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Article

Colletotrichum siamense causing anthracnose in postharvest of 'Hass' avocado

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Abstract

Mexico is the leading producer and exporter of avocados in the world. The main producing area is the Central Pacific Region of Mexico (Jalisco, Michoacán, and Nayarit), where 96% of the national production is harvested. Anthracnose in avocado postharvest can reach between 20 and 80% losses due to the deterioration of the quality of the avocado fruit. The objective of the research was to diagnose the causative agent of anthracnose of avocado postharvest in the Central Pacific Region of Mexico, the study was conducted between 2019 and 2020. Completely healthy avocado fruits were sampled and pathogenic fungi that cause anthracnose were isolated, a morphological, molecular, and phylogenetic identification was carried out, as well as their development under fungicide stress. Morphological characteristics indicated that the fungus that causes anthracnose in postharvest belongs to *Colletotrichum gloeosporioides sensu lato*. Molecular and phylogenetic tests identified the fungi as *Colletotrichum siamense*, an endophytic fungus capable of existing in two conditions of fruit life (pre- and postharvest). This fungus under fungicide stress remains in an inactive state in response until its effect wears off.

Palabras clave:

Persea americana Miller, synthetic fungicide, postharvest.

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Introduction

Mexico is the leading producer and exporter of avocados in the world. The main producing area is the Central Pacific Region of Mexico, which includes the states of Jalisco, Michoacán, and Nayarit, where 96% of the national production is harvested (SAGARPA, 2018; SIAP-producción agrícola, 2021). Anthracnose disease in the postharvest stage of avocados can reach between 20 and 80% losses due to the deterioration of the quality of the avocado fruit.

The species complex of *C. gloeosporioides* is the cause of this disease (Bill *et al*., 2014), which is characterized by visible symptoms such as black spots on the skin and soft rot in the pulp of immature fruits. During the ripening process, it develops rapidly in the tissues of the pulp and skin until it affects 100% of the fruit (Kimaru *et al*., 2018). *C. gloeosporioides* infects the fruit from preharvest (penetration through natural openings, wounds, or direct rupture of the cuticle) and remains dormant (Prusky *et al*., 2013).

In preharvest, *C. gloeosporioides*, *C. acutatum*, *C. boninense*, *C. hymenocallidis*, *C. siamense* and *C. tropicale* have been identified as causative agents of anthracnose in Michoacán, Nayarit and Hidalgo (Silva-Rojas and Ávila-Quezada, 2011; Jaimes *et al*., 2015; Campos-Martínez *et al*., 2016; Trinidad-Angel *et al*., 2017; Fuentes-Aragón *et al*., 2018). For the implementation of control methods (chemical or biological), precise identification of the pathogen is required (Fuentes-Aragón *et al*., 2020a b).

Chemical control at harvest and postharvest is limited to three molecules. Copper (in its different salts, with multiple sites of action, it is applied at a concentration of 1 mL L^{-1} of water) is allowed days before harvest in conventional and organic production. It is considered low risk with no signs of developing resistance. The other two molecules, azoxystrobin (affects cellular respiration) and fludioxonil (acts on transduction signals, MAP/histidine), in a single mixture, are applied at a concentration of 0.75-1.5 mL L^{-1} of water in postharvest.

The maximum permissible residual limit is 0.4 ppm in the United States of America, 0.2 ppm in Japan, and 0.1-0.4 ppm in Europe (APEAM, 2016; FRAC, 2022). The objective of the research was to diagnose the causative agent of postharvest anthracnose of apparently healthy avocado fruits, from the Central Pacific Region of Mexico, by morphological characteristics, pathogenicity tests, molecular and phylogenetic identifications, as well as their development under fungicide stress.

Materials and methods

Sampling sites, pathogen isolation and identification

In 2019, physiologically ripe avocado fruits, without mechanical damage, visibly healthy and without apparent damage (thrips), were sampled in five orchards in Michoacán, one in Jalisco, and two in Nayarit, Mexico. Twenty fruits per sampling site were stored at 25 °C ±3 °C until symptoms of anthracnose developed (circular brown lesions on the skin that change to darker colors during the ripening process).

