Torres-Rodriguez JA *et al.* (2024)
Notulae Botanicae Horti Agrobotanici Cluj-Napoca
Volume 52, Issue 2, Article number 13562
DOI:10.15835/nbha52213562
Research Article

Marine actinomycetes for biocontrol of *Fusarium solani* in tomato plants: *In vitro* and *in vivo* studies

Juan A. TORRES-RODRIGUEZ[1]*, Juan J. REYES-PÉREZ[1], Luis HERNÁNDEZ ADAME[2], Bryan L. LLERENA-FUENTES[1], Luis G. HERNANDEZ-MONTIEL[2]*

[1]*Universidad Técnica Estatal de Quevedo, Quevedo EC 120501, Los Ríos, Ecuador; jatorres@uteq.edu.ec (*corresponding author); jreyes@uteq.edu.ec; bryan.llerena2018@uteq.edu.ec*
[2]*Nanotechnology & Microbial Biocontrol Group, Centro de Investigaciones Biológicas del Noroeste, La Paz, Baja California Sur, 23096, México; ladame@cibnor.mx; lhernandez@cibnor.mx (*corresponding author)*

Abstract

Using microorganisms as biocontrol agents of phytopathogens has been an alternative to synthetic fungicides. Actinomycetes isolated from soil and plants have reduced diseases caused by phytopathogens; however, microorganisms from marine environments may be an option as biocontrol agents. The tomato crop possesses an important economic impact worldwide, being Mexico the main exporter. Several species of *Fusarium* cause damage to tomato crops and are controlled with synthetic fungicides. The objective of this work was to determine the effect of marine actinomycetes as biocontrol on *Fusarium solani* in tomato plants. Four strains of marine actinomycetes (A20, A19, A18, and A15) and one terrestrial actinomycete (ED48) were used. The actinomycetes strains used, produced siderophores. The greatest inhibition of mycelial growth of *F. solani* due to iron competition was obtained by strain A19 with 74.28%. Only two actinomycetes showed antifungal activity by VOCs (A19 and A18), strain A19 showed the highest antagonistic activity with PICR of 76.75%. Actinomycetes treatments showed significant differences with synthetic fungicide application in growth, disease severity (SE), and disease incidence (DI) variables. The application of marine actinomycete (A19) on plants infested with *F. solani* increased the levels of enzyme activity (SOD, POD, CAT, and PAL) versus plants in that only *F. solani* and distilled water (control) were applied. Actinomycetes of marine origin are an option as biocontrol agents for *F. solani*.

Keywords: antioxidant enzymes; siderophores; *Solanum lycopersicum* L.; *Streptomyces*; volatile organic compounds

Introduction

Tomato (*Solanum lycopersicum* L.) crop possesses an important economic impact worldwide (Campos *et al*., 2022; García-Estrada *et al*., 2022), however, there are economic losses caused by fungal diseases,

Received: 18 Dec 2024. Received in revised form: 05 Mar 2024. Accepted: 21 May 2024. Published online: 27 Jun 2024.
From Volume 49, Issue 1, 2021, Notulae Botanicae Horti Agrobotanici Cluj-Napoca journal uses article numbers in place of the traditional method of continuous pagination through the volume. The journal will continue to appear quarterly, as before, with four annual numbers.

highlighting the vascular root wilt disease caused by *Fusarium* spp. (Li *et al*., 2023), causing 80% crop losses (Akbar *et al*., 2016). Moreover, it is adapted to survive in the soil in the absence of a host plant, making it difficult to control (Cruz *et al*., 2018).

Currently, the application of agrochemicals is the main control method for *Fusarium* spp. (Ismaila *et al*., 2022). However, the use of synthetic fungicides causes resistance in phytopathogens and negative effects on the environment, and human, and animal health (Torres-Rodriguez *et al*., 2022a; Cech *et al*., 2023). Therefore, the search for alternatives to reduce the application of synthetic fungicides is a priority worldwide (Maluin *et al*., 2020; Torres-Rodriguez *et al*., 2022a).

Biocontrol offers advantages over synthetic fungicides and phytopathogen control. Biocontrol agents can control a specific group of microorganisms, present long-term sustainability, lower risk to human and animal health, suppress phytopathogens, and induce plant defense responses, causing less ecosystem damage than synthetic fungicides (He *et al*., 2021). In recent years, actinomycetes application as biocontrol agents against phytopathogens has been an option to reduce in the crops the application of synthetic fungicides (Boukaew *et al*., 2022; Wang *et al*., 2023). Various species of *Streptomyces* have been used to control phytopathogenic fungi, such as *Botrytis* sp., *Pyricularia* sp., *Penicillium* sp., *Alternaria* sp., *Fusarium* sp., *Colletotrichum* sp., among others (Allali *et al*., 2019; Alblooshi *et al*., 2022; Qi *et al*., 2022; Torres-rodriguez *et al*., 2022b).

Among the main antagonistic mechanisms of actinomycetes towards phytopathogens are the production of volatile organic compounds (VOCs) and siderophores. VOCs are low molecular weight compounds that at normal temperatures and pressure volatilize easily, giving them the ability to disperse through the atmosphere and soil (Li *et al*., 2020). VOCs have been shown to increase plant growth, induce systemic resistance (ISR) in the host, and exhibit antifungal activity towards phytopathogenic fungi (Gong *et al*., 2022; Salwan *et al*., 2023). Siderophores are iron-chelating molecules synthesized by microorganisms and are important in positive and negative interactions between them (Puja *et al*., 2023). Siderophores are important in the growth and virulence of phytopathogens, as well as in plant-phytopathogen interactions by limiting iron availability (Hernández Montiel *et al*., 2018; Meena *et al*., 2022). In addition, actinomycetes also exhibit antagonistic activity towards phytopathogens through competition for space and nutrients (Fadhilah *et al*., 2021) antibiotic production (Xia *et al*., 2022), lytic enzymes (Gebily *et al*., 2021), and induction of host resistance (Kaari *et al*., 2022).

Marine actinomycetes are poorly analyzed microorganisms that may be an option as biocontrol agents (Ameen *et al*., 2021; Torres-Rodriguez *et al*., 2022b). The objective of this work was to determine the effect of marine actinomycetes biocontrol on *Fusarium solani* in tomato plants.

Materials and Methods

Fusarium solani

The fungus was previously isolated from diseased tomato plants with *Fusarium* wild disease (Torres-Rodriguez *et al*., 2022a) and was donated to the phytopathology laboratory of the Centro de Investigaciones Biológicas del Noroeste (CIBNOR), La Paz, Baja California Sur, México.

Antagonistic actinomycetes

Marine actinomycetes were previously isolated from marine mangrove sediment (Torres-Rodriguez *et al*., 2022a) and were donated to the phytopathology laboratory of the CIBNOR. Four strains of marine actinomycetes (*Nocardiopsis lucentensis* -A20 and A15-, *Streptomyces* sp. -A19-, and *Streptomyces griseoflavus* -

A18-) were used. A reference strain of terrestrial origin (ED48) of *Streptomyces* sp. was used as a control. Actinomycetes were stored in ISP-2 at 4 °C and in 20% glycerol at -80 °C for further analysis.

Siderophore production by marine actinomycetes

The chrome azurol S (CAS) agar medium assay was used to determine siderophore production (Schwyn and Neilands, 1987). Each marine actinomycete was grown in ISP2 medium (composed of malt extract 10 g, yeast extract 4 g, dextrose 4 g, agar 20 g, marine water 1 L, and pH 7.2) at 28 °C for 15 days. Subsequently, equidistantly four plugs of each strain were placed into CAS agar plate (composed of CAS 0.0605 g, $C_{19}H_{42}BrN$ 0.0729 g, $FeCI_3{\cdot}6H_2O$ 0.0027 g, $NaH_2PO_4{\cdot}2H_2O$ 0.2953 g, $Na_2HPO_4{\cdot}12H_2O$ 1.2135 g, NH_4Cl 0.1250 g, $KH_2{\cdot}PO_4$ 0.0375 g, NaCl 0.0625 g, agar 15 g, distillate water 1 L, and pH 6.8), and were incubated at 28 °C for 15 days. Five replicates were used by actinomycete. The experiment was replicated three times. Siderophore production was evaluated according to whether yellow or orange halos formed around the colonies.

Effect of iron on the antifungal activity of marine actinomycetes

The antifungal activity of marine actinomycetes against *F. solani* was evaluated on potato dextrose agar (PDA-Fe) Petri dishes supplemented with $FeCl_3{\cdot}6H_2O$ (0.05%) or EDTA-Na2 (0.05%) (Qi *et al*., 2022). *F. solani* was inoculated on PDA at 28 °C for 7 days and all actinomycetes were grown in ISP2 medium at 28 °C for 15 days. A plug of target fungus was placed in the center of PDA-Fe Petri dishes and two plugs of each actinomycete were inoculated at the symmetric points of the *F. solani* disc. PDA without $FeCl_3{\cdot}6H_2O$ or EDTA-Na_2 were used as controls. After incubation at 28 °C for 7 days, the growth diameter of *F. solani* was measured. The percent of radial growth inhibition (PICR, %) of *F. solani* was determined. The mycelial growth inhibition percentage (PICR, %) of the phytopathogen was determined with the formula: [(R1-R2) /R1] × 100%, where R1 = radial growth of *F. solani* on the control plate and R2 = growth of *F. solani* in the direction toward the actinomycete colonies. Five replicates per treatment were used and the experiment was repeated three times.

VOCs production by marine actinomycetes

PDA Petri dishes were centrally inoculated with a plug of *F. solani* from a 7-day-old PDA culture. At the same time, another Petri plate with ISP2 medium was inoculated with each actinomycete, covering the entire surface of the plate (Djebaili *et al*., 2021). The lids of both plates were removed, and the two inoculated bases were brought into contact so that the fungus remained below. The junction of the two bases was sealed with Parafilm and incubated at 28 °C for 7 days. PDA plates with *F. solani* with one base containing only the ISP2 medium were used as a control. The percentage of radial growth inhibition (PICR, %) of *F. solani* was determined. Five replicates per treatment were used, and the experiment was repeated three times.

Biocontrol of marine actinomycetes against F. solani in tomato

Microorganism growth conditions

Marine actinomycete *Streptomyces* sp. A19 strain was selected for the experiments *in vivo* conditions because that showed high antifungal activity against *F. solani* in the *in vitro* assays. Terrestrial origin *Streptomyces* sp. ED48 strain was used as a control. Both actinomycetes were grown in ISP2 broth at 28 °C for 7 days and 150 rpm. Each actinomycete strain was adjusted to 1×10^8 CFU mL^{-1} (Díaz-Díaz *et al*., 2022). *F. solani* was grown on PDA at 28 °C for 7 days. Then 5 mL of sterile water was added, and spores were collected and adjusted to 1×10^6 conidia mL^{-1}.

Treatments and growing conditions

Tomato plants cv. 'Saladettes' were grown in 200-cavity germination trays using COSMOPEAT substrate at 25 °C, 80% RH (relative humidity), and 12 h of light intensity in a plant growth chamber. After 25 days, the plants had one-third of their roots trimmed and were immersed in the *F. solani* conidia suspension for 15 min before transplanting.

After (24 h) inoculation of *F. solani* the following treatments were applied in the root's plants: (1) A19 + *F. solani* (A19+F); (2) ED48+F; (3) Synthetic fungicide (Carbendazim) + *F. solani*; (4) *F. solani*, and (5) Control (without treatment -sterile distiller water-). 1 mL of the actinomycete inoculum was inoculated near the root collar of tomato plants. Synthetic fungicide Carbendazim (methyl benzimidazol-2-ylcarbamate) was used at 6 mg. mL^{-1}. Plants were maintained at 28 °C, 80% RH, and 12 h light in a plant growth chamber for 28 days. Six replicates per treatment were used, and the experiment was repeated three times.

Effect of actinomycetes on growth of tomato plants inoculated with *F. solani*

Growth variables in the plants inoculated with marine actinomycetes and *F. solani* such as plant height, stem diameter, dry weight, and root length were quantified at 28 days after the treatment′s application. Leaf samples were taken and stored at -80 °C for enzymatic quantification.

Evaluation of the severity and incidence of the disease

Disease severity (DS) was determined 28 days after application of treatments using the scale of Marlatt *et al*. (1996); 1 = Plants without symptoms; 2 = Slight chlorosis and wilting or stunting; 3 = Moderate chlorosis and wilting or stunting; 4 = Severe chlorosis and wilting or stunting; 5 = Dead plants. Subsequently, a DS index was estimated using the following formula:

$$\text{DS (\%)} = \left[\sum_{i=1}^{5} ni(sti)\,/(N \times K)\right] \times 100$$

where ni = number of plants in the DS stage of development, sti= DS stage value (1-5), N = total number of plants evaluated and K = highest scale level (5).

The percentage disease incidence (% DI) (Saravanakumar *et al*., 2016) was determined by the following formula:

$$\%DI = (Pi / TP) \times 100\%$$

where Pi = the number of infected plants and TP = the total number of plants. The experimental design was completely randomized with six replicates per treatment and the experiment was repeated twice.

Antioxidant enzyme activity in tomato plants

Leaf samples frozen at -80 °C from the treatments described above were homogenized with glass beads and mechanical agitation, followed by a homogenizer to disintegrate the tissue. To each Eppendorf tube with the sample, 1 mL of phosphate buffer (100mM pH 7.0) was added. The samples were centrifuged at 3800 rpm for 20 min at 4 °C, the supernatant was subjected to enzymatic assays. Protein content was determined using the bicinchoninic acid (BCA) technique. Catalase (CAT) enzyme activity was determined according to the methodology described by Johansson and Borg (1988). One unit of CAT activity is defined as the amount of enzyme that reacts with 1 nmol of formaldehyde per minute and is expressed as U mg^{-1} of protein. Peroxidase (POD) enzyme activity was determined according to the methodology of Srivastava and Dwivedi (1988). One unit of POD activity is defined as the amount of enzyme that causes tetraguaiacol formation in the presence of H_2O_2 per minute and is expressed in U mg^{-1} of protein. Superoxide dismutase (SOD) enzyme activity was determined according to the methodology of Paoletti *et al*. (1986). One unit of SOD activity is defined as the amount of enzyme required to inhibit 50% of the O_2 reaction in the presence of nitro-blue tetrazolium (NBT) reagent and is expressed as U mg^{-1} of protein. Phenylalanine ammonia lyase (PAL) enzyme activity was determined according to the methodology of Yamada *et al*. (1981). One unit of PAL activity is defined as μmol of cinnamic acid formed per minute per milligram of protein (min mg^{-1} of protein).

Statistical analysis

Data were analyzed by one-way analysis of variance (ANOVA) using STATISTICA 10.0 software (StatSoft software, Tulsa, OK) and Fisher LSD test ($p < 0.05$) was used for the separation of means. Data were tested for normality using the Shapiro-Wilk test and homogeneity of variances using Bartlett's test before analysis of variance (ANOVA). For percentage inhibition of VOCs, disease severity (DS), and disease incidence (DI) from *in vivo* experiments, data were analyzed separately using the nonparametric Kruskal-Wallis test because the assumptions of normality and homogeneity of variances were not met even though they were log, arcsine, or square root transformed. Mean values were compared using Dunn's comparison test at $p < 0.05$.

Results

Antagonistic activity of marine actinomycetes towards F. solani

All strains of actinomycetes (A20, A19, A18, A15, and ED48) produced siderophores. The results of co-culture of the actinomycetes and *F. solani* under iron-deficient (EDTA-Na_2) or iron-rich ($FeCl_3$ $6H_2O$) conditions showed that the $FeCl_3$ $6H_2O$-enriched culture medium had a negative effect on the antagonism of the actinomycetes towards the phytopathogen (Figure 1). However, the antagonistic activity of actinomycetes was increased in the presence of EDTA-Na_2. These results show that competition for iron through siderophore production by actinomycetes is involved in the inhibition of *F. solani*.

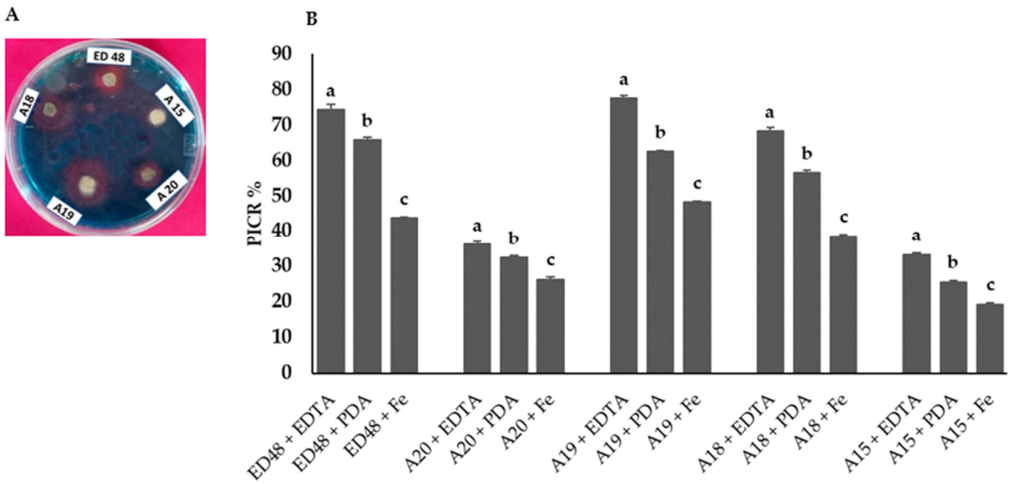

Figure 1. A: Siderophore production by actinomycetes. B: Inhibition of radial growth of *F. solani* by siderophores

ED48: terrestrial *Streptomyces* sp.; A20: marine *N. lucentensis*; A19: marine *Streptomyces* sp.; A18: marine *S. griseoflavus*; A15: marine *N. lucentensis*. ± Standard deviation. Columns with the same letters do not differ significantly according to Fisher ($p < 0.05$).

Only two actinomycetes showed antifungal activity by VOCs (A19 and A18) towards *F. solani*. Strain A19 showed the highest antagonistic activity with PICR of 76.75%, which presented significant differences with the rest of the actinomycetes. The marine actinomycete strain A18 showed a PICR of 63.62% (Figure 2).

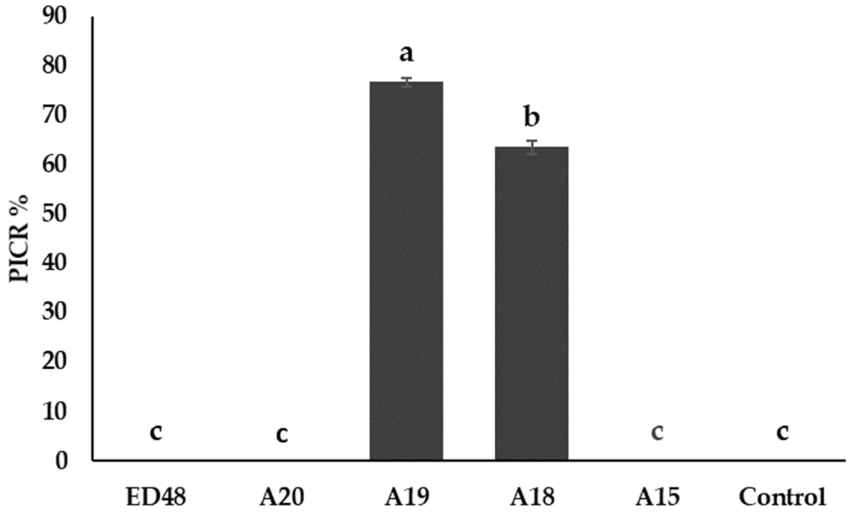

Figure 2. Percentage inhibition of actinomycete VOCs towards *F. solani*
ED48: terrestrial *Streptomyces* sp.; A20: marine *N. lucentensis*; A19: marine *Streptomyces* sp.; A18: marine *S. griseoflavus*; A15: marine *N. lucentensis*. ± Standard deviation. Columns with the same letters do not differ significantly according to Dunn ($p < 0.05$).

Biocontrol of Actinomycetes towards F. solani in tomato

The marine actinomycete A19 was used for the in vivo tests, which showed the best results in the *in vitro* tests. The actinomycete treatments (A19 and ED48) showed a greater protection effect on tomato plants against *F. solani* than the application of the synthetic fungicide (Carbendazim). The greatest protection effect on tomato plants against *F. solani* was obtained with the treatment (A19+F) in the variables plant height (355.80 mm), root dry weight (72.04 mg), and root length (51.13 mm), which showed significant differences with the rest of the applied treatments; however, it did not show significant differences between the treatment ED48+F and the control in the variable stem diameter. The lowest results in the growth variables of tomato plants were obtained with the application of the phytopathogen (Table 1).

Table 1. Morphometric variables of tomato plants inoculated with marine actinomycetes and *F. solani*

Treatment	Plant height (mm)	Stem diameter (mm)	Root dry weight (mg)	Root length (mm)
A19+F	335.80 ±1.07 a	4.28 ±0.12 a	72.04 ±0.96 a	51.13 ±1.21 a
ED48+F	307.78 ±0.52 b	4.25 ±0.15 a	67.27 ±0.81 b	45.25 ±0.49 b
F. solani	165.90 ±0.46 c	2.03 ±0.16 b	32.14 ±1.34 c	18.48 ±0.92 c
SynFun+F	301.48 ±1.11 d	3.99 ±0.11 c	59.32 ±0.78 d	39.24 ±0.53 d
Control	359.82 ±0.96 e	4.40 ±0.09 d	74.70 ±2.18 e	56.08 ±0.92 e

*A19+F: marine *Streptomyces* sp.+*F. solani*; ED48+F: terrestrial *Streptomyces* sp.+*F. solani*; SynFun+F: synthetic fungicide+*F. solani*; Control: sterile distilled water. ± Standard deviation. Columns with the same letters do not differ significantly according to Fisher ($p < 0.05$).

The treatment of marine actinomycete (A19+F) on tomato plants inoculated with *F. solani* showed the lowest result in disease severity (20%) compared to the application of the synthetic fungicide. Actinomycete treatments showed significant differences in disease reduction compared to plants treated with the phytopathogen (*F. solani*). Marine actinomycete (A19+F) and terrestrial actinomycete (ED48+F) treatments were superior to the synthetic fungicide application (Figure 3).

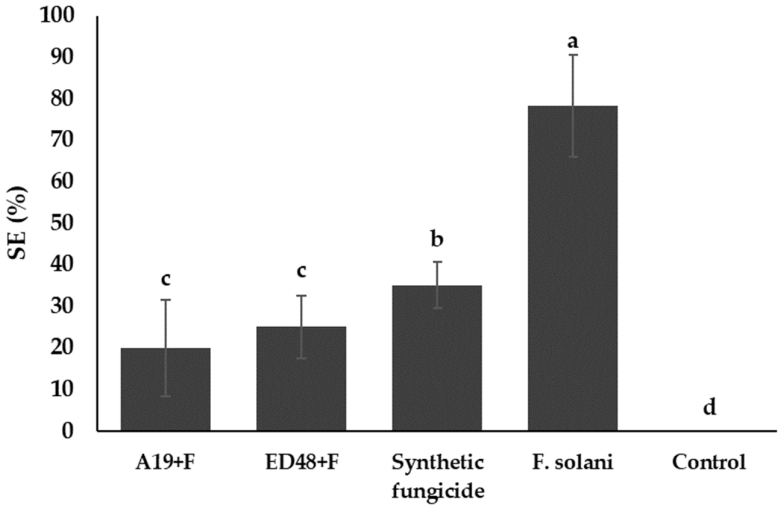

Figure 3. Disease severity (DS) caused by *F. solani* on tomato plants treated with actinomycetes
A19+F: marine *Streptomyces* sp.+*F. solani*; ED48+F: terrestrial *Streptomyces* sp.+*F. solani*; Synthetic fungicide: Carbendazim+*F. solani*; Control: sterile distilled water. ± Standard deviation. Columns with the same letters do not differ significantly according to Dunn ($p < 0.05$).

Disease incidence (DI) was lower in tomato plants treated with actinomycete treatments, surpassing the control treatment. The marine actinomycete treatment (A19+F) and the terrestrial actinomycete (ED48+F) presented the lowest DI values (50%), showing significant differences with the rest of the treatments, however they did not show significant differences with the synthetic fungicide. The control treatment (*F. solani*) presented 100% DI in tomato plants (Figure 4).

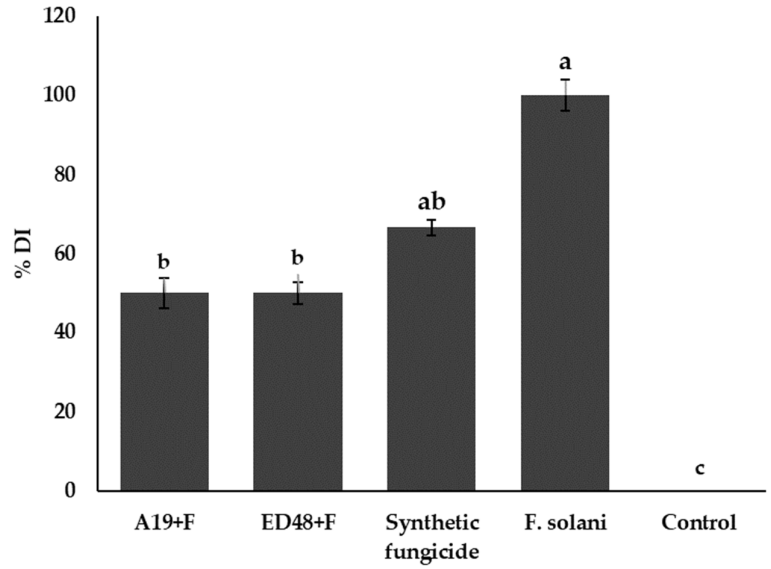

Figure 4. Incidence of disease caused by *F. solani* in tomato plants treated with actinomycetes
A19+F: marine *Streptomyces* sp.+*F. solani*; ED48+F: terrestrial *Streptomyces* sp.+*F. solani*; Synthetic fungicide: Carbendazim+*F. solani*; Control: sterile distilled water. ± Standard deviation. Columns with the same letters do not differ significantly according to Dunn ($p < 0.05$).

The activity of antioxidant enzymes SOD, CAT, POD, and PAL increased when actinomycetes or phytopathogen were applied compared to the control treatment (dis-tilled water). SOD activity increased significantly when marine actinomycete and *F. solani* (A19+F) treatment was applied. CAT activity increased with the treatment (A19+F), which presented significant differences with the rest of the remaining treatments. POD activity increased with the application of the actinomycetes and phytopathogen treatments. The highest result was obtained with the marine actinomycete and phytopathogen treatment (A19+F). PAL activity was increased with the actinomycete and *F. solani* treatments compared to the control treatment. The maximum result was reached with the A19+F treatment, showing significant differences compared to the rest of the remaining treatments (Table 2).

Table 2. Effect of marine actinomycetes and *F. solani* on antioxidant enzyme activity in tomato plants

Treatment	SOD activity (U mg^{-1} protein)	CAT activity (U mg^{-1} protein)	POD activity (U mg^{-1} protein)	PAL activity (min mg^{-1} protein)
A19+F	1.83 ±0.23 a	5.89 ±0.20 a	4.61 ±0.20 a	2.58 ±0.14 a
ED48+F	1.45 ±0.18 b	5.27 ±0.15 b	4.07 ±0.43 b	2.31 ±0.20 b
F. solani	1.00 ±0.42 c	4.29 ±0.59 c	3.11 ±0.36 c	1.73 ±0.24 c
Control	0.61 ±0.19 d	1.59 ±0.29 d	1.81 ±0.26 d	0.91 ±0.13 d

*A19+F: marine *Streptomyces* sp.+*F. solani*; ED48+F: terrestrial *Streptomyces* sp.+*F. solani*; Control: sterile distilled water; SOD: superoxide dismutase activity; CAT: catalase activity; POD: peroxidase activity; PAL: phenylalanine ammonia lyase activity. ± Standard deviation. Columns with the same letters do not differ significantly according to Fisher ($p < 0.05$).

Discussion

Antagonistic activity of marine actinomycetes towards F. solani

The excessive use of synthetic fungicides to control phytopathogenic fungi such as *F. solani* leads to resistance development by phytopathogens, and soil and water contamination (Fang *et al*., 2016), therefore the use of new environmentally friendly alternatives will reduce their application. The main studies of actinomycetes as biocontrol agents have focused on isolates from terrestrial environments (Torres-Rodriguez *et al*., 2022b). However, the study of actinomycetes from marine environments will allow the characterization of new biocontrol agents for agriculture (Liu *et al*., 2020).

