Characterization of the coffee berry disease pathogen, *Colletotrichum kahawae* sp. nov.

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A range of *Colletotrichum* isolates from coffee, including the coffee berry disease (CBD) pathogen, and representative isolates of *C. gloeosporioides* from some other tropical crops are compared. Isolates of the CBD pathogen taken from across its range of distribution in Africa have common morphological, biochemical and pathogenic characteristics. These distinguish them from other *Colletotrichum* isolates. The nomenclature of the CBD pathogen, often referred to as a form of *C. coffeanum*, is confused. Its taxonomic position is discussed and the new species name *Colletotrichum kahawae* is introduced.

A range of different *Colletotrichum* strains can be found on coffee, which can be separated into groups on the basis of the morphology of their fresh single-spore-derived isolates on malt extract agar (MEA). The slow-growing, cottony, dark greenish grey colonies of the coffee berry disease (CBD) pathogen were recognized as distinctive by early workers such as McDonald (1926) and Rayner (1952) in Kenya. This strain causes a serious anthracnose disease of young developing berries of *Coffea arabica* L. in many African countries. Gibbs (1969) defined four groups of *Colletotrichum* strains from coffee, based on the morphology of their colonies on MEA. These were ccm, having fast-growing, profuse, pale aerial mycelium with conidia borne directly on hyphae; cca, having fast-growing, sparse, pale aerial mycelium with rather short conidia borne in acervuli; ccp, having slow-growing, pink aerial mycelium with conidia borne directly on hyphae; and the CBD strain. These groups have since been used by coffee pathologists as a basis for much subsequent work on CBD. Hindorf (1970) defined the different strains of *Colletotrichum* further and recognized that the ccp strain was *Colletotrichum acutatum* Simmonds, ccm and cca were morphs of *Colletotrichum gloeosporioides* Penz. and the CBD strain was referred to as *Colletotrichum coffeanum* Noack.

The species *Colletotrichum coffeanum* (Noack, 1901) and *Gloeosporium coffeanum* (Delacroix, 1897) under which *Colletotrichum* from coffee was originally described, are apparently both synonymous with *C. gloeosporioides*. This occurs as a saprobe or weak pathogen of ripe berries or damaged coffee tissue worldwide. Noack's material came from Brazil, where CBD does not exist, and coffee leaves were the source of Delacroix's material. Thus it is clear that the name *Colletotrichum coffeanum* was not based on type material associated with coffee berry disease, and in view of the distinctive characteristics of the CBD pathogen the applicability of the name is questionable. Several authors have recognized this apparent anomaly and have referred to the CBD pathogen as 'a form of *C. coffeanum*' (Nutman & Roberts, 1960) or as 'var. *virulans*' (Rayner, unpublished report, 1941).

Conventional taxonomic criteria used to differentiate species of *Colletotrichum* are based primarily on conidial and appressorial morphology. On these criteria isolates of the CBD pathogen fall within the broad concept of *C. gloeosporioides* and von Arx (1957) included *C. coffeanum* in synonymy with *C. gloeosporioides*. Many strains of this species are known to be anamorphs of *Glomerella cingulata* (Stonem.) Spauld. & Schrenk, and the CBD pathogen has frequently been referred to as a conidial state of *G. cingulata*. However, despite some earlier claims, there are no conclusive reports of the existence of a teleomorph of the CBD pathogen (Firman & Waller, 1977).

A further complication is that strains of *Colletotrichum* other than the CBD strain are often isolated from older CBD lesions, particularly if techniques are used which utilize the growth of mycelium from diseased tissue explants on to nutrient agar. These may select faster-growing, saprobic secondary invaders, particularly *C. gloeosporioides*, which is a very common inhabitant of the phylloplane of many tropical perennial plants. Older CBD lesions are rapidly colonized by this and other species, and these have been shown to compete saprobically with the CBD pathogen (Waller, 1972; Masaba & Waller, 1992). In common with other *Colletotrichum* species, the CBD pathogen becomes variable when maintained in culture. Colonies become pale grey to white, and frequently lose their capacity to sporulate after a few subculturings. This makes them morphologically indistinguishable from strains of *C. gloeosporioides*, and this cultural variability has contributed to the confused taxonomic position.

