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Alternative hosts of *Erysiphe quercicola* in the Brazilian cashew ecosystem

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Abstract

Powdery mildew is currently the most important disease of the cashew plant across all producing regions of Brazil. A recent study reported the occurrence of *Erysiphe quercicola* as the causal agent of the symptoms on leaves, inflorescences, pseudofruits and kernels. Morphological evidence raised the question of whether different hosts of the fungus occur in areas near to cashew orchards. This study was developed to compare the fungi that cause powdery mildew in plants in the cashew ecosystem in order to understand the host relationships, and raising the possibility that alternative hosts are involved in the epidemics verified in the cashew tree. The work consisted of collecting samples of plants with symptoms of powdery mildew and carrying out morphological, phylogenetic and cross-pathogenicity analysis of the fungal pathogens. The results of this characterization showed that annatto (*Bixa orellana*), sombrero (*Clitoria fairchildiana*) and mango (*Mangifera indica*) are possible alternative hosts of *E. quercicola* pathogenic to cashew and can therefore represent a source of inoculum for cashew powdery mildew. In addition, the occurrence of this pathogen in mango in Brazil was identified for the first time.

KEYWORDS
cross inoculation, phylogeny, powdery mildew

1 | INTRODUCTION

Cashew powdery mildew has become one of the main phytopathological problems of cashew (*Anacardium occidentale*), due to damage to leaves and new shoots, inflorescences, maturis, mature fruits and peduncles (Cardoso et al., 2012, 2017). The damage caused by powdery mildew in cashew production is even more worrying, because both the peduncle and the nut, the main commercialized products, are severely affected (Cardoso et al., 2013). Although it was first described in cashew at the end of the 19th century in Brazil, when its causal agent was designated as the fungus *Oidium anacardii* (Noack, 1898), powdery mildew only became the main cashew disease in the mid-twentieth century in East Africa (Casulli, 1979). High losses in cashew production due to powdery mildew were observed in Tanzania, with reductions of 5%–70% in production due to severe attack of the disease (Martin et al., 1997). More recently in Brazil, areas such as the south-eastern region of Piauí and the coast of Ceará have seen losses of up to 100% in some orchards (Viana et al., 2016).

In later years, the disease has been reported in other tropical plants, the original description and nomenclature being based only on morphological characteristics and the host. However, more recent morphological and molecular studies indicate that *O. anacardii* on cashew (*A. occidentale*, Anacardiaceae), *O. mangiferae* on mango (*Mangifera indica*, Anacardiaceae), *O. bixae* on annatto (*Bixa orellana*, Bixaceae), *O. citri* on *Citrus* spp. (Rutaceae) and *Oidium* sp. on *Acacia* spp. (Fabaceae) have

rDNA internal transcribed spacer (ITS) sequences that are identical or very similar to those of *Erysiphe* sp. in *Quercus phillyraeoides* (Limkaisang et al., 2006), which was later classified as *E. quercicola* by Takamatsu et al. (2007). Although powdery mildews in tropical plants have been classified as separate species according to their hosts, they were reclassified as asexual forms of *E. quercicola* by Takamatsu et al. (2007). On the other hand, cross-inoculation studies in conjunction with molecular analyses have identified polyphagous species such as *E. quercicola* that exhibit a host range beyond the plant family level (Kirschner & Liu, 2014; Meeboon & Takamatsu, 2015; Siahaan et al., 2016).

A recent study based on morphological and molecular characteristics reported the occurrence of the fungus *E. quercicola* causing powdery mildew in cashew trees in Brazil (Cardoso et al., 2017), although it has already been reported as the cause of epidemics verified in Tanzania (Limkaisang et al., 2006). In another later study carried out by Fonseca, Cardoso, Ootani, Brasil, et al. (2019) based on morphological, phylogenetic and pathogenic analyses, it was shown that two species are associated with cashew powdery mildew: *E. quercicola*, which infects young immature tissues such as young leaves, flowers and young fruits, and *E. necator*, which infects mature and shaded leaf tissues. This same study reported the first occurrence of both *E. quercicola* and *E. necator* causing powdery mildew in cashew trees, and the first detection of *E. necator* in this host.