Samples of 0.5 cm^2 of mesocarp were taken when the first symptoms appeared and were disinfected with 1.5% v/v sodium hypochlorite for 2 min. They were then washed three times with sterile distilled water, dried with sterile blotting cloth, and seeded in Petri dishes with potato dextrose agar medium (PDA; DIBICO, Mexico). They were incubated at 27 °C ±2 °C until mycelium and spores were observed. The culture was isolated by successive reseeding and purified using the monosporic culture technique (Zhang *et al*., 2013).

Morphological identification

For each pathogen isolated, growth rate was measured in PDA medium incubated at 27 °C ±1 °C for 7 days. Every 24 h, the diameter of the colony was evaluated and the growth rate (mm day^{-1}) was

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calculated. The morphological description was made based on the color of the colony (mycelium), color of conoidal masses, presence of acervuli, size and shape of the spore.

Molecular identification

The PCR technique was used to confirm the identity of the isolated strains (*Colletotrichum*). Genomic DNA was extracted from the mycelium of colonies of 8 d of incubation at 27 °C for each *Colletotrichum* strain isolated using the CTAB method (Doyle, 1990). The DNA of all isolates was amplified by rDNA-ITS, which included ITS1 (5'CAACTCCCAAACCCCTGTGA-3') and ITS4 (5'GCGACGATTACCAGTAACGA-3'); and glyceraldehyde-3-phosphate dehydrogenase, where GDF1 (5'-GCCGTCAACGACCCCTTCATTGA-3') and GDR1 (5'-GGGT GGAG TCGT ACTT GAGC ATGT-3') were used.

The amplification and cleaning conditions were carried out as indicated by the following authors (Silva-Rojas and Ávila-Quezada, 2011; Fuentes-Aragón *et al*., 2018; Juárez-Vázquez *et al*., 2019). The study was conducted at the Comprehensive Phytosanitary Diagnostic Laboratory at the facilities of the College of Postgraduates in the State of Mexico, Mexico.

Phylogenetic analysis

The evolutionary history was inferred with the Neighbor-Joining method. The Bootstrap consensus tree inferred from 100 replicates was taken to represent the evolutionary history of the analyzed taxa. Branches corresponding to reproductive partitions in less than 50% of collapsed boot replicates. The percentage of replicated trees in which the associated taxa were clustered in the bootstrap test (100 replicates) was shown next to the branches.

Evolutionary distances were calculated using the Tamura-Nei substitution model as tree inference options. The analysis involved 22 nucleotide sequences. All positions containing gaps and missing data were removed. There were a total of 442 positions in the final dataset. Evolutionary analyses were performed in the molecular evolutionary genetics analysis (MEGA) 7.0 software (Weir *et al*., 2012; Kumar *et al*., 2016).

Pathogenicity tests

Koch's postulates were used to corroborate the isolated agent as the cause of the observed symptoms. Pathogenicity tests were performed on completely healthy fruits with no visible damage, with a pulp dry matter content between 23-25% (NMX-FF-016-SCFI-2016, 2016). Three wounds (3 mm) were made in the longitudinal area of the fruit and spore suspension (10^6 spores ml^{-1}) was placed over the wounds. The experiment was repeated twice. All fruits were incubated at 27 °C and 90% relative humidity until anthracnose disease appeared. The development of anthracnose was recorded for each isolate and the pathogen was reisolated to confirm morphological identity and cultural characteristics.

Mycelium growth under fungicide stress

Inhibition of mycelium growth in the presence of two fungicides, copper sulfate and the mixture of fludioxonil + azoxystrobin, was performed in PDA with the concentration of each fungicide; for copper sulfate, they were 20, 40, 60, and 80 ppm; for fludioxonil + azoxystrobin, they were 10, 20, 50, and 70 ppm. PDA alone was included as a control. Five repetitions were performed per *C. siamense* isolate. A 7-day-old mycelium sample was added to each Petri dish and they were incubated at 27 °C ±1 °C for 48 h (Han *et al*., 2021). After this incubation period, treatments with fungicides were reinoculated in PDA without fungicide, to verify the fungicidal or fungistatic effect.

