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SHORT COMMUNICATION

Multilocus phylogenetic analyses suggest the presence of *Colletotrichum chrysophilum* causing banana anthracnose in Mexico

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Abstract

Postharvest anthracnose disease caused by *Colletotrichum* species is one of the main threats to banana production because it reduces the quality, the marketability, and the consumption of the fruit. From June to September 2017, coalescent sunken necrotic lesions were observed on the banana fruit cv. Tabasco (*Musa acuminata*), harvested in two orchards in Teapa, Tabasco, southeast of Mexico. Thus, this research aimed to identify the causal agents of necrotic lesions that affect banana production. Isolates of *Colletotrichum* spp. obtained from the sunken necrotic lesions were studied by morphological and multilocus phylogenetic approaches. Amplification and sequencing of the six (*GAPDH*, *CHS-1*, *ACT*, *TUB*, *GS*, and *APMAT*) partial genes were performed. Later, individual alignment for each gene was created and concatenated. Bayesian inference and maximum likelihood analyses revealed that the three representative strains belong to *C. chrysophilum*, a member of *C. gloeosporioides* species complex. To determine whether *C. chrysophilum* strains were responsible for the symptoms on banana fruit, a pathogenicity test was conducted by inoculation of wounded fruit. Typical necrotic lesions were observed 8 days after inoculation, while the control fruit remained healthy. This finding represents the first report of *C. chrysophilum* causing anthracnose of banana in Mexico; therefore, it should be considered an integrated management program to reduce losses caused by this disease.

Keywords Anthracnose · *Colletotrichum gloeosporioides* species complex · *Musa acuminata* · Pathogenicity · Phylogenetic analyses

Mexico is the 12th largest producer of banana fruit worldwide, providing 2.3 million t annually, of which approximately 25% is exported (FAOSTAT 2018). However, fungal diseases such as Fusarium wilt (*Fusarium oxysporum* f. sp. *cubense*), black sigatoka (*Pseudocercospora fijiensis*), and anthracnose (*Colletotrichum spp.*) are the main threats to banana production, causing yield losses and reduced fruit marketability.

Anthracnose caused by *Colletotrichum musae* (Berk. & M.A. Curtis) Arx, a host-specific pathogen, is the most worldwide dangerous disease in the postharvest stage due to the quiescent infections caused by the pathogen during fruit ripening (Bellaire et al. 2007; Su et al. 2011). Nevertheless, other species have also been associated with anthracnose symptoms: *Colletotrichum aotearoa* B. Weir & P.R. Johnst in Japan and India (Sharma et al. 2015); *Colletotrichum chrysophilum* W.A.S. Vieira, W.G. Lima, M.P.S. Cãmara & V.P. Doyle, *Colletotrichum tropicale* Rojas, Rehner & Samuels, *Colletotrichum theobromicola* Delac., and *Colletotrichum siamense* Prihast., L. Cai & K.D. Hyde in Brazil (Vieira et al. 2017); *Colletotrichum gloeosporioides* (Penz.) Penz. & Sacc. sensu stricto in Malaysia and Ecuador (Intan et al. 2013; Riera et al. 2019); *Colletotrichum paxtonii* Damm, P.F. Cannon & Crous in Saint Lucia (Damm

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et al. 2012); *Colletotrichum plurivorum* Damm, Alizadeh & Toy. Sato in Japan (Damm et al. 2019); and *Colletotrichum scovillei* Damm, P.F. Cannon & Crous in China (Zhou et al. 2017). Furthermore, other species, such as *Colletotrichum karsti* You L. Yang, Zuo Y. Liu, K.D. Hyde & L. Cai, *Colletotrichum gigasporum* Rakotonir. & Munaut, and *Colletotrichum musicola* Damm have been reported in Mexico (Damm et al. 2012, 2019; Liu et al. 2014).

From June to September 2017, banana fruits cv. Tabasco from two orchards in Teapa, Tabasco state, Mexico, with anthracnose symptoms, were sampled in an advanced stage of ripeness. The disease incidence was estimated at around 10%. The sunken necrotic tissue was washed thoroughly with tap water. Small pieces (0.5 cm in length) were cut from the outer margin of the lesions, disinfested in 2% NaClO for 2 min, rinsed three times with distilled sterilized water, and then dried in a biosafety chamber. The tissues were placed on potato dextrose agar (PDA, Bioxon, USA) plates and subsequently incubated in the dark at ~ 25 °C for 8 days. Twenty-seven isolates were obtained according to the monoconidial method (Lim et al., 2002).

Morphological characterization was carried out on PDA media and synthetic nutrient-poor agar (SNA, Nirenberg et al. 1976) amended with pine needles (Liu et al. 2013) previously autoclaved two times to 15 psi for 10 min each. The SNA and PDA plates were incubated at ~ 25 °C under a 12 h fluorescent light/dark photoperiod for 7 and 15 days, respectively. The development of appressoria was induced via the slide culture technique where the size and shape were recorded (Cai et al. 2009). Morphological structures were measured using ImageJ software (https://imagej.nih.gov/ij/index.html) from pictures taken with an Infinity 1–2 camera mounted on a BX51 microscope (Olympus, Japan). On PDA, colonies were a pale brown colour on the upper side, a dark brown in the centre, and a pale brown in the periphery on the reverse side. The growth rate was 5.9 mm day $^{-1}$ ($n = 5$). The conidia were hyaline and aseptate with a smooth-walled shape, measuring 17.2–11.4 µm (length) × 5.8–2.9 µm (width) ($n = 30$), and some of them had a constricted centre. On SNA, cylindrical conidia were hyaline and aseptate, measuring 17.0–11.1 µm × 4.1–2.5 µm ($n = 30$). The appressoria were solitary, dark brown, and ovoid or pyriform in shape, measuring 11.2–7.2 µm × 6.8–3.9 µm ($n = 20$) (Fig. 1). The sexual morph was absent, and setae and conidia masses occurred on both media. The size and growth rate of the CPO 27.222, CPO 27.223, and CPO 27.224 strains were similar to those of *C. chrysophilum* holotype URM89949 in PDA and SNA media but different in conidia shape and cultural characteristics. This difference may be due to the culture medium used (Vieira et al. 2017); or the high intraspecific genetic changes resulting in different

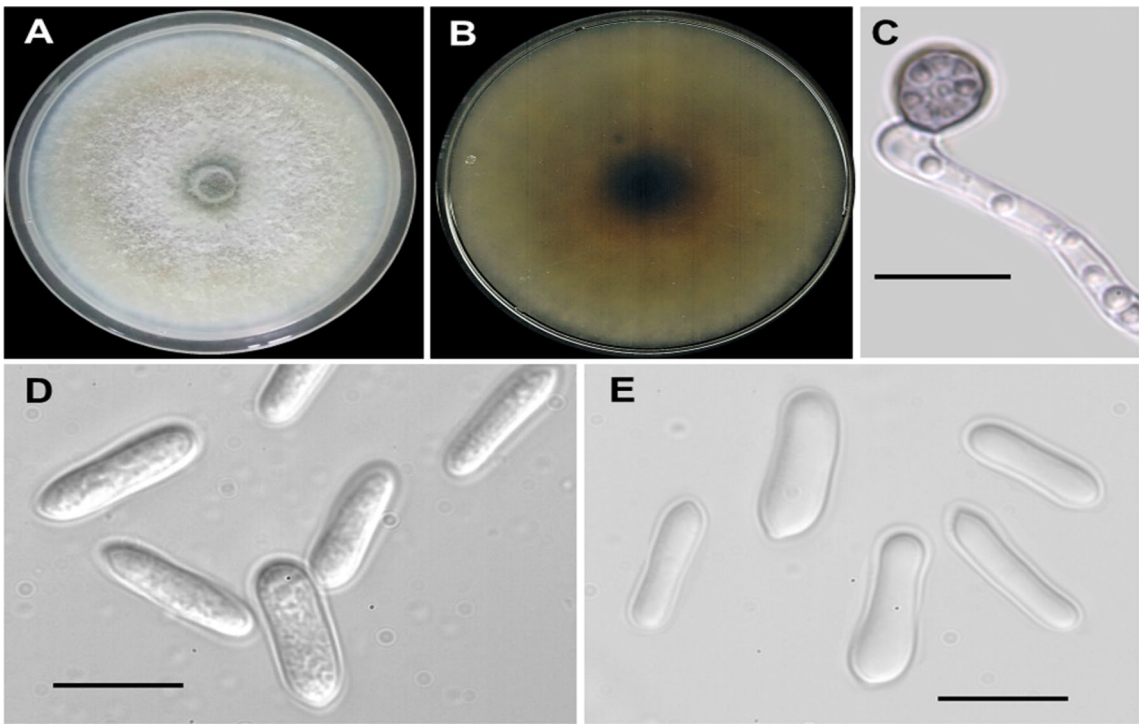

Fig. 1 Cultural and morphological characteristics of *Colletotrichum chrysophilum*. *a* Upper side of colony growing on potato dextrose agar (PDA) medium, **b** reverse side of colony growing on PDA, **c** conidia on PDA, **d** conidia on synthetic nutrient-poor agar (SNA), **e, f, g** solitary appressorium. Scale bars = 10 µm

morphotypes, as demonstrated in other *Colletotrichum* species (Damm et al. 2012).

For molecular identification, DNA extraction was performed according to the 2% cetyltrimethylammonium bromide (CTAB) method (Doyle and Doyle 1990). PCR mixtures and thermocycler programmes of the annealing temperatures were previously standardized for the six loci amplified (Fuentes-Aragón et al. 2018). The glyceraldehyde-3-phosphate dehydrogenase (*GAPDH*), chitin synthase (*CHS-1*), actin (*ACT*), β-tubulin (*TUB2*), and glutamine synthetase (*GS*), as well as the *Apn2-MAT1-2* intergenic spacer and mating type MAT1-2 (*APMA*T) partial genes were amplified and sequenced using the primers GDF1/GDR1 (Guerber et al. 2003), CHS-783F/CHS-248R (Carbone and Kohn 1999), ACT-512F/ACT-783R (Carbone and Kohn 1999), T1/Bt2b (O'Donnell and Cigelnik 1997; Glass and Donaldson 1995), GSF1/GSR1 (Guerber et al. 2003), and AMF1/AMR1 (Silva et al. 2012), respectively. The PCR products were purified with ExoSAP-IT (Affymetrix, USA) and directly sequenced in a 3130 Genetic Analyser (Applied Biosystems, USA) at the facilities of the Postgraduates College in Mexico, following the procedures described by Juárez-Vázquez et al. (2019).

Maximum likelihood (ML) and Bayesian inference (BI) analyses were carried out using the raxmlGUI (Silvestro and Michalak 2012) and MrBayes v.3.2 (Ronquist et al. 2012), respectively. Consensus sequences were obtained using Geneious v.9.1. (Kearse et al. 2012), and alignments were performed via MAFFT (Katoh et al. 2002). A concatenated alignment was achieved with Mesquite v3.6 (Maddison and Maddison 2018). For the ML method, the GTR + G + I nucleotide substitution model was implemented with 1,000 bootstrap repetitions to determine a posterior probability. For BI, two simultaneous runs were executed based on the four Markov chain Monte Carlo methods with 450,000 generations (standard deviation of split frequencies = 0.009120) that were sampled every 1,000 generations. The 25% of the resultant trees were discarded as 'burn-in' phase option. Nucleotide substitution models were previously selected for each partition via Jmodel Test (Posada 2008) and implemented in the BI analyses. *C. theobromicola* CMM4242 was used as an outgroup for ML and BI methods. The trees were visualised in FigTree v1.4.4 (https://tree.bio.ed.ac.uk/software/figtree/).

The concatenated multilocus analyses, performed with *GAPDH*, *CHS-1*, *ACT*, *TUB2*, *GS*, and *APMAT* datasets contained 30 taxa and 3,023 characters composing the matrix. It includes sequences of *Colletotrichum* ex-type strains retrieved from GenBank, the representative strains generated in this study (CPO 27.222, CPO 27.223, and CPO 27.224), and the *Colletotrichum* species belonging to the Musae clade (Table 1). For BI analyses, the substitution models implemented were the HKY + I with an invariable site for *GAPDH*, the SYM + G with gamma distribution rates for *CHS-1*, the HKY for *ACT*, the GTR for *TUB2*, the GTR + G for *GS*, and the HKY + G for *APMAT*. This analyses generated 902 trees, of which 25% were discarded as 'burn-in' phase, and the posterior probabilities were calculated with the remaining trees (678 trees). The sequences generated in this study clustered into the *C. chrysophilum* clade, whose posterior probability and bootstrap support values are high (1/100, respectively) (Fig. 2).

Koch's postulate was achieved to evaluate the pathogenicity of the CPO 27.222, CPO 27.223, and CPO 27.224 strains. Five unripe detached banana fruit cv. Tabasco per strain were washed with tap water, disinfested with 70% ethanol for 1 min, followed by 1.5% NaClO for 3 min, and then rinsed three times with distilled sterilized water. The inoculation method consisted of making a wound into the pericarp with a diameter of ~ 3 mm and a depth of 2 mm using a sterile dissection needle. The three strains in the present study were reactivated on fresh PDA plates, which were incubated at ~ 25 °C under a 12 h light/dark photoperiod for 4 days. For inoculation, a mycelial plug 0.5 cm in diameter was taken from the margin of an actively growing culture and placed on the disinfested fruit surface. A PDA plug without mycelium was used as control. The five inoculated fruit and controls were placed in a growth chamber at ~ 25 °C in the dark for 8 days. All inoculated strains were pathogenic on unripe detached banana fruit cv. Tabasco. The inoculated fruit displayed initial necrotic lesions at 4 days after inoculation (dai), and typical black lesions with acervuli and conidia on the fruit surface at 8 dai. The control fruit did not display symptoms (Fig. 3). The strains were reisolated, and the *GAPDH* partial gene was amplified and sequenced for each strain. The sequences of the inoculated strains were identical to those of the original inoculated.

Colletotrichum chrysophilum was recently considered a new species in Brazil, causing anthracnose on banana (Vieira et al. 2017). Later, it was reported on *Anacardium occidentale* and *Anacardium humble* in the same country (Veloso et al. 2018), and on *Mangifera indica* in Mexico (Fuentes-Aragón et al. 2020). In conclusion, this species was demonstrated for the first time to cause anthracnose on banana fruit in Mexico. These results provide a basis for studies on the epidemiology and management of this species, contributing to the knowledge of the host range of *C. chrysophilum*.

Table 1 *Colletotrichum* species and their gene accession numbers used for phylogenetic analyses in this study

Species	Culture no	Host	Locality	GenBank accesion numbers					
				GAPDH	*CHS-1*	*ACT*	*TUB*	*GS*	*APMAT*
C. aenigma	ICMP 18608 [T]	*Persea americana*	Israel	JX010044	JX009774	JX009443	JX010389	JX010078	KM360143
C. alienum	ICMP 12071 [T]	*Malus domestica*	New Zealand	JX010028	JX009882	JX009572	JX010411	JX010101	KM360144
C. aeschynomenes	ICMP 17,673, ATCC 201874 [T]	*Aeschynomene virginica*	USA	JX009930	JX009799	JX009483	JX010392	JX010081	KM360145
C. asianum	ICMP 18,580, CBS 130418 [T]	*Coffea arabica*	Thailand	JX010053	JX009867	JX009584	JX010406	JX010096	FR718814
C. chrysophilum	CMM 4268 [T], URM7362	*Musa* sp.	Brazil	KX094183	KX094083	KX093982	KX094285	KX094204	KX094325
	E183	*Genipa americana*	Panama	KX094178	KX094108	KX093978	GU994472	KX094208	GU994443
	Coll919	*Terpsichore taxifolia*	Puerto Rico	KX094177	KX094107	KX093977	KX094288	KX094207	JX145317
	CMM4309	*Musa* sp.	Brazil	KX094185	KX094086	KX093984	KX094287	KX094206	KX094327
	CMM4363	*Musa* sp.	Brazil	KX094180	KX094071	KX093962	KX094283	KX094201	KX094323
	CPO 27.240	*Mangifera indica*	Mexico	MK948838	MK948805	MK948795	MK948822	MK948814	MK948829
	CPO 27.408	*Persea americana*	Mexico	MN737343	MN746551	MN746518	MN848364	MN848394	MN854411
	CPO 27.222	***Musa acuminata***	**Mexico**	**MK507867**	**MK507870**	**MK507873**	**MK507879**	**MK507876**	**MK507882**
	CPO 27.223	***Musa acuminata***	**Mexico**	**MK507868**	**MK507871**	**MK507874**	**MK507880**	**MK507877**	**MK507883**
	CPO 27.224	***Musa acuminata***	**Mexico**	**MK507869**	**MK507872**	**MK507875**	**MK507881**	**MK507878**	**MK507884**
C. fructicola	CBS 130,416, ICMP 18581 [T]	*Coffea arabica*	Thailand	JX010033	JX009866	FJ907426	JX010405	JX010095	JQ807838
	CPC 28,644	*Capsicum annuum*	Thailand	MH707465	MH805851	MH781481	MH846564	MH748265	MH728830
C. makassarense	CBS 143664 [T], CPC 28,612	*Capsicum annuum*	Indonesia	MH728820	MH805850	MH781480	MH846563	MH748264	MH728831
C. musae	CBS 116,870, ICMP 19119 [T]	*Musa* sp.	USA	JX010050	JX009896	JX009433	HQ596280	JX010103	KC888926
	CMM4452	*Musa* sp.	Brazil	KX094193	KX094084	KX093969	KX094291	KX094236	KX094330
C. nupharicola	CBS 470.96, ICMP 18187 [T]	*Nuphar lutea*	USA	JX009972	JX009835	JX009437	JX010398	JX010088	JX145319
C. queenslandicum	ICMP 1778 [T]	*Carica papaya*	Australia	JX009934	JX009899	JX009447	JX010414	JX010104	KC888928
C. salsolae	ICMP 19051 [T]	*Salsola tragus*	Hungary	JX009916	JX009863	JX009562	JX010403	JX010093	KC888925
C. siamense	ICMP 18,642, CBS 125378 [T]	*Hymenocallis americana*	China	JX010019	GQ856730	GQ856775	JX010410	JX010100	JQ899283
	ICMP 18,578, CBS 130,417	*Coffea arabica*	Thailand	JX009924	JX009865	FJ907423	JX010404	JX010094	JQ899289
	ICMP 19,118, CBS 130,420	*Jasminum sambac*	Vietnam	HM131497	JX009895	HM131507	JX010415	JX010105	JQ807841
	CMM4247	*Musa* sp.	Brazil	KX094155	KX094073	KX093973	KX094261	KX094196	KX094301
C. tainanense	CPC 30,245, CBS 14366 [T]	*Capsicum annuum*	Taiwan	MH728823	MH805845	MH781475	MH846558	MH748259	MH728836
C. theobromicola	CMM4242	*Musa* sp.	Brazil	KX094173	KX094069	KX093971	KX094278	KX094197	KX094320
C. tropicale	ICMP 18,653, CBS 124,949 T	*Theobroma cacao*	Panama	JX010007	JX009870	JX009489	JX010407	JX010097	KC790728
	CMM4243	*Musa* sp.	Brazil	KU213601	KU213600	KU213596	KU213604	KU213602	KU213597

[T] ex-type culture

Sequences generated in this study are in bold font

ATCC, American Type Culture Collection; CBS, Westerdijk Fungal Biodiversity Institute; CPC, Culture Collection of Pedro W. Crous; CMM, Culture Collection of Phytopathogenic Fungi; GZAAS, Guizhou Academy of Agricultural Sciences Herbarium; ICMP, International Collection of Microorganisms from Plants; JZB, Beijing Academy of Agriculture and Forestry Sciences culture collection; CPO, Postgraduate College in Agricultural Sciences

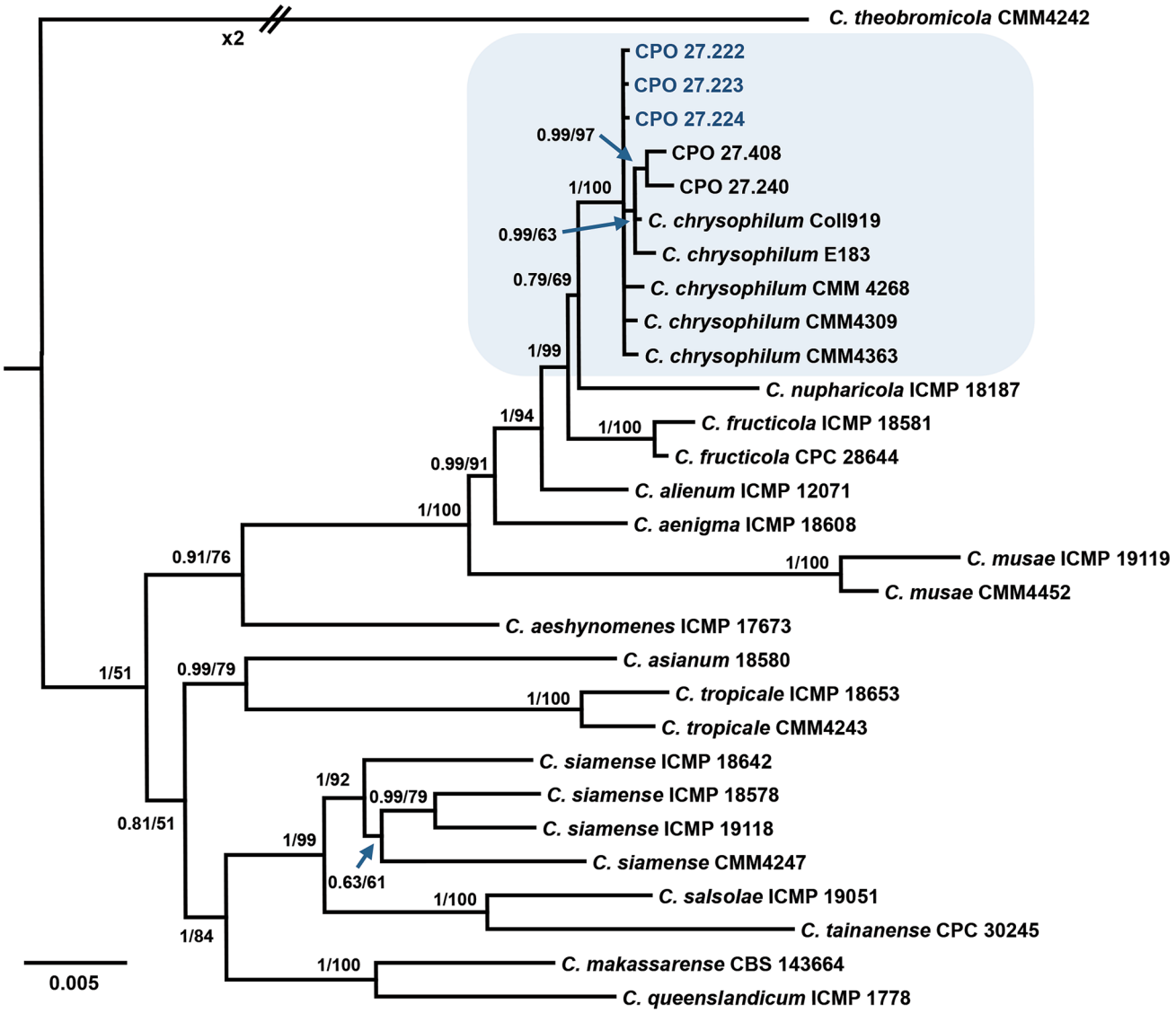

Fig. 2 Bayesian phylogenetic tree of the Musae clade of the *Colletotrichum gloeosporioides* species complex generated via concatenate *GAPDH*, *ACT*, *CHS-1*, *TUB2*, *GS*, and *APMAT* sequences. *Colletotrichum theobromicola* strain CMM4242 isolated from *Musa* sp. was used as an outgroup. Posterior probability and bootstrap support values (PP/BS) are shown at the nodes. The banana strains from Mexico sequenced in this study are indicated in blue. The scale bar indicates the expected changes per site

Fig. 3 Symptoms of anthracnose on banana caused by *Colletotrichum chrysophilum* strain CPO 27.222 8 days after inoculation

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Compliance with ethical standards

Conflict of interest All authors declare that they have no conflict of interest in any part of the research.

Ethical approval This article does not contain any studies performed by any of the authors that include human participants or animals.

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