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Distribution and Pathogenicity of *Colletotrichum* Species Associated With Mango Anthracnose in Mexico

J. M. Tovar-Pedraza,[1] J. A. Mora-Aguilera,[2] C. Nava-Díaz,[2] N. B. Lima,[3] S. J. Michereff,[4] J. S. Sandoval-Islas,[2] M. P. S. Câmara,[5] D. Téliz-Ortiz,[2] and S. G. Leyva-Mir[6,†]

[1] Laboratorio de Fitopatología, Coordinación Culiacán, Centro de Investigación en Alimentación y Desarrollo, Culiacán, 80110 Sinaloa, Mexico
[2] Fitopatología, Campus Montecillo, Colegio de Postgraduados, Texcoco, 56230 Estado de México, Mexico
[3] CONICET–Instituto de Patología Vegetal, CIAP-INTA, X5020ICA Córdoba, Argentina
[4] Centro de Ciências Agrárias e da Biodiversidade, Universidade Federal do Cariri, Crato, 63130-025 Ceará, Brazil
[5] Departamento de Agronomia, Universidade Federal Rural de Pernambuco, Recife, 52171-900 Pernambuco, Brazil
[6] Departamento de Parasitología Agrícola, Universidad Autónoma Chapingo, Texcoco, 56230 Estado de México, Mexico

Abstract

Mango anthracnose, caused by *Colletotrichum* spp., is the most significant disease of mango (*Mangifera indica* L.) in almost all production areas around the world. In Mexico, mango anthracnose has only been attributed to *C. asianum* and *C. gloeosporioides*. The aims of this study were to identify the *Colletotrichum* species associated with mango anthracnose symptoms in Mexico by phylogenetic inference using the *ApMat* marker, to determine the distribution of these species, and to test their pathogenicity and virulence on mango fruits. Surveys were carried out from 2010 to 2012 in 59 commercial orchards in the major mango growing states of Mexico, and a total of 118 isolates were obtained from leaves, twigs, and fruits with typical anthracnose symptoms. All isolates were tentatively identified in the *C. gloeosporioides* species complex based on morphological and cultural characteristics. The Bayesian inference phylogenetic tree generated with *Apn2*/MAT intergenic spacer sequences of 59 isolates (one per orchard) revealed that *C. alienum*, *C. asianum*, *C. fructicola*, *C. siamense*, and *C. tropicale* were associated with symptoms of mango anthracnose. In this study, *C. alienum*, *C. fructicola*, *C. siamense*, and *C. tropicale* are reported for the first time in association with mango tissues in Mexico. This study represents the first report of *C. alienum* causing mango anthracnose worldwide. The distribution of *Colletotrichum* species varied among the mango growing states from Mexico. Chiapas was the only state in which all five species were found. Pathogenicity tests on mango fruit cultivar Manila showed that all *Colletotrichum* species from this study could induce anthracnose lesions. However, differences in virulence were evident among species. *C. siamense* and *C. asianum* were the most virulent, whereas *C. alienum* and *C. fructicola* were considered the least virulent species.

Keywords: *Mangifera indica*, morphology, phylogeny, pathogenicity, *Colletotrichum*

The mango (*Mangifera indica* L.) is one of the five most economically important fruit crops worldwide, with production occurring in most countries in the tropics and subtropics (Mukherjee and Litz 2009; Paull and Duarte 2011). During the period from 2010 to 2016, Mexico was the fifth largest producer and the largest exporter of mangos worldwide (Food and Agriculture Organization of the United Nations 2017). In Mexico, mango production is distributed in 23 states; however, more than 97% of the production is concentrated in 10 states (Guerrero, Nayarit, Chiapas, Oaxaca, Sinaloa, Michoacán, Veracruz, Jalisco, Colima, and Campeche) (Servicio de Informacion Agroalimentaria y Pesquera 2017).

Anthracnose, caused by *Colletotrichum* spp., is the most important disease of mango in almost all production areas, because it attacks leaves, twigs, flowering panicles, and fruits (Arauz 2000; Paull and Duarte 2011; Ploetz 2003; Ploetz and Freeman 2009). Yields are drastically reduced when the inflorescence is attacked. Disease occurs as quiescent infections on immature fruit, but the damage is more economically significant in postharvest fruits (Prusky et al. 2009). The incidence of mango anthracnose can reach almost 100% in fruit produced in areas with high humidity during the flowering period, particularly in poorly managed orchards (Arauz 2000; Ploetz and Freeman 2009).

Anthracnose symptoms in mango orchards may be observed on leaves, twigs, panicles, and fruits. On leaves, lesions are irregular, necrotic, and often surrounded by chlorotic haloes. Lesions may coalesce and form large necrotic areas, especially along the leaf margins. Under favorable conditions, salmon to orange fruiting bodies (acervuli) of the pathogen are formed on the lesions. On twigs, symptoms begin as small, enlarged oval and necrotic lesions that expand and coalesce. During severe infections, the fungus can invade twigs and cause dieback. Small, circular dark lesions also develop on pedicels and peduncles. On panicles, the fungus induces blossom blight and can affect both inflorescence stalk and individual flowers. Fruits may be infected at any stage of their development. Infection on young fruits is often observed as mummification. Infections on larger fruits usually remain latent until the fruit ripens, and it appears as black, irregular, and sunken lesions (Arauz 2000; Ploetz 2003; Ploetz and Freeman 2009; Prakash 2004; Prusky et al. 2009).

Accurate identification of the plant pathogen species is critical to understand the epidemiology of mango anthracnose and develop effective control measures (Cai et al. 2009). Species circumscription and identification of *Colletotrichum* species has historically been based on host range, symptoms of infection on particular hosts, and a suite of morphological characters (Hyde et al. 2009a, b). However, the use of these conventional taxonomic characters in *Colletotrichum* species has failed to support the development of a robust species concept because of their plasticity (Cannon et al. 2012; Damm et al. 2012a, b; Hyde et al. 2009a, b; Rojas et al. 2010). According to Marin-Felix et al. (2017) and Damm et al. (2019), there are 14 *Colletotrichum* species complexes and 15 accepted singleton

†Corresponding author: S. G. Leyva-Mir; lsantos@correo.chapingo.mx

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species. All of the complexes can be distinguished from each other by using internal transcribed spacer (ITS) sequence data alone, whereas the species-within-species complex can be resolved by sequence differences in additional genes.

