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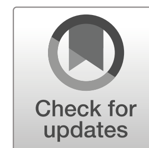

Antifungal potential of Lauraceae rhizobacteria from a tropical montane cloud forest against *Fusarium* spp.

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Abstract

The occurrence of pests and diseases can affect plant health and productivity in ecosystems that are already at risk, such as tropical montane cloud forests. The use of naturally occurring microorganisms is a promising alternative to mitigate forest tree fungal pathogens. The objectives of this study were to isolate rhizobacteria associated with five Lauraceae species from a Mexican tropical montane cloud forest and to evaluate their antifungal activity against *Fusarium solani* and *F. oxysporum*. Fifty-six rhizobacterial isolates were assessed for mycelial growth inhibition of *Fusarium* spp. through dual culture assays. Thirty-three isolates significantly reduced the growth of *F. solani*, while 21 isolates inhibited that of *F. oxysporum*. The nine bacterial isolates that inhibited fungal growth by more than 20% were identified through 16S rDNA gene sequence analysis; they belonged to the genera *Streptomyces*, *Arthrobacter*, *Pseudomonas*, and *Staphylococcus*. The volatile organic compounds (VOC) produced by these nine isolates were evaluated for antifungal activity. Six isolates (*Streptomyces* sp., *Arthrobacter* sp., *Pseudomonas* sp., and *Staphylococcus* spp.) successfully inhibited *F. solani* mycelial growth by up to 37% through VOC emission, while only the isolate INECOL-21 (*Pseudomonas* sp.) inhibited *F. oxysporum*. This work provides information on the microbiota of Mexican Lauraceae and is one of the few studies identifying forest tree–associated microbes with inhibitory activity against tree pathogens.

Keywords Actinobacteria · *Pseudomonas* · *Persea schiedeana* · Rhizosphere · Volatile organic compounds

Introduction

Tropical montane cloud forests, despite their limited distribution, have been acknowledged as one of the world's most diverse ecosystems [10]. They cover about 2.5% of tropical forest land worldwide and are characterized by the frequent presence of clouds and mist, a high level of species endemism, and the presence of very diverse communities [58]. The importance of tropical montane cloud forests as critical providers of ecosystem services is widely recognized, for example, because of their role in the maintenance of the hydrological cycle [9]. However, this ecosystem is considered as one of the most threatened ecosystems globally [13], climate change, illegal logging, and conversion to pastures being the main causes behind the disturbance of tropical montane cloud forests [11].

Another threat facing these forests is the occurrence of pests and diseases that could affect plant health and productivity, and ultimately forest stability. Examples of such diseases are laurel wilt and *Fusarium* dieback, both caused by fungi associated with invasive ambrosia beetles. Laurel wilt is a disease affecting the Lauraceae family, caused by the fungus *Raffaelea lauricola* T.C. Harr., Fraedrich & Aghayeva and vectored by the beetle *Xyleborus glabratus* Eichhoff [28]. On the other hand, *Fusarium* dieback is caused by various fungi, including *Fusarium euwallaceae* Freeman, Mendel, Aoki & O'Donnell and *F. kuroshium* F. Na, J. D. Carrillo &

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A. Eskalen, which form a symbiotic relationship with the polyphagous shot hole borer (PSHB) and the Kuroshio shot hole borer (KSHB) (*Euwallacea* spp. nr. *fornicatus*) respectively [40, 43]. *Fusarium* dieback affects a large number of plant species, such as those belonging to the Lauraceae, and is considered to present a real threat to natural forests [45]. Since Lauraceae species are relevant members of the tree community of tropical montane cloud forests [39], it is critical to find strategies to protect them against the attack of fungal pathogens.

Different management strategies have been explored in order to mitigate the negative impacts caused by fungal phytopathogens in forest ecosystems. The application of agrochemicals, in addition to silvicultural management, is a common practice [14]. The use of naturally occurring microorganisms as biological control agents is a promising alternative that could protect tree health and productivity while meeting the increasing demand for environment friendly methods [14]. The rhizosphere is a particularly interesting habitat to isolate microorganisms, since it harbors a large microbial diversity which is critical for plant growth and health [50].

