

Fungi and oomycetes causing root rot in avocado (*Persea americana* Mill) in Nayarit, Mexico

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Abstract: Avocado is a crop of great importance in Nayarit, Mexico. Trees with root rot symptoms have recently been observed, but the causal agent remains unknown. Therefore, this research aimed to identify the putatively pathogenic fungi and oomycetes that cause root rot in avocados in Nayarit, Mexico. From June to July 2022, in orchards located in the main producing municipalities of Nayarit, symptomatic root sections were collected from trees with apparent root rot. Fifteen microorganisms associated with diseased roots were isolated and morphologically identified. Subsequently, pathogenicity tests of the fungal isolates and oomycetes were performed on young (≈four-month-old) avocado trees. Isolates showing pathogenicity were molecularly identified by sequencing the internal transcript spacer regions (primers ITS5 and ITS4). All oomycete and fungal isolates caused symptoms, but with different levels of virulence. Molecular identification revealed three genera, isolates of *Phytophthora cinnamomi* (Oomycete), *Fusarium oxysporum* species complex, *F. solani* species complex, *Fusarium* sp., and *Lasiodiplodia* sp., associated with avocado root rot in Nayarit.

Index Terms: molecular characterization, distribution, *Fusarium*, phytopathogen.

Fungos e oomicetos causando podridão radicular em abacate (*Persea americana* Mill) em Nayarit, México

Resumo: O abacate é uma cultura de grande importância em Nayarit, México. Árvores com sintomas de podridão radicular foram observadas recentemente, mas o agente causal permanece desconhecido. Portanto, esta pesquisa teve como objetivo identificar os fungos e oomicetos supostamente patogênicos que causam podridão radicular em abacates em Nayarit, México. De junho a julho de 2022, em pomares localizados nos principais municípios produtores

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de Nayarit, foram coletadas seções de raízes sintomáticas de árvores com aparente podridão radicular. Quinze microrganismos associados a raízes doentes foram isolados e identificados morfológicamente. Posteriormente, testes de patogenicidade dos isolados fúngicos e oomicetos foram realizados em abacateiros jovens ($\approx$ quatro meses de idade). Os isolados que apresentaram patogenicidade foram identificados molecularmente por meio do sequenciamento das regiões espaçadoras do transcrito interno, com os primers ITS5 e ITS4. Todos os isolados oomicetos e fúngicos causaram sintomas, mas com níveis de virulência distintos. A identificação molecular permitiu identificar três gêneros, isolados de *Phytophthora cinnamomi* (Oomiceto), complexo de espécies *Fusarium oxysporum*, complexo de espécies *F. solani*, *Fusarium* sp. e *Lasiodiplodia* sp., associados à podridão da raiz do abacate em Nayarit.

Termos para indexação: caracterização molecular, distribuição, *Fusarium*, fitopatógeno.

The avocado (*Persea americana* Mill) is one of the major perennial crops in Mexico. The country stands out as the world's leading producer, yielding approximately 2.9 million metric tons over an established area exceeding 250,000 hectares (SIAP, 2024). However, its production has been constrained by various phytosanitary issues. The disease commonly known as "avocado root rot," caused by the oomycete soilborne *Phytophthora cinnamomi* Rands, is a significant limiting factor in avocado cultivation and is widely distributed, with a broad range of alternative host species (RAMÍREZ et al., 2014; RODRÍGUEZ et al., 2017).

The damage caused by this pathogen to avocado trees in Mexico has been documented in the roots and the base of the stem. Such damage causes leaf wilting, reducing the quality and quantity of fruit produced. As the disease progresses, the tree wilts and loses foliage, with apparent branch dieback. In severe cases, they cause significant losses in the harvest, and the tree dies (OSORIO et al., 2017; ZAPATA et al., 2018).