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Table 1. Isolates of *Colletotrichum* spp. studied

IMI no.	Preliminary identification	Country of origin	Host	Symptom/organ
108201	*C. coffeanum*	Tanzania	*Coffea* sp.	CBD*
170660	*C. coffeanum*	Kenya	*Coffea arabica*	CBD
180269	*G. cingulata*	Belize	*Citrus sinensis*	Premature fruit drop
190857	*C coffeanum*	Ethiopia	*Coffea arabica*	CBD
202931	*G. cingulata*	Dominica	*Citrus paradisi*	Premature fruit drop
216370	*C. acutatum*	Tanzania	*Coffea arabica*	Berry lesion*
226803	*G. cingulata*	Belize	*Citrus* sp	Premature fruit drop
275791	*G. cingulata*	Malawi	*Coffea arabica*	Twigs
299393	*C. coffeanum*	Cameroon	*C. arabica*	CBD
300964	*C. coffeanum*	Zimbabwe	*C. arabica*	CBD
301220	*C. coffeanum*	Malawi	*C. arabica*	CBD
302910	*G. cingulata*	Dominica	*Mangifera indica*	Blossom blight
303105	*G. cingulata*	Colombia	*C. arabica*	Ripe berry lesion
303106	*G cingulata*	Colombia	*C. arabica*	Ripe berry lesion
309622	*G cingulata*	Costa Rica	*Coffea* sp.	Ripe berry lesion
309792a	*C. acutatum*	Malaysia	*M. indica*	Leaf lesion
311655	*C. coffeanum*	Tanzania	*Coffea* sp.	Berry lesion
313839	*G. cingulata* var. *minor*	Australia	*M. indica*	Fruit, anthracnose
313840	*C. acutatum*	Australia	*M. indica*	Fruit, anthracnose
313841	*C. acutatum*	Australia	*M. indica*	Fruit, anthracnose
315974	*G. cingulata*	Costa Rica	*C. arabica*	Twigs
319401	*C. coffeanum*	Kenya	*C. arabica*	CBD
319406	*C. coffeanum*	Kenya	*C. arabica*	CBD
319418	*C. coffeanum*	Kenya	*C. arabica*	CBD
319423	*C. acutatum*	Kenya	*C. arabica*	Berry lesion
321880	*G. cingulata*	Trinidad	*M. indica*	Fruit, anthracnose
321881	*G. cingulata*	Trinidad	*M. indica*	Fruit, anthracnose
321882	*G. cingulata*	Trinidad	*M. indica*	Fruit, anthracnose
321884	*G. cingulata*	Trinidad	*M. indica*	Fruit, anthracnose
321885	*G. cingulata*	Trinidad	*M indica*	Fruit, anthracnose
323017	*G. cingulata*	Reading University	*C. arabica*	Seedling, stem
325944	*C. coffeanum*	Malawi	*C. arabica*	CBD
325945	*Colletotrichum* sp.	Malawi	*C. arabica*	Old berry lesion
333347	*Colletotrichum* sp.	Malawi	*C. arabica*	Old berry lesion
334134	*G. cingulata*	Barbados	*Dioscorea alata*	Leaves, anthracnose
334135	*G. cingulata*	St. Vincent	*D. alata*	Leaves, anthracnose
334963a	*C. coffeanum*	Malawi	*C. arabica*	CBD
334963b	*C. coffeanum*	Malawi	*C. arabica*	CBD
334963c	*C. coffeanum*	Malawi	*C arabica*	CBD
334963d	*C. coffeanum*	Malawi	*C. arabica*	CBD
334963e	*C. coffeanum*	Malawi	*C. arabica*	CBD
334964	*G. cingulata*	Malawi	*C. arabica*	Berry lesion
337195	*C. coffeanum*	Malawi	*C. arabica*	CBD
338730	*C. coffeanum*	Zambia	*C. arabica*	CBD
338731	*C. coffeanum*	Malawi	*C. arabica*	CBD

* Typical dark sunken CBD lesions are distinguished from other coffee berry lesions not showing these symptoms.