Therefore, it is necessary to carry out research with the objective of studying the aetiology of powdery mildew in tropical plants in Brazil, allowing for possible involvement of alternative hosts of *E. quercicola* with the epidemics observed in cashew trees. In areas where cashew is cultivated, morphological evidence has raised the question of the existence of different hosts of the *E. quercicola* fungus. This ecological factor is of paramount importance to the survival of the fungus and represents a serious problem in the management of this disease. The identification of possible alternative hosts of *E. quercicola* contributes to the search for new alternatives to control the fungus for the integrated management of cashew powdery mildew.

Therefore, the objectives of this research were to compare the fungi associated with powdery mildew that occur in tropical plants in ecosystems where cashew is cultivated, in order to determine (a) their relationship with cashew and (b) the possible participation of alternative hosts in the epidemiology of powdery mildew in cashew.

2 | MATERIALS AND METHODS

2.1 | Sampling and storing powdery mildew-infected plants

Field surveys in three states of the north-east region of Brazil were carried out in 2017 and 2018, during the period favourable to cashew powdery mildew epidemics (September to November), that is, under conditions of dry weather, strong winds and temperatures ranging from 23°C to 26°C.

Samples of powdery mildew in cashew and other tropical plants were collected. Species of powdery mildew hosts included southern sandbur grass (*Cenchrus echinatus*), Indian heliotrope (*Heliotropium indicum*), coffee senna (*Senna occidentalis*), mango (*M. indica*), Jesuit's tea (*Dysphania ambrosioides*), bellyache bush (*Jatropha gossypiifolia*), stone breaker (*Phyllanthus niruri*), lilac tasselflower (*Emilia sonchifolia*), orchid tree (*Clitoria fairchildiana*), annatto (*B. orellana*) and goatweed (*Scoparia dulcis*). Twenty-one samples were collected from Buíque in the state of Pernambuco, from São João da Varjota in the state of Piauí and from Amontada, Fortaleza, Guaramiranga, Pacajus and Russas in the state of Ceará. Sampled tissues were herborized and stored at the Phytopathology Laboratory of Embrapa Agroindústria Tropical, in Fortaleza, Ceará State.

2.2 | Morphological characterization

For morphological characterization, infected tissues were scraped and mounted on a slide with 40% lactophenol in cotton blue (200 ml/L phenol, 200 ml/L lactic acid, 400 ml/L white glycerin, 0.5 g/L cotton blue and 200 ml/L water) for morphological studies in light microscopy with 10×, 20× and 40× phase contrast objectives. A previous observation was carried out to select only the powdery mildew specimens that showed typical characteristics of the genus *Erysiphe*, according to the description by Braun and Cook (2012). The criterion used for selection was the nature of conidiogenesis, a morphological character of taxonomic consistency according to Takamatsu (2013). The genus *Erysiphe* has *Pseudodium*-type conidiogenesis (noncatenulate, i.e., solitary conidia formed at the apex of the conidiophore) (Braun & Cook, 2012).

Powdery mildew specimens obtained from sandbur grass, Indian heliotrope, coffee senna, Jesuit's tea, bellyache bush, stonebreaker, lilac tasselflower and goatweed had *Euoidium*-type conidiogenesis (catenulate, i.e., conidia maturing in chains), while those obtained from cashew, mango, sombrero and annatto had *Pseudoidium*-type conidiogenesis. Therefore, among 21 specimens, only 13, collected from cashew, annatto, sombrero and mango trees, were selected and used for morphological and phylogenetic analyses (Table 1).

Morphological characteristics and measurements were performed by microscopic examination and photomicrographs with a photographic camera (Moticam 1000 1.3 megapixel USB 2.0) coupled to a trilocular optical microscope (LEICA DM LS). The size and shape of conidia, presence of fibrous bodies, nature of conidiogenesis, characteristics of the conidiophore (number of septa, shape and size of the basal cell) and form of appressoria in the mycelium were observed. Fifty conidiophores and conidia were measured per sample. Scanning electron microscopy examinations were also performed.