Currently, there are at least 12 *Colletotrichum* species that have been previously associated with mango tissues worldwide. These species belong to the gloeosporioides (*C. asianum* Prihastuti, Cai & Hyde; *C. fructicola* Prihastuti, Cai & Hyde; *C. gloeosporioides* Penz. & Sacc.; *C. theobromicola* Delacr.; *C. siamense* Phoulivong, Cai & Hyde; *C. tropicale* Rojas, Rehner & Samuels; *C. queenslandicum* Weir & Johnst.; and *C. grossum* Diao, Zhang, Cai & Liu), boninense (*C. karstii* Yang, Liu, Hyde & Cai), and acutatum (*C. fioriniae* Shivas & Tan; *C. simmondsii* Shivas & Tan; and *C. scovillei* Damm, Cannon & Crous) species complexes, as well as one singleton species as *C. cliviicola* Damm & Crous (Jayawardena et al. 2016; Lima et al. 2013; Manzano León et al. 2018; Marin-Felix et al. 2017; Mo et al. 2018; Pardo-De la Hoz et al. 2016; Qin et al. 2019; Sharma et al. 2013; Shivas et al. 2016; Vieira et al. 2014).

In previous studies, the taxonomy of *Colletotrichum* species associated with mango was identified by phylogenetic multilocus analyses (ACT, TUB2, CAL, CHS, GAPDH, ITS) in conjunction with recognizable phenotypic characters (Cai et al. 2009; Damm et al. 2012a, b; James et al. 2014; Lima et al. 2013; Phoulivong et al. 2010; Udayanga et al. 2013; Weir et al. 2012). However, studies involving *Colletotrichum* isolates associated with several tropical hosts, including mango, demonstrated that the *ApMat* marker provided better phylogenetic information compared with other loci used and can resolve species within the *C. gloeosporioides* complex (Doyle et al. 2013; Pardo-De la Hoz et al. 2016; Rojas et al. 2010; Sharma et al. 2013, 2015, 2017; Silva et al. 2012; Vieira et al. 2014).

Until 2014, *C. gloeosporioides* was identified as the only species associated with mango anthracnose in Mexico (Gutiérrez-Alonso et al. 2001; Rojas-Martínez et al. 2008). In 2014, *C. asianum* was also identified from mango fruit from Mexico based on multilocus phylogenetic analysis (Honger et al. 2014). The aims of this study were to identify the *Colletotrichum* species associated with mango anthracnose in Mexico based on phylogenetic analysis using *Apn2*/MAT intergenic spacer sequence data, to determine the distribution of these species, and to test their pathogenicity and virulence on mango fruits.

Materials and Methods

Sampling and fungal isolation. Mango leaves, twigs, and fruits with typical anthracnose symptoms (Fig. 1) were collected during several surveys carried out from 2010 to 2012 in various mango cultivars in 59 commercial orchards in the major mango growing states of Mexico (Table 1). Fungal isolates were obtained from infected tissues without visible sporulation using the procedure described by Cai et al. (2009) and Prihastuti et al. (2009). Pure cultures were established from single spores for isolates identified as *Colletotrichum* species based on morphological characteristics. For samples of symptomatic tissues with reproductive structures (acervuli) on lesions, monoconidial cultures were obtained following the technique of Goh (1999).

Representative cultures of each isolate were deposited in the Culture Collection of Phytopathogenic Fungi of the Department of Agricultural Parasitology at the Chapingo Autonomous University (Texcoco, Estado de México, Mexico). Cultures were maintained as spore suspensions and mycelial plugs in 15% glycerol at −80°C.

Morphology and cultural characteristics. Macroscopic and microscopic characteristics were examined for 118 *Colletotrichum* isolates. All isolates were subcultured onto potato dextrose agar (PDA) from conidia suspensions stored at −80°C. To determine the growth rate of each isolate, mycelial plugs (5 mm in diameter) were taken from 5-day-old cultures and placed onto PDA and malt extract agar (MEA; Difco, Bordeaux, France). The plates were incubated at 25°C in darkness. Colony diameters of a three-replicate culture of each isolate were recorded at 24-h intervals over 6 days. Growth rate was calculated as the 6-day average of mean daily growth (in millimeters per day). After 6 days, colony growth characteristics, including surface and reverse colony appearance on each type of agar, were recorded. The experiment was conducted twice.

To study the conidial morphology, conidia per isolate were harvested from actively growing colonies, mounted in 100% lactic acid, and examined for size and shape at 100× magnification using a compound microscope (BX41; Olympus, Tokyo, Japan) equipped with differential-interference-contrast optics. Measurements of 50 conidia were made with Motic Image Plus version 5.0 (Motic Group Co., Jiangsu, China).

DNA extraction, PCR amplification, and sequencing. Aerial mycelium from 6-day-old culture was scraped directly from the medium using a sterile spatula and was placed in 2-ml microtubes. Genomic DNA was extracted from 59 isolates (one isolate per orchard) using the hexacetyltrimethylammonium bromide method described by Doyle and Doyle (1990). DNA concentrations were quantified using a NanoDrop Lite Spectrophotometer (Thermo Fisher Scientific, Madison, WI) and the samples were diluted to 50 ng μl^{-1} for PCR reaction.

PCR amplification of the intergenic spacer between the 3′ end of the DNA-lyase and the mating type locus *Mat*1-2 (*Apn2*/Mat-IGS) of the *Apn2* and MAT1-2-1 (*ApMat* marker) was carried out with cycling parameters and primers specified by Doyle et al. (2013). PCR amplifications were conducted in a Bio-Rad C1000 thermocycler (Bio-Rad Laboratories, Hercules, CA). The PCR products were separated by electrophoresis in 1% agarose gel stained with ethidium bromide and viewed under ultraviolet light. The amplified PCR products were purified using the QIAquick PCR Purification Kit (Qiagen, Valencia, CA) and sequenced by Macrogen Inc. (Seoul, Korea) in both directions with the same primers that were used for the PCR reactions.

Phylogenetic analysis. The quality of the nucleotide sequences and the contig assembly was assessed using the Staden Package (Staden et al. 1998). Multiple sequence alignments of each gene used ClustalW as implemented in MEGA 7 (Kumar et al. 2016) and were manually adjusted to allow maximum sequence similarity. Bayesian phylogenetic estimates were inferred with MrBayes 3.2.6 (Ronquist et al. 2012) implemented on the CIPRES cluster (https://www.phylo.org/portal2/home.action) using the best-fit models of nucleotide substitution selected according to AICc by MrModeltest 2.3 (Nylander 2004). Four parallel runs were conducted with one cold and three heated Markov chain Monte Carlo search chains per run for 5×10^6 generations, sampling every 1,000 generations. Posterior probabilities were calculated after discarding the first 25% of generations as burn-in. Phylogenetic trees were viewed with TreeView (Page 1996). Sequences generated in this study were deposited in GenBank (Table 1). Alignments and tree files are available in TreeBASE (study no. 23366).