This paper reports comparisons of a range of *Colletotrichum* isolates using both morphological and pathological criteria, and some biochemical methods based on substrate utilization. Results facilitate further differentiation of the CBD pathogen from other, similar *Colletotrichum* strains which occur on coffee, often in close association with it, and from other isolates of *C. gloeosporioides*. They also show that it should be recognized as a distinct species, formally named as *C. kahawae* sp. nov. here.

MATERIALS AND METHODS

Colletotrichum *isolates*

Table 1 lists isolates of *Colletotrichum* used in this study, showing their identification based on conventional criteria, source, and disease symptoms with which they were associated. Some of these originated from overseas workers, but most were isolated from material collected by the senior author or from material sent to IMI. These were initially cultured on MEA from single conidium isolates derived from dilution plates of conidial suspensions made from sporulating lesions. All cultures are maintained in a lyophilized state since initial isolation, except isolates IMI 108201–216370, which were originally kept as agar cultures preserved under oil. Cultures were resuscitated as needed on 2% MEA.

Morphological characters including colony type were recorded on 1 to 3-wk-old cultures maintained at 25 °C on 2% MEA. Cytological studies were undertaken using slide cultures stained with the Giemsa technique for nuclear material (Punithalingam, 1983).

Substrate utilization tests

Initial studies by Hakiza (1985) on eight *Colletotrichum* isolates indicated that the CBD isolates could not metabolize certain organic acids, and this aspect was further investigated with the following method.

Substrate utilization was assessed in stationary liquid cultures according to the method of Bridge (1985). Medium B (Lynch *et al.*, 1981) was used as the basal medium, supplemented with either ammonium tartrate or citric acid (1% w/v). Positive and negative controls containing, respectively, glucose or no additional carbon source were included for every isolate. All liquid media contained 0·005% (w/v) bromocresol purple and were adjusted to pH 4·5 prior to sterilization by autoclaving at 105° for 20 min. Utilization media were inoculated with agar plugs (4 mm diam.), taken from 7 d single-conidium-derived cultures grown on unsupplemented Medium B solidified with 1% (w/v) Oxoid no. 3 agar. Utilization was assessed by visual comparison of growth in relation to the positive and negative controls.

Pathogenicity

Pathogenicity tests were conducted using a modification of the hypocotyl infection test originally devised to select resistance to CBD (Cook, 1973; Van der Vossen, Cook & Murakaru, 1976). Seedlings of the CBD-susceptible cultivar SL28 with elongating hypocotyls (6–7 wk from planting) were inoculated by spraying with a fresh aqueous conidial suspension (*ca* 10^4 spores ml^{-1}) obtained from cultures on 2% MEA. They were maintained in a saturated atmosphere at 20–25° for 2 d and then exposed to normal greenhouse conditions. Fifteen to twenty seedlings were inoculated with each test culture; controls were sprayed with sterile water. The number of surviving seedlings was recorded after 2 wk, and cultures were deemed pathogenic if more than 25% of the seedlings were killed. In practice, typical pathogenic isolates invariably killed more than 30% of seedlings, whereas non-pathogens had no effect.