Osorio et al. (2017) mention that besides *P. cinnamomi*, there are unidentified microorganisms associated with "avocado root rot" have unknown roles. Additionally, *Phytophthora heveae* Thompson,

Phytophthora citricola Sawada, *Verticillium* sp., and *Cylindrocarpon destructans* Zinss pathogens inducing similar symptoms have been suggested (RAMÍREZ et al., 2014). Studies on the incidence, causal agents, and pathogenicity of the microorganisms causing root rot in avocado orchards in Nayarit, Mexico, are scarce. Therefore, this research aimed to identify the microorganisms associated with avocado root rot in the producing areas of Nayarit and to evaluate their pathogenicity.

During June and July 2022, root samples from avocado trees were collected in 13 orchards in the main producing municipalities in Nayarit, Mexico (Figure 1) (Table 1). Trees showing symptoms of "avocado root rot" were selected. Symptoms included defoliation, chlorosis, wilting, dieback, and necrotic new roots (Figure 2). Samples were taken from five trees per orchard. Roots were washed, sterilized with a 3% sodium hypochlorite solution, rinsed with sterile distilled water, and dried. Segments of 5-10 mm were cut, focusing on the advancing zone of the disease, and placed on potato dextrose agar (PDA) and V8-PARPH media. Petri dishes with tissue samples were incubated at 28 ± 2 °C in the dark until fungal and oomycete colonies became visible.

Table 1. Characteristics of sampling sites of avocado trees with symptomatic roots in Nayarit, Mexico.

Municipality	Geographical coordinates	Age (years)	Technical level	Altitude (masl)
Ixtlán Del Río	21° 02' 09" N, 104° 20' 09" O	13	High ^x	1148
Jala	21° 05' 57" N, 104° 20' 17" O	6	Medium ^y	1905
Jala	21° 06' 43" N, 104° 19' 35" O	6	Medium ^y	1925
Jala	21° 05' 53" N, 104° 19' 12" O	6	Medium ^y	1908
Jala	21° 05' 36" N, 104° 19' 13" O	7	Medium ^y	1893
Jala	21° 06' 12" N, 104° 21' 50" O	7	Medium ^y	1871
Jala	21° 06' 22" N, 104° 21' 04" O	7	Medium ^y	1902
Ahuacatlán	21° 07' 12" N, 104° 35' 36" O	8	Medium ^y	810
Santa María Del Oro	21° 11' 08" N, 104° 35' 25" O	12	Medium ^y	1290
Tepic	21° 29' 58" N, 104° 46' 46" O	17	Medium ^y	1000
Xalisco	21° 23' 45" N, 104° 55' 48" O	19	Medium ^y	1260
Xalisco	21° 23' 38" N, 104° 55' 52" O	22	Medium ^y	1190
Xalisco	21° 22' 26" N, 104° 54' 56" O	19	Medium ^y	1110

masl: meters above sea level.

^xHigh: Micro-sprinkler irrigation and fertigation.

^yMedium: Irrigation during the rainy season, without fertigation and casual technical assistance.