2.3 | DNA extraction, amplification and sequencing

The genomic DNA of the selected specimens (Table 1) was extracted from hyphae, conidiophores and conidia of the fungus collected from infected tissues, using a DNeasy plant mini kit (Qiagen), according to the manufacturer's instructions. The total DNA extracted was quantified using the

TABLE 1 *Erysiphe quercicola* specimens used in this study, herbarium accession number, affected organs, host plant, collection site and GenBank accession number

Accession number on herbarium	Infected tissue	Host	Place of collection (city, state)[a]	GenBank accession number	
				ITS	28S
OID01	Leaf	Sombrero	Pacajus, CE	KY765028	MK559479
OID101	Inflorescence	Cashew	Fortaleza, CE	KY312007	KY692191
OID104	Leaflet	Cashew	Pacajus, CE	KY172852	KY692192
OID111	Leaflet	Cashew	Guaramiranga, CE	MK559486	MK559480
OID116	Leaf	Annatto	Fortaleza, CE	KY741537	KY741538
OID125	Leaf	Sombrero	Guaramiranga, CE	MH569421	MK085085
OID128	Leaf	Sombrero	Fortaleza, CE	MK085083	MK085086
OID147	Inflorescence	Mango	São João da Varjota, PI	MK559487	MK559481
OID148	Inflorescence	Cashew	São João da Varjota, PI	MK240381	MK240388
OID155	Leaf	Mango	Guaramiranga, CE	MK559488	MK559482
OID156	Leaf	Annatto	Buíque, PE	MK559489	MK559483
OID157	Leaflet	Cashew	Buíque, PE	MK559490	MK559484
OID163	Leaf	Annatto	Guaramiranga, CE	MK559491	MK559485

[a]CE, Ceará; PE, Pernambuco; PI, Piauí.

NanoDrop 2000c spectrophotometer (Thermo Fisher Scientific). The DNA was diluted to 10 ng/μl and stored at −20°C until use.

The rDNA ITS region, including ITS1-5.8S-ITS2, was amplified using the primers ITS1F (5′-TCCGTAGGTGAACCTGCGG-3′; White et al., 1990) and P3R (5′-GCCGCTTCACTCGCCGTTAC-3′; Kusaba & Tsuge, 1995). For amplification of the 28S region of rDNA (including the D1 and D2 domains), primers PM3 (5′-GKGCTYTMCGCGTAGT-3′; Takamatsu & Kano, 2001) and TW14 (5′-GCTATCCTGAGGGAAACTTC-3′; Mori et al., 2000) were used. PCR mixes (50 μl) contained 6.25 μl genomic DNA (10 ng/μl), 10 μl 5× buffer, 1 μl dNTP (10 mM), 2 μl $MgCl_2$ (25 mM), 0. 8 μl of each primer (10 mM), 0.5 μl of GoTaq polymerase (5 U/μl) and 28.65 μl of sterile ultrapure water.

The Flexigene thermocycler programme used in the amplification of the PCR products included an initial denaturation step at 94°C for 2 min; followed by 35 cycles of denaturation at 94°C for 60 s, annealing at 52°C for 28S and 60°C for ITS for 60 s; and a final extension at 72°C for 10 min (Mori et al., 2000). PCR products were separated by electrophoresis on 1.5% agarose gel in Tris borate EDTA buffer, stained with ethidium bromide (0.5 mg/ml) for 1 min and visualized under a UV transilluminator. After checking the amplified bands, 40 μl aliquots of each PCR product were sent to Macrogen Inc., South Korea (http://www.macrogen.com) to be purified and sequenced in the sense and antisense directions.