RESULTS

The dark, greenish grey, cottony colonies characteristic of the CBD pathogen were easily distinguishable from the other isolates which had pale grey to white colonies or pinkish adpressed colonies in the case of *C. acutatum*. Growth rates of the CBD isolates also tended to be slower than those of other isolates (2–4 mm d^{-1} compared to 3–6 mm d^{-1}). The two oldest CBD isolates, originally kept under oil, had deteriorated; IMI 108201 now producing pale colonies and no appressoria, and IMI 170660 showing some cultural variation to produce pale flecking of the colony. A more recent isolate, IMI 319406, also showed mixed colony characteristics and subsequent single conidium-derived colonies taken from this showed it to be a mixed isolate. Isolates IMI 325945 and 333347 recovered from old diseased berries had pale, faster-growing colonies (Table 2).

All isolates had conidia and appressoria which fell within the broad range of those normally encompassed by *C. gloeosporioides*, except those of *C. acutatum* and IMI 333347, which had small fusiform conidia and produced no appressoria. There were no clear cytological differences between isolates; all had a small proportion of conidia with more than one nucleus except for IMI 108201, which had a high proportion which were binucleate.

The pathogenicity of all CBD isolates was confirmed by the seedling hypocotyl test, except for IMI 338731, which gave an inconclusive result. The old, abnormal CBD isolate IMI 108201 and the pale isolates IMI 325945 and 333347 from old diseased berries were not pathogenic. The latter were presumed to be secondary saprobic colonizers of old lesions. None of the other isolates was pathogenic to coffee seedling hypocotyls (Table 2).

Biochemical tests showed that none of the 19 CBD isolates could metabolize citrate as a sole carbon source and only one, the mixed culture IMI 319406, could metabolize tartrate. Only one of the non-CBD coffee isolates could not metabolize either citrate or tartrate. This was isolate IMI 216370, an old *C. acutatum* culture. Other isolates gave variable reactions as indicated in Table 3. Two non-coffee isolates, both from yams in the Caribbean, gave a negative result for both citrate and tartrate.

Table 2. Pathogenic characteristics and colony morphology of *Colletotrichum* isolates from coffee

IMI no.	*Colletotrichum* taxon	Pathogenicity	Colony morphology
108201	CBD	−	Off-white, cottony (no appressoria)
170660	CBD	+	Dark with white flecking, cottony
190857	CBD	+	Dark grey cottony
216370	*acutatum*	−	Pink adpressed
275791	*gloeosporioides*	−	Pale grey floccose
299393	CBD	+	Dark grey cottony
300964	CBD	+	Dark grey cottony
301220	CBD	+	Dark grey cottony
303105	*gloeosporioides*	−	Pale grey adpressed
303106	*gloeosporioides*	−	Off-white floccose
309622	*gloeosporioides*	−	Off-white cottony
311655	CBD	+	Dark grey cottony
315974	*gloeosporioides*	−	Pale grey floccose
319401	CBD	+	Dark grey cottony
319406	CBD	+	Grey and white mixed
319418	CBD	+	Dark grey cottony
319423	*acutatum*	−	Pink adpressed
323017	*gloeosporioides*	−	Off-white floccose
325944	CBD	+	Dark grey cottony
325945	*gloeosporioides*	−	Pale grey floccose
333347	*gloeosporioides*	−	Pale grey cottony
334963 abcde	CBD	+	Dark grey cottony
334964	*gloeosporioides*	−	Grey to white variable
337195	CBD	+	Dark grey cottony
338730	CBD	+	Dark grey cottony
338731	CBD	(−)*	Grey cottony

+, Pathogenic, more than 25% seedlings killed; −, non-pathogenic, no seedling killed.

* Pathogenicity test inconclusive, as only 10% of coffee seedlings killed, with another 15% having non-lethal stem lesions.