The antagonistic activity of actinomycetes against phytopathogens depends on their capacity to produce diverse antagonistic mechanisms such as the production of lytic enzymes, antifungal metabolites, competition for nutrients, siderophores, volatile compounds, among others (Igarashi *et al*., 2021).

In the absence of iron, microorganisms release high-affinity ferric iron-chelating compounds called siderophores into the environment. These siderophores transport Fe^{3+} into the microbial cell (Ghosh *et al*., 2020). Iron is important for microorganisms to perform processes such as nucleic acid synthesis and repair, respiration, photosynthetic transport, and nitrate reduction or free radical detoxification, therefore, the limitation of this element reduces the growth and infection process of phytopathogens (Hernández Montiel *et al*., 2018).

In our study, all actinomycetes produced siderophores, showing yellow halos around the strain colonies. The siderophores produced by the actinomycetes mediated the antifungal activity toward *F. solani* and it decreased after adding iron to the culture medium. The antagonistic activity of the actinomycetes increased with the application of EDTA-Na_2 to the culture medium. This could be because the actinomycetes competed for iron with the phytopathogen by secreting siderophores to suppress its growth. Similar results, under iron-deficient or iron-rich conditions, showed that the application of $FeCl_3$ $6H_2O$ to the culture medium had a negative effect on the antagonism of *F. oxysporum* f. sp. *cubense* by the actinomycete strain *Sarracenia*

sichuanensis, on the contrary, the antagonistic activity of *S. sichuanensis* was enhanced along with increasing EDTA-Na_2 concentrations and its extracts induced apoptosis of the phytopathogen cells (Qi *et al*., 2022).

Streptomyces species have been shown to produce siderophores which are important in the phytopathogens biocontrol (Zhou *et al*., 2022). Allali *et al*. (2019) demonstrated that *Nepenthes dassonvillei* species inhibited the growth of the phytopathogens *Rhizoctonia solani*, *F. graminearum*, and *F. oxysporum* under *in vitro* conditions. This effect may be related to the production of siderophores by an antagonist. In another work, *S. rameus* presented antifungal activity towards *R. bataticola*, this antifungal activity was related to the production of siderophores, since iron competition is a mechanism to inhibit the growth of phytopathogens (Meena *et al*., 2022). Similar results have been reported by Al-Dhabi *et al*. (2019) where *Streptomyces* species produced siderophores, showing the potential to inhibit the growth of phytopathogens like *F. oxysporum*, *Aspergillus niger*, *A. flavus*, and *F. solani*.

The production of antifungal VOCs by actinomycetes is a complex process influenced by a variety of genetic, metabolic, and environmental factors, which may explain why only two of the four actinomycetes evaluated in the study showed this activity (Zhao *et al*., 2022). The capacity of actinomycetes to produce VOCs that exhibit antifungal activity by causing structural alterations in the cells of the phytopathogens has been demonstrated (Gong *et al*., 2022). Some VOCs, such as dimethyl disulfide (DMDS) and 2-methyl-pentanoate, are highly toxic to phytopathogens in plants, moreover, VOCs such as acetoin, 2,3-butanediol, and tridecane, induce systemic host resistance (Ossowicki *et al*., 2017). Only actinomycetes (A19 and A18) of marine origin produced VOCs with antifungal activity towards *F. solani*, actinomycete ED48 of terrestrial origin did not produce VOCs. Similar results to those reported in this work, regarding the inhibition of *F. solani* growth by VOCs, were obtained by Yang *et al*. (2021), showing that VOCs from *S. aureoverticillatus* inhibited the mycelial growth of *F. oxysporum* by 63.11%; the VOCs identified with the greatest antifungal activity were acridine and 9-methyl.

Also, *Streptomyces* sp. VOCs inhibited mycelial growth of *R. solani* by 95%, *F. solani* by 69% and *F. oxysporum* by 20%, and in *in vivo* assays, VOCs inhibited the development of gray mold disease caused by *Botrytis cinerea* on strawberry (*Fragaria ananassa*) fruits by 87% compared to the control treatment (not inoculated with *B. cinerea*) (Ayed *et al*., 2021). Also, *Streptomyces* sp. VOCs have been shown to reduce mycelial growth of *C. acutatum* by 77% (Jepsen *et al*., 2022). VOCs produced by *S. lavendulae* inhibited mycelial growth and sporulation of *Ceratocystis fimbriata* under *in vitro* conditions, inducing morphological changes in hyphae (Li *et al*., 2020).

Biocontrol of Actinomycetes Towards F. solani in Tomato

Actinomycetes A19 and ED48 presented the lowest SE and DI towards *F. solani*, showing significant differences with the synthetic fungicide. The least damage to tomato plants caused by *F. solani* was reported when the marine actinomycete (A19+F) was applied, demonstrating its potential as a biocontrol agent. Actinomycetes can present a greater protective effect on plants than synthetic fungicides, due to the wide range of bioactive compounds they produce such as antibiotics, siderophores, enzymes, and VOCs, which have multiple mechanisms of action against phytopathogens. In addition, they induce defense responses in the plant, making them more resistant to infections by phytopathogens (Gong *et al*., 2022; Torres-Rodriguez *et al*., 2022b; Salwan *et al*., 2023).

Similar results were reported by Qi *et al*. (2022), who demonstrated in an *in vivo* experiment that the *S. sichuanensis* strain significantly reduced the infection of *F. oxysporum* f. sp. *cubense* in the roots and bulbs of banana (*Musa paradisiaca* L.) seedlings, regarding the control treatment (without application of actinomycetes), reducing the disease index by 25.83%. Similarly, in a pot experiment with rice seedlings, strains of *S. chilikensis* reduced the severity of the disease caused by *F. oxysporum*. Plant growth parameters (root length,

root fresh weight, and root dry weight) were also increased by 53-91, 62-5, and 73-46%, respectively, in the *S. chilikensis*-treated plant groups compared to those infected with *F. oxysporum* (Behera *et al*., 2022).

Korayem *et al*. (2020) demonstrated the biocontrol activity of *S. parvulus* towards *R. solani* in green beans, plants treated with *S. parvulus* presented the highest survival, showing significant differences with plants treated with synthetic fungicides, in addition, growth variables such as plant height, number of leaves and dry weight of plants, increased with the *S. parvulus* treatment, regarding the control and synthetic fungicide.

It has been demonstrated in chickpea (*Cicer arietinum* L.) plants that *Streptomyces* sp. from terrestrial environments significantly decreased the incidence of disease caused by *B. cinerea* by 47% compared to the control treatment. In addition, they induce resistance mechanisms in plants, such as antioxidant enzymes and phenolic compounds (Vijayabharathi *et al*., 2018). The application of *Streptomyces* sp. from marine environments significantly decreased the disease index of *F. oxysporum* in banana crops, the secondary metabolites of *Streptomyces* sp. caused cell membrane rupture and leakage of intracellular components of the phytopathogen (Li *et al*., 2021).

Similar results to those reported in this work were obtained by Yandigeri *et al*. (2015), who demonstrated that the application of *S. vinaceusdrappus* from marine environments in tomato plants reduced root rot disease caused by *R. solani* by 71%. Application of *S. puniceus* from wetland environments decreased early blight disease caused by *A. solani* on tomato leaves relative to the control treatment (Hao *et al*., 2019).

Plants treated with actinomycetes and the phytopathogen presented the highest levels of enzymatic activity (SOD, POD, CAT, and PAL) compared to plants treated with only *F. solani* and distilled water (control). The first defense response of plants towards phytopathogens is the oxidative burst, causing high levels of reactive oxygen species (ROS). Low ROS concentrations intervene as a signal molecule in cell proliferation, differentiation, apoptosis, and stress adaptation (Li *et al*., 2020). However, the imbalance of ROS production and the defense system can destroy biological functional molecules, causing cellular damage. Antioxidant enzymes like SOD, POD, and CAT can reduce ROS and decrease cell damage. PAL products are modified into secondary metabolites (lignin, flavonoids, and phytoalexins), which are involved in plant resistance to phytopathogens (Morrison and Buxton, 1993). The application of VOCs from *S. lavandulae* on sweet potato (*Solanum tuberosum* L.) increased SOD, POD, and CAT antioxidant enzymes regarding the control treatment, results that correspond to those reported in this work (Li *et al*., 2020). The application of *Streptomyces* sp. on banana crop infested with *Fusarium oxysporum* f. sp. *cubense* tropical race 4 (TR4) increased the activities of defense-related enzymes (PPO, POD, and SOD) compared to plants treated alone with *F. oxysporum* TR4 or the control treatment (distilled water), results in correspondence to those obtained in this work (Zhang *et al*., 2021).

Research on marine actinomycetes has focused on *in vitro* conditions, therefore, there are few works on the study of marine actinomycetes *in vivo* conditions. The application of marine actinomycete is an option as a biocontrol agent for *F. solani* in tomato crops.

Conclusions

The four strains of marine actinomycetes produced siderophores and inhibited the mycelial growth of *F. solani* by iron competition in the culture media. Strain A19 showed the highest inhibition of *F. solani* by iron competition with a PICR of 74.28%. Only two strains of marine actinomycetes inhibited the phytopathogen by VOCs production, A19 presented the highest PICR with 76.75%. The actinomycete of marine origin (A19) and the terrestrial actinomycete (ED48) showed the greatest reduction of the disease caused by *F. solani*, compared to the synthetic fungicide. In the growth variables evaluated, the marine

actinomycete (A19) had the greatest protective effect on tomato plants against *F. solani*. The actinomycetes presented lower DI than the synthetic fungicide treatment. The marine actinomycete with the phytopathogen treatment (A19+F) presented the highest activity of the enzymes evaluated (SOD, CAT, POD, and PAL) showing significant differences with the rest of the treatments. The application of marine actinomycetes reduced plant damage caused by *F. solani.* Marine environments are a source of microorganisms that can act as biocontrol agents against phytopathogens.

Authors' Contributions

Conceptualization, J.A.T.-R., L.G.H.-M. and J.J.R.-P.; methodology, J.A.T.-R., L.G.H.-M. and J.J.R.-P.; validation, L.H.-A. and B.L.LL.-F.; writing, J.A.T.-R., L.G.H.-M. and B.L.LL.-F.; review and editing, L.G.H.-M. and J.J.R.-P; visualization, L.G.H.-M. and J.A.T.-R.; supervision, L.G.H.-M. and J.A.T.-R.; project administration, L.G.H.-M. All authors read and approved the final manuscript.

Ethical approval (for researches involving animals or humans)

Not applicable.

Acknowledgements

The first author is grateful to Consejo Nacional de Ciencia y Tecnologia (CONACYT), Mexico for Grant No. 2021910046 to carry out the Doctoral thesis project and to the State Technical University of Quevedo, for the support granted through the Competitive Fund for Scientific and Technological Research (FOCICYT) 8th Call, through the project PFOC8-10-2021 "Stimulation of biological and agricultural productivity by the application of silicon in horticultural crops.

Conflict of Interests

The authors declare that there are no conflicts of interest related to this article.

References

Akbar K, Abbasi FM, Sajid M, Ahmad M, Khan ZU, Ali H (2016). Marker-assisted selection and pyramiding of I1 and Ph3 genes for multiple disease resistance in tomato through PCR analysis. International Journal of Biosciences 9(3):108-113.

Alblooshi AA, Purayil GP, Saeed EE, Ramadan GA, Tariq S, Altaee AS, ... AbuQamar SF (2022). Biocontrol potential of endophytic actinobacteria against *Fusarium solani*, the causal agent of sudden decline syndrome on date palm in the UAE. Journal of Fungi 8(1):8. *https://doi.org/10.3390/jof8010008*

Al-Dhabi NA, Esmail GA, Mohammed Ghilan AK, Valan Arasu M (2019). Composting of vegetable waste using microbial consortium and biocontrol efficacy of *Streptomyces* Sp. Al-Dhabi 30 isolated from the Saudi Arabian environment for sustainable agriculture. Sustainability 11(23):6845. *https://doi.org/10.3390/su11236845*

Allali K, Goudjal Y, Zamoum M, Bouznada K, Sabaou N, Zitouni A (2019). *Nocardiopsis dassonvillei* strain MB22 from the Algerian Sahara promotes wheat seedlings growth and potentially controls the common root rot pathogen *Bipolaris sorokiniana*. Journal of Plant Pathology 101:1115-1125. *https://doi.org/10.1007/s42161-019-00347-x*

Ameen F, AlNadhari S, Al-Homaidan AA (2021). Marine microorganisms as an untapped source of bioactive compounds. Saudi Journal of Biological Sciences 28(1):224-231. *https://doi.org/10.1016/j.sjbs.2020.09.052*

Ayed A, Kalai-Grami L, Ben Slimene I, Chaouachi M, Mankai H, Karkouch I, ... Limam F (2021). Antifungal activity of volatile organic compounds from *Streptomyces* sp. strain S97 against *Botrytis cinerea*. Biocontrol Science and Technology 31(12):1330-1348. *https://doi.org/10.1080/09583157.2021.1947982*

Behera HT, Mojumdar A, Behera SS, Das S, Ray L (2022). Biocontrol of wilt disease of rice seedlings incited by *Fusarium oxysporum* through soil application of *Streptomyces chilikensis* RC1830. Letters in Applied Microbiology 75(5):1366-1382. *https://doi.org/10.1111/lam.13807*

Boukaew S, Yossan S, Cheirsilp B, Prasertsan P (2022). Impact of environmental factors on *Streptomyces* spp. metabolites against *Botrytis cinerea*. Journal of Basic Microbiology 62(5):611-622. *https://doi.org/10.1002/jobm.202100423*

Campos MD, Félix MDR, Patanita M, Materatski P, Albuquerque A, Ribeiro JA, ... Varanda C (2022). Defense strategies: The role of transcription factors in tomato–pathogen interaction. Biology 11(2):235. *https://doi.org/10.3390/biology11020235*

Cech R, Zaller JG, Lyssimachou A, Clausing P, Hertoge K, Linhart C (2023). Pesticide drift mitigation measures appear to reduce contamination of non-agricultural areas, but hazards to humans and the environment remain. Science of the Total Environment 854:158814. *https://doi.org/10.1016/j.scitotenv.2022.158814*

Cruz AF, Silva LF, Sousa TV, Nicoli A, de Paula Junior TJ, Caixeta ET, ... Zambolim L (2018). Molecular diversity in *Fusarium oxysporum* isolates from common bean fields in Brazil. European Journal of Plant Pathology 152:343-354. *https://doi.org/10.1007/s10658-018-1479-7*

Díaz-Díaz M, Bernal-Cabrera A, Trapero A, Medina-Marrero R, Sifontes-Rodríguez S, Cupull-Santana RD, ... Agustí-Brisach C (2022). Characterization of actinobacterial strains as potential biocontrol agents against *Macrophomina phaseolina* and *Rhizoctonia solani*, the main soil-borne pathogens of *Phaseolus vulgaris* in Cuba. Plants 11(5):645. *https://doi.org/10.3390/plants11050645*

Djebaili R, Pellegrini M, Ercole C, Farda B, Kitouni M, Del Gallo M (2021). Biocontrol of soil-borne pathogens of *Solanum lycopersicum* L. and *Daucus carota* L. by plant growth-promoting actinomycetes: *In vitro* and in planta antagonistic activity. Pathogens 10(10):1305. *https://doi.org/10.3390/pathogens10101305*

Fadhilah QG, Santoso I, Maryanto AE, Abdullah S, Yasman Y (2021). Evaluation of the antifungal activity of marine actinomycetes isolates against the phytopathogenic fungi *Colletotrichum siamense* KA: A preliminary study for new antifungal compound discovery. Pharmacia 68(4):837-843.

Fang H, Han L, Cui Y, Xue Y, Cai L, Yu Y (2016). Changes in soil microbial community structure and function associated with degradation and resistance of carbendazim and chlortetracycline during repeated treatments. Science of the Total Environment 572:1203-1212. *https://doi.org/10.1016/j.scitotenv.2016.08.038*

García-Estrada RS, Diaz-Lara A, Aguilar-Molina VH, Tovar-Pedraza JM (2022). Viruses of economic impact on tomato crops in Mexico: From diagnosis to management—A review. Viruses 14(6):1251. *https://doi.org/10.3390/v14061251*

Gebily DA, Ghanem GA, Ragab MM, Ali AM, Soliman NEDK, 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. Egyptian Journal of Biological Pest Control 31:1-15.

Ghosh SK, Bera T, Chakrabarty AM (2020). Microbial siderophore–A boon to agricultural sciences. Biological Control 144:104214. *https://doi.org/10.1016/j.biocontrol.2020.104214*

Gong Y, Liu JQ, Xu MJ, Zhang CM, Gao J, Li CG, ... Qin S (2022). Antifungal volatile organic compounds from *Streptomyces setonii* WY228 control black spot disease of sweet potato. Applied and Environmental Microbiology 88(6):e02317-21. *https://doi.org/10.1128/aem.02317-21*

Hao L, Zheng X, Wang Y, Li S, Shang C, Xu Y (2019). Inhibition of tomato early blight disease by culture extracts of a *Streptomyces puniceus* isolate from mangrove soil. Phytopathology 109(7):1149-1156. *https://doi.org/10.1094/PHYTO-12-18-0444-R*

He DC, He MH, Amalin DM, Liu W, Alvindia DG, Zhan J (2021). Biological control of plant diseases: An evolutionary and eco-economic consideration. Pathogens 10(10):1311. *https://doi.org/10.3390/pathogens10101311*

Hernández Montiel LG, Rivas García T, Romero Bastidas M, Chiquito Contreras CJ, Ruiz Espinoza FH, Chiquito Contreras RG (2018). Antagonistic potential of bacteria and marine yeasts for the control of phytopathogenic fungi. Revista Mexicana de Ciencias Agrícolas 9:4311-4321. *https://doi.org/10.29312/remexca.v0i20.1000*

Igarashi M, Sawa R, Umekita M, Hatano M, Arisaka R, Hayashi C, ... Kato C (2021). *Sealutomicins*, new enediyne antibiotics from the deep-sea actinomycete *Nonomuraea* sp. MM565M-173N2. The Journal of Antibiotics 74(5):291-299. *https://doi.org/10.1038/s41429-020-00402-1*

Ismaila AA, Ahmad K, Siddique Y, Wahab MAA, Kutawa AB, Abdullahi A, ... Abdullah SNA (2023). *Fusarium* wilt of banana: Current update and sustainable disease control using classical and essential oils approaches. Horticultural Plant Journal 9(1):1-28. *https://doi.org/10.1016/j.hpj.2022.02.004*

Jepsen T, Jensen B, Jørgensen NO (2022). Volatiles produced by *Streptomyces* spp. delay rot in apples caused by *Colletotrichum acutatum*. Current Research in Microbial Sciences 3:100121. *https://doi.org/10.1016/j.crmicr.2022.100121*

Johansson LH, Borg LH (1988). A spectrophotometric method for determination of catalase activity in small tissue samples. Analytical biochemistry 174(1):331-336. *https://doi.org/10.1016/0003-2697(88)90554-4*

Kaari M, Joseph J, Manikkam R, Sreenivasan A, Venugopal G, Alexander B, ... Krishnan S (2022). Anti-biofilm activity and biocontrol potential of *Streptomyces* cultures against *Ralstonia solanacearum* on tomato plants. Indian Journal of Microbiology 62:32-39. *https://doi.org/10.1007/s12088-021-00963-1*

Korayem AS, Abdelhafez AA, Zaki MM, Saleh EA (2020). Biological control of green bean damping-off disease caused by *Rhizoctonia solani* by *Streptomyces parvulus* strain 10d. Egyptian Journal of Microbiology 55:87-94. *https://dx.doi.org/10.21608/ejm.2020.22329.1145*

Li W, Ren L, Li Q, Zhang D, Jin X, Fang W, ... Cao A (2023). Evaluation of ethylicin as a potential soil fumigant in commercial tomato production in China. Science of the Total Environment 854:158520. *https://doi.org/10.1016/j.scitotenv.2022.158520*

Li X, Li B, Cai S, Zhang Y, Xu M, Zhang C, ... Qin S (2020). Identification of rhizospheric actinomycete *Streptomyces lavendulae* sps-33 and the inhibitory effect of its volatile organic compounds against *Ceratocystis fimbriata* in postharvest sweet potato (*Ipomoea batatas* (L.) Lam.). Microorganisms 8(3):319. *https://doi.org/10.3390/microorganisms8030319*

Li X, Li K, Zhou D, Zhang M, Qi D, Jing T, ... Xie J (2021). Biological control of banana wilt disease caused by *Fusarium oxyspoum* f. sp. *Cubense* using *Streptomyces* sp. H4. Biological Control 155:104524. *https://doi.org/10.1016/j.biocontrol.2020.104524*

Liu Q, Tian JH, Liu HC, Zhou YG, Xin YH (2020). *Cryobacterium ruanii* sp. nov. and *Cryobacterium* breve sp. nov., isolated from glaciers. International Journal of Systematic and Evolutionary Microbiology 70(3):1918-1923. *https://doi.org/10.1099/ijsem.0.003994*

Maluin FN, Hussein MZ (2020). Chitosan-based agronanochemicals as a sustainable alternative in crop protection. Molecules 25(7):1611. *https://doi.org/10.3390/molecules25071611*

Marlatt ML, Correll JC, Kaufmann P, Cooper PE (1996). Two genetically distinct populations of *Fusarium oxysporum* f. sp. *lycopersici* race 3 in the United States. Plant Disease 80(12):1336-1342.

Meena LI, Rajeswari E, Ahiladevi P, Kamalakannan A, Kalaiselvi T (2022). Antifungal potential of *Streptomyces rameus* GgS 48 against mungbean root rot [*Rhizoctonia bataticola* (Taub.) Butler]. Journal of Biosciences 47(1):1-17.

Morrison TA, Buxton DR (1993). Activity of phenylalanine ammonia-lyase, tyrosine ammonia-lyase, and cinnamyl alcohol dehydrogenase in the maize stalk. Crop Science 33(6):1264-1268. *https://doi.org/10.2135/cropsci1993.0011183X003300060030x*

Ossowicki A, Jafra S, Garbeva P (2017). The antimicrobial volatile power of the rhizospheric isolate *Pseudomonas donghuensis* P482. PloS One 12(3):e0174362. *https://doi.org/10.1371/journal.pone.0174362*

Paoletti F, Aldinucci D, Mocali A, Caparrini A (1986). A sensitive spectrophotometric method for the determination of superoxide dismutase activity in tissue extracts. Analytical Biochemistry 154(2):536-541. *https://doi.org/10.1016/0003-2697(86)90026-6*

Puja H, Mislin GL, Rigouin C (2023). Engineering siderophore biosynthesis and regulation pathways to increase diversity and availability. Biomolecules 13(6):959. *https://doi.org/10.3390/biom13060959*

Qi D, Zou L, Zhou D, Zhang M, Wei Y, Li K, ... Xie J (2022). Biocontrol potential and antifungal mechanism of a novel *Streptomyces sichuanensis* against *Fusarium oxysporum* f. sp. *cubense* tropical race 4 *in vitro* and *in vivo*. Applied Microbiology and Biotechnology 106(4):1633-1649. *https://doi.org/10.1007/s00253-022-11788-3*

Salwan R, Sharma M, Sharma A, Sharma V (2023). Insights into plant beneficial microorganism-triggered induced systemic resistance. Plant Stress 7:100140. *https://doi.org/10.1016/j.stress.2023.100140*

Saravanakumar K, Yu C, Dou K, Wang M, Li Y, Chen J (2016). Synergistic effect of *Trichoderma*-derived antifungal metabolites and cell wall degrading enzymes on enhanced biocontrol of *Fusarium oxysporum* f. sp. *cucumerinum.* Biological Control 94:37-46. *https://doi.org/10.1016/j.biocontrol.2015.12.001*

Schwyn B, Neilands JB (1987). Universal chemical assay for the detection and determination of siderophores. Analytical biochemistry 160(1):47-56. *https://doi.org/10.1016/0003-2697(87)90612-9*

Srivastava MK, Dwivedi UN (1998). Salicylic acid modulates glutathione metabolism in pea seedlings. Journal of Plant physiology 153(3-4):409-414. *https://doi.org/10.1016/S0176-1617(98)80168-5*

Torres-Rodriguez JA, Reyes-Pérez JJ, Castellanos T, Angulo C, Quinones-Aguilar EE, Hernandez-Montiel LG (2022a) Identi-fication and morphological characterization of marine actinomycetes as biocontrol agents of *Fusarium solani* in tomato. Revista de la Facultad de Agronomía, Universidad del Zulia 39:e223915.

Torres-Rodriguez JA, Reyes-Pérez JJ, Quiñones-Aguilar EE, Hernandez-Montiel LG (2022b). Actinomycete potential as biocontrol agent of phytopathogenic fungi: mechanisms, source, and applications. Plants 11(23):3201. *https://doi.org/10.3390/plants11233201*

Vijayabharathi R, Gopalakrishnan S, Sathya A, Vasanth Kumar M, Srinivas V, Mamta S (2018). *Streptomyces* sp. as plant growth-promoters and host-plant resistance inducers against *Botrytis cinerea* in chickpea. Biocontrol Science and Technology 28(12):1140-1163. *https://doi.org/10.1080/09583157.2018.1515890*

Wang S, Fang X, Liang K, Li S, Han S, Zhu T (2022). Cloning, expression and antifungal effect of the recombinant chitinase from *Streptomyces sampsonii* KJ40. Ciência Rural 53:e20210663. *https://doi.org/10.1590/0103-8478cr20210663*

Xia X, Liu J, Huang L, Zhang X, Deng Y, Li F, ... Huang R (2022). Molecular details of actinomycin D-Treated MRSA revealed via high-dimensional data. Marine Drugs 20(2):114. *https://doi.org/10.3390/md20020114*

Yamada S, Nabe K, Izuo N, Nakamichi K, Chibata I (1981). Production of L-phenylalanine from trans-cinnamic acid with *Rhodotorula glutinis* containing L-phenylalanine ammonia-lyase activity. Applied and environmental microbiology 42(5):773-778. *https://doi.org/10.1128/aem.42.5.773-778.1981*

Yandigeri MS, Malviya N, Solanki MK, Shrivastava P, Sivakumar G (2015). Chitinolytic *Streptomyces vinaceusdrappus* S5MW2 isolated from Chilika lake, India enhances plant growth and biocontrol efficacy through chitin supplementation against *Rhizoctonia solani*. World Journal of Microbiology and Biotechnology 31:1217-1225. *https://doi.org/10.1007/s11274-015-1870-x*

Yang D, Wang L, Wang T, Zhang Y, Zhang S, Luo Y (2021). Plant growth-promoting rhizobacteria HN6 induced the change and reorganization of *Fusarium microflora* in the rhizosphere of banana seedlings to construct a healthy banana microflora. Frontiers in Microbiology 12:685408. *https://doi.org/10.3389/fmicb.2021.685408*

Zhang L, Zhang H, Huang Y, Peng J, Xie J, Wang W (2021). Isolation and evaluation of rhizosphere actinomycetes with potential application for biocontrolling *Fusarium* wilt of banana caused by *Fusarium oxysporum* f. sp. *cubense* tropical race 4. Frontiers in Microbiology 12:763038. *https://doi.org/10.3389/fmicb.2021.763038*

Zhao X, Zhou J, Tian R, Liu Y (2022). Microbial volatile organic compounds: Antifungal mechanisms, applications, and challenges. Frontiers in Microbiology 13:922450. *https://doi.org/10.3389/fmicb.2022.922450*

Zhou D, Jing T, Chen Y, Yun T, Qi D, Zang X, ... Xie J (2022). Biocontrol potential of a newly isolated *Streptomyces* sp. HSL-9B from mangrove forest on postharvest anthracnose of mango fruit caused by *Colletotrichum gloeosporioides*. Food Control 135:108836. *https://doi.org/10.1016/j.foodcont.2022.108836*

Notes:

- Material disclaimer: The authors are fully responsible for their work and they hold sole responsibility for the articles published in the journal.
- Maps and affiliations: The publisher stay neutral with regard to jurisdictional claims in published maps and institutional affiliations.
- Responsibilities: The editors, editorial board and publisher do not assume any responsibility for the article's contents and for the authors' views expressed in their contributions. The statements and opinions published represent the views of the authors or persons to whom they are credited. Publication of research information does not constitute a recommendation or endorsement of products involved.