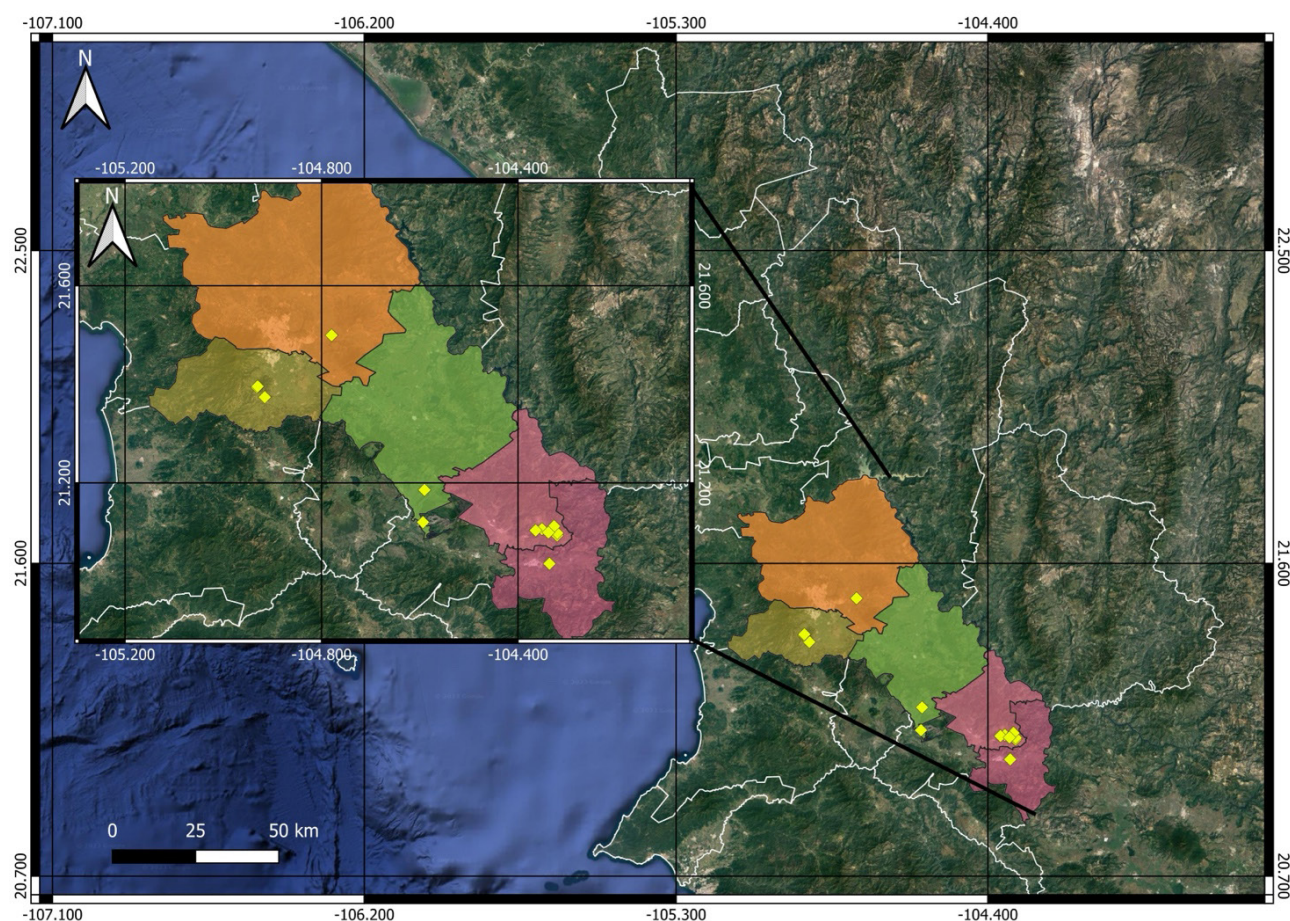
**Figure 1.** Geographic location of avocado orchard sampling sites in Nayarit, Mexico.



Figure 2. Characteristic symptoms of avocado root rot.

The isolated microorganisms were purified on PDA using the monoconidial culture and incubated at 28 ± 2 °C for 72 hours. Their identification was performed at the genus level by observing morphological characteristics under a light microscope (Leica, DME 13595, Wetzlar, Germany) and using taxonomic keys (WATANABE, 2010; BARNETT; HUNTER, 1998; ERWIN; RIBEIRO, 1996).