Table 3. Utilization of tartrate (T) and citrate (C) by isolates of *Colletotrichum* species after 7 d incubation at 25°

	CBD isolates		Other *Colletotrichum* isolates from			
			(*a*) coffee		(*b*) other hosts	
Utilization*	No. of isolates (total 19)	% of total	No. of isolates (total 11)	% of total	No. of isolates (total 15)	% of total
T 0	18	94·7	1	9·1	2	13·3
C 0	19	100·0	6	54·6	6	40·0
T +	1†	5·3	8	72·8	4	26·7
C +	0	0·0	2	18·2	0	0·0
T v	0	0·0	2	18·2	9	60·0
C v	0	0·0	3	27·3	9	60·0

* 0 No utilization by colour reaction; may be weak growth. + Utilization of substrate. v Variable result.
† IMI 319406 (mixed culture – see text).

DISCUSSION

Representative isolates of the coffee berry disease pathogen obtained from across the range of its distribution and examined in this study show common morphological, cultural and biochemical characteristics. These can be used to distinguish it from other *Colletotrichum* strains occurring on coffee and some other tropical crops. This reinforces the conclusions drawn from earlier work on the fungus reviewed by Firman & Waller (1977) and particularly that of Hindorf (1970, 1973, 1974) on the differentiation of the pathogen in Kenya, that the CBD pathogen exists as a distinct and quite separate population in the coffee mycobiota. More recent work (Masaba, 1991) has shown that there is active competition between the CBD pathogen and other *Colletotrichum* strains both *in vivo* and *in vitro*.

The inability of the CBD pathogen to utilize either citrate or tartrate as sole carbon sources is a feature that may be only indirectly related to pathogenicity but may be directly related to a reduced saprobic capability. These biochemical characteristics, however, are all of a negative nature, need careful assessment and should not be used as a sole diagnostic character. The previous study by Hakiza (1985) and unpublished work by the authors show that other enzyme functions tend to be deficient in the CBD pathogen, including ability to metabolize lactate and RNA. These criteria, however, were not sufficiently clear cut to give good differentiation between the *Colletotrichum* strains studied.

Although this study has been concerned with demonstrating the similarity of isolates of the CBD pathogen from different areas, relative to other *Colletotrichum* isolates, variability within the pathogen population is known. Variation of colony morphology of cultures maintained on agar has been well documented (Firman & Waller, 1977); variation in aggressiveness of isolates in Kenya has also been found (D. M. Masaba, pers. comm.). Recently, Rodriguez *et al.* (1991) have reported variation in both aggressiveness and some cultural characters such as rates of sporulation and growth, although the history of their cultures is not clear. Some degree of variation within the CBD pathogen is normal, particularly with *Colletotrichum* species, which are known to be very plastic (Sutton, 1992). Ecotypes suited to the different climatic conditions under which coffee is grown in Africa may develop, but there is no evidence for pathogenic adaptation to different coffee cultivars. This aspect of variability needs further investigation, particularly as the CBD pathogen extends its range and becomes exposed to a wider range of environmental conditions and host germplasm.

The range of natural variability within the CBD pathogen is less than that occurring between the different *Colletotrichum* strains, which is sufficient to distinguish the CBD pathogen from other *Colletotrichum* strains. However, there are close similarities with the broad species concept of *C. gloeosporioides*, as emphasized in the study by Sreenivasaprasad, Brown & Mills (1993) which showed close homology in ribosomal DNA. This study also grouped a range of CBD isolates together, but distinguished them from other *Colletotrichum* isolates based on analysis of restriction fragment-length polymorphisms of ribosomal and mitochondrial DNA.

The most distinctive characteristic of the CBD pathogen, one which enables it to occupy a unique ecological niche, and which separates it on a functional basis from all other *Colletotrichum* species, is its pathogenicity towards developing coffee berries and seedling hypocotyls. The fungus has only been found in association with CBD and its characteristics are consistent among isolates from across its range of distribution. Evidence suggests that the CBD pathogen is a unique co-evolved pathogen of *Coffea* which is slowly spreading out from its centre of origin in the forests of Central Africa (Robinson, 1974; Firman & Waller, 1977; Masaba & Waller, 1992). Coffee berry disease has not occurred where selection pressure for the emergence of the disease has been greatest, as would be expected if it were a pathogenic form of *C. gloeosporioides*; the disease does not occur in South America, where *Coffea arabica* is grown most extensively, and only reached the centre of diversity of *C. arabica* in the Ethiopian highlands in about 1970. When the CBD pathogen did reach the wild population much of it was susceptible to the disease (Van der Graaff, 1981).