Statistical analysis

All experiments were performed using a completely randomized design with three repetitions, considering the origin of the isolate as a factor of variation for the radial diameter of the colony, the

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growth rate, the area of the colony at seven days, and the length and diameter of the spore. Mean comparisons were made with the LSD Fisher test ($p \leq 0.05$).

Results and discussion

Morphological identification

Nine pathogenic fungal strains belonging to the species complex of *C. gloeosporioides* were identified. Of these, six pathogens corresponded to the state of Michoacán, in five sampling sites, one pathogenic fungus in Jalisco, and two pathogenic fungi from Nayarit. Fruit disease symptoms, colony characteristics, and spore shape are shown in Figure 1 and described in Table 1. Most of the isolates showed aerial mycelium, white to dark gray color at 7 d of incubation, with orange cone-shaped masses and only in two cases they were black.

Figure 1. A) Symptoms of anthracnose in avocado fruits from which *C. gloeosporioides sensu lato* strains were isolated; B) morphological characteristics of the colonies after seven days of incubation at 27 °C on potato dextrose agar; and C) spores.

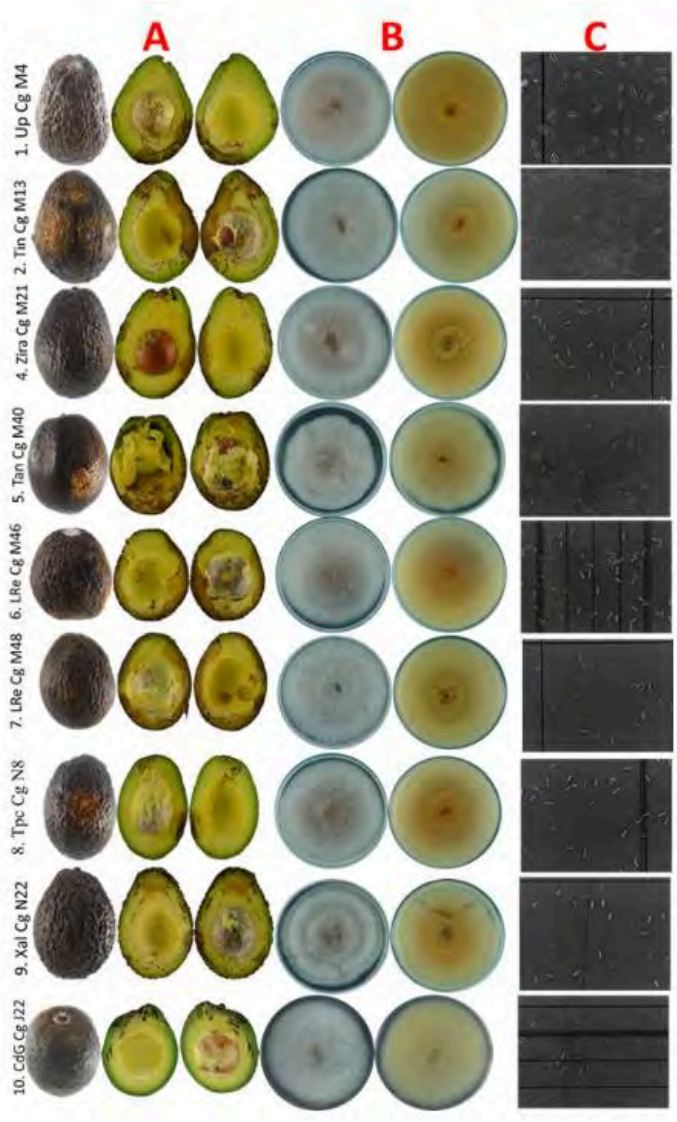

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Table 1. Morphological characterization of nine pathogenic fungi isolated causing anthracnose in avocado fruits from three states of the Central Pacific region of Mexico.

Strain	State of origin	Colony characteristics	Conoidal mass color	Acervuli	Spore shape
1. Up Cg M4	Michoacán	White to dark gray, aerial mycelium	Orange	Yes	Cylindrical to ellipsoidal
2. Tin Cg M13	Michoacán	White to dark gray, aerial mycelium, with concentric rings	Orange	Yes	Cylindrical to ellipsoidal
4. Zira Cg M21	Michoacán	White to dark gray, aerial mycelium, with concentric rings	Orange	Yes	Cylindrical to ellipsoidal
5. Tan Cg M40	Michoacán	White to dark gray, aerial mycelium	Orange	Yes	Cylindrical to ellipsoidal
6. LRe Cg M46	Michoacán	White to dark gray, aerial mycelium, with concentric rings	Orange	Yes	Cylindrical to ellipsoidal
7. LRe Cg M48	Michoacán	White to dark gray, aerial mycelium	Black	Yes	Cylindrical to ellipsoidal
8. Tpc Cg N8	Nayarit	White to dark gray, aerial mycelium, with concentric rings	Orange	Yes	Cylindrical to ellipsoidal
9. Xal Cg N22	Nayarit	White to dark gray, aerial mycelium, with concentric rings	Orange	Yes	Cylindrical to ellipsoidal
10. CdG Cg J22	Jalisco	White to dark gray, aerial mycelium	Black	Yes	Cylindrical to ellipsoidal

All had acervuli. The shape of the spores was cylindrical to ellipsoidal. Growth rate ranged from 11.7 to 12.9 mm day^{-1}, with statistical differences between them ($p< 0.05$). The length and equatorial diameter of the spore also showed significant differences ($p< 0.05$). The spores ranged in length from 40.3 to 46.1 µm and from 11 to 15.3 µm in equatorial diameter.

The final diameter of the colony on day seven was different between the strains and ranged from 69 to 83 mm. The concentration of spores at the end of incubation was different between the strains ($p< 0.05$) (Table 2). Based on these morphological and cultural characteristics, the isolates were identified as *C. gloeosporioides sensu lato*. Under this classification, different species that cause anthracnose in avocados are grouped.

Table 2. *In vitro* development of nine pathogenic fungus isolated causing anthracnose in postharvest of avocado from three states of the Central Pacific Region of Mexico.

Strain	Mycelium growth (mm d^{-1})	Spore size		Final diameter 7 d (mm)	Concentration (10^6 spores ml^{-1})
		Length (µm)	Diameter (µm)		
1. Up Cg M4	11.7 ±2.3 c	46.1 ±4.5 a	13.8 ±2.1 c	69.1 ±1.8 e	20 ±9.8 b

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Strain	Mycelium growth (mm d^{-1})	Spore size		Final diameter 7 d (mm)	Concentration (10^6 spores ml^{-1})
		Length (µm)	Diameter (µm)		
2. Tin Cg M13	11.8 ±2.8 c	40.4 ±2.8 d	11 ±1.4 e	73.6 ±1 c	6.2 ±6.8 f
4. Zira Cg M21	12.9 ±3.3 a	45.8 ±4.8 b	13.2 ±1.8 c	76.4 ±1.5 b	18 ±8 c
5. Tan Cg M40	12.3 ±3.2 b	45.4 ±4 b	12.8 ±1.7 d	72.7 ±2.9 d	6.8 ±4.9 f
6. LRe Cg M46	12.5 ±2.9 b	44.5 ±3.5 b	14.3 ±1.9 b	74.4 ±1.7 c	14 ±3.4 d
7. LRe Cg M48	12.9 ±3.2 a	43 ±4.4 c	13.3 ±2.5 c	70.4 ±1.8 e	25 ±24 a
8. Tpc Cg N8	12.8 ±3.6 a	40.3 ±3 d	11.5 ±2 e	72.2 ±1.8 d	26 ±11 a
9. Xal Cg N22	12.1 ±3.3 b	42.1 ± 4.1 c	14 ±1.7 b	73 ±1.9 c	14 ±10 d
10. CdG Cg J22	11.7 ±3.2 c	44.7 ± 3.2 b	15.3 ±1.2 a	83.2 ±1.8 a	9.3 ±3.2 e

[i] Means with equal letters within columns are not statistically different (Fisher LSD, $p \leq 0.05$).

Pathogenicity tests

In pathogenicity tests, typical characteristics of anthracnose disease developed after five days of storage, such as black spots on the pericarp and soft rot on the mesocarp, which spread rapidly throughout the fruit. No other symptoms were observed among the isolates (Figure 2).

Figure 2. Pathogenicity tests performed on nine pathogenic fungi isolated after 5 days of incubation on 'Hass' avocado: A) 1- Up Cg M4; B) 2- Tin Cg M13; C) 4- Zira CG M21; D) 5- Tan CG M40; E) 6- LRe Cg M46; F) 7-LRe Cg M48; G) 8- Tpc Cg N8; H) 9- Xal Cg N22; and I) 10- CdG Cg J22.

Molecular identification and phylogenetic tree

Based on the ITS nucleotide sequences and a BLAST search, the isolates obtained in this study were identified as *C. gloeosporioides* species complex. The nine isolates showed a percentage coverage between 99 and 100% and an identity of 98 to 100% with the genus *Colletotrichum* and were classified in the *gloeosporioides* clade based on the ITS nucleotide sequence. With the GAPDH sequence, they showed a percentage of coverage of 79 to 100% with *C. siamense*, as well as an identity of 98 to 100% with this species (Table 3 and Figures 3 and 4).

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Table 3. Accession number, percentage of coverage and identity of nine strains of *C. siamense* causing anthracnose in postharvest of avocado from the Central Pacific Region of Mexico.

Strain	No. accession (GenBank)		Coverage (%)		Identity (%)		Assigned species
	ITS	GAPDH	ITS	GAPDH	ITS	GAPDH	
1. Up Cg M4	KX022506.1	KP703347.1	100	79	99.8	98	*C. siamense*
2. Tin Cg M13	MK426765.1	KP703277.1	100	97	100	100	*C. siamense*
4. Zira Cg M21	MK426765.1	KP703277.1	100	100	99.82	100	*C. siamense*
5. Tan Cg M40	KX022506.1	KP703347.1	100	100	99.7	100	*C. siamense*
6. LRe Cg M46	KU662388.1	KP703347.1	99	98	100	99.5	*C. siamense*
7. LRe Cg M48	KU662388.1	KP703277.1	99	100	100	100	*C. siamense*
8. Tpc Cg N8	KX022503.1	KP703277.1	100	100	99.8	100	*C. siamense*
9. Xal Cg N22	KU662388.1	KP703347.1	100	100	99.8	100	*C. siamense*
10. CdG Cg J22	KU662377.1	KP703277.1	99	91	99.8	100	*C. siamense*

Figure 3. Sequence annealing.

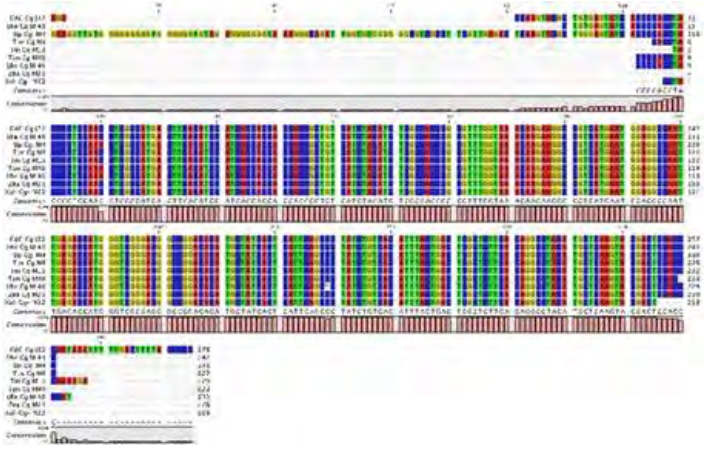

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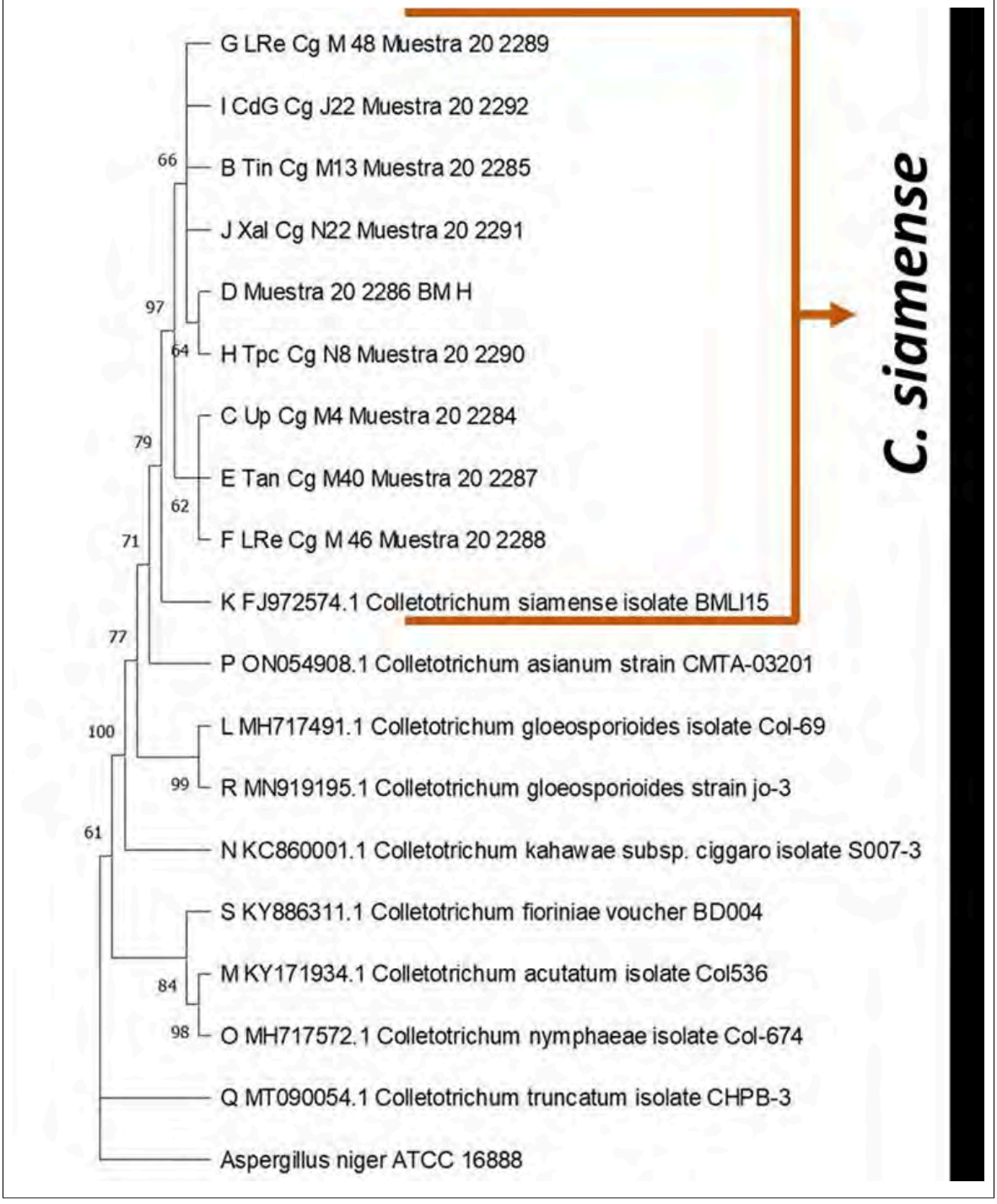
Figure 4. Maximum likelihood tree of the aminergic toxin family.



Mycelium growth under fungicide stress

In all the strains isolated and evaluated, in both fungicides, they achieved 100% inhibition compared to the control (Figure 5). When mycelium samples of the tested pathogens were reseeded in PDA only, the strains developed mycelium within 48 h of incubation. The higher the concentration of the fludioxonil + azoxystrobin fungicide exposed, the lower the mycelium development compared to

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the control (Figure 6). The Up Cg M4 and Tin Cg M13 strains showed greater susceptibility to low concentrations of the fungicide, compared to the rest of the strains, which, at high concentrations, also developed mycelium, although scarce and disordered.

Figure 5. Inhibition of mycelial growth of *C. siamense* under fungicide stress. A) fludioxonil + azoxystrobin; and B) copper sulfate, after 48 h of incubation at 27 °C ±1 °C.

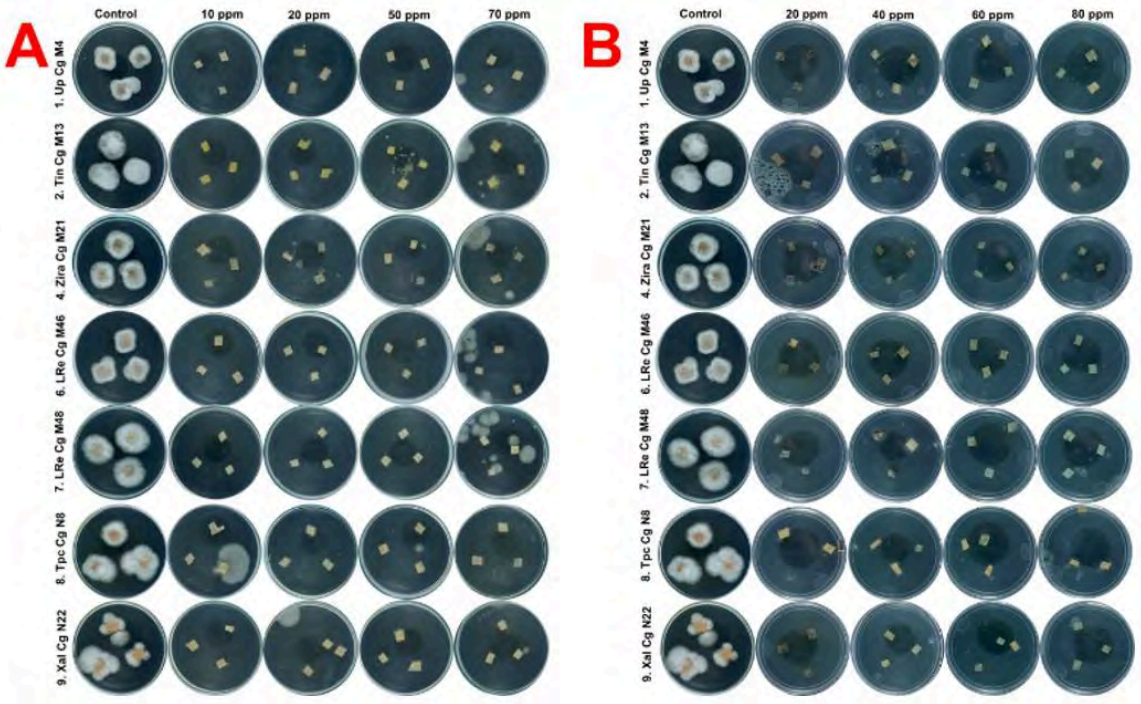
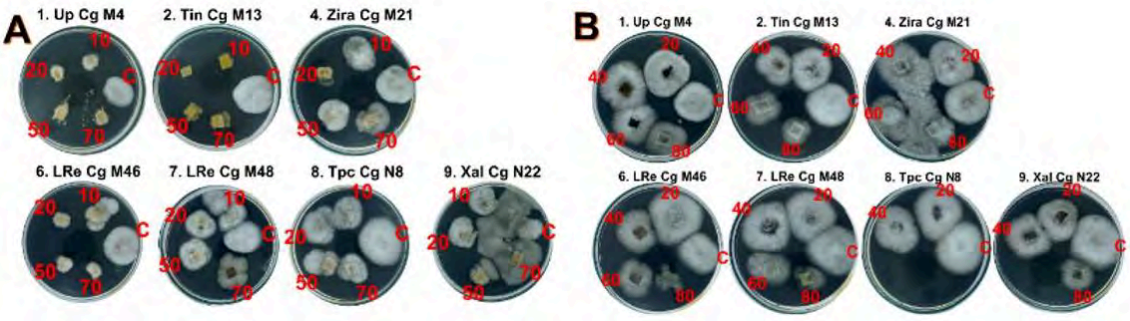


Figure 6. Growth of mycelium in PDA medium after 48 h exposed to fungicide stress. A) fludioxonil + azoxystrobin (10, 20, 50, and 70 ppm); and B) copper sulfate (20, 40, 60, and 80 ppm).



With the copper sulfate fungicide, all strains developed mycelium after reinoculation in PDA without fungicide. Increased development after exposure to low concentrations of fungicides and decreased development of mycelium after exposure to high concentrations of fungicides. One explanation for this phenomenon of inhibition under stress of both fungicides is that the evaluated strains entered an inactive state in response to the high concentration of the fungicide. This is because, in the field, the concentration of the fungicide decreases over time due to the degradation of the molecule, exposure to ultraviolet light or dilution by rain or environment (Arjona-López *et al*., 2020; Han *et al*., 2021).

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The identification of *C. siamense* in the Central Pacific Region of Mexico indicated that the fungus has dispersed within the main avocado-producing regions in Mexico. Research by Weir *et al*. (2012) mentioned that *C. siamense* is represented by 30 isolates from a wide range of hosts from various tropical regions and forms a monophyletic clade that cannot be genetically subdivided without being considered a species complex of *C. siamense*. ITS sequences do not reliably separate *C. siamense* from the rest of *C. gloeosporioides sensu lato* (*C. alienum*, *C. fructicola* and *C. tropicale*).

The GAPDH gene sequence was more efficient in distinguishing *C. siamense* (Lee *et al*., 2020). Fuentes-Aragón *et al*. (2020b) reported for the first time in preharvest the presence of *C. siamense* in fruits with visible symptoms of anthracnose in the Central Pacific Region of Mexico. The results of this research coincided with the studies already mentioned, which indicate that *C. siamense* is the most abundant pathogen in the Central Pacific Region of Mexico, the one with the highest production and export of 'Hass' avocado in Mexico.

The presence of *C. siamense*, isolated from avocado fruits with visible symptoms of anthracnose in the preharvest stage, was reported in Australia (Giblin and Coates, 2007), New Zealand (Hofer *et al*., 2021); Mexico (Trinidad-Ángel *et al*., 2017; Fuentes-Aragón *et al*., 2020b); Ghana (Honger *et al*., 2016) and Israel (Sharma *et al*., 2017). Unlike these studies, this research used avocado fruits without visible symptoms of anthracnose and harvested at physiological maturity, which confirms that *C. siamense* is an endophytic pathogenic fungus, capable of existing in two conditions of life of the fruit (pre- and postharvest); in addition, it can enter the immature tissue of the fruit (lenticels, pedicels, and direct penetration) and remain dormant for months (dormancy) (Prusky *et al*., 2013) and further colonize the fruit during storage when the fruit begins to ripen, making it a necrotrophic fungus.

It is evident that the control of anthracnose in preharvest does not eliminate the postharvest problem; therefore, different strategies must be used, one for the control of anthracnose in preharvest and another in postharvest with asymptomatic fruits and thus, keep the quality of the fruits for longer storage, to allow reaching international markets.

On the other hand, in postharvest, due to existing regulations, chemical control is rarely used. Therefore, it is necessary to use alternative methods to the use of chemical compounds to control anthracnose in avocado storage with high efficiency, low cost, and low risk to health and the environment (Herrera-González *et al*., 2021).

Conclusions

Based on their morphological, molecular and phylogenetic characteristics, they were identified as *C. siamense* causing anthracnose in postharvest of avocado from the Central Pacific Region of Mexico. In addition, it was evidenced that these strains remain dormant under the stress of the azoxystrobin-fludioxonil and copper sulfate fungicides, but when the stress was removed, growth restarted.

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