Industrial Crops & Products 143 (2020) 111914

Contents lists available at ScienceDirect

Industrial Crops & Products

journal homepage: www.elsevier.com/locate/indcrop

Fungicidal properties and insights on the mechanisms of the action of volatile oils from Amazonian Aniba trees

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ARTICLE INFO

Keywords:
Antifungal
Essential oil
Leaves
Linalool
Membrane active
1-Nitro-2-phenylethane

ABSTRACT

The Amazonian *Aniba* species are world-renowned for their essential oils (EOs). The molecules derived from EOs have been intensively investigated in regards to their potential for disease control in plants. The aim of this study was to investigate the antifungal properties of *Aniba canelilla* EO (ACEO) and *Aniba parviflora* EO (APEO) when used against eight phytopathogenic fungi. Gas chromatography-mass spectrometry (GC–MS) analysis of oils showed that 1-nitro-2-phenylethane (~80%) and linalool (~40%) are the major compounds in ACEO and APEO, respectively. The ACEO and APEO treatments displayed remarkable antifungal effects against *Aspergillus flavus*, *Aspergillus niger, Fusarium oxysporum, Fusarium solani, Alternaria alternata, Colletotrichum gloeosporioides, Colletotrichum musae* and *Colletotrichum guaranicola*, for which the IC_{50} values ranged from 0.05 to 0.28 μL mL^{-1} and 0.17 to 0.63 μL mL^{-1}, respectively. Furthermore, the oil caused the inhibition of conidial germination by at least 83% for ACEO and 78% for APEO. The ACEO and APEO at 5 μL mL^{-1} induced leakage of nucleic acids and protein, suggesting that inhibition could be linked to the breakdown of membrane integrity of the conidia. In addition, the detection of fluorescent dye **p**ropidium **i**odide (PI) on *F. solani* conidia treated with ACEO and APEO indicates damage on the conidia cytoplasmic membrane. The findings of this study may be of biotechnological interest for the development of new plant protection products, with the advantage of being less harmful than the agrochemicals currently available.

1. Introduction

Various fungi are specialized in infecting crops, and cause substantial losses in agricultural production, mainly in postharvest fruit and vegetables, affecting trade and marketing worldwide (Abdullah et al., 2016; James and Zikankuba, 2017). Application of inorganic fungicides immediately after harvest is a way to prevent the contamination of perishable produce, and avoid significant post-harvest losses (Zhang et al., 2018a, 2018b). Indiscriminate use of chemical fungicides causes various health hazards, environmental pollution, and selection of pathogens resistant to the fungicides (Calvo-Irabien, 2018; Roy et al., 2018).

Therefore, significant advances are being made to establish alternative methods for the control of postharvest diseases. In recent years, research in the field of biotechnology has shown that natural phytochemical compounds can be a good alternative to the use of chemicals. The application of molecules from plant secondary metabolism in organic farming and agrofood industries offers a promising approach due to wide-spectrum biological activities and low toxicity to the environment and human health (Donsì and Ferrari, 2016; Grande-Tovar et al., 2018).

The essential oils are a plant secondary metabolism-derived mixture that is characterized by a multiplicity of volatile compounds and a strong, characteristic aroma. These blends are, generally lipophilic, water-insoluble and highly volatile, and usually classified as terpene hydrocarbons, alcohols, aldehydes, ketones, esters, phenols and organics acids (Valderrama and Ruiz, 2018). They are synthesized in different plant organs (*e.g.* seeds, flowers, leaves, stems, roots), and

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https://doi.org/10.1016/j.indcrop.2019.111914
Received 1 July 2019; Received in revised form 25 October 2019; Accepted 27 October 2019
Available online 11 November 2019

stored in various types of structures (*e.g.* epidermal cells, canals, glandular trichomes, secretory ducts) (Morone-Fortunato et al., 2010). The functional role of EOs seems to be in attraction of pollinators (Amaral et al., 2015; Giuliani et al., 2018) and in plant defense by providing protection against UV light, herbivores, and pathogens (Asbahani et al., 2015; Zaynab et al., 2018).

Numerous studies have shown the antifungal properties of EOs from Piperaceae, Poaceae, Myrtaceae, Lamiaceae and Lauraceae (Elguea-Culebras et al., 2016; Ribeiro-Santos et al., 2017; Sharma et al., 2017; Basak, 2018). A number of plant EOs have shown deleterious effect *in vitro* by inhibiting growth, sporulation and germination of necrotrophic and hemibiotrophic plant fungi (Ben Ghnaya et al., 2016; Boubaker et al., 2016; Boukaew et al., 2017). *In vivo* activity of EOs against biotrophs, hemibiotrophic and necrotrophic fungal is well documented (Tariq et al., 2019; Tohidi et al., 2019). The essential oils are capable of reducing the infection process, and thus prevent the early degradation of fruits and vegetables (Al-Reza et al., 2010; Castro et al., 2017; Xu et al., 2018). Furthermore, the use of nanosystem-associated EO (*e.g.* microcapsules, microspheres, nanoemulsions, nanoliposomes and solid lipid nanoparticles) represents an advantageous approach to enhance their performance as a natural food preservative (Mohammadi et al., 2015; Jemaa et al., 2018; Pisoschi et al., 2018; Rezaei et al., 2019).

Brazil has a prominent position worldwide due to its biological diversity, especially in the Amazon rainforest, where it is estimated that there are around 50,000 plant species (Hubbell et al., 2008). A large number of tropical plant species are widely explored as a source of valuable biomolecules and active ingredients, with applications in cosmetic, agriculture and pharmaceutical industries (Bataglion et al., 2014; Da Silva et al., 2018; Nascimento et al., 2019). In this context, Lauraceae is plant family with many large tree species which stand out for their high production of bioactive metabolites (Grecco et al., 2016; Llorent-Martínez et al., 2017). *Aniba* is a genus of trees belonging to the Lauraceae family, known for its production of EOs, and represents an important economic source for the Amazon region (Marques, 2001; Krainovic et al., 2018). The essential oils from *Aniba* species showed a great variety of biological properties and has been used in perfume and pharmaceutical industries (May and Barata, 2004; Pereira et al., 2018). *Aniba canelilla* (H.B.K.) Mez and *Aniba parviflora* (Meiss.) Mez are EO-producing trees abundant in the Amazon region, and both are used in the fragrance industry (Maia and Andrade, 2009). The *A. canelilla* EO consists mainly of 1-nitro-2-phenylethane (~ 80%), a rare benzenoid in plants which confers the characteristic cinnamon odor. In the Amazon region, leaf and bark infusions have been used for the treatment of diarrhea, stomachache, fevers, nauseas, headaches and infections (Taveira et al., 2003; Pedrollo et al., 2016). *Aniba parviflora*, popularly known as “macaca poranga”, has an EO rich in linalool (~ 40%) and is used as an ingredient in homemade perfume and flavoring sachets (Sarrazin et al., 2016; da Silva et al., 2016). Amazonian linalool-rich EOs are used in traditional medicine for their pharmacological properties, which include sedative and antidepressant effects (Santos et al., 2018).

Historically, the extraction of EOs from *Aniba* species is carried out with wood from the branch, after cutting the entire trunk (Krainovic et al., 2017), which can lead to extinction or endanger the species, as is the case with *A. rosaeodora* (Varty, 1998; Martinelli and Moraes, 2013). A sustainable strategy for obtaining EOs in the Amazon without the felling of the tree would be to extract the EO from leaves and thin branches, since the yield from these parts of the tree is similar to the yield of oil from the trunk (Chantraine et al., 2009; Pimentel et al., 2018). In addition, this approach can provide a source of income for the local community, favoring the sustainable development of the region, besides contributing to the conservation of Amazonian species. Despite previous studies on chemical composition of *A. canelilla* EO and *A. parviflora* EO (*Aniba* EOs), very little information is available on their potential antifungal effect and their mechanism of action. Therefore, this paper presents the study of the chemical composition, antifungal activity and inferences about the mode of action of EOs from two Amazonian *Aniba* species.

2. Materials and methods

2.1. Plant material identification and authentication

Plant EOs were extracted from leaves of *A. canelilla* and *A. parviflora* collected in the Adolpho Ducke Forest Reserve, Manaus, Amazonas, Brazil. Healthy leaves were collected in wet season (February and March, 2016). Two samples of *Aniba* reproductive material was initially identified from its morphological features and was then authenticated by INPA’s taxonomist by comparison with the vouchers N. 177252 (*A. canelilla*) and N. 59574 (*A. parviflora*) at INPA’s herbarium, Manaus, Amazonas, Brazil.

2.2. Extraction of essential oil

A total of 300 g of air-dried leaves (at 26 ± 3 °C for 7 days) from two *Aniba* trees were ground separately using an analytical mill. The powdered material was subjected to hydrodistillation for approximately 3 h using Clevenger-type apparatus. Each extracted *Aniba* EOs was dried over anhydrous sodium sulphate and stored in amber vials at 4 °C until used for GC–MS analysis, and the yield (%, v/w) was estimated on a dry weight basis. The phytochemical content of the *Aniba* EOs was determined as the mean of three replicates.

2.3. Gas chromatography-mass spectrometry (GC–MS) analysis and Identification of volatile components

The composition of the volatile constituents from each *Aniba* EO was analyzed by GC–MS using a Shimadzu QP2010 Ultra GC–MS (Kyoto, Japan), and a HP-5MS capillary column (30 m x 0.25 mm; i.d., 0.25 µm). The GC–MS conditions were in accordance with the detailed method described by Pimentel et al. (2018). One microliter of ACEO and APEO, which were dissolved in ethyl acetate (10 µL mL^{-1} final concentration), were injected directly in split mode (1:40), helium was used as the carrier gas at a constant flowrate of 1.0 mL min^{-1}. The initial oven temperature was programmed to start at 60 °C, then raised to 240 °C at 3 °C min^{-1}. Ionization energy and mass scan range were set as 70 eV and 30–500 amu, respectively. The compounds were identified by comparing their mass spectra with the ones from the NIST 8.0 spectral library and comparing their retention indexes with those from literature (Adams, 2007; Babushok et al., 2011).

2.4. In vitro antifungal activities of Aniba EOs

2.4.1. Microorganisms

Plant pathogenic fungi *Aspergillus flavus*, *Aspergillus niger, Fusarium oxysporum, Fusarium solani, Alternaria alternata, Colletotrichum gloeosporioides, Colletotrichum musae* and *Colletotrichum guaranicola* were obtained from the Microbiological Collections at the National Institute for Amazonian Research (MCTI-INPA), Amazonas, Brazil. Fungi were maintained in potato dextrose agar (PDA) at 26 ± 2 °C.

2.4.2. Standardization of fungal inoculum

The fungal conidia were washed from the surface of 7-day-old PDA plates with 10 mL of sterile distilled water containing 0.1% Tween-80 (v/v). The conidia suspensions were adjusted with sterile saline solution to a final concentration of 2×10^5 conidia mL^{-1} using a Neubauer chamber and a light microscope (Zeiss AxioLab A1).

2.4.3. Antifungal activity in solid media

In order to examine the antifungal activity of the *Aniba* EOs, the wells-diffusion method in dishes was used (Engelmeier and Hadacek, 2006). The conidia suspensions of fungi were equally spread on the

Table 1
Chemical composition of essential oil from leaves of *A. canelilla* (ACEO) and *A. parviflora* (APEO).

Compound name[a]	RI exp.	RI lit.	Molecular formula	ACEO Relative area (%)	APEO	Identification
Ethyl butanoate	800	802	$C_4H_8O_2$	3.10 ± 0.02	3.2 ± 0.12	RI, MS
Ethylbenzene	823	846	C_8H_{10}	0.37 ± 0.03	0.48 ± 0.02	RI, MS, BI
α-Pinene	934	939	$C_{10}H_{16}$	0.61 ± 0.02	1.22 ± 0.04	RI, MS, BI
Camphene	948	954	$C_{10}H_{16}$	–	0.90 ± 0.03	RI, MS, BI
Benzaldehyde	962	952	C_7H_6O	0.48 ± 0.05	–	RI, MS
β-Pinene	980	978	$C_{10}H_{16}$	0.63 ± 0.12	1.72 ± 0.03	RI, MS, BI
β-Myrcene	988	988	$C_{10}H_{16}$	–	1.93 ± 0.02	RI, MS
α-Phellandrene	1005	1002	$C_{10}H_{16}$	–	2.74 ± 0.02	RI, MS, BI
o-Cymene	1023	1026	$C_{10}H_{14}$	–	2.65 ± 0.13	RI, MS, BI
D-Limonene	1027	1029	$C_{10}H_{16}$	0.55 ± 0.16	1.22 ± 0.04	RI, MS
β-Phellandrene	1029	1029	$C_{10}H_{16}$	–	4.01 ± 0.04	RI, MS, BI
Eucalyptol	1031	1031	$C_{10}H_{18}O$	–	4.02 ± 0.02	RI, MS
Benzene acetaldehyde	1043	1042	C_8H_8O	0.43 ± 0.02	–	RI, MS, BI
E-β-Ocimene	1045	1050	$C_{10}H_{16}$	–	3.02 ± 0.02	RI, MS, BI
cis-Linalool oxide	1071	1072	$C_{10}H_{18}O_2$	–	1.42 ± 0.03	RI, MS
trans-Linalool oxide	1088	1086	$C_{10}H_{18}O_2$	–	1.64 ± 0.02	RI, MS
Linalool	1100	1096	$C_{10}H_{18}O$	0.44 ± 0.22	40.02 ± 1.22	RI, MS
Borneol	1165	1169	$C_{10}H_{18}O$	–	1.3 ± 0.02	RI, MS, BI
Terpinen-4-ol	1177	1177	$C_{10}H_{18}O$	–	0.99 ± 0.05	RI, MS, BI
α-Terpineol	1190	1188	$C_{10}H_{18}O$	0.64 ± 0.03	2.32 ± 0.04	RI, MS, BI
1-Nitro-2-phenylethane	1304	1295	$C_8H_9NO_2$	87.34 ± 2.33	–	RI, MS, BI
α-Copaene	1375	1376	$C_{15}H_{24}$	0.66 ± 0.04	1.95 ± 0.02	RI, MS
Z-Caryophyllene	1406	1408	$C_{15}H_{24}$	0.27 ± 0.05	–	RI, MS
β-Caryophyllene	1418	1417	$C_{15}H_{24}$	0.52 ± 0.04	3.05 ± 0.04	RI, MS, BI
Aromadendrene	1437	1441	$C_{15}H_{24}$	–	0.96 ± 0.05	RI, MS, BI
α- Humulene	1453	1454	$C_{15}H_{24}$	0.68 ± 0.05	2.3 ± 0.05	RI, MS
β-Selinene	1485	1490	$C_{15}H_{24}$	0.59 ± 0.02	0.85 ± 0.02	RI, MS, BI
α-Selinene	1493	1492	$C_{15}H_{24}$	0.54 ± 0.02	–	RI, MS, BI
Bicyclogermacrene	1495	1500	$C_{15}H_{24}$	–	2.75 ± 0.03	RI, MS, BI
β-Bisabolene	1508	1505	$C_{15}H_{24}$	0.46 ± 0.02	–	RI, MS, BI
Elemicin	1554	1557	$C_{12}H_{16}O_3$	–	1.31 ± 0.03	RI, MS, BI
trans-Nerolidol	1564	1563	$C_{15}H_{26}O$	–	1.47 ± 0.02	RI, MS, BI
Spathulenol	1576	1578	$C_{15}H_{24}O$	–	3.83 ± 0.04	RI, MS
Caryophyllene oxide	1582	1583	$C_{15}H_{24}O$	0.53 ± 0.02	4.33 ± 0.02	RI, MS
α-Acorenol	1629	1633	$C_{15}H_{26}O$	–	1.2 ± 0.04	RI, MS, BI
Cubenol	1636	1644	$C_{15}H_{26}O$	–	1.27 ± 0.06	RI, MS, BI
β-Eudesmol	1649	1650	$C_{15}H_{24}O$	–	0.65 ± 0.07	RI, MS, BI
α-Eudesmol	1652	1653	$C_{15}H_{24}O$	–	0.62 ± 0.06	RI, MS, BI
α-Cadinol	1654	1654	$C_{15}H_{26}O$	0.42 ± 0.02	–	RI, MS, BI
ni	1657		–	0.31 ± 0.02	–	–
Monoterpene hydrocarbons				2.3	17.2	
Oxygenated monoterpenes				1.1	51.7	
Sesquiterpene hydrocarbons				4.2	10.6	
Oxygenated sesquiterpenes				0.9	15.4	
Others (Aromatic components)				91.19	5.1	
Total identification %				99.69	100	

RI exp., linear retention index on HP-5MS column, experimentally determined using homologous series of *n*-alkanes.
RI lit., Adams mass spectral-retention index library (Adams, 2007).
RI, identification based on comparison of RI exp with those described by Adams, 2007.
MS, identification based on comparison with NIST 08 MS databases.
BI, identification based on comparison with Babushok' *s* retention Index (Babushok et al., 2011).
[a] Compounds are listed in order of their elution from a HP-5MS column.

Table 2
Inhibition of fungal growth on potato dextrose agar by essential oil from leaves of *A. canelilla* (ACEO) and *A. parviflora* (APEO).

	ACEO	APEO	Mancozeb*
	Diameter of inhibition zone (mm) at 20 μL mL^{-1}		
A. flavus	22.2 ± 0.7^{A}	17.2 ± 0.8^{B}	24.2 ± 1.1^{A}
A. niger	20.4 ± 1.1^{B}	16.3 ± 1.0^{C}	24.1 ± 0.8^{A}
F. oxysporum	19.8 ± 0.6^{B}	16.4 ± 0.4^{C}	23.5 ± 1.2^{A}
F. solani	21.7 ± 2.3^{A}	15.9 ± 0.5^{B}	23.7 ± 1.0^{A}
A. alternata	12.3 ± 1.1^{B}	11.0 ± 0.4^{B}	15.5 ± 0.8^{A}
C. gloeosporioides	14.7 ± 1.3^{B}	10.4 ± 1.1^{C}	22.7 ± 2.2^{A}
C. musae	11.5 ± 1.8^{B}	10.4 ± 1.1^{B}	21.4 ± 2.6^{A}
C. guaranicola	16.1 ± 1.1^{B}	10.3 ± 1.2^{C}	22.8 ± 1.9^{A}

Values are presented as mean (n = 3) ± standard deviation; Different letters in each row indicate a significant difference ($p < 0.05$) by the Tukey test.
* Mancozeb (2 mg mL^{-1}) was used as positive control.

surface of the PDA plates separately, and 50 μL of ACEO and APEO at 20 μL mL^{-1} in 0.1% v/v Tween-80 were dropped in the center of PDA medium. Stock solutions of 2 mg mL^{-1} mancozeb and 0.1% Tween-80 (v/v) were prepared in distilled water and tested as positive and negative controls, respectively. The inoculated plates were maintained for 7 days at 26 ± 2 °C, and the diameter of inhibition growth zones (DIZ) were measured in mm. The experiments were run in triplicate.

2.4.4. Determination of the minimum inhibitory concentration (MIC), minimum fungicidal concentration (MFC) and IC_{50}

The MIC values of *Aniba* EOs were determined by quantitative 96-well microtiter plate assay developed by Broekaert et al. (1990). Ten microliters of conidia suspension (2×10^5 conidia mL^{-1}) of each test strain was inoculated in 96-well microtiter plates containing 90 μL of yeast potato dextrose broth (YPD) for 16 h at 26 ± 2 °C. Next, 100 μL aliquots of ACEO and APEO at 0.156–20 μL mL^{-1} final concentration

Table 3
Minimal inhibitory concentration (MIC) and minimal fungicidal concentration (MFC) of essential oil from leaves of *A. canelilla* (ACEO) and *A. parviflora* (APEO).

	ACEO		APEO		Mancozeb*	
	MIC	MFC	MIC	MFC	MIC	MFC
A. flavus	0.15	0.15	0.62	0.62	0.3	0.3
A. niger	0.3	0.3	1.25	1.25	0.3	0.3
F. oxysporum	0.62	0.62	0.62	0.62	0.3	0.3
F. solani	0.62	0.62	0.62	0.62	0.3	0.3
A. alternata	5.0	5.0	5.0	5.0	0.3	0.3
C. gloeosporioides	0.62	0.62	2.5	2.5	0.3	0.3
C. musae	0.62	0.62	5.0	5.0	0.3	0.3
C. guaranicola	0.15	0.15	1.25	1.25	0.3	0.3

MIC and MFC expressed in μL mL^{-1}.
* Mancozeb (2 mg mL^{-1}) was used as positive control.

were incubated at 26 ± 2 °C in the dark and the growth was determined by measurement of absorbance at 630 nm every 12 h up to 96 h using an automated microplate reader (Thermo Plate Reader – Elx800, Biotek). After incubation, to check the presence of viable fungi, 10 μL of 1% TTC (2,3-5-triphenyl tetrazolium chloride), which is an indicator of the activity of dehydrogenase enzymes involved in the cellular respiration process, was added to each well of the microtiter plate and incubated at 37 °C for 1 h. The MIC values were considered to be the lowest concentration of *Aniba* EOs showing no color change. The MFC values were determined by subsequent subculturing of 5 μL cultures onto PDA plates at 26 ± 2 °C for 5 days, and defined as the lowest concentration that completely inhibited subculture growth. The 2 mg mL^{-1}mancozeb and 0.1% Tween-80 (v/v) were used as positive and negative controls.

The inhibition percentage was calculated using absorbance at λ = 630 nm (A_{630}) by the following equation: % fungal inhibition: 100 – [100 × (A_{630} of treated well – Average A_{630} of background absorption) / A_{630} of growth wells - Average A_{630} of background absorption)]. The fungi inhibition curves and concentration that causes 50% mycelial inhibition (IC_{50}) were modeled using the following equation:

$$Y = \text{bottom} + (\text{top} - \text{bottom}) /1 + 10^{[\text{Log (IC}-\text{X)} \times \text{Hill Slope}]},$$

fitting the model parameters by non-linear regression (Rautenbach et al., 2006). Bottom and top represent inhibition at low and high antifungal concentration, respectively. The hill slope is the slope of the curve. Each experiment was performed in triplicate.

2.4.5. Conidial germination assay

To evaluate effects of each *Aniba* EOs on the germination, 5 μL of conidia supensions (2×10^5 conidia mL^{-1}) were incubated at 26 ± 2 °C for 24 h with 5 μL of ACEO and APEO at 5 μL mL^{-1} final concentration in sterile depression slides. After incubation, conidia from each slide were studied under light microscopy on an AxioLab A1 microscope (Zeiss, Germany). The 2 mg mL^{-1} mancozeb and 0.1% Tween-80 (v/v) were used as positive and negative controls. Then, at least 100 conidia per replicate were counted to determine germination inhibition percentage (GI) according to the equation:

$$GI\ (\%) = [(Gc - Gt)/Gc \times 100]$$

Where Gc and Gt represent the number of germinated conidia in negative control slides and *Aniba* EOs-treated slides, respectively. Each experiment was performed in triplicate.

2.4.6. Release of cellular contents

The conidial integrity was examined by determining the release of nucleic acids and proteins into the supernatant according to the method of Ma et al. (2018), however with modifications. Two hundred microliter of *Aniba* EOs (50 μL mL^{-1} in 0.1% Tween-80) was incubated with 2 mL of conidial suspensions (5×10^7 conidia mL^{-1} in 10 mM phosphate buffered saline, pH 7.4) at 28 °C for 24 h. After incubation, the samples were centrifuged at 4000 × *g* for 10 min at 4 °C. The 0.22 μm-filtered supernatants were used for determining the nucleic acid and protein. Tween-80 0.1% (v/v) was used as negative control. The nucleic acid content was measured by absorbance at 260 nm (A260 mm), and the protein concentration was determined by the method Bradford et al.,(1976) . Tween-80 (0.1% v/v) was used as negative control. Each experiment was performed in triplicate.

2.4.7. Conidial membrane permeability assay

Conidia membrane permeability was determined according to the method of Qin et al. (2010). *F. solani* conidia (5×10^7 conidia mL^{-1} in 20 mM sodium phosphate buffer, pH 7.0) were treated for 24 h with ACEO and APEO at 5 μL mL^{-1} final concentration. After exposure, conidia were collected by centrifugation at 10,000 rpm for 10 min at 25 °C, washed twice with 20 mM sodium phosphate buffer (pH 7.0) and incubated with 1 mM PI, in the dark, at 30 °C for 15 min. Finally, conidia were collected by centrifugation, washed twice with the buffer to remove residual dye and assessed under fluorescent microscopy (Olympus System Microscopy) at excitation and emission wavelengths of 480 and 580 nm, respectively.

2.5. Experimental design and statistical analyses

The experimental design was completely randomized with two treatments (*A. canelilla* EO and *A. parviflora* EO) and eight pathogenic fungi (*A. flavus*, *A.niger, F. oxysporum, F. solani, A. alternata, C. gloeosporioides, C. musae* and *C. guaranicola*). All analyses were carried out in triplicate and all results, expressed as mean ± standard error and compared using an analysis of variance (ANOVA) followed by Tukey's post tests using Graphpad Prism 7.0 software (Graphpad Software, Inc.).

3. Results and discussion

3.1. Phytochemical Composition of the Aniba EOs

The essential oils composition from leaves of two *Aniba* species, characterized by GC/MS, are reported in Table 1. In the study with ACEO (yield of 0.81 ± 0.2% dry mass), 19 components were identified and the major volatile constituents were the 1-nitro-2-phenylethane (87.34%) and ethyl butanoate (3.1%), comprising of about 90% of the ACEO. The noteworthy minor components (amount < 1.0%) found were α- humulene (0.68%), α-copaene (0.66%), α-terpineol (0.64%) and β-pinene (0.63%). Previous study of phytochemical composition of leaves from *A. canelilla* EO revealed that the main component of the oil is 1-nitro-2-phenylethane, with percentages ranging from 70% to 92% (Barbosa et al., 2017; de Silva et al., 2009; da Silva et al., 2007). The content of 1-nitro-2-phenylethane from ACEO found in this study was perfectly in line with studies cited above. On the other hand, ethyl butanoate found here was not reported in previous chemical profiles of *Aniba canelilla*. The methyleugenol, frequently reported in the chemical profile of bark/trunk from *A.canelilla* (Giongo et al., 2017; Kreutz et al., 2018), was described in leaves of this species with levels that ranged between 0.5% to 3.4% (Taveira et al., 2003), however, this compound was not detected in the analyzed samples. These findings are in agreement with the chemistry of *A. canelilla* EO previously described (Barbosa et al., 2017; da Silva et al., 2007; de Silva et al., 2009).

In the case of APEO (yield of 1.03% ± 0.3 dry mass), a total of 32 components were identified in the EO (Table 1), with linalool (40.02%) as the predominat compound. Among the minor components, caryophyllene oxide (4.33%), eucalyptol (4.02%) and β-phellandrene (4.01%) were detected. Indeed, the linalool is the main compound described in *A. parviflora* EO with levels ranging from 40% to 45%, as well as the presence of β-phellandrene being commonly reported with

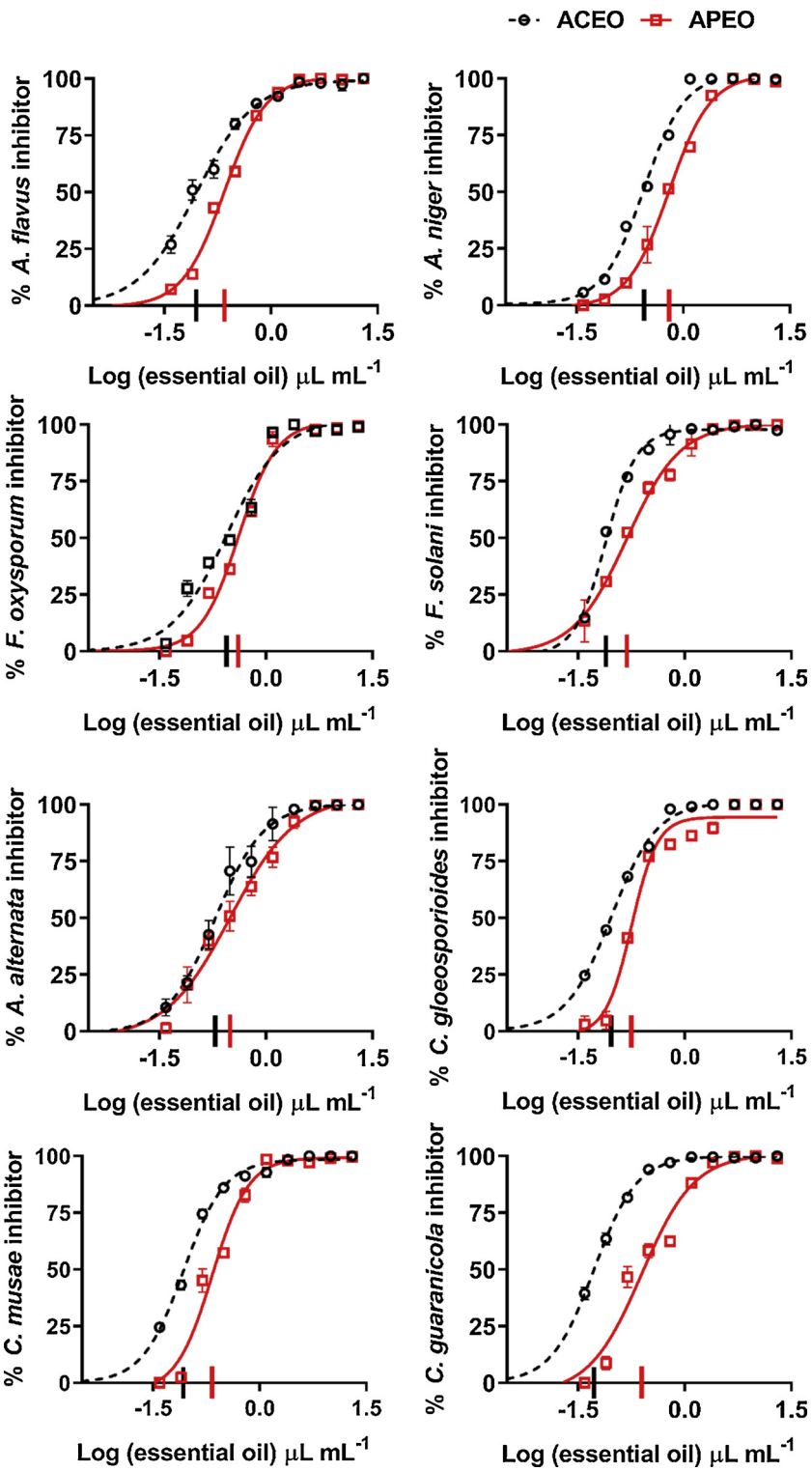

Fig. 1. Dose-response curves of essential oil from leaves of *A. canelilla* (ACEO) and *A. parviflora* (APEO) against phytopathogenic fungi. Extra-long ticks (black for ACEO and red for APEO) on the x-axis represent the IC_{50} valor. Each data point is the mean of three determinations and the error bar represents the standard deviation.

levels ranging from 15% to 17% (Santos et al., 2018; da Silva et al., 2016). In this study, the percentage of β-phellandrene (~ 4%) in APEO was lower than the levels reported in previous studies.

The qualitative and quantitative composition of EO may present significant differences depending on the sites, temperature, precipitation, plant parts, harvest period (Krainovic et al., 2018; Zhang et al., 2018a, 2018b). Plants can respond to different environmental conditions by producing and/or accumulating volatile organic compounds, which exert their biological functions by mediating plastic adaptive responses and plant-herbivore/pathogen interactions (Meléndez-González and Espinosa-García, 2018; Sharifi-Rad et al., 2017). Volatile organic compounds are the substrates and byproducts of cell metabolism, mainly from enzymatic reaction, and directly influence the phenotype which makes these metabolites essential for growth

Table 4
Antifungal activity of essential oil from leaves of *A. canelilla* (ACEO) and *A. parviflora* (APEO) against phytopathogenic fungi.

	ACEO				APEO				Mancozeb*			
	IC_{50}	95% CI	R^2	RMSE	IC_{50}	95% CI	R^2	RMSE	IC_{50}	95% CI	R^2	RMSE
A. flavus	0.08	0.07 - 0.09	0.99	3.155	0.21	0.20 - 0.23	0.99	2.511	0.16	0.14 - 0.18	0.98	3.927
A. niger	0.28	0.25- 0.3	0.99	3.323	0.63	0.58 - 0.68	0.99	3.035	0.12	0.09 - 0.15	0.97	5.294
F. oxysporum	0.27	0.22 - 0.34	0.97	6.301	0.41	0.37 - 0.45	0.98	4.334	0.07	0.06 - 0.07	0.99	2.661
F. solani	0.07	0.07 - 0.08	0.99	2.872	0.15	0.13 - 0.17	0.98	3.883	0.1	0.09 - 0.11	0.98	3.851
A. alternata	0.19	0.16 - 0.22	0.98	5.283	0.31	0.25 - 0.38	0.97	5.391	0.13	0.1 - 0.15	0.97	4.88
C. gloeosporioides	0.09	0.08 - 0.09	0.99	1.97	0.17	0.16 - 0.19	0.98	5.304	0.08	0.07 - 0.1	0.98	4.402
C. musae	0.08	0.07 - 0.09	0.99	2.65	0.21	0.19 - 0.24	0.98	5.548	0.15	0.13 - 0.17	0.97	5.864
C. guaranicola	0.05	0.05 - 0.06	0.99	1.357	0.24	0.2 - 0.3	0.97	6.701	0.06	0.06 - 0.07	0.99	2.465

IC_{50}, Concentration of essential oils (μL mL^{-1}) that causes 50% inhibition of fungal growth.
95% CI, 95% confidence intervals, the values are considered significantly different when the 95% CI fail to overlap.
IC_{50} values and 95% confidence intervals obtained by non-linear regression from dose-response curves from three independent experiments.
R^2, coefficient of determination.
RMSE, root mean square error.
* Mancozeb (2 mg mL^{-1}) was used as positive control.

Table 5
In vitro effect of essential oil from leaves of *A. canelilla* (ACEO) and *A. parviflora* (APEO) on conidial germination of phytopathogenic fungi.

	ACEO	APEO	Mancozeb*
	Inhibition of conidia germination (%) at 5 μL mL^{-1}		
A. flavus	93.0 ± 2.8^A	78.0 ± 1.1^B	100.0 ± 0.0^C
A. niger	92.6 ± 1.7^A	79.1 ± 1.9^B	100.0 ± 0.0^C
F. oxysporum	93.4 ± 2.2^A	82.7 ± 1.7^B	100.0 ± 0.0^C
F. solani	96.7 ± 1.3^A	84.6 ± 1.1^B	100.0 ± 0.0^A
A. alternata	83.5 ± 3.3^A	69.9 ± 0.6^B	100.0 ± 0.0^C
C. gloeosporioides	95.2 ± 2.3^A	76.5 ± 1.7^B	100.0 ± 0.0^C
C. musae	96.2 ± 2.1^A	85.3 ± 0.6^B	100.0 ± 0.0^C
C. guaranicola	96.3 ± 1.7^A	84.9 ± 2.3^B	100.0 ± 0.0^A

Values are presented as mean (n = 3) ± standard deviation; Different letters in each row indicate a significant difference ($p < 0.0001$) by the Tukey test.
* Mancozeb (2 mg mL^{-1}) was used as positive control.

and development (Verma and Shukla, 2015).

3.2. Antifungal activity of Aniba EOs on mycelial growth

The essential oils extracted from the leaves of *Aniba* were studied for its capacity to inhibit eight plant pathogenic fungi by using an agar-well diffusion technique using 20 μL mL^{-1} doses. The essential oils of the two *Aniba* species exhibited important activity against all the fungi analyzed (Table 2). The ACEO was as effective as mancozeb (control positive) ($p < 0.05$) against *A. flavus* and *F. solani* with DIZ values of 22.2 ± 0.7 mm and 21.7 ± 2.3 mm, respectively. *C. musae* was less sensitive among the fungi tested to ACEO with a diameter of inhibition zone of 11.5 ± 1.8 mm. The APEO inhibited the growth of all fungi, with DIZ values ranging from 10.3 ± 1.2 mm to 17.2 ± 0.8 mm. The ACEO showed stronger antifungal activity than the APEO ($p < 0.05$) on the six strains of fungi. The essential oils are widely known for their antifungal properties against various fungi (Calvo-Irabien, 2018; Lagrouh et al., 2017). In general, volatile blends are rich in terpenes, aliphatic hydrocarbons, alcohols, acids, aldehydes, acyclic esters, and their fungicidal activity has generally been attributed to the major components present in EOs (Wang et al., 2018; An et al., 2019). The studies on the potential inhibitory effect of ACEO and APEO against plant pathogenic fungi are still incipient. However, the bioactive potential of EOs from *Aniba* species has been reported (Giongo et al., 2017; Santos et al., 2018). The *A. parviflora* EO showed antibacterial activity against human pathogenic bacteria (Sarrazin et al., 2016; da Silva et al., 2016).

The MIC and MFC values (Table 3) highlight the fungicidal effect of ACEO and APEO, since the MIC values and corresponding MFC are equivalent for each species of fungi (Adrar et al., 2016). The ACEO exhibited higher activity (lower MIC and MFC values) than APEO against five fungal strains tested in this study. As presented in Table 3, the ACEO exhibited strong inhibitory effect against *A. flavus*, *A. niger* and *C. guaranicola* with MIC and MFC values equal to, or less than, those of the positive control (Mancozeb). The APEO exhibited MIC and MFC values ranging from 0.62 to 5.0 μL mL^{-1} against the fungi tested, and the MIC and MFC values of mancozeb was 0.3 μL mL^{-1}. Until now, there have been no reports in regards to the effects of ACEO and APEO on phytopathogenic fungi. Recently, Pimentel el al. (2018) described antifungal properties of EO from *A. rosaeodora*. The *A. rosaeodora* EO exhibited fungicidal effects for *C.guaranicola*, *C. gloeosporioides*, *Colletotrichum* sp., and *Al. alternata*, with MIC and MFC values ranging from 0.62 to 5.0 μL mL^{-1}.

To detail the magnitude of the antifungal effect of the *Aniba* EOs, the IC_{50} values were calculated from the dose–response inhibition curves of vegetative growth of phytopathogens under the influence of ACEO and APEO (Fig. 1). Inhibitory dose-response curves of ACEO and APEO have $R^2 \geq 0.97$ (coefficient of determination) and RMSE ≤ 6.701 (root mean square error) for all fungi, suggesting a good fit of the equation with raw data. Aligned with the data obtained in aforementioned experiments, the ACEO showed stronger antifungal activities than APEO [See 95% CI (95% confidence intervals), Table 4], with lower IC_{50} values for all phytopathogens tested (Table 4). The IC_{50} values of ACEO ranging from 0.05 to 0.28 μL mL^{-1}, while IC_{50} values of APEO ranging from 0.15 to 0.63 μL mL^{-1}. With ACEO, the lowest IC_{50} was 0.05 μL mL^{-1} on *C. guaranicola*, a 4.8-fold diference between IC_{50} value of APEO (0.24 μL mL^{-1}) for the same fungi. The mancozeb showed strong inhibitory effects, with IC_{50} values of 0.06 to 0.16 μL mL^{-1}. The IC_{50} values of ACEO on *C. guaranicola* and *C. gloeosporioides* has a magnitude equivalent to that of mancozeb (See 95% CI in Table 4), one of the most frequently used broad-spectrum commercial fungicides. It is worth stressing that mancozeb and other fungicides cause a variety of toxic effects (Gündel et al., 2019). In this context, *Aniba* EOs have good potential for application in the field for controlling plant diseases caused by phytopathogenic fungi.

A second approach used in this study for measuring the antifungal potential of *Aniba* EOs was the deleterious effect on asexual spores (conidia). Conidia are vital structures produced abundantly by a wide variety of fungi, which have high capacity for inoculation due to easy dispersion by air and water (Nguyen Van Long et al., 2017). The effects of *Aniba* EOs at 5.0 μL mL^{-1} on conidial germination are shown in Table 5. Conidial germination after a 24-h incubation varied according to each *Aniba* EO. The ACEO presented the highest percentage of inhibition on all fungi compared with APEO ($p < 0.001$). On *F. solani* and *C. guaranicola*, ACEO inhibited as strongly as mancozeb ($p >$

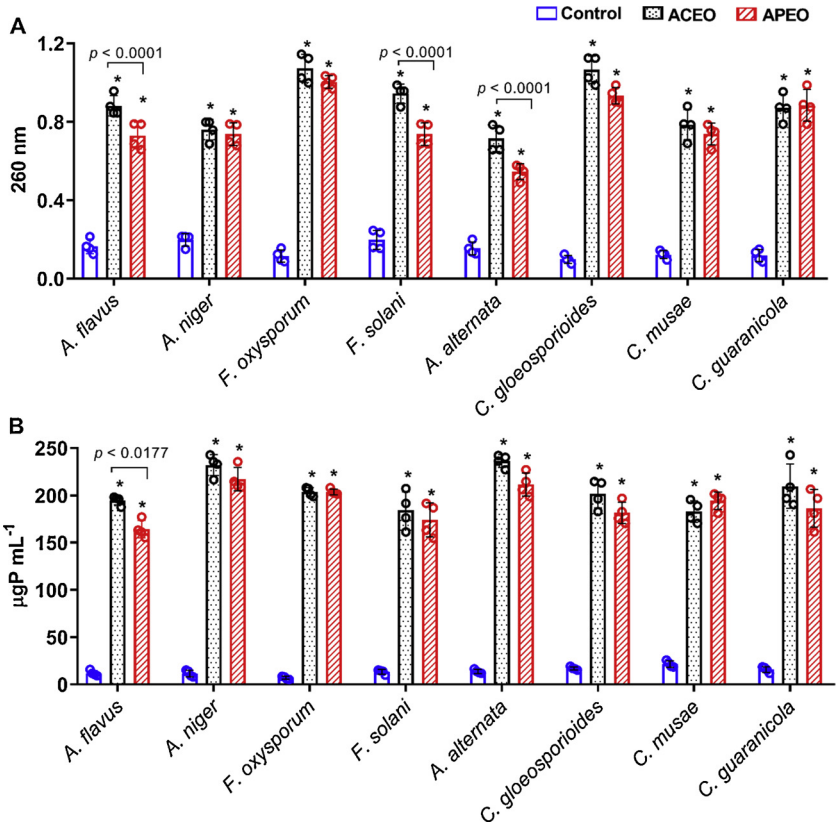

Fig. 2. Effects of essential oil from leaves of *A. canelilla* (ACEO) and *A. parviflora* (APEO) at 5 µL mL^{-1} on leakage of nucleic acids (A) and leakage of soluble protein (B). Each value is the mean for three replicates. *$p < 0.05$ indicates statistical difference compared with control (0.1% Tween-80).

0.05), with the reduction of germination in 96.7 ± 1.3% and 96.3 ± 1.7%, respectively. The mancozeb (2 mg mL^{-1}), as a positive control, fully inhibited the conidial germination of all of the pathogenic fungi tested. In general, the percentage of conidial germination inhibition by ACEO ranged from 83.5% to 96.7% and from 69.9% to 85.3% for conidia treated with APEO. The effectiveness of EOs on conidia germination inhibition is well reported in the literature (Basak, 2018; Black-Solis et al., 2019; Gahukar, 2018). At 10 µL mL^{-1}, *A. rosaeodora* EO completely inhibited germination of *Al. alternata* conidia (Pimentel et al., 2018). Efficacy of ACEO against spore germination was found to be promising when compared to earlier studies on the inhibitory effect on conidial germination by essential oil from different plant sources (Rguez et al., 2018).

The hypothesis that EOs may cause changes in cell membrane permeability was verified with a cellular components leakage assay, including nucleic acids and proteins. The results showed that after being treated with *Aniba* EOs (5 µL mL^{-1}) for 24 h (Fig. 2A), nucleic acids in suspensions of all fungi were released in a superior quantity than in the negative control ($p < 0.05$). After exposure to ACEO and APEO, the absorbance values for nucleic acids (A260 nm) ranged from 0.76 to 1.07 and 0.54 to 1.00, respectively, while negative control ranged from 0.098 to 0.19. In *A. flavus*, *F. solani* and *A. alternata*, the A260 nm values of conidia supernatant was higher in ACEO than in APEO ($p < 0.001$). A similar phenomenon in *Aniba* EO-treated conidia was also observed for released protein (Fig. 2B). In general, leakage of soluble protein after treatment with ACEO and APEO was much higher than the negative control ($p < 0.05$). The soluble protein in suspensions ranged from 6.9 to 21.54 µgP mL^{-1} for control, while for conidia treated with ACEO and APEO this ranged from 182.73 to 236.34 µg P mL^{-1} and from 164.14 to 217.1 µg P mL^{-1}, respectively. The propidium iodide (PI) was used to determine whether *Aniba* EOs led to a damage of membrane permeability on *F. solani* conidia. The fluorescent dye (PI) is membrane impermeable, which is detected (red fluorescence) only after changes in membrane permeability. As a result, *Aniba* EOs-treated *F. solani* conidia were easily stained by PI, whereas the control *F. solani* conidia were not stained (Fig. 3), indicating a considerable lost membrane permeability. The propidium iodide internalization is associated disruption of the cell membrane and cell dead (Almeida et al., 2019; Ji et al., 2018). The cell membrane permeability is essential for the viability of fungal conidia, where injury to the phospholipid bilayer may result in leakage of cell material, cellular collapse and eventually death of the fungal cells (Li et al., 2018; Xiang et al., 2018). In this study, nucleic acids and protein were released at multi-fold levels higher than in the control, indicating modification or disruption of the structure of plasma membrane, leading to the leakage of cytoplasmic constituents.

In general, the potential antifungal effect is attributed to the main compounds present in EO (Rguez et al., 2018; Xu et al., 2018). In the case of ACEO, the 1-nitro-2-phenylethane, a rare natural nitro derivate compound which determines its cinnamon-like fragrance, makes up ~ 87% of the ACEO, may be responsible for the antifungal activity against the phytopathogens reported in this study. Few studies have documented the action of 1-nitro-2-phenylethane against microorganisms; however, studies reported in the literature are focused on their pharmacological properties, *e.g.* vasorelaxant (Brito et al., 2013), cytoprotective (Cosker et al., 2014), antinociceptive (de Lima et al., 2009) and hypnotic, anticonvulsant and anxiolytic effects (Oyemitan et al., 2013). Oger et al. (1994) reported the fungistatic effect of 1-nitro-2-phenylethane against *Candida albicans*, *C. parasilosis*, *C. tropicalis and A. fumigatus*. The essential oil, 1-nitro-2-phenylethane and methyleugenol, isolated from stems of *A. canellila*, showed trypanocidal activity against *Trypanosoma evansi* comparable to the positive control (diminazene aceturate). The authors suggest that molecules isolated (1-nitro-2-phenylethane and methyl eugenol) from the *A. canellila* EO may be responsible for the trypanocidal action (Giongo et al., 2017).

Linalool, the major phytoconstituent of APEO (~ 40%), is well known for its broad number of relevant biological activities

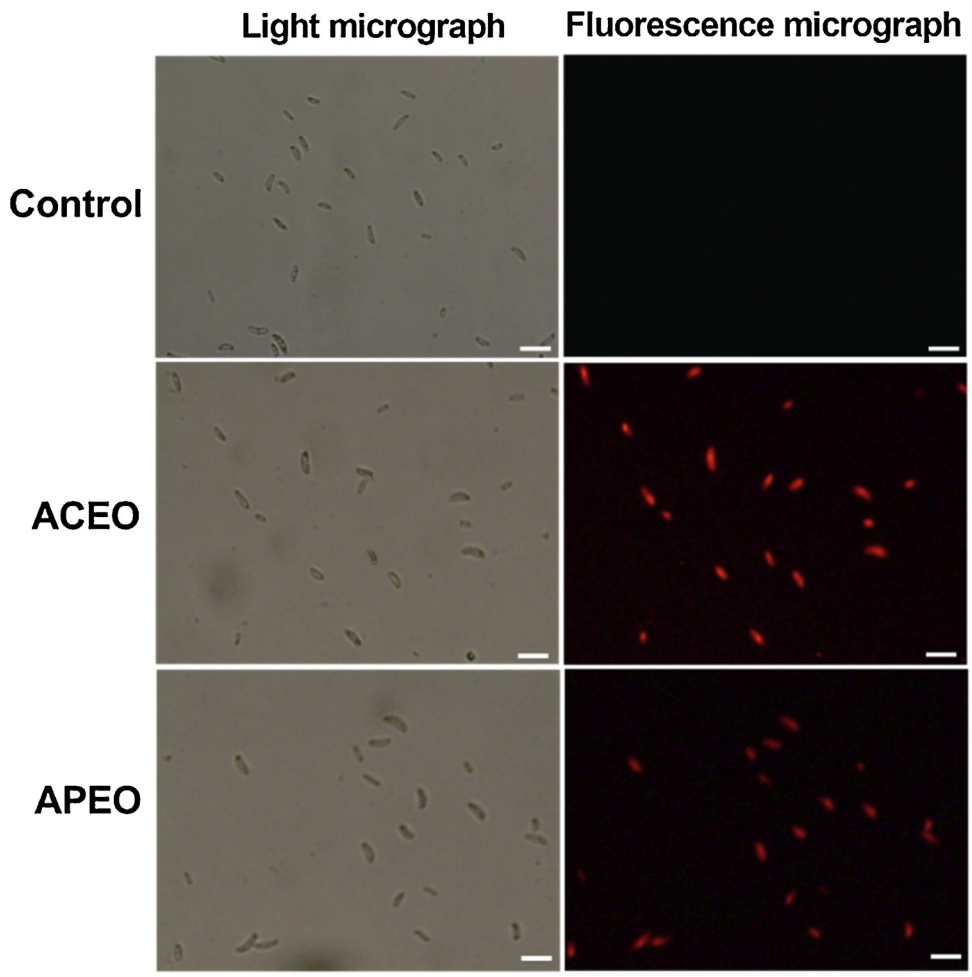

Fig. 3. Fluorescence microscopy of *F. solani* conidia treated with essential oil of *A. canelilla* (ACEO) and *A. parviflora* (APEO) at 5 µL mL^{-1}. The red fluorescence indicates changes on conidia membrane permeability. Images are representative of two independent experiments. Control: 0.1% Tween-80. Bars, 40 µm (200 × magnification).

(Aprotosoaie et al., 2014; Pereira et al., 2018). Linalool, an acyclic monoterpene frequently found in several plants, presents an alcohol functional group which confers polarity to the molecule, making it a chemically reactive compound (Aprotosoaie et al., 2014). In linalool-rich EO, linalool's presence may be responsible for much of the bioactive properties (Prachayasittikul et al., 2018; Santos et al., 2018; Yadav et al., 2019) and has the potential to enhance the scale of antimicrobial effect (Herman et al., 2016). *A. rosaeodora* EO is constituted mainly of linalool (~ 70–80 %) (Krainovic et al., 2018; Sarrazin et al., 2016) and the magnitude of its antifungal effect was proportional to the percentages of linalool present in *A. rosaeodora* EO, *i.e.*, ~ 75% linalool for *A. rosaeodora* EO (wet season) was more effective in inhibiting fungi than ~ 48% linalool for *A. rosaeodora* EO (dry season) (Pimentel et al., 2018). Similarly, other studies involving linalool-rich EOs showed this similar effect (Duarte et al., 2016; Hussain et al., 2008). Linaool is a lipophilic metabolite and its deleterious effect is associated with changes in the physical properties of cell membranes, altering the selective permeability, which allows for an abnormal flow of cytoplasmic components and cell death (Kalily et al., 2016; Lima et al., 2017; Pereira et al., 2018). In short, the antimicrobial activity of EOs is closely related to the activity of their main components. Thus, 1-nitro-2-phenylethane and linalool may play a key role in antifungal activity because of their reactive chemical properties. However, the synergistic action with other components of the EO may have relevance to its biological properties. Thus, future studies focused on the isolation and analysis of the main compound of each oil are fundamental for a deeper understanding on the biological effect of the *Aniba* EOs.

4. Conclusions

The ACEO and APEO strongly inhibited the vegetative growth and the conidial germination of all phytopathogens tested. In general, the ACEO was more effective in inhibiting fungi than the APEO. The mechanisms of action based on the cellular components leakage assay showed that *Aniba* EOs can induce the release of nucleic acids and proteins. Such release may be due to damage to the cell membrane integrity and lead to lethal effect on the pathogens. The *Aniba* EOs are potential candidates for environmentally friendly antifungal agents for controlling postharvest diseases in fruits and vegetables, as an alternative to chemical additives.

Author's contributions

José F. C. Gonçalves, Diego P. Souza and Renah B. Q. Pimentel conceived and designed the experiments; Diego P. Souza and Renah B. Q. Pimentel performed the experimental collection and assembled the data; José F. C. Gonçalves, Diego P. Souza, Renah B. Q. Pimentel, Patricia M. Albuquerque, Sergio D. Junior, Andreia V. Fernandes analyzed and interpreted the data; José Francisco C. Gonçalves, Alberdan S. Santos, José T. A. Oliveira, Marcio V. Ramos contributed reagents/materials/analysis tools; José F. C. Gonçalves, Diego P. Souza and Renah B. Q. Pimentel wrote the paper. Alberdan S. Santos, José T. A.

Oliveira, Marcio V. Ramos, Bala Rathinasabapathi contributed to deepen the hypothesis/discussions and revised the paper.

Declaration of Competing Interest

The authors declare that they have no conflict of interest.

Acknowledgements

We are grateful to the National Institute for Amazonian Research (MCTIC-INPA), the Amazonas State University - School of Technology of Amazonas for logistical support, the Coordination for the Improvement of Higher Level Personnel (CAPES)- Brazil (Project Pro-Amazonia Nº52), National Council for Scientific and Technological Development (CNPq, Brazil) and Amazonas State Research Support Foundation (FAPEAM) for finantial supporting this study. Alberdan S. Santos, José T. A. Oliveira, Marcio V. Ramos, José F. C. Gonçalves acknowledge fellowships provided by CNPq.

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