Although the CBD pathogen appears to be closely related to *C. gloeosporioides* and possibly evolved from it fairly recently, it is sufficiently distinct in its pathogenicity and

Table 4. Features of *Colletotrichum kahawae* enabling it to be distinguished from *C. gloeosporioides* isolates from coffee

Colletotrichum kahawae	*Colletotrichum gloeosporioides*
(1) Colony characteristics (fresh single-conidial isolates on 2% MEA)	
Slow-growing (2–4 mm d^{-1} at 25°); profuse olivaceous to greenish dark grey mycelium; no acervular conidiomata produced; sporulation occurs from simple hyphae.	Faster growing (3–6 mm d^{-1} at 25°); white to pale grey mycelium; sporulation from acervuli or simple hyphae.
(2) Metabolism	
Cannot utilize citrate or tartrate as sole carbon source.	Can utilize tartrate, citrate or both as sole carbon sources.
(3) Pathogenicity	
Pathogenic to young expanding green berries and developing seedling hypocotyls of *Coffea arabica* cv. SL28 and other susceptible cultivars, causing dark sunken anthracnose lesions.	Not pathogenic to young expanding coffee berries or seedling hypocotyls.

related ecology, colony morphology and biochemical characteristics to warrant recognition as a distinct species. The features distinguishing the CBD pathogen from *C. gloeosporioides* are summarized in Table 4. The name *C. coffeanum* cannot be used as it evidently refers to *C. gloeosporioides* (see above) and the name *C. coffeanum* var. *virulans* was not validly published. The new name *Colletotrichum kahawae* is now proposed here as follows.

Colletotrichum kahawae J. M. Waller & P. D. Bridge, sp. nov.

Etym.: kahaw'a – coffee (Swahili et Arabic), locus CBD fungi et substrati.

Coloniae primae ex laesionibus sporiferis dense floccosae, griseae vel atro-olivaceo griseae, reversum atro-viride griseum, in agaro 2% MA post 7 dies 25° 14–28 mm diam. In subculturis successivis variabilibus, saepe pallidioribus vel brunneis. *Conidiomata* acervularia absentia sed conidia ex hyphis simplicibus oriunda. *Conidia* recta, cylindrica, aseptata, saepe guttulata, ad apicum obtusa, 12·5–19·0 × 4·0 µm. *Appressoria* modice abundantia, pallide vel medio brunneo, circularia vel leniter irregularia, 8·0–9·5 × 5·5–6·5 µm, complescentia.

Non posse uti citrate et tartrate ut pote tantum origines carbonis. Laesiones atrae depressae anthracnosae in baccis viridibus juvenilibus et hypocotylis plantularum *Coffeae arabicae* formatae.

Ex baccis *Coffeae arabicae* cv. SL 28, Kakuzi Estate, Ruiru, Kenya, 29 Jan. 1987, D. M. Masaba 22/87 CBD, IMI 319418, holotypus.

First colonies from sporulating lesions densely floccose, grey to dark olivaceous grey, dark greenish in reverse, on 2% MA at 25° attaining 14–28 mm diam. in 7 d. With successive transfer cultures becoming variable, often paler or brownish. Acervular conidiomata not formed, conidia produced from simple hyphae. Conidia straight, cylindrical, aseptate, invariably guttulate, obtuse at the apex, 12·5–19·0 × 4·0 µm. Appressoria moderately abundant, pale to medium brown, circular or slightly irregular, 8·0–9·5 × 5·5–6·5 µm, often becoming complex. Unable to metabolize citrate and tartrate as sole carbon sources. Pathogenic to young green berