus* subsp. *rimosus*

(AB184745.2), and *S. platensis* (AB163439.1). In addition, phylogenetic analysis showed that *Streptomyces* sp. CACIS-2.15CA from a separate clade belongs to *S. roseocinereus* (AB184513.1), *S. sioyaensis* (NR_043498.1), and *S. albus* (AB184522) species (Fig. 2).

The phenotypic characterization of *Streptomyces* sp. CACIS-2.15CA on ISP2 culture media showed colonies with dry and rough surfaces and a crusty appearance. The 14th day vegetative mycelium developed white aerial hyphae and a gray spore mass. Branched and non-fragmented well-developed vegetative mycelia were observed; the color on the reverse side of the colony was brown. Regarding their microscopic morphology, these mycelia showed abundant branched spiral-type hyphae arranged in chains with 10–20 spores, oval to cylindrical in shape with a smooth surface (Fig. 3).

Additional morphological features on different culture media and sensitivity to antibiotics are shown in Additional file 1: Table S1. Furthermore, *Streptomyces* sp. CACIS-2.15CA grew in the presence of 62 compounds as carbon sources (Additional file 1: Fig. S1).

Detection of SeM biosynthetic gene clusters in *Streptomyces* sp. CACIS-2.15CA

The presence of biosynthetic gene clusters for PKS type I, PKS type II, and NRPS in the genome of *Streptomyces* sp. CACIS-2.15CA was detected by PCR (Additional file 1: Fig. S2). The amplified DNA fragments obtained by PKS type I and NRPS synthases were ~ 1400 and ~ 700 bp, respectively. No DNA amplification for PKS type II PKS was obtained using a specific pair of primers (KSα/KSβ).

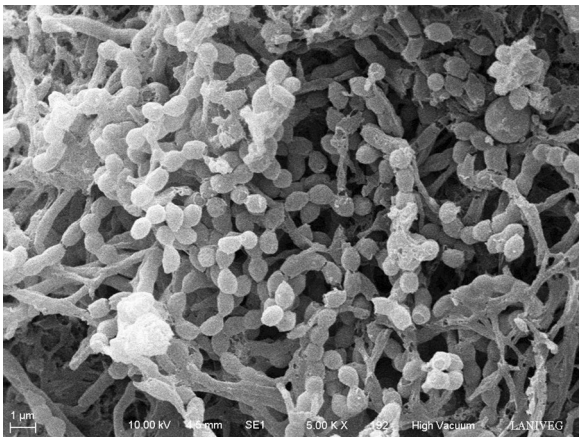

Fig. 3 Scanning electron micrograph showing spore morphology of *Streptomyces* sp. CACIS-2.15CA

Discussion

Studies assessing the ability of some actinomycetes to inhibit the growth of phytopathogenic fungi and oomycetes have been conducted worldwide. *S. corchorusii* AUH-1 exhibited an antagonistic activity against *Fusarium*, *Phytophthora*, *Rhizoctonia*, *Botryosphaeria*, and *Verticillium* by SeM (Yang et al. 2019). In addition, *Streptomyces* sp. CB-75 is another strain that inhibited the growth of 11 species of fungal pathogens, accounting for 73 to 81% (Chen et al. 2018). *Streptomyces rochei* MN700192 DG4 and *Streptomyces* griseus MT210913 DG5 have also shown a broad-spectrum antagonistic activity against phytopathogenic fungi that affect some vegetables and fruits at the postharvest stage (Ghanem et al. 2022). Therefore, in controlling the spread of *F. oxysporum*, the causal agent of gladiolus corm rot,

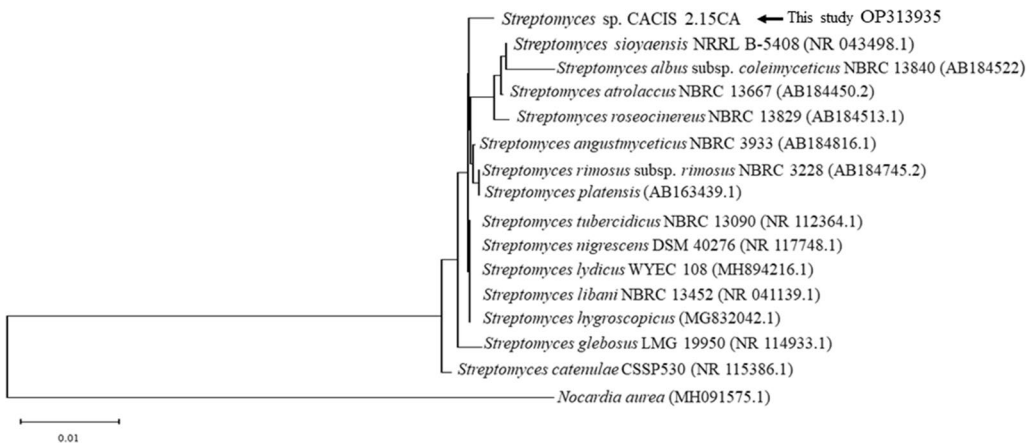

Fig. 2 Phylogenetic relationship among *Streptomyces* sp. CACIS-2.15 CA isolate and other *Streptomyces* strains

a bioactive extract produced by a novel streptomycete and applied to infected gladiolus corms, controls' fungal diseases and maintains corm hardness (Rios-Hernández et al. 2021). Recently, the bioactive extract produced by *Streptomyces* sp. AGS-58 controls anthracnose-causing *Colletotrichum siamense* in postharvest mango fruits (Evangelista-Martínez et al. 2022).

SeM produced by *Streptomyces* is considered as the principal group of molecules that induce an antimicrobial effect against fungal phytopathogens. On the contrary, the PIs of the CACIS-2.15CA isolate were lower than those reported in other studies, which indicates the importance of in vitro antagonism assays. Moreover, the inhibitory effect mediated by SeM varies depending on the medium used to develop the assay (Santos et al. 2020). The production of SeM by actinomycetes results from global changes in gene expression, which are induced by variations in the environment where they grow (van der Meij et al. 2017). Therefore, under in vitro culture conditions, the source of carbon, nitrogen, and phosphate, as well as temperature and pH, will either enhance or reduce the yield in the production of SeM (Souagui et al. 2019).

Phylogenetic analysis showed that *Streptomyces* sp. CACIS-2.15CA from a separate clade belongs to *S. roseocinereus*, *S. sioyaensis*, and *S. albus* species. These species have shown bioactivity that improves the health and productivity of field plants. The *S. sioyaensis* fermentation broth inhibited *Valsa sordida* by increasing the cell permeability and disrupting the metabolic pathways of the pathogen, which can be considered as potent BCAs for poplar tree canker (Li et al. 2020). Moreover, *S. roseocinereus* showed a great application potential as a biofertilizer, which increased plant growth, P uptake, and yield (Chouyia et al. 2020). Furthermore, a novel isolate of *Streptomyces albus* S4, a symbiotic bacterium with leaf-cutting ants, *Acromyrmex octospinosus*, produces the polyene antifungal candicidin (Barke et al. 2010). Candicidin binds to ergosterol, which affects membrane permeability and integrity and leads to a rapid efflux of K+ ions, thereby causing fungal cell death. Notably, *S. lydicus* WYEC108 and *S. platensis* belong to this clade. The former is considered as a biocontrol fungal agent from the commercial biofungicide Actinovate®, whereas the latter can produce platensimycin or platencin, which is a class of broad-spectrum antibiotics against gram-positive bacteria (Smanski et al. 2009).

The biosynthesis of SeM with biological activity in Actinobacteria is associated with the presence of biosynthetic gene clusters in their genome, most of which were synthesized for PKS type I and II and NRPS synthases (Dhakal et al. 2019). In addition, the presence of these genes has been reported in various studies; for example, Ayuso-Sacido and Genilloud (2004) detected the presence of NRPS and PKS type I genes in 210 reference strains of actinomycetes, with a frequency of 79.5 and 56.7%, respectively. The detection of gene clusters in the antagonist of plant fungal pathogens, *Streptomyces* sp. CACIS-1.15CA, was also reported (Evangelista-Martínez et al. 2020). Therefore, the presence of NRPS and PKS I genes could play an important role in the antifungal activity of *Streptomyces* sp. CACIS-2.15CA.

Conclusion

The detection of PKS type I and NRPS gene clusters for SeM biosynthesis and the antagonism on fungal growth represent a natural alternative as a BCA to control fungal pathogens, including species-causing plant diseases from the genus *Colletotrichum*, *Lasiodiplodia*, *Fusarium*, *Phytophthora*, and *Botrytis*. Therefore, *Streptomyces* sp. CACIS-2.15CA has a great application potential as a BCA.

Abbreviations

BCA: Biocontrol agents; ISP 2: International *Streptomyces* Project; PCR: Polymerase chain reaction; PDA: Papa dextrose agar; PI: Percentage of inhibition; PKS: Polyketide synthase; NRPS: Non-ribosomal peptide synthase; SeM: Secondary metabolites; SS: Spore suspensions.

Supplementary Information

The online version contains supplementary material available at https://doi.org/10.1186/s41938-022-00630-7.

Additional file 1. Antifungal activity of soil *Streptomyces* sp. CACIS-2.15CA, as a potential biocontrol agent, against some soil-borne fungi.

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Author contributions

This study was conceived and designed by Z. E-M. D.E. R-M conducted the experiments. Data were analyzed by Z. E-M and D.E. R-M. D.E. R-M prepared the manuscript draft. The final manuscript was revised by D.E. R-M and Z. E-M. All authors have read and approved the final manuscript.

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Availability of data and materials

The datasets supporting the conclusion of the article are included within the article and supplementary material.

Declarations

Ethics approval and consent to participate

Not applicable.

Consent for publication

Not applicable.

Competing interests
The authors declare that they have no competing interests.

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