The isolates' identities were confirmed molecularly by extracting genomic DNA from the seven-day-old PDA cultures using the DNeasy Plant kit (QIAGEN®) per the manufacturer's instructions. Molecular identification involved sequencing internal transcribed spacers (ITS). These regions were amplified using universal primers ITS1 (5'-TCCGTAGGTGAACCTGCGG-3') and ITS4 (5'-TCCTCCGCTTATTGATATGC-3') (WHITE et al., 1990) with the following conditions: 1x buffer, 3.5 mM MgCl₂, 10 mM dNTPs, 2.5 μ M of each primer, and 1U Taq platinum (Invitrogen®). The amplification protocol in-

involved one cycle at 94 °C for 5 min, followed by 35 cycles at 94 °C for 30 secs, 60 °C for 45 secs, 72 °C for 1.5 min, and a final extension at 72 °C for 8 min. PCR products were visualized on 2 % agarose gels and purified using magnetic beads before sequencing. Sequences were edited with MEGA 11 (TAMURA et al., 2021) to obtain a consensus sequence for each sample and analyzed using BLAST on the NCBI database; all the sequences generated in this study were deposited in the NCBI database (Table 2).

For *Phytophthora* species identification, we followed the methodology described on the IDphy tool, which provides molecular resources for identifying *Phytophthora* species based on the type strains and well-authenticated specimens (ABAD et al. 2023). Therefore, the strains morphologically identified as belonging to the genus *Phytophthora* were aligned and phylogenetically compared with the sequence of the type strain of *Phytophthora cinnamomi* and all the members of Clade 7 of *Phytophthora*, where this species is grouped (ABAD et al. 2023).

Additionally, we constructed a maximum-likelihood model tree on the IQ-TREE server (TRIFINOPOULOS et al. 2016) with sequences of all species from Clade 7 and our sequences. Concerning *Fusarium* species complexes, their sequences were aligned with MAFFT v7 (KATO et al. 2019) and then used to reconstruct a maximum-likelihood model on the IQ-TREE server. The best-fitting model obtained with Modelfinder was the K2P+I+G4, and an ultrafast bootstrap test (HOANG et al. 2018) with 10,000 replicates was performed. For the phylogenetic reconstruction, we included previously reported sequences of the *Fusarium solani* Mart species complex (FSSC), including the type of strain (SCHROERS et al. 2016) and sequences of the *Fusarium oxysporum* Schlecht species complex (FOSC), all downloaded from GenBank.

Table 2. Identification, pathogenicity, GenBank accession numbers, and virulence level of fungal and oomycete isolates from symptomatic avocado roots.

Municipality	Type	Scientific Name	GenBank (Acc. No.)	First Symptoms (dai)	Mortality (dai)	Virulence Level
Ixtlán del Río	Fungus	<i>Lasiodiplodia</i> sp.	PP965121	135	No	Low virulence
Jala	Fungus	<i>Fusarium oxysporum</i>	PP965113	35	143	Highly virulent
Jala	Oomycete	<i>Phytophthora cinnamomi</i>	PP965124	21	159	Highly virulent
Jala	Fungus	<i>Fusarium oxysporum</i>	PP965115	98	No	Moderately virulent
Jala	Oomycete	<i>Phytophthora cinnamomi</i>	PP965126	21	No	Moderately virulent
Jala	Fungus	<i>Fusarium</i> sp.	PP965116	35	No	Moderately virulent
Jala	Fungus	<i>Fusarium oxysporum</i>	PP965118	21	159	Highly virulent
Jala	Fungus	<i>Fusarium oxysporum</i>	PP965122	98	No	Moderately virulent
Ahuacatlán	Fungus	<i>Fusarium solani</i>	PP965120	28	No	Moderately virulent
Santa María del Oro	Fungus	<i>Fusarium solani</i>	PP965119	135	No	Low virulence
Santa María del Oro	Oomycete	<i>Phytophthora cinnamomi</i>	PP965127	143	No	Low virulence
Tepic	Fungus	<i>Fusarium</i> sp.	PP965123	59	No	Moderately virulent
Xalisco	Fungus	<i>Fusarium</i> sp.	PP965114	28	No	Moderately virulent
Xalisco	Fungus	<i>Fusarium</i> sp.	PP965117	113	No	Low virulence
Xalisco	Oomycete	<i>Phytophthora cinnamomi</i>	PP965125	143	No	Low virulence

Note: dai = days after inoculation; 'No' = no plant mortality observed.