Pathogenicity and virulence on detached fruits. Pathogenicity tests were carried out on detached fruits of mango (cultivar Manila) at the first color break stage of ripening. Mango fruits were thoroughly washed under running water, surface disinfested in 1% sodium hypochlorite solution for 2 min followed by immersion in 70% ethanol for 2 min, rinsed two times in sterile distilled water, and dried in a laminar flow hood. The fruits were inoculated using the colonized agar plug method because some isolates had no satisfactory sporulation on the culture medium. Fruits were wounded in two allocated areas with a sterile toothpick (3 mm in depth). A mycelial plug (5 mm in diameter) removed from the margin of a 6-day-old PDA culture was placed onto the fruit surface on each wound. A noncolonized agar plug was placed on the wounds of 10 fruits used as the control. The fruits were incubated at 25°C in the dark on plastic trays lined with two layers of paper towel moistened with sterile distilled water and enclosed in a plastic bag. Six days after inoculation, the virulence of each isolate was assessed by measuring lesion diameter. Each isolate was inoculated on three fruits and the experiment was repeated twice. Differences in virulence caused by *Colletotrichum* species were determined by one-way analysis of variance, and mean values were compared by the least significant difference test at the 5% significance level using SAS version 9.1 software.

Results

Fungal isolates. A total of 118 *Colletotrichum* isolates were obtained from symptomatic mango tissues (110 leaves, five fruits, and three twigs) collected from 59 orchards distributed in the states

of Chiapas ($n = 11$), Sinaloa ($n = 9$), Nayarit ($n = 9$), Veracruz ($n = 9$), Michoacán ($n = 6$), Oaxaca ($n = 6$), Colima ($n = 5$), and Guerrero ($n = 4$) in Mexico (Table 1).

Morphology and cultural characteristics. In PDA media, colonies generally showed dense, white to grayish growth (Fig. 2). The mycelium growth rate varied from 8.3 to 11.6 mm day^{-1} (average = 10.2 mm day^{-1}). In MEA media, the colonies exhibited a growth rate that ranged between 10.6 and 15.0 mm day^{-1} (average = 13.7 mm day^{-1}), and they also exhibited greater variation in color from white to gray and beige. Conidia were hyaline, unicellular, and cylindrical (12.5 to 18.4 × 3.5 to 5.4 µm), with rounded extremes and inconspicuous hilum (Fig. 2).

All 118 isolates obtained from mango were tentatively identified in the *C. gloeosporioides* species complex based on morphological and cultural features. However, none of the morphological and cultural features tested allowed discrimination between the species belonging to the *C. gloeosporioides* complex.

Phylogenetic analysis. A total of 59 isolates were characterized for phylogenetic analysis of *Apn2*/MAT intergenic spacer sequences. The phylogeny provided sufficient information to distinguish five *Colletotrichum* species associated with symptoms of mango anthracnose in Mexico. All 59 isolates were nested within the Musae clade of the *C. gloeosporioides* complex with a high level of support with the Bayesian posterior probability values. The five clades corresponded to previously described species: *C. alienum*, *C. asianum*, *C. fructicola*, *C. siamense*, and *C. tropicale*. Thirty-three isolates were identified as *C. siamense*. Nineteen isolates were identified as *C. asianum*. Four isolates clustered with the type strain of *C. tropicale*. Two isolates were identified as *C. alienum*. Finally, only one isolate clustered with *C. fructicola* (Fig. 3).

Distribution of *Colletotrichum* species. The distribution of *Colletotrichum* species varied among the mango growing states from Mexico (Fig. 4). Chiapas was the only state in which all five species were found. *C. siamense* was found in all mango growing states, and all isolates from Guerrero belonged to this species. *C. asianum* was found in all sites, except in Guerrero and Oaxaca. *C. tropicale* was recorded only in the isolates from Sinaloa, Veracruz, and Chiapas. *C. alienum* was only isolated in samples from Chiapas and Oaxaca, whereas *C. fructicola* was identified only in Chiapas.