2.4 | Phylogenetic analysis

The nucleotide sequences of the ITS and 28S regions of rDNA were edited using the BioEdit program v. 7.0.5 (Hall, 2012) and manually aligned using ClustalW with previously published *Erysiphe* sequences deposited in GenBank (NCBI, http://www.ncbi.nlm.nih.gov) (Table 2). Phylogenetic relationships were inferred by maximum-parsimony (MP) analysis and performed using a tree-bisection-reconnection (TBR) heuristic search option in the MEGA 7 program (Kumar et al., 2016). The statistical support of the tree was tested using bootstrap analysis with 1000 repetitions. *E. australiana* was used as an outgroup. Tree scores, including tree length, consistency index (CI), retention index (RI) and rescaled consistency index (RC), were also calculated. All sequences obtained here were deposited in GenBank (Table 1).

2.5 | Pathogenic tests and cross-inoculations

Pathogenicity tests were performed in cross-inoculations between all four hosts (cashew, annatto, sombrero and mango) evaluated (Table 1). The cashew seedlings susceptible to powdery mildew were produced from cashew seeds of the clone BRS189 and inoculated at 30 days old. Inoculation was performed by transferring conidia by foliar contact between discs (6.5 mm in diameter) of infected leaves with the adaxial epidermis of young, uninfected leaves. Two tests were performed: for the first one, naturally infected leaf samples (OID104, OID116, OID128 and OID155; Table 1) were collected and used to inoculate separately onto four seedlings of each host to ensure the pathogenicity of each specimen. The inoculum produced in the first test was used for the next one through cross-inoculation between alternative hosts. Again, four plants were inoculated and four healthy plants were kept separately as an uninoculated control. The plants were kept in incubation chambers at a temperature of 22 ± 2°C and 68 ± 4% relative humidity. Macroscopic examination of symptoms and signs was performed every day. After the development of symptoms, samples of infected tissues were examined under light microscopy to confirm the presence of the inoculated pathogen, thus fulfilling Koch's postulates.

TABLE 2 *Erysiphe* species, specimen number, host plant, country of origin and GenBank accession number of the sequences used in the phylogenetic study

Species	Specimen	Host	Origin	GenBank accession no.		Reference[a]
				ITS	28S	
E. quercicola	VPRI30172	*Citrus limon*	Indonesia	AB237791	AB237818	1
E. quercicola	VPRI30173	*Citrus reticulata*	Indonesia	AB237792	AB237819	1
E. quercicola	MUMH 3210	*Citrus sinensis*	Malaysia	AB237793	AB237820	1
E. quercicola	MUMH 3188	*Mangifera indica*	Argentina	AB237794	AB237821	1
E. quercicola	MUMH2419	*Hevea brasiliensis*	Brazil	AB193607	AB197134	1
E. quercicola	MUMH3165	*Bixa orellana*	Argentina	AB237787	AB237815	1
E. quercicola	MUMH 124	*Quercus phillyraeoides*	Japan	AB193590	AB197135	1
E. quercicola	MUMH2546	*Acacia auriculiformis*	Malaysia	AB237803	AB237830	1
E. quercicola	VPRI20907	*Acacia mangium*	Australia	AB237808	AB237833	1
E. quercicola	–	*Anacardium occidentale*	Brazil	KY172852	–	2
E. quercicola	–	*Quercus robur*	Brazil	KT714236	–	3
E. quercicola	LGM-005	*Delonix regia*	Brazil	JQ034229	–	4
E. quercicola	–	*Cinnamomum camphora*	Brazil	MF183968	–	5
E. alphitoides	VPRI20379	*Mangifera indica*	Australia	AB237799	AB237826	6
E. necator	MUMH 530	*Vitis vinifera*	Japan	LC028996	LC028996	7
E. necator	MUMH s141	*Vitis coignetiae*	Japan	LC028995	LC028995	7
E. baliensis	MUMH 5705	*Gliricidia sepium*	Indonesia	LC060726	LC060726	6
E. hypogena	MUMH 900	*Quercus acutissima*	Japan	AB292727	AB292727	8
E. epigena	MUMH 1958	*Quercus variabilis*	Japan	AB292719	AB292719	8
E. sedi	MUMH 2575	*Sedum aizoon*	Russia	LC010045	LC010045	1
E. thaxteri	MUMH 2465	*Berberis darwinii*	Argentina	LC010017	LC010017	1
E. limonii	MUMH 2568	*Limonium platyphyllum*	Ukraine	LC010039	LC010039	1
E. australiana	LPF 665	*Lagerstroemia speciosa*	Brazil	KT941419	KT941421	9