After isolating microorganisms, fifteen isolates (eleven fungi and four oomycetes) were selected to undergo pathogenicity testing under greenhouse conditions. Five young avocado trees (var. *Drymifolia*, $\approx$ 4 months old) grown from seeds of healthy trees and planted individually in black polyethylene bags (18×26 cm; $\approx$ 2 L) containing sterile loam-clay soil were used. The base of each tree's stem was inoculated with a 6 mm PDA disc with mycelium from each microorganism.

Before inoculation, the bark of the stems was superficially injured with 2 mm cross-shaped cuts using a sterile scalpel. Inoculated stems were wrapped with Parafilm®. Control trees received PDA discs without inoculum. Inoculated trees were maintained in a greenhouse for six months after inoculation. During this time, the presence or absence of typical infection symptoms caused by the tested fungi and oomycetes was monitored weekly. Fungal and oomycete isolates that caused severe damage to roots, stems, leaves, and shoots after inoculation, including tree death, were considered pathogenic.

To classify the virulence level of each isolate, two criteria were considered: the number of days until the appearance of first symptoms (dai), and whether the inoculated tree eventually died. Isolates were categorized as follows: highly virulent if they caused symptoms within 35 days and induced plant mortality; moderately virulent if symptoms appeared between 36 and 98 days, regardless of whether mortality occurred; low virulence was assigned to isolates that produced symptoms after 98 days without inducing mortality; and avirulent (zero virulence) was assigned when no symptoms or mortality were observed (Table 2).

The microorganisms (fungi and oomycetes) isolated from the roots of avocado trees with symptoms of "avocado root rot" belonged to the genera *Phytophthora*, *Fusarium*, and *Lasiodiplodia*.

Analysis of the ITS sequences revealed 97-100% nucleotide similarity between the fungal and oomycete isolates and previously published sequences, including the ex-type strain of *Phytophthora cinnamomi*

(oomycete), *Fusarium oxysporum* species complex, *F. solani* species complex, and *Lasiodiplodia* sp. *P. cinnamomi* identification was corroborated by the grouping of our sequences with the ex-type strain sequence of *P. cinnamomi* in a ML analysis (Figure 3).

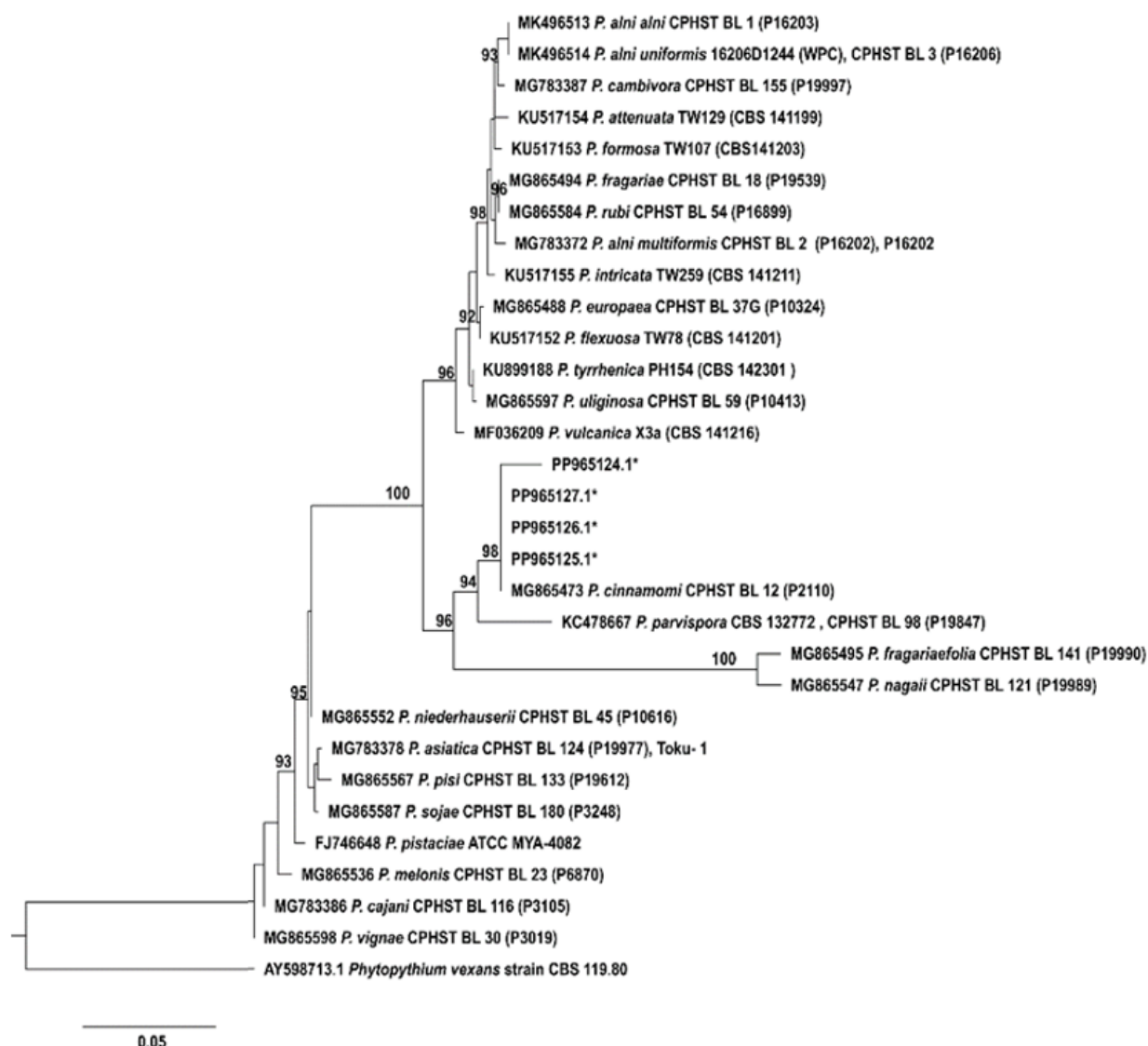


Figure 3. Maximum Likelihood phylogenetic tree of *Phytophthora* clade 7. The tree shows the grouping of the sequences from this study with the *Phytophthora cinnamomi* ex-type sequence. *Phytophythium vexans* was used as an external group. The best-fit model by Modelfinder was TIM3+F+G4, the ultrafast bootstrap test (HOANG et al. 2018) consisted of 10,000 replicates, numbers above branches indicate ultrafast bootstrap values >95 and asterisks * indicate sequences generated in this study.

Fusarium sp. was the most frequently observed genus (66.6%, 10 isolates), with four isolates identified as *F. oxysporum* species complex and two as *F. solani* species complex, all supported by the phylogenetic analysis (Figure 4), as well as four identified only at the genus level. Similarly, *Fusarium* has been associated with diseased avoca-

do trees in other regions. Hernández et al. (2015) in Colombia documented the association of the genus *Fusarium* with various avocado organs. *Fusarium austroamericanum*, *F. decemcellulare*, *F. incarnatum*, *F. oxysporum*, *F. solani*, *F. subglutinans*, and *F. verticillioides* were reported in fruits; while *F. incarnatum*, *F. solani*, and *F. subglutinans*

were found in leaves. *Fusarium solani* was reported in both the peduncle and the root. Olalde et al. (2020) reported *F. oxysporum* and *F. solani* as root rot pathogens in avocado trees in Michoacán, Mexico. Ceja et al. (2000) found *F. oxysporum* and *F. solani* causing trunk lesions in avocado. León; Mattos (2016) documented seed

and seedling infection by *F. verticillioides* in Peru. *Phytophthora* was the second most frequent genus with four isolates (26.6%) belonging to *P. cinnamomi*. Members of the genus *Phytophthora* are significant pathogens for agricultural and forestry crops worldwide, causing substantial economic losses.

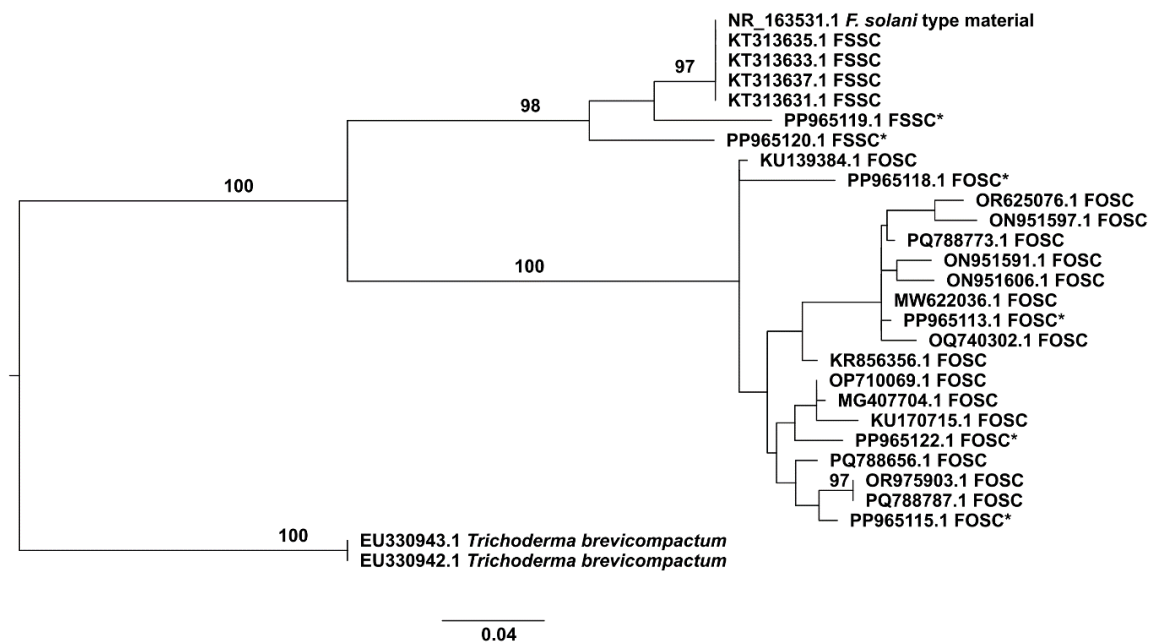


Figure 4. ITS Maximum Likelihood phylogenetic tree, showing the grouping of strain sequences from this study with members of the *Fusarium solani* species complex (FSSC) and *Fusarium oxysporum* species complex (FOSC). *Trichoderma brevicompactum* was used as an external group. Numbers above branches indicate ultrafast bootstrap values >95, asterisks * indicate sequences generated in this study.

The *P. cinnamomi* isolates were differentially distributed among the orchards sampled in this study. This species has been reported as the main cause of root rot in avocados in other countries (BERG et al., 2021; KURBETLI et al., 2020; RODRÍGUEZ et al., 2017). In Mexico, the first epidemiological report of this pathogen was in 1952, documenting a 90% loss in avocado production (AGAPITO et al., 2022). Other species, such as *P. heveae* and *P. citricola* have also been associated with root rot in avocado in Colombia (RAMÍREZ et al., 2014). Finally, one isolate (6.6%) belonged to the genus *Lasiodiplodia*. This fungus is considered the causal agent of dieback and fruit rot in vari-

ous host plants (PICOS et al., 2015). Medina et al. (2018) reported *L. theobromae* causing soft rot symptoms in jackfruit (*Artocarpus heterophyllus*) in Nayarit, Mexico.