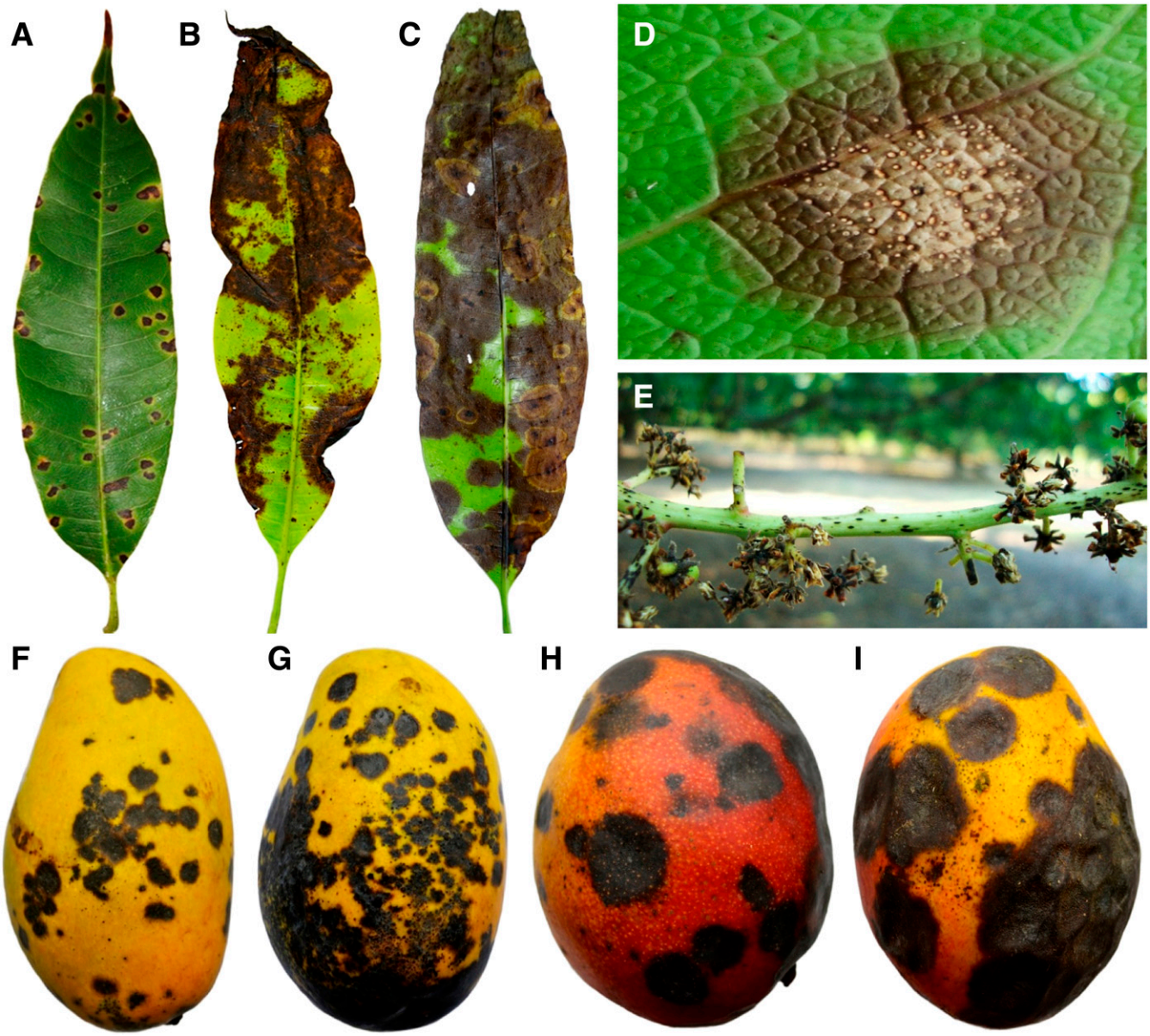

Fig. 1. Anthracnose symptoms caused by *Colletotrichum* spp. on mango tissues of the following cultivars: **A,** Tommy Atkins; **B, C, D, and E,** Ataulfo; **F and G,** Manila; and **H and I,** Haden. A, Irregular necrotic lesions on leaves. B and C, Leaf blight. D, Acervuli on a necrotic foliar lesion. E, Blight of panicles. F, G, H, and I, Fruits showing irregular and sunken necrotic lesions.

Although *C. siamense* was found in all mango growing states, no preference of this species with a specific tissue, cultivar, or collection site was observed, because it was obtained specifically from mango leaves and fruits as well as from various cultivars (Ataulfo, Manililla, Haden, Kent, Keitt, Manila, and Tommy Atkins) and collection sites of the main producing states of Mexico. Furthermore, it was not possible to relate their specificity to tissues and mango cultivars because of the low number of isolates analyzed.

Pathogenicity and virulence on fruits. All *Colletotrichum* isolates were pathogenic to mango fruits. Inoculated fruits developed sunken necrotic lesions on pericarp, whereas control fruits remained disease free. Fungal colonies were reisolated from all symptomatic fruits and were found to be morphologically identical to the original isolates inoculated on mango fruits, thus fulfilling Koch's postulates.

There were significant differences ($P \leq 0.05$) in lesion diameter produced by the different *Colletotrichum* species tested in this study. *C. siamense* and *C. asianum* were the most virulent species, with a mean lesion diameter of 17.4 and 16.9 mm, respectively. *C. tropicale* exhibited intermediate virulence, with a mean lesion diameter of 13.9 mm, whereas *C. fructicola* and *C. alienum* were significantly less virulent than all other species (Fig. 5).

Discussion

Our phylogenetic analysis using the *ApMat* marker revealed that *C. alienum*, *C. asianum*, *C. fructicola*, *C. siamense*, and *C. tropicale* were associated with symptoms of mango anthracnose. Thus, this study represents the first report of *C. siamense*, *C. tropicale*, *C. alienum*, and *C. fructicola* associated with mango in Mexico. Previous studies recommend the use of the *ApMat* marker for

Table 1. *Colletotrichum* isolates included in the analysis of *ApMat* sequence data, along with information on the taxon, host, geographic location, and GenBank accession number

Taxon	Isolate code[z]	Host	Geographic location	GenBank accession no.
C. aenigma	**ICMP18608**	*Persea americana*	Israel	KM360143
C. aeschynomenes	**ICMP17673**	*Aeschynomene virginica*	United States	KM360145
C. alienum	**ICMP12071**	*Malus domestica*	New Zealand	KC888927
	LF322	*Camellia sinensis*	China	KJ954545
	UACH376	*Mangifera indica*	Mexico	MK016305
	UACH360	*Mangifera indica*	Mexico	MK016306
C. asianum	**CBS130418**	*Coffea arabica*	Thailand	FR718814
	LC0037	Coffee berry	Thailand	JQ899285
	LC0038	Coffee berry	Thailand	JQ899286
	MTCC11680, GM595	*Mangifera indica*	India	JQ894554
	UACH307	*Mangifera indica*	Mexico	MK016307
	UACH348	*Mangifera indica*	Mexico	MK016308
	UACH318	*Mangifera indica*	Mexico	MK016309
	UACH337	*Mangifera indica*	Mexico	MK016310
	UACH305	*Mangifera indica*	Mexico	MK016311
	UACH341	*Mangifera indica*	Mexico	MK016312
	UACH323	*Mangifera indica*	Mexico	MK016313
	UACH310	*Mangifera indica*	Mexico	MK016314
	UACH299	*Mangifera indica*	Mexico	MK016315
	UACH311	*Mangifera indica*	Mexico	MK016316
	UACH295	*Mangifera indica*	Mexico	MK016317
	UACH340	*Mangifera indica*	Mexico	MK016318
	UACH335	*Mangifera indica*	Mexico	MK016319
	UACH308	*Mangifera indica*	Mexico	MK016320
	UACH338	*Mangifera indica*	Mexico	MK016321
	UACH336	*Mangifera indica*	Mexico	MK016322
	UACH312	*Mangifera indica*	Mexico	MK016323
	UACH339	*Mangifera indica*	Mexico	MK016324
	UACH315	*Mangifera indica*	Mexico	MK016325
C. chrysophilum	**URM7362**	*Musa* sp.	Brazil	KX094325
C. chrysophilum	CMM4292	*Musa* sp.	Brazil	KX094324
C. conoides	MYL24	*Actinidia chinensis*	China	MG198007
C. endophyticum	YN1A4	*Camellia sinensis*	China	KU251734
C. fructicola	**CBS130416**	*Coffea arabica*	Thailand	JQ899290
C. fructicola	Coll996	*Rhexia virginica*	United States	JX145324
C. fructicola	CollP1	*Vaccinium corymbosum*	United States	JX145316
C. fructicola	UACH298	*Mangifera indica*	Mexico	MK016326
C. gloeosporioides	**CBS112999**	*Citrus sinensis*	Italy	JQ807843
C. hebeiense	JZB330024, SD4S2	*Vitis vinifera*	China	KF377573
C. hebeiense	JZB330028, K3	*Vitis vinifera*	China	KF377562
C. horii	**ICMP10492**	*Diospyros kaki*	Japan	JQ807840
C. musae	**CBS116870**	*Musa* sp.	United States	KC888926
C. musae	CMM4423	*Musa* sp.	Brazil	KX094328
C. nupharicola	OAC1	*Areca catechu*	India	KU239773