[a]1, Takamatsu et al. (2015); 2, Cardoso et al. (2017); 3, Piveta et al. (2018); 4, Dallagnol et al. (2012); 5, Dorneles et al. (2018); 6, Siahaan et al. (2016); 7, Takamatsu et al. (2015); 8, Takamatsu et al. (2007); 9, Fonseca et al. (2016).

The fungal incubation period for each evaluated host was recorded in the two pathogenicity tests. In the second test, in addition to the incubation period, the severity of the disease at 15 days after inoculation was also evaluated, based on a descriptive scale of severity of symptoms, according to classes ranging from 0 to 4, where 0 = absence of symptoms, 1 = presence of small lesions (2 cm), covering up to 2% of the evaluated leaf area; 2 = larger lesions (>2 cm), covering up to 5% of the evaluated leaf area; 3 = coalesced lesions, covering 5% to 25% of the evaluated leaf area; and 4 = large lesions (>4 cm), covering more than 25% of the evaluated leaf area (Cardoso et al., 2006).

3 | RESULTS

3.1 | Morphological characterization

In the surveys carried out, the symptoms were characterized by intense mycelial growth and sporulation in the leaves and stems of annatto and sombrero, as well as in young leaves and inflorescences of cashew and mango trees. The morphological characterization of powdery mildew specimens in these hosts was performed based on conidiophores and conidia (Table 3). The morphological characteristics of these specimens were typical of the genus *Erysiphe*, as described by Braun and Cook (2012).

The fungal hyphae were hyaline, septate and branched with erect conidiophores with conidia at the apex (Figure 1e,f). Cylindrical conidiophore basal cells measured 16.7–36.6 μm in length by 5.6–8.8 μm in width, followed by one or two shorter cells (Figure 1f, Table 3). The conidia were ellipsoid in shape, with a rounded apex and truncated base, without fibrous bodies and measuring 21.2–37.9 μm in length by 10.9–21.8 μm in width, with a length:width ratio of 1.3–2.6 (Table 3). Appressoria in the mycelium were lobed. Chasmothecia were not found.

3.2 | Phylogenetic analysis

Phylogenetic analysis of 13 sampled specimens was performed to identify the fungus at species level. After constructing the most parsimonious phylogenetic tree (length = 141, CI = 0.7865, RI = 0.8662, RC = 0.7495) obtained from the combined dataset of ITS and 28S

TABLE 3 Morphological characteristics of powdery mildew specimens collected from tropical plants in the cashew powdery mildew ecosystem

Accession number in herbarium	Host	Conidia		Conidiophore basal cell
		Length (L) × width (W) (μm)	L:W	L × W (μm)
OID101	Cashew	22.4–34.1 × 10.9–19.1	1.6–2.4	20.5–33.7 × 6.6–7.8
OID104	Cashew	21.2–37.3 × 11.5–20.4	1.4–2.6	19.2–36.6 × 5.9–7.7
OID111	Cashew	21.5–32.1 × 12.4–16.5	1.5–2.4	22.2–29.2 × 6.5–7.9
OID148	Cashew	22.4–31.8 × 10.9–18.5	1.6–2.4	19.4–36.2 × 6.3–7.5
OID157	Cashew	25.5–32.0 × 13.4–18.3	1.6–2.3	21.4–34.1 × 6.7–7.8
OID116	Annatto	22.7–33.9 × 13.4–21.5	1.3–2.0	19.1–35.1 × 6.3–7.8
OID156	Annatto	22.3–32.1 × 12.6–19.2	1.4–2.5	20.1–34.6 × 6.4–7.8
OID163	Annatto	20.5–32.9 × 12.4–18.7	1.3–2.5	19.7–34.0 × 6.2–7.7
OID01	Sombrero	23.9–37.1 × 13.3–17.4	1.6–2.2	17.8–30.2 × 6.1–8.6
OID125	Sombrero	25.0–37.9 × 13.4–17.0	1.7–2.6	16.9–30.5 × 5.6–8.7
OID128	Sombrero	24.4–39.8 × 13.3–19.4	1.9–2.1	16.7–32.4 × 5.7–8.8
OID147	Mango	25.7–35.7 × 13.7–19.2	1.5–2.4	20.7–33.1 × 6.3–7.9
OID155	Mango	25.3–34.6 × 13.1–21.8	1.3–2.1	20.3–35.7 × 6.5–8.0
Braun and Cook (2012)[a]	–	25.0–40.0 × 12.0–22.0	1.5–2.3	20.0–40.0 × 7.0–11