Recently, Betancourt et al. (2024) reported *L. theobromae* as the cause of dieback in sour-sop (*Annona muricata* L.) in Nayarit, Mexico, and Cambero et al. (2024) reported it as a root pathogen in *Annona muricata* L. in Nayarit, Mexico. In this regard, Alama et al. (2006) recorded *L. theobromae* as the causal agent of canker and dieback in avocado crops in Peru, with an incidence exceeding 80%. In Colombia, *L. theobromae* was associated with damage to the graft area in avocado was recorded (RAMÍREZ; MORALES,

2021). Similar data are reported by Monir et al. (2021), who indicate that *L. theobromae* was the phytopathogen frequently isolated from graft failure seedlings in different avocado cultivars. Arjona et al. (2019) observed branch dieback in several avocado orchards in southern Spain, with a low incidence of *L. theobromae* with these symptoms. Valencia et al. (2019) documented the infection of *L. theobromae* in avocado cankers and dieback in Chile.

All isolates were pathogenic to avocado trees (Table 2), with varying degrees of virulence in the time required to induce the first symptoms. The time to appearance of initial symptoms, such as chlorosis and wilting, in inoculated avocado plants (var. *drymifolia*), varied among pathogens. *Fusarium oxysporum* strains induced the first infection symptoms in avocado trees between 21 and 98 days after inoculation (dai). *F. solani* isolates ranged from 28 to 135 dai. Isolates of *Phytophthora cinnamomi* induced disease symptoms from 21 to 143 dai. The *Lasiodiplodia* sp. (005) isolate triggered the appearance of initial infection symptoms at 135 dai. Isolates of *Fusarium* sp. (006) and *Phytophthora cinnamomi* (007) isolated from trees in the municipality of Jala were the most virulent, causing chlorosis in all tested trees between 21 and 35 dai, followed by tree death between 143 and 159 dai. Therefore, the identification of this *Fusarium* sp. strain is needed.

Based on days until symptoms, pathogenicity testing revealed significant variability in intrinsic virulence among isolates, even within the same species and originating from the same locality. This variability can be attributed to the strains' specific ability to induce pathological symptoms, potentially depending on their region of origin. Dissanayake et al. (2009) documented differences in virulence among *Fusarium*

strains on the Welsh onion (*Allium fistulosum*) cultivated in different regions, interestingly, the five isolates with the highest virulence were members of *F. oxysporum*. Hernández et al. (2015) suggested that the variability among *F. oxysporum* isolates is influenced by the environmental conditions where the fungus develops, leading to distinct virulence characteristics.

These include colony adaptation, the production of microconidia and macroconidia for propagation, and the formation of chlamydospores for survival under stress factors. In *P. cinnamomi*, pathogenic variation has also been demonstrated. Huberli et al. (2001) documented pathogenicity differences among Australian isolates from plant species *Eucalyptus marginata* and *Corymbia calophylla*, suggesting three response categories based on the duration necessary for the pathogen to induce plant death: i) High pathogenicity, where isolates caused plant death at ≤ 59 days after inoculation (dai); ii) Intermediate pathogenicity, where isolates induced plant death between 60 and 182 dai; and iii) low pathogenicity, where isolates did not cause plant death after 182 dai.

According to the results obtained from morphological characterization, ITS sequence analysis, and pathogenicity tests, *Phytophthora cinnamomi* (Oomycete), strains related to the *Fusarium oxysporum* species complex, and the *F. solani* species complex, *Fusarium* sp., and *Lasiodiplodia* sp. were identified as the phytopathogens responsible for causing the symptoms of root rot and wilting of *Persea americana* plants in Nayarit, Mexico. However, to ensure greater reliability of molecular identification, the use of additional markers such as EF1 α , β -tubulin, rDNA, among others, is recommended. This information could be useful for producers of this crop, enabling

the development of targeted disease control strategies, such as chemical or genetic control (e.g., resistant rootstocks).

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Data Availability: The data that support the findings of this study are available from the corresponding author, Rosales, F.A.P., upon reasonable request.

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