(*Continued on next page*)

[z] Type isolates are shown in bold. ICMP = International Collection of Microorganisms From Plants, Landcare Research, Auckland, New Zealand; LF = Working collection of Fang Liu, housed at the Chinese Academy of Sciences (CAS), China; UACH = Culture Collection of Phytopathogenic Fungi of Department of Agricultural Parasitology, Chapingo Autonomous University, Mexico; CBS = Centraalbureau voor Schimmelcultures, Utrecht, Netherlands; LC = Working collection of Lei Cai, housed at CAS, China; MTCC = Microbial Type Culture Collection and Gene Bank, Chandigarh, India; URM = Culture collection "University Recife Mycologia," Recife, Brazil; and CMM = Culture Collection of Phytopathogenic Fungi "Professora Maria Menezes," Universidade Federal Rural de Pernambuco, Recife, Brazil.

accurate identification of *C. siamense* (Sharma et al. 2015, 2017) and for delimitation of cryptic species within the *C. gloeosporioides* species complex (Doyle et al. 2013; Pardo-De la Hoz et al. 2016; Rojas et al. 2010; Sharma et al. 2013, 2017; Silva et al. 2012; Vieira et al. 2014). In addition, Liu et al. (2015) demonstrated that 22 *Colletotrichum* species, including *C. alienum*, *C. asianum*, *C. fructicola*, *C. siamense*, and *C. tropicale*, were clearly delimitated with the *ApMat* marker; however, other species in the *C. gloeosporioides* species complex such as *C. jiangxiense* Liu & Cai and *C. kahawae* Waller & Bridge cannot be distinguished from each other by the *ApMat* marker and their identification requires a phylogenetic analysis using *ApMat* and glutamine synthetase concatenated alignments.

Pathogenicity tests performed with isolates of *C. siamense*, *C. asianum*, *C. tropicale*, *C. alienum*, and *C. fructicola* confirmed that these species are responsible for causing mango anthracnose in Mexico. Furthermore, the present findings showed that *C. gloeosporioides* sensu stricto is not a common pathogen of mango fruits in Mexico and demonstrated that at least five *Colletotrichum* species causing mango anthracnose can be found, as reported for Brazil (Lima et al. 2013), India (Sharma et al. 2013), Australia (Shivas et al. 2016), and Colombia (Pardo-De la Hoz et al. 2016).

C. siamense was the most frequently isolated species from mango tissues with anthracnose symptoms in Mexico. This fungal species has been previously associated with mango tissues in Brazil (Lima et al. 2013; Vieira et al. 2014), India (Sharma et al. 2013, 2015), Colombia (Pardo-De la Hoz et al. 2016), China (Mo et al. 2018), and Australia (Giblin et al. 2018). In our study, *C. siamense* showed a similar virulence as *C. asianum* producing the larger lesions on mango fruit, in contrast to the study by Lima et al. (2013), who determined *C. asianum* as a species more virulent than *C. siamense* (syn. *C. dianesei*) in Brazil.

C. asianum was the second most prevalent species found in symptomatic tissues from mango in this study. Similarly, Lima et al.

Table 1. (*Continued from previous page*)

Taxon	Isolate code[z]	Host	Geographic location	GenBank accession no.
C. nupharicola	**CBS470.96**	*Nuphar lutea*	United States	JX145319
C. nupharicola	CBS472.96	*Nymphaea odorata*	United States	JX145320
C. perseae	GA100	*P. americana*	Israel	KX620177
C. queenslandicum	**ICMP1778**	*Carica papaya*	Australia	KC888928
C. salsolae	**ICMP19051**	*Salsola tragus*	Hungary	KC888925
C. siamense	**CBS130417**	*Coffea arabica*	Thailand	JQ899289
	GN1	*Azadirachta indica*	India	KC790673
	UACH345	*Mangifera indica*	Mexico	MK016327
	UACH302	*Mangifera indica*	Mexico	MK016328
	UACH320	*Mangifera indica*	Mexico	MK016329
	UACH321	*Mangifera indica*	Mexico	MK016330
	UACH325	*Mangifera indica*	Mexico	MK016331
	UACH326	*Mangifera indica*	Mexico	MK016332
	UACH324	*Mangifera indica*	Mexico	MK016333
	UACH301	*Mangifera indica*	Mexico	MK016334
	UACH350	*Mangifera indica*	Mexico	MK016335
	UACH316	*Mangifera indica*	Mexico	MK016336
	UACH330	*Mangifera indica*	Mexico	MK016337
	UACH314	*Mangifera indica*	Mexico	MK016338
	UACH331	*Mangifera indica*	Mexico	MK016339
	UACH329	*Mangifera indica*	Mexico	MK016340
	UACH333	*Mangifera indica*	Mexico	MK016341
	UACH334	*Mangifera indica*	Mexico	MK016342
	UACH294	*Mangifera indica*	Mexico	MK016343
	UACH309	*Mangifera indica*	Mexico	MK016344
	UACH328	*Mangifera indica*	Mexico	MK016345
	UACH313	*Mangifera indica*	Mexico	MK016346
	UACH346	*Mangifera indica*	Mexico	MK016347
	UACH349	*Mangifera indica*	Mexico	MK016348
	UACH322	*Mangifera indica*	Mexico	MK016349
	UACH342	*Mangifera indica*	Mexico	MK016350
	UACH351	*Mangifera indica*	Mexico	MK016351
	UACH317	*Mangifera indica*	Mexico	MK016352
	UACH296	*Mangifera indica*	Mexico	MK016353
	UACH327	*Mangifera indica*	Mexico	MK016354
	UACH303	*Mangifera indica*	Mexico	MK016355
	UACH332	*Mangifera indica*	Mexico	MK016356
	UACH343	*Mangifera indica*	Mexico	MK016357
	UACH319	*Mangifera indica*	Mexico	MK016358
	UACH304	*Mangifera indica*	Mexico	MK016359
C. tropicale	**CBS124949**	*Theobroma cacao*	Panama	GU994425
	CMM3780	*Mangifera indica*	Brazil	KJ155467
	Coll918	*Terpsichore taxifolia*	Puerto Rico	JX145307
	UACH297	*Mangifera indica*	Mexico	MK016360
	UACH300	*Mangifera indica*	Mexico	MK016362
	UACH306	*Mangifera indica*	Mexico	MK016361
	UACH347	*Mangifera indica*	Mexico	MK016363
C. theobromicola	GJS0843, CBS124944	*Theobroma cacao*	Panama	GU994447
	GJS0850, CBS124945	*Theobroma cacao*	Panama	GU994448

(2013) and Vieira et al. (2014) recorded that *C. asianum* was the second most frequently isolated species from mango tissues in Brazil. In addition, this species has been associated with mango anthracnose in Australia (Giblin et al. 2018; James et al. 2014; Shivas et al. 2016; Weir et al. 2012), Philippines, Panama (Weir et al. 2012), Thailand (Phoulivong et al. 2010; Weir et al. 2012), India (Sharma et al. 2013), Ghana (Honger et al. 2014), Colombia (Pardo-De la Hoz et al. 2016), and China (Mo et al. 2018), enlisting this *Colletotrichum* species as the most widely distributed in major mango producing countries. In our pathogenicity tests, isolates of *C. asianum* showed high virulence, which is in agreement with the results reported by Sharma et al. (2013) and Vieira et al. (2014) for *Colletotrichum* isolates obtained from mango from India and Brazil, respectively.

C. tropicale was the third most common species of all of the isolates identified in our study. This is in line with the studies published by Lima et al. (2013) and Vieira et al. (2014), who reported a lower

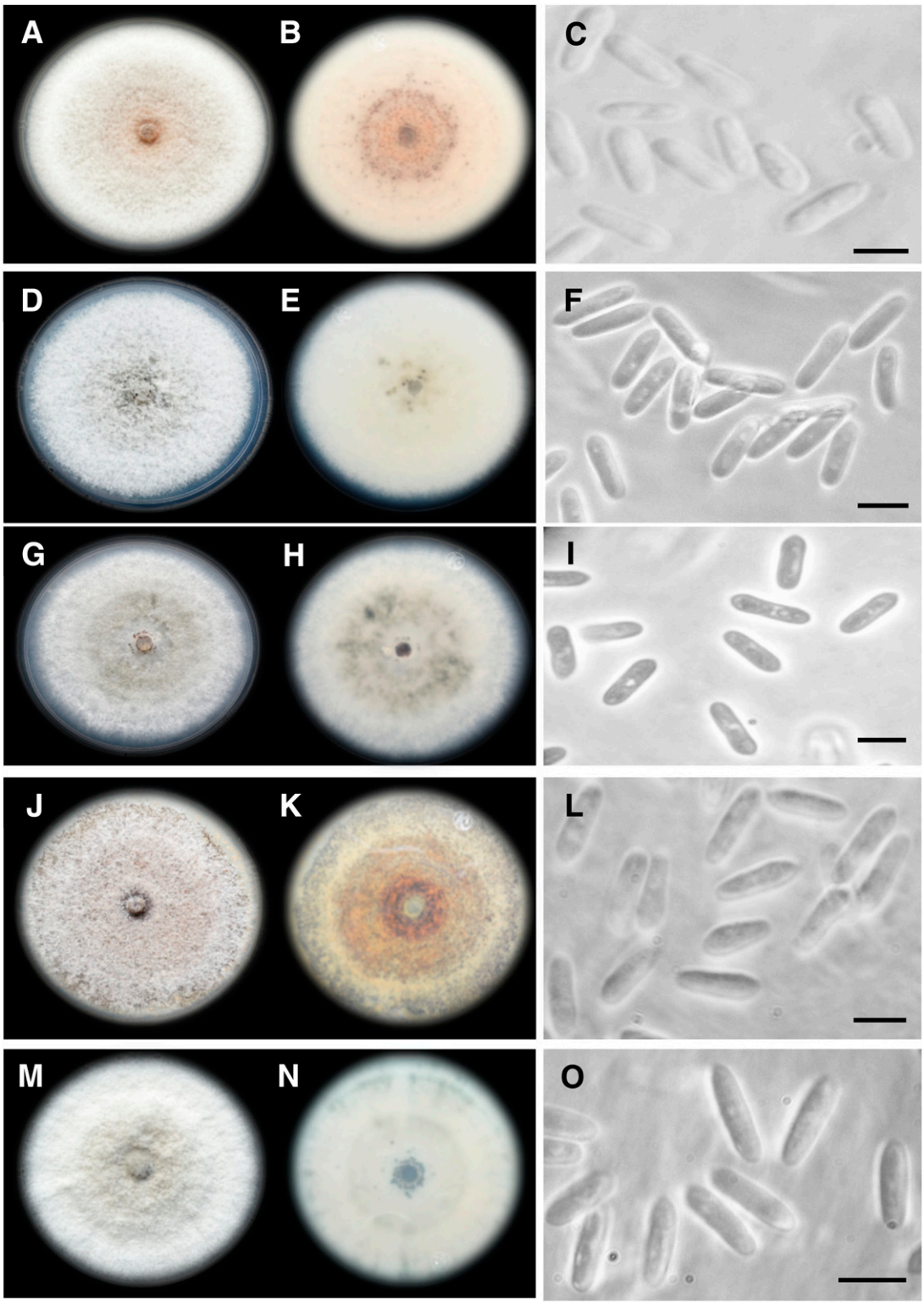

Fig. 2. Colony morphology and conidia of five *Colletotrichum* species after 9 days of incubation at 25°C under continuous dark (left, upper view of colony; center, reverse view of colony; and right, conidia). **A, B, and C,** *Colletotrichum siamense.* **D, E, and F,** *C. asianum.* **G, H, and I,** *C. tropicale.* **J, K, and L,** *C. fructicola.* **M, N, and O,** *C. alienum.* Scale bars = 10 μm.

prevalence of *C. tropicale* with respect to *C. siamense* (syn. *C. dianesei*) and *C. asianum* in mango tissues from Brazil. Pathogenicity tests showed that *C. tropicale* was more virulent than *C. fructicola*, which is in agreement with the results reported by Lima et al. (2013) and Vieira et al. (2014), with isolates obtained from symptomatic and asymptomatic mango tissues, respectively.

C. alienum was represented by two isolates in this study. This fungus has been previously associated with several hosts, including fruit

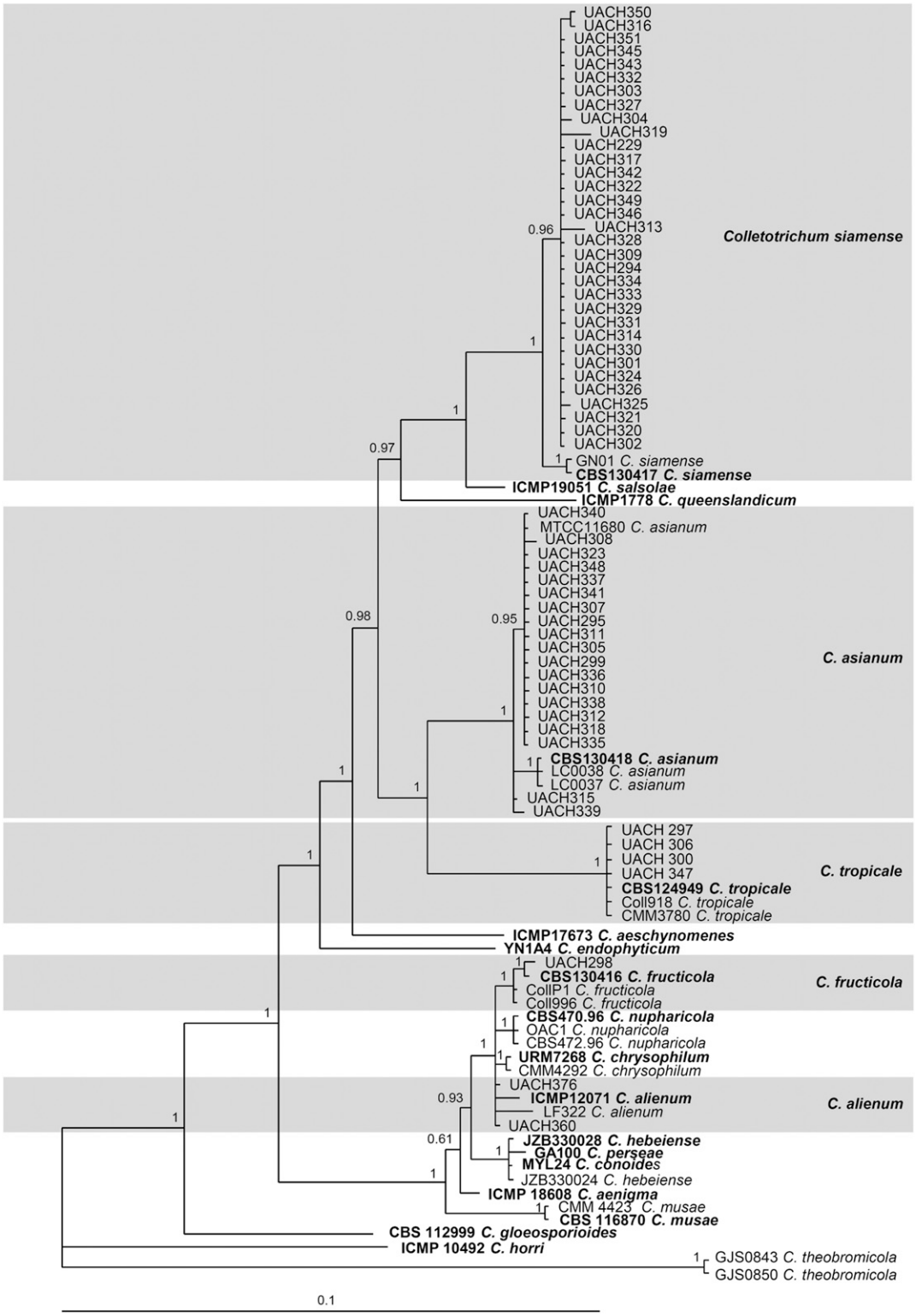

Fig. 3. Phylogenetic tree constructed based on Bayesian inference of sequence data of the *Apn2*/MAT intergenic spacer from 93 *Colletotrichum* isolates. The tree shows the phylogenetic relationships of *Colletotrichum* species isolated from *Mangifera indica* and selected *Colletotrichum* species. Bayesian posterior probability values ≥ 0.5 are shown in each node. Ex-type or ex-epitype sequences are emphasized in bold. Culture accession numbers are listed. *C. theobromicola* is used as outgroup. The scale bar indicates the number of expected changes per site. UACH = Culture Collection of Phytopathogenic Fungi of Department of Agricultural Parasitology, Chapingo Autonomous University, Mexico; CBS = Centraalbureau voor Schimmelcultures, Utrecht, Netherlands; ICMP = International Collection of Microorganisms From Plants, Landcare Research, Auckland, New Zealand; MTCC = Microbial Type Culture Collection and Gene Bank, Chandigarh, India; LC = Working collection of Lei Cai, housed at the Chinese Academy of Sciences (CAS), China; CMM = Culture Collection of Phytopathogenic Fungi "Professora Maria Menezes," Universidade Federal Rural de Pernambuco, Recife, Brazil; URM = Culture collection "University Recife Mycologia," Recife, Brazil; and LF = Working collection of Fang Liu, housed at CAS, China.

crops such as strawberry (*Fragaria* × *ananassa*), avocado (*Persea americana*), and apple (*Malus domestica*) (Farr and Rossman 2019). However, this study represents the first report worldwide of this fungal species causing mango anthracnose.

C. fructicola was represented only by one isolate in this study. This species was previously reported to cause mango anthracnose in Brazil (Lima et al. 2013), India (Sharma et al. 2013), Korea (Jao et al. 2016), and China (Mo et al. 2018). However, Vieira et al. (2014) referred to *C. fructicola* as an endophytic fungus of mango tissues in northeastern Brazil. This species has also been identified on apple and avocado fruits in Japan (Yokosawa et al. 2017) and Israel (Sharma et al. 2017), respectively. In addition, Fuentes-Aragón et al. (2018) identified this fungal species as the causal agent of anthracnose and soft rot in avocado fruits in Mexico. Results of pathogenicity tests in our study revealed that the isolate of *C. fructicola* caused the smallest lesions on mango fruits, which is in agreement with the findings of Sharma et al. (2013) and Vieira et al. (2014), who reported that this fungal species was the least virulent of *Colletotrichum* isolates inoculated on mango fruits in India and Brazil, respectively.

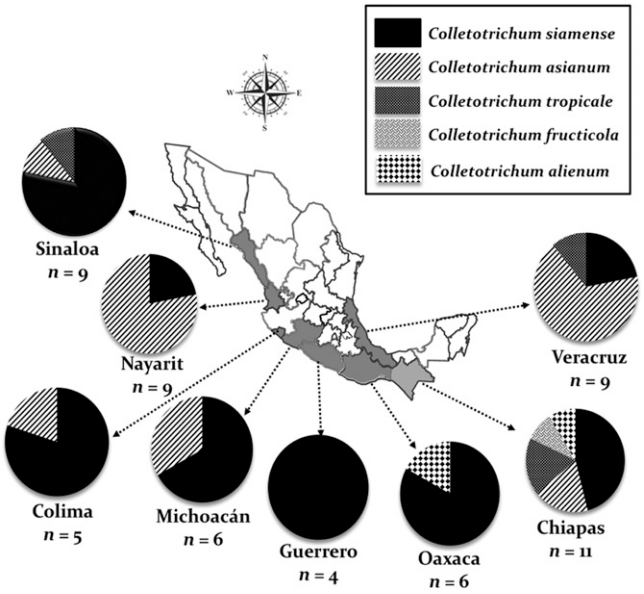

Fig. 4. Collection sites of *Colletotrichum* isolates associated with mango anthracnose in eight states from Mexico. Circles represent the association frequency of each species with plants exhibiting symptoms of anthracnose in each site sampled. *n* is the number of isolates analyzed in each mango growing state.

In the current study, the virulence assessment of the isolates of five *Colletotrichum* species causing mango anthracnose in Mexico was estimated. However, these results may not reflect the true virulence potential of these species because the symptoms developed in mango fruits can vary greatly, according to various factors such as the fruit type, fruit condition, humidity, temperature, inoculum concentration, and inoculation method (Freeman et al. 1998; Giblin et al. 2010; Sanders and Korsten 2003). For this reason, further research is suggested to estimate the potential virulence of *Colletotrichum* species in a natural infection experiment instead of by artificially generated infections, as mentioned by Prihastuti et al. (2009), Lima et al. (2013), and Vieira et al. (2014). It is also necessary to evaluate the response of the major mango cultivars produced in Mexico to the infection by *Colletotrichum* spp., in order to identify the levels of resistance and tolerance of those cultivars to this disease.

Overall, this study represents the most detailed research of *Colletotrichum* species associated with mango anthracnose in Mexico and the findings have comprehensive relevance in various aspects of the disease, since accurate identification of closely related *Colletotrichum* species is important to determine the geographical distribution of a particular fungal species and to formulate quarantine regulations, as well as to understand the epidemiology and to establish strategies for the integrated management of diseases in mango orchards. In addition, further studies are needed to determine the fungicide sensitivity of *Colletotrichum* isolates from mango in Mexico.

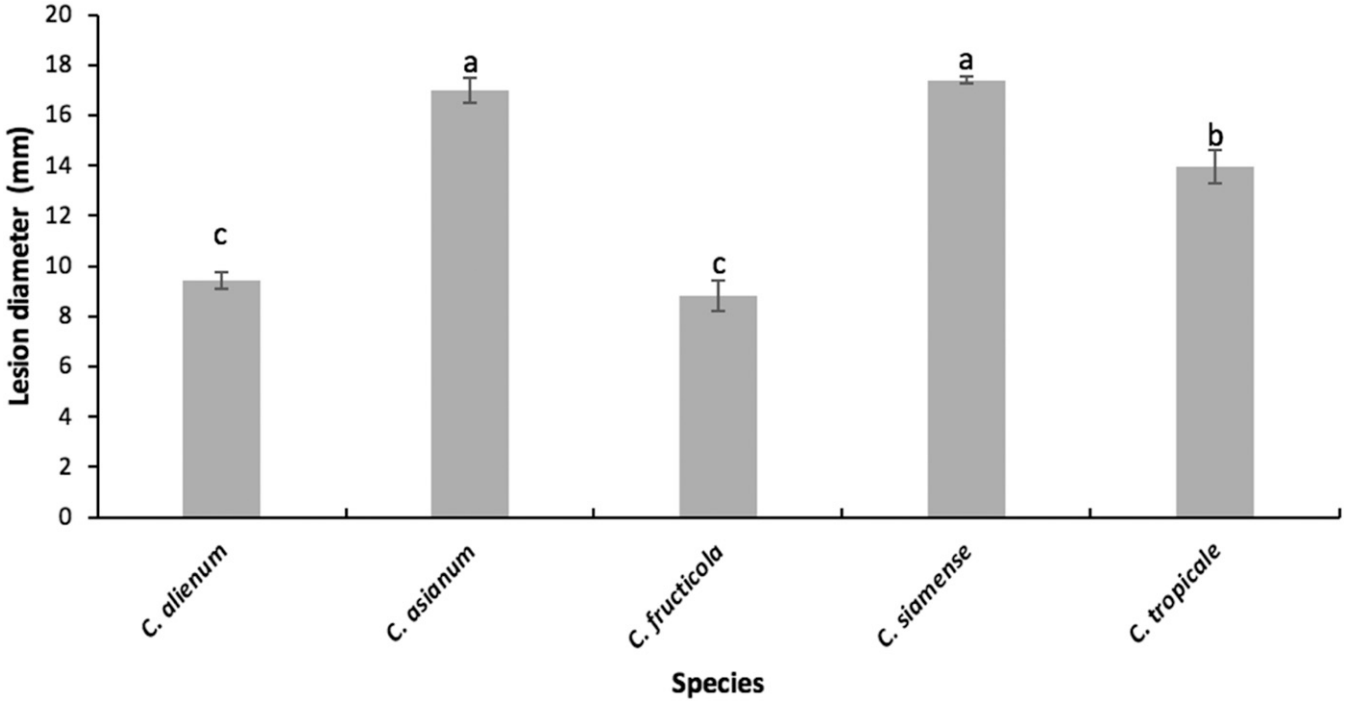

Fig. 5. Mean lesion diameter (in millimeters) caused by five *Colletotrichum* species associated with mango anthracnose in Mexico, 5 days after inoculation with mycelium colonized agar plugs onto wounded fruits of Manila cultivar. Bars above columns are the standard error of the mean. Columns with the same letter do not differ significantly according to Fisher's least significant difference test ($P \leq 0.05$).

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