Plant–microbe interactions are mediated by the secretion of different chemical compounds, which may present biological activities such as plant growth promotion or fungal inhibition [3, 5, 41]. Rhizobacteria such as *Bacillus* spp., *Pseudomonas* spp., and Actinobacteria have been shown to successfully inhibit the growth of pathogenic fungi *Fusarium circinatum* Nirenberg & O'Donnell and *Monilia perniciosa* (Stahel) Aime & Phillips-Mora, oomycete *Phytophthora infestans* (Mont.) de Bary, or bacteria *Ralstonia solanacearum* (Smith) Yabuuchi et al. [12, 15, 30, 32, 54], through the emission of antifungal diffusible or volatile compounds. Rhizobacteria have shown to be effective antagonists of diverse *Fusarium* species. For example, avocado rhizobacteria have shown to successfully inhibit the growth of *F. euwallaceae* and *Fusarium* sp., causal agents of *Fusarium* dieback in *Persea americana* Mill. [25, 26]. Bacterial strain *Streptomyces goshikiensis* YCXU, isolated from the rhizosphere of cucumber, significantly reduced the incidence of *Fusarium* wilt caused by *F. oxysporum* f. sp. *niveum*, in watermelon, by producing antifungal compounds and inducing stress resistance in the plant [21]. Other reports demonstrated the potential of native rhizobacteria, mainly from the genera *Bacillus* and *Pseudomonas*, as biological control agents of *F. solani* in turmeric or chili plants [16, 56] and as antagonists of *F. oxysporum* f. sp. *cubense*, responsible of *Fusarium* wilt in banana and watermelon, through the emission of volatile organic compounds (VOC) [61, 65].

Although the plant and animal diversity of tropical montane cloud forests has been widely studied [24], little is known about the diversity of its microorganisms and the biotechnological potential they may represent. Cazorla and Mercado-Blanco [14] recently highlighted the scarcity of studies investigating biological control options for tree diseases. Focusing the search for microbial biological control agents on the microorganisms inhabiting tropical montane cloud forests could tackle two issues: gaining information on the existing microbial diversity in this threatened ecosystem and finding naturally occurring microorganisms with inhibitory activity against tree pathogens. The objectives of the present work were therefore to isolate rhizobacteria associated with five Lauraceae species from a tropical montane cloud forest in Xalapa, Mexico, and to evaluate their antifungal activity through in vitro antagonism assays against the ubiquitous fungal phytopathogens *F. solani* and *F. oxysporum.*

Materials and methods

Isolation of rhizobacteria

Five trees from different species of Lauraceae were selected within the Santuario del Bosque de Niebla, a protected area of tropical montane cloud forest located in Xalapa, State of Veracruz, Mexico. Species were identified as *Ocotea psychotrioides* Kunth, *Persea schiedeana* Nees, *Damburneya salicifolia* (Kunth) Trofimov & Rohwer, *Persea longipes* (Schltdl.) Meisn, and *Aiouea effusa* (Meisn.) R. Rohde & Rohwer.

Four rhizosphere samples were taken per tree, approximately 50 cm away from the trunk and at a depth of 5–10 cm, where most of the feeder roots could be found, following the method reported in Guevara-Avendaño et al. [25]. Samples from a same tree were mixed to obtain one composite sample of rhizosphere soil per tree. Samples were transported to the laboratory in a cooler and immediately processed upon arrival. Loose soil was removed from the roots by shaking them gently, and the remaining soil, which was strongly adhered to the roots, was considered as rhizosphere soil. Solutions were prepared from 1 g of rhizosphere soil and 99 ml of distilled water and homogenized by shaking vigorously. Dilutions of 1×10^{-4} were then streaked onto Petri dishes with Luria–Bertani agar (LB, Sigma–Aldrich), in duplicate, and plates were incubated at 30 °C for 7 days. Bacterial isolates were taken from the plates as they grew and subcultured in LB until pure cultures were obtained. Bacterial isolates from the same tree were then grouped into morphotypes, based on colonial morphology (form, color, and texture) and cellular morpho-anatomical criteria (shape and Gram-staining results) (Online Resource 1).

In vitro direct antagonism assays against *F. solani* and *F. oxysporum*

One bacterial isolate per morphotype (56 morphotypes in total) was randomly selected to be screened for antifungal

activity against *F. solani* and *F. oxysporum*. Strains of *F. solani* and *F. oxysporum*, isolated from chili (*Capsicum annum* L.) and vanilla (*Vanilla planifolia* Jacks. ex. Andrew) respectively, were provided by Dr. Mauricio Luna-Rodríguez (Universidad Veracruzana, Mexico). Chili is known to be affected by *Fusarium* wilt and vanilla by root and stem rot caused by these *Fusarium* species [1, 2, 56]. The fungal strains were cultured on potato dextrose agar (PDA) with 150 ppm chloramphenicol (Sigma–Aldrich) and incubated at 28 °C, 7 days before dual plating. Bacterial isolates were first re-streaked onto LB and incubated at 30 °C, 48 h prior to the implementation of the dual culture assays.

One plug of 5 mm of diameter was taken from the border of the mycelium of each fungus and placed on the center of a PDA plate. Each one of the 56 bacterial isolates to be tested for antifungal activity was then streaked on two opposite sides of the mycelial plug, at a distance of approximately 2 cm from the plug. A duplicate plate with the same combination (bacterial isolate × fungal species) was established so that two Petri dishes were prepared per bacterial isolate. Petri dishes were then incubated at 30 °C for 7 days.

At day 7, mycelium radial growth was measured from the center of mycelial disc towards the bacterial treatment (r) and the control (R), which corresponded to the maximum growth of the fungus away from the bacteria. Two measurements were taken per plate (for the two bacterial streaks), for a total of four measurements per bacterial treatment. The percentage of mycelial growth inhibition was then calculated with the following formula: % inhibition = $[(R - r) \quad R] \times 100$.

Molecular identification of bacterial isolates with antifungal activity

Bacterial isolates presenting inhibition percentages higher than 20% for at least one of the tested fungi were identified through 16S rRNA gene sequencing. DNA was extracted from bacterial isolates using the DNeasy® Blood and Tissue kit (Qiagen, Germany), as reported in Méndez-Bravo et al. [41] and following the manufacturer's instructions. The 16S rRNA region was amplified by PCR using universal primers 27F (5′-AGAGTTTGATCMTGGCTCAG-3′) and 1492R (5′-TACGGYTACCTTGTTACGACTT-3′), in 50-μl reactions containing 25 ng of template DNA, 1× of Taq buffer, 200 μM of each dNTP, 1.25 mM of $MgCl_2$, 0.4 μM of each primer, and 0.5 U of Taq DNA polymerase (Qiagen, Germany). Sterile milli-Q water was used as template in controls. Reactions were performed in a SureCycler 8800 (Agilent, CA) under the following conditions: initial denaturation at 95 °C for 4 min; 30 cycles of denaturation at 95 °C for 45 s, annealing at 53 °C for 45 s, and extension at 72 °C for 2 min; and a final extension step at 72 °C for 5 min. Successfully amplified DNA products were purified using QiaQuick® Purification kit (Qiagen, Hilden, Germany), following the manufacturer's instructions. Purified DNA amplicons were then sent to Macrogen Inc. for sequencing. Sequences were deposited in GenBank (accession numbers MF767291 to MF767299).

In vitro indirect antagonism assays against *F. solani* and *F. oxysporum*

The bacterial isolates that showed inhibition of *F. solani* or *F. oxysporum* larger than 20% in the direct antagonism assays were further evaluated to determine their antifungal activity against both pathogenic fungi through the emission of VOC. These bacterial isolates were re-streaked onto LB and incubated for 48 h at 30 °C prior to implementing the antagonism assays. The isolates of *F. solani* and *F. oxysporum* were incubated on PDA plates, at room temperature, for 7 days. The indirect antagonism assays were carried out with the two-sealed-baseplates method described in Guevara-Avendaño et al. [26]. Briefly, each bacterial isolate ($n = 9$) was streaked onto a baseplate containing LB medium. Another baseplate was prepared with a disc of 5-mm diameter of fungal mycelium placed in its center, on PDA medium. Both baseplates were sealed with Parafilm® and incubated at 30 °C, during 7 days. Each bacterial isolate was tested for antifungal activity in triplicate against both *F. solani* and *F. oxysporum*. Three assays were set up without bacterial treatments (LB only) and used as controls.

At day 7, mycelium diameter was measured in treatments where mycelium was exposed to the bacterial VOC (d) and in control conditions where mycelium was growing in the absence of bacteria (D). The percentage of mycelial growth inhibition was then calculated with the following formula: % inhibition = $[(D - d) \quad D] \times 100$.

Data analysis

Data from the direct and indirect antagonism assays were analyzed with the SigmaStat v.4 software. Mycelial growth inhibition produced by each bacterial was contrasted against its respective control with a Student t test or a Mann–Whitney U test according to the normality of the data ($n = 4$ in direct antagonism assays; $n = 3$ in indirect antagonism assays). Differences were considered as significant when $P \leq 0.05$.

Sequences were manually checked in BioEdit 7.2.5. [27] and aligned with the multiple alignment program MUSCLE in MEGA 7 [35]. The edited sequences and their best matches in GenBank nucleotide database (www.ncbi.nlm.nih.gov) were used to construct the alignment. Subsequently, a Neighbor-Joining tree was constructed in MEGA 7, using a Kimura two-parameter model with Gamma distribution and a bootstrap method with 1000 replicates.

Results

A total of 83 bacterial isolates were obtained from the rhizosphere of the five selected Lauraceae species. Nine bacterial isolates were obtained from *O. psychotrioides*, seven isolates from that of *P. schiedeana*, 20 isolates from that of *D. salicifolia*, 21 from that of *P. longipes*, and 26 from the rhizosphere of *A. effusa*. After grouping the isolates into morphotypes, 56 isolates (one representative of each morphotype) were selected to be evaluated in antagonism assays against *Fusarium* spp. (seven isolates obtained from *O. psychotrioides* and from *P. schiedeana* respectively, 13 from *D. salicifolia*, 12 from *P. longipes*, and 17 from *A. effusa*).

The mycelial growth of *F. solani* was significantly inhibited by 33 of the 56 tested bacterial isolates (Online Resource 2), with inhibition percentages ranging from 6 to 31%. On the other hand, 21 isolates significantly reduced the growth of *F. oxysporum*, with inhibition percentages ranging from 6 to 20%; 18 of these 21 isolates also presented antifungal activity against *F. solani* (Online Resource 2).

Nine bacterial isolates presented inhibition percentages that were larger than 20%, for at least one of the fungal pathogens (Table 1; Fig. 1). Bacterial isolates INECOL-8, INECOL-11, INECOL-19, INECOL-21, INECOL-27, INECOL-57, INECOL-65.2, and INECOL-100 reduced the growth of *F. solani* by more than 20%. Five of these isolates also presented significant antagonistic activity against *F. oxysporum*. However, bacterial isolate INECOL-65.1 was the only isolate to reduce by 20% the growth of *F. oxysporum* (Figs. 1 and 2). The 16S rDNA sequences from these nine isolates showed that they belonged to the bacterial genera *Arthrobacter*, *Pseudomonas*, *Staphylococcus*, and *Streptomyces* (Table 2; Fig. 3). Isolates INECOL-21, identified as *Pseudomonas* sp., and INECOL-27, identified as *Arthrobacter* sp., exerted the strongest antagonistic activity against *F. solani* (Fig. 2). Both isolates were obtained from the rhizosphere of *P. schiedeana*;

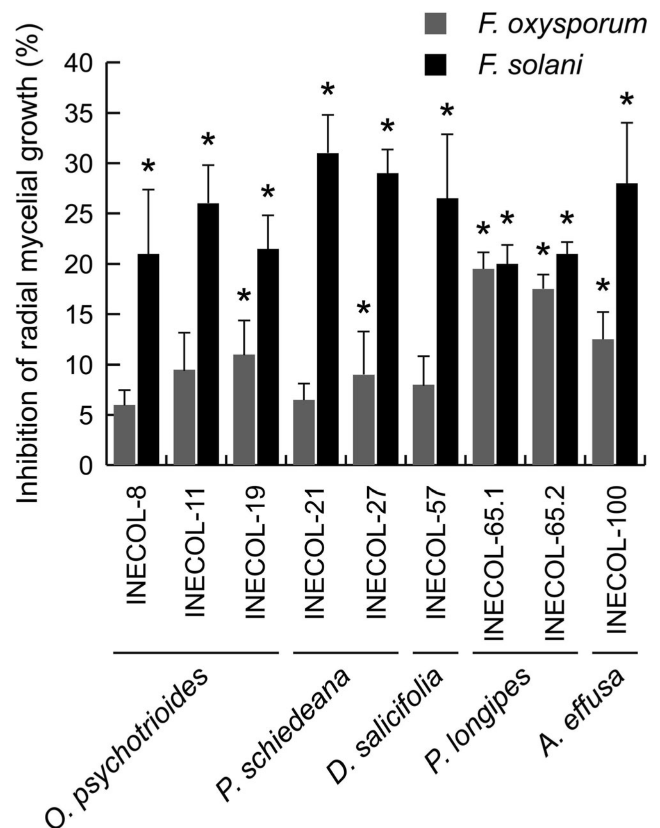

Fig. 1 Inhibition percentage of mycelial radial growth of *Fusarium solani* and *F. oxysporum* by the nine sequenced bacterial isolates ($n = 4$ replicates). Bars represent standard errors (s.e.). Asterisk sign represents a significant inhibition of mycelial radial growth in comparison with a control (Student's *t* test or the Mann–Whitney *U* test depending on data distribution, $P \leq 0.05$)

Table 1 Mycelial radial growth of *F. solani* and *F. oxysporum* confronted with the rhizobacterial isolates that were able to reduce fungal growth by more than 20% in direct antagonism assays

Bacterial isolate	Mycelial radial growth of *F. solani* (cm)		Mycelial radial growth of *F. oxysporum* (cm)	
	Treatment	Control	Treatment	Control
INECOL-8	*2.53 ± 0.40†*	*3.15 ± 0.13*	3.35 ± 0.13	3.48 ± 0.21
INECOL-11	*2.20 ± 0.22**	*2.83 ± 0.24*	3.28 ± 0.10	3.58 ± 0.15
INECOL-19	*2.10 ± 0.22**	*2.60 ± 0.25*	*3.20 ± 0.16**	*3.50 ± 0.14*
INECOL-21	*2.43 ± 0.10**	*3.35 ± 0.37*	3.38 ± 0.17	3.65 ± 0.17
INECOL-27	*2.18 ± 0.17†*	*3.08 ± 0.15*	*3.20 ± 0.14**	*3.48 ± 0.15*
INECOL-57	*1.83 ± 0.05†*	*2.50 ± 0.36*	3.20 ± 0.18	3.45 ± 0.10
INECOL-65.1	*2.25 ± 0.13**	*2.78 ± 0.10*	*2.00 ± 0.00†*	*2.48 ± 0.05*
INECOL-65.2	*2.18 ± 0.05**	*2.73 ± 0.05*	*1.98 ± 0.10**	*2.35 ± 0.13*
INECOL-100	*2.28 ± 0.30**	*3.10 ± 0.22*	*3.05 ± 0.13**	*3.40 ± 0.14*

Values represent the average of four replicates ± standard error. Italicized values show significant differences between the treatment and its respective control

*$P \leq 0.05$, Student's *t* test (normal distribution)

†$P \leq 0.05$, the Mann–Whitney *U* test (non-parametric distribution)

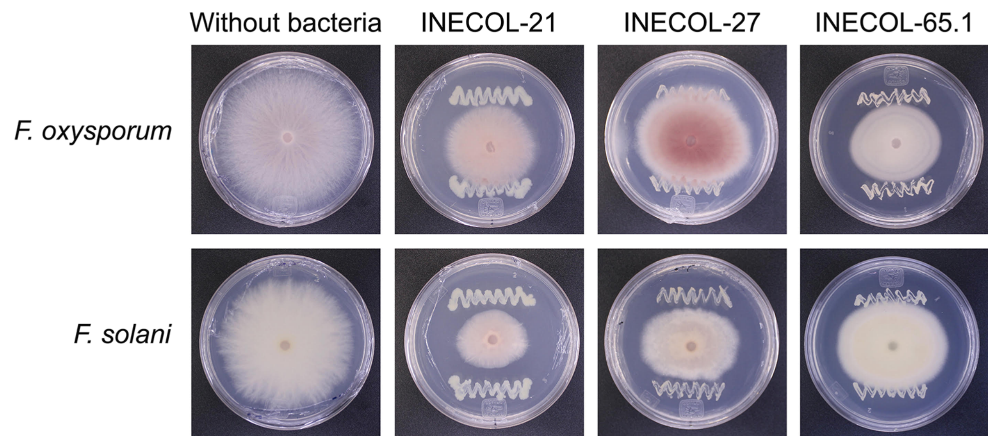

Fig. 2 Dual culture assays to evaluate the antagonism of isolates INECOL-21 (*Pseudomonas* sp.), INECOL-27 (*Arthrobacter* sp.), and INECOL-65.1 (*Staphylococcus* sp.) against *F. solani* and *F. oxysporum*. Asterisk sign represents a significant inhibition of mycelial radial growth in comparison with a control. Fungi growing without the presence of bacteria are shown as a reference

isolate INECOL-27 was also able to significantly inhibit the mycelial growth of *F. oxysporum*. Isolate INECOL-65.1, which showed the strongest antagonistic activity against *F. oxysporum*, was identified as *Staphylococcus* sp. and was obtained from the rhizosphere of *P. longipes*.

Bacterial VOC produced by six isolates were able to significantly inhibit mycelial growth of *F. solani* in indirect antagonism assays (Table 3). Bacterial isolates INECOL-8 (*Streptomyces* sp.). INECOL-11 (*Staphylococcus* sp.), INECOL-21 (*Pseudomonas* sp.), INECOL-27 (*Arthrobacter* sp.), INECOL-57 (*Staphylococcus* sp.), and INECOL-65.2 (*Staphylococcus* sp.) reduced *F. solani* mycelial growth by up to 37%. Isolate INECOL-21 was the only isolate able to inhibit the growth of *F. oxysporum* through VOC emission. Interestingly, the VOC emitted by four other bacterial isolates, all belonging to the genus *Staphylococcus*, promoted the growth of *F. oxysporum* (Table 3).

Discussion

The use of rhizobacteria as biocontrol agents against fungal phytopathogens has been increasingly documented [30, 32]. The antifungal compounds that rhizobacteria may produce, and their potential ability to promote plant growth, have made them interesting candidates in the search for more sustainable control methods of fungal diseases [4]. Rhizobacteria belonging to the genera *Bacillus* [37, 66], *Pseudomonas* [17], *Streptomyces* [62], and *Paenibacillus* [53] have been reported to successfully inhibit the growth of fungi such as *Gaeumannomyces graminis* (Sacc.) Arx & Olivier, *Fusarium verticillioides* (Sacc.) Nirenberg, *F. solani*, and *F. oxysporum*. More recently, rhizobacteria associated with avocado (a Lauraceae species), all identified as *Bacillus* spp., were found to exhibit antifungal activities against *F. euwallaceae*, the causal agent of *Fusarium* dieback [25]. Another avocado rhizobacterial strain, identified as *Bacillus* sp. and closely related to *B. acidiceler* Peak et al., was also reported to reduce the mycelial growth of *Phytophthora cinnamomi* Rands, through the emission of antifungal diffusible and volatile compounds [41]. While the relevance of rhizobacteria for sustainable management in agricultural settings has been extensively highlighted, few studies have focused on forest tree–associated microbes for biocontrol application in forest management, despite the economic and ecological importance of forest ecosystems [57].

Table 2 Lauraceae rhizobacteria able to reduce the growth of *Fusarium solani* or *F. oxysporum* by more than 20% and their closest matches based on the NCBI database "16S ribosomal RNA sequences (bacteria and archaea)"

Bacterial isolate	GenBank Accession number	NCBI best match		Identity %
		Taxonomy	Accession number	
INECOL-8	MF767291	*Streptomyces cirratus*	KU877577.1	100
INECOL-11	MF767292	*Staphylococcus xylosus*	KX770743.1	100
INECOL-19	MF767293	*Staphylococcus pasteuri*	MF109913.1	100
INECOL-21	MF767294	*Pseudomonas koreensis*	MF193902.1	100
INECOL-27	MF767295	*Arthrobacter kerguelensis*	HF937010.1	100
INECOL-57	MF767296	*Staphylococcus* sp.	KY315825.1	100
INECOL-65.1	MF767297	*Staphylococcus* sp.	KY682067.1	100
INECOL-65.2	MF767298	*Staphylococcus pasteuri*	MF109913.1	100
INECOL-100	MF767299	*Staphylococcus saprophyticus*	KF476046.1	99

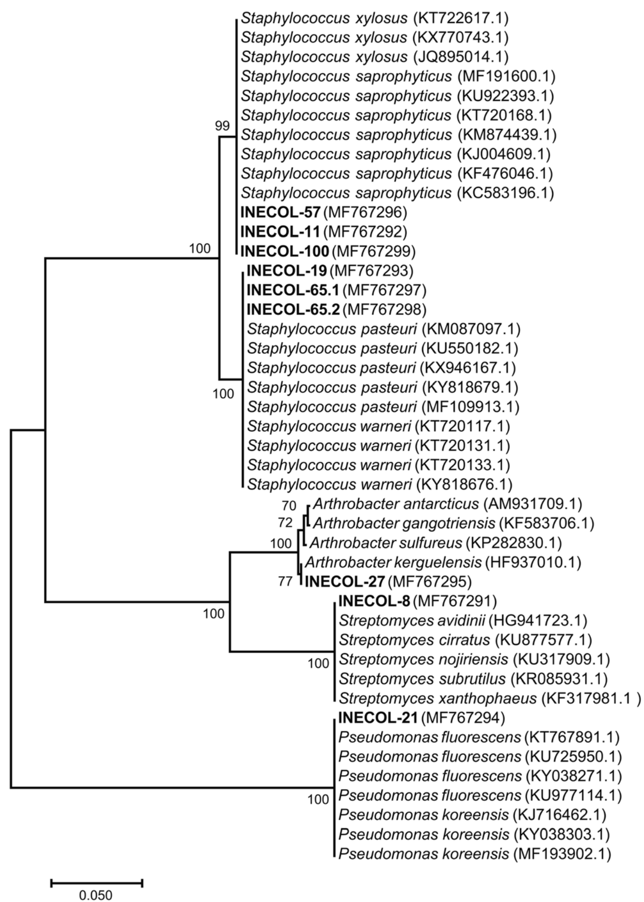

Fig. 3 Neighbor-Joining tree of partially sequenced 16S rRNA genes. Bold letters indicate bacterial isolates that were obtained in this study and presented a percentage of inhibition higher than 20% against *F. solani* or *F. oxysporum*. Values above nodes correspond to bootstrap values obtained from 1000 replicates

In the present study, we identified nine bacterial isolates with antifungal activity against the widespread fungal pathogens *Fusarium* spp. These fungi were selected as model organisms, due to the phylogenetic closeness of *F. solani* to *F. euwallaceae* [44] and to their frequency on avocado roots [18, 19]. The antagonistic isolates obtained in this study belonged to the bacterial genera *Arthrobacter*, *Pseudomonas*, *Staphylococcus*, and *Streptomyces*. Surprisingly, unlike the above-mentioned reports of avocado rhizobacteria displaying antifungal activities [25, 41], none of the sequenced isolates belonged to the genus *Bacillus*.

Most bacterial isolates with antifungal activity that were obtained in this study belonged to the genus *Staphylococcus*. While *Staphylococcus* species are mostly known for causing a wide range of human opportunistic diseases, they are also relatively frequent in the soil and in the rhizosphere [7]. *Staphylococcus epidermis* (Winslow and Winslow) Evans, *S. pasteuri* Chesneau et al., and *S. xylosus* Schleifer & Kloos have been isolated from the rhizosphere of potato [8], mangrove [29], and vanilla [2]. In some cases, *Staphylococcus* strains have been shown to promote plant growth, through the improvement of plant mineral nutrition or the enhancement of plant tolerance to halophilic conditions [31, 46]. The antifungal activity of some *Staphylococcus* species was also demonstrated, such as that of *S. equorum* Schliefer et al. against *Botrytis cinerea* Pers. [55]. The VOC emitted by some *Staphylococcus* species in our study were able to successfully inhibit the growth of *F. solani*, but promoted that of *F. oxysporum*. Fungal growth promotion by VOC produced by *S. epidermis* had been previously demonstrated for *Rhizoctonia solani* Kühn and *Penicillium waksmanii* K.W. Zaleski [34, 60]. As Berg et al. [7] stated, the rhizosphere constitutes a unique, nutrient-rich environment which may select for opportunistic pathogens, as these microorganisms are highly competitive and emit a wide array of antimicrobial substances. However, as these microorganisms are possible human pathogens, it is critical to understand their route of transmission and to assess their potential risk before using them for biotechnological purposes.

Table 3 Mycelial diameter growth of *F. solani* and *F. oxysporum* confronted with bacterial VOC in indirect antagonism assays

Bacterial isolate	Mycelial radial growth of *F. solani* (cm)		Mycelial radial growth of *F. oxysporum* (cm)	
	Treatment	Control	Treatment	Control
INECOL-8	_5.77 ± 0.32*_	_7.00 ± 0.00_	8.00 ± 0.00	8.00 ± 0.00
INECOL-11	_4.93 ± 0.23*_	_6.20 ± 0.12_	7.93 ± 0.07	8.00 ± 0.00
INECOL-19	6.03 ± 0.39	_6.20 ± 0.12_	7.53 ± 0.47	8.00 ± 0.00
INECOL-21	_3.90 ± 0.12*_	_6.20 ± 0.12_	_7.03 ± 0.77*_	8.00 ± 0.00
INECOL-27	_5.47 ± 0.12*_	_6.67 ± 0.19_	7.87 ± 0.13	8.00 ± 0.00
INECOL-57	_5.67 ± 0.18*_	_6.20 ± 0.12_	_8.00 ± 0.00*_	7.43 ± 0.07
INECOL-65.1	6.73 ± 0.28	_7.00 ± 0.00_	_7.97 ± 0.03*_	7.43 ± 0.07
INECOL-65.2	_6.40 ± 0.10*_	_7.00 ± 0.00_	_8.00 ± 0.00*_	7.43 ± 0.07
INECOL-100	6.50 ± 0.50	_6.20 ± 0.12_	_8.00 ± 0.00*_	7.43 ± 0.07

Values represent the average of three replicates ± standard error. Italicized values show significant differences between the treatment and its respective control

*$P \leq 0.05$, Student's *t* test (normal distribution)

Isolate INECOL-21, identified as *Pseudomonas* sp. and obtained from the rhizosphere of *P. schiedeana* (a wild relative of *P. americana*), exhibited the strongest inhibition of *F. solani* mycelial growth in direct antagonism assays. This isolate also showed the strongest inhibition of *F. solani* by VOC emission (37%) and was the only one to successfully inhibit *F. oxysporum* mycelial growth in indirect antagonism assays. *Pseudomonas* strains have been frequently reported to be plant growth promoters or fungal antagonists [6]. *Pseudomonas* spp., particularly fluorescent Pseudomonads, have been associated with soil suppressiveness of *Fusarium* wilt [64], due to their capacity to produce a wide range of antimicrobial compounds such as 2,4-diacetilfloroglucinol (DAPG), phenazines, or pyoluteorin [51]. *Pseudomonas* species have also been shown to exhibit antifungal activity through the emission of VOC such as aldehydes, alcohols, ketones, and sulfides [22, 26, 48]. Both *P. fluorescens* Migula and *P. koreensis* Kwon et al., phylogenetically close relatives of isolate INECOL-21, have been reported to be promising agents for the biological control of *Fusarium* spp. [36, 52].

Actinobacteria such as *Streptomyces* spp. or *Arthrobacter* spp. (isolates INECOL-8 and INECOL-27) are promising candidates for the production of bioactive formulations, due to their capacity to sporulate, to promote plant growth through the production of indole acetic acid, soluble phosphate, and siderophores, and to emit a wide range of antimicrobial compounds [33, 38, 47, 63]. Antifungal compounds produced by Actinobacteria may include volatile molecules such as dimethylpyrazine and dimethylhexadecylamine (activity reported against *B. cinerea* and *Fusarium* sp.; [47, 59]), S,S-dipropyl carbonodithioate (activity reported against *F. solani* and *F. oxysporum*, among other fungi; [42]), or other diffusible metabolites (activity reported against *F. oxysporum*; [23]). *Streptomyces* spp. are also known for their ability to produce fungal cell wall–degrading enzymes such as chitinases, cellulases, and glucanases [20].

This study contributed to gain information about the bacterial diversity associated with Lauraceae species in a tropical montane cloud forest and allowed us to identify several bacterial strains with antagonistic activity against ubiquitous fungal pathogens. The bacterial isolates that successfully inhibited the growth of *Fusarium* spp., either through the production of diffusible compounds or the emission of VOC, should thus be considered in further evaluations to assess their antagonistic activity in vivo in greenhouse bioassays, in order to confirm their potential application as biocontrol agents. These future studies should focus on those isolates that are not reported as opportunistic pathogens and elucidate whether the selected bacterial isolates also display plant growth–promoting abilities. Combining multiple biocontrol mechanisms such as the production of antibiotics, siderophores, or lytic enzymes, with plant growth promotion through the production of phytohormones or the induction of the plant defense system, has been shown to be critical for rhizobacteria to successfully compete their fungal antagonist [16, 49]. The use in field conditions of rhizobacteria with antifungal activity and plant growth–promoting capacity is therefore a promising approach for the control of *Fusarium* phytopathogens. The utilization of microorganisms as biological control agents against forest tree diseases is still scarce [14] and little is known about the mechanisms through which fungal inhibition by bacterial biocontrol agents could occur in field conditions. It is therefore necessary to focus future research efforts on the interactions between trees and their associated microbiota, to be able to design new strategies to improve forest tree health in an environmentally friendly manner.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Research involving human participants and/or animals This article does not contain any studies with human participants or animals performed by any of the authors.

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