[a]Refer to morphological characteristics of *Erysiphe quercicola*.

rDNA sequences, the samples obtained from the different hosts grouped into a clade with *E. quercicola* specimens with 99% bootstrap support (Figure 2). Based on both morphological and molecular information, the species *E. quercicola* was identified as the causal agent of powdery mildew in these hosts.

3.3 | Pathogenicity

In the pathogenicity tests performed, symptoms and signs of the fungus similar to those found in tissues naturally infected with *E. quercicola* were observed in seedlings of cashew (Figure 1a), annatto (Figure 1b), sombrero (Figure 1c) and mango (Figure 1d) at 5 days after inoculation. Uninoculated plants remained symptomless.

3.4 | Cross-inoculations

The results of the cross-inoculation test (Table 4) demonstrated the pathogenicity of *E. quercicola* for all combinations evaluated among the alternative hosts, with an incubation period ranging from 4 to 7 days, and with different severity patterns at 15 days after inoculation. The annatto (severity 4), sombrero (severity 3) and mango (severity 3) hosts were highly susceptible to inoculum from cashew, with an incubation period ranging from 4 to 6 days. At the same time, inoculum from annatto, sombrero and mango infected cashew seedlings between 4 and 6 days, with severities of 3, 2 and 4, respectively. The lowest severities (2) were observed in cashew and mango trees with inoculum from sombrero, in mango with inoculum from annatto, and in sombrero with inoculum from mango.

4 | DISCUSSION

The morphological, phylogenetic and pathogenicity tests revealed that the fungus that causes powdery mildew in cashew, annatto, sombrero and mango is the fungus *E. quercicola*. This occurrence confirms recent reports on the occurrence of this species causing powdery mildew in annatto and sombrero in Brazil (Fonseca, Cardoso, Ootani,

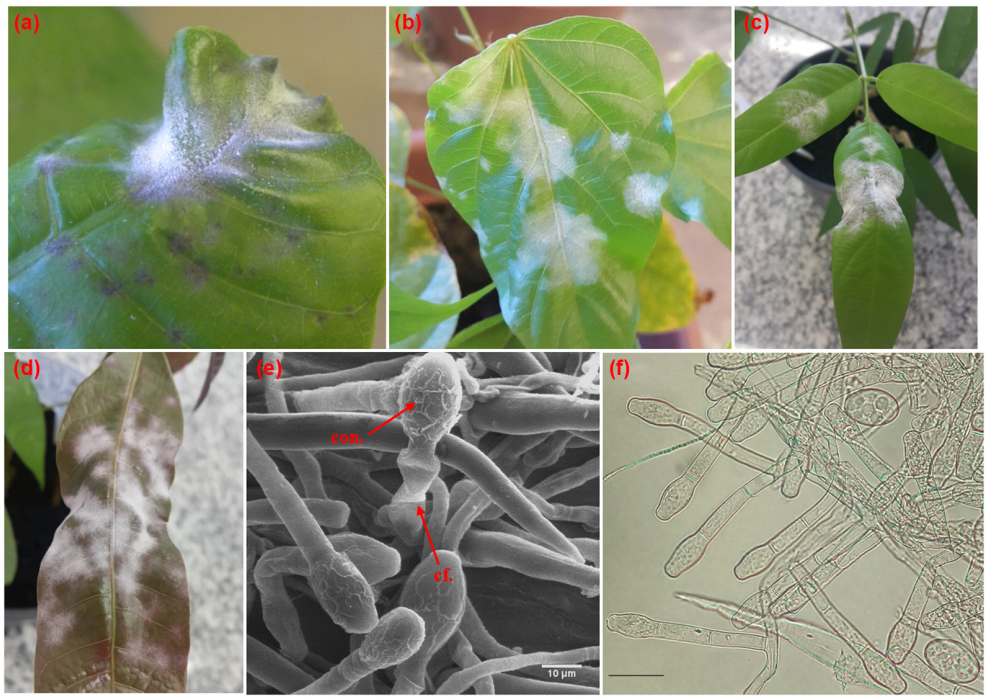

FIGURE 1 (a–d) Powdery mildew symptoms in cashew, annatto, sombrero and mango seedlings inoculated with *Erysiphe quercicola*. (e) Scanning electron microscopy showing conidiophores (cf.) and conidia (con.) of *E. quercicola*. (f) Conidiophores and conidia of *E. quercicola* (scale bar: 30 µm). [Colour figure can be viewed at wileyonlinelibrary.com]

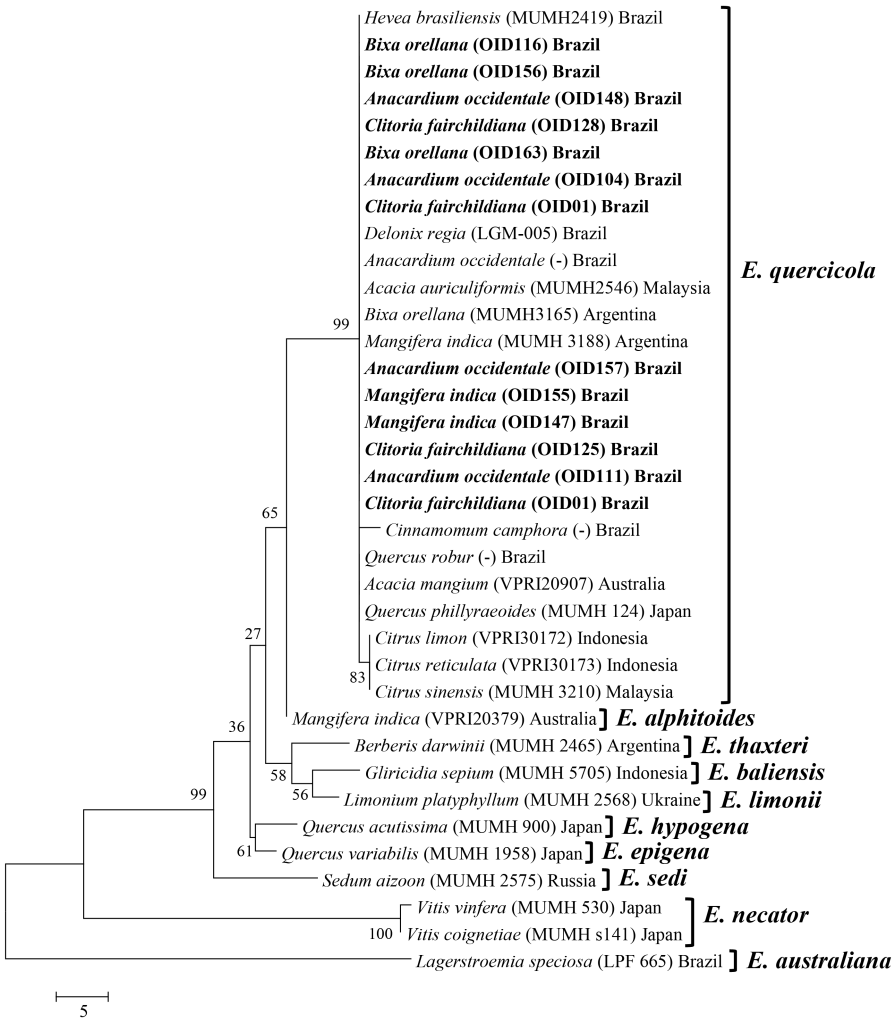

FIGURE 2 Phylogenetic tree inferred by maximum parsimony (MP) from combined data from the ITS and 28S genomic regions of the rDNA for species of the genus *Erysiphe*. Bootstrap values with 1000 repetitions are shown on the nodes. *E. australiana* was used as the outgroup. The specimens obtained in this study are highlighted in bold. Three specimens do not have codes and are indicated by (–).

TABLE 4 Cross inoculations among hosts of *Erysiphe quercicola* isolated in the cashew ecosystem

Host (source of inoculum)	Host	Other hosts		
	Cashew	Annatto	Sombrero	Mango
Incubation period (days)				
Cashew	4	4	4	6
Annatto	4	4	7	5
Sombrero	6	5	4	6
Mango	6	5	7	5
Severity[a]				
Cashew	4	4	3	3
Annatto	3	4	3	2
Sombrero	2	3	4	2
Mango	4	4	2	4

[a]Severity of symptoms 15 days after inoculation: 0, no symptoms; 1, small lesions up to 2% of leaf area; 2, 2%–5% of leaf area; 3, 5%–25% of leaf area; 4, >25% of leaf area.

Viana, et al., 2019; Fonseca, Cardoso, Viana, Brasil, et al., 2019). This is the first report of *E. quercicola* in mango. Although *O. mangiferae* (Berthet, 1914) in mango, synonymous with *E. quercicola* according to Braun and Cook (2012), has been reported in Brazil, no morphological, molecular and pathogenic characterization of the aetiological agent of powdery mildew in this host has been carried out until the present study. In other countries, including Argentina, Australia, Spain and Thailand (Desprez-Loustau et al., 2017; Takamatsu et al., 2018), the occurrence of *E. quercicola* has already been reported in mango. In recent years, new hosts of *E. quercicola* have been reported such as cashew, flamboyant tree (*Delonix regia*), rubber tree (*Hevea brasiliensis*), camphor (*Cinnamomum camphora*) and oak (*Quercus robur*) in Brazil (Cardoso et al., 2017; Dallagnol et al., 2012; Dorneles et al., 2018; Limkaisang et al., 2005; Piveta et al., 2018).

The characterization of the aetiological agent of powdery mildew in this study reveals that *E. quercicola* extends its host list in Brazil to mango. Cross-inoculation pathogenicity tests were carried out to investigate the existence of alternative hosts of the fungus that causes powdery mildew in cashew. The results of the cross-inoculation tests show that annatto, sombrero and mango can serve as alternative hosts of *E. quercicola* and as an inoculum source for cashew powdery mildew in orchards established close to areas with the presence of such plants. Consequently, these hosts are involved in the cashew powdery mildew epidemics seen in recent years.

The information observed in cross-inoculation tests suggests a possible cause of the recent introduction of *E. quercicola* causing powdery mildew in cashew trees in Brazil (Cardoso et al., 2017), because the symptoms of the disease that were limited only to mature cashew leaves until the year 2006 (Freire et al., 2002) started to manifest themselves in leaves and new shoots, inflorescences, maturis, mature fruits and peduncles in all producing regions of the north-east (Cardoso et al., 2013). The ability of powdery mildew specimens from alternative hosts to cause infection in cashew trees raises the important hypothesis that this could have been the main cause of the primary origin of the cashew epidemics in Brazil.

This work showed, through morphological, molecular and pathogenic characterization, the possible participation of alternative hosts of *E. quercicola* in the occurrence of cashew powdery mildew epidemics in north-east Brazil, in addition to identifying for the first time the occurrence of this pathogen in mango trees in Brazil. Subsequent works, aiming to expand the list of alternative hosts of cashew powdery mildew, should be conducted, so that a complete relationship can be achieved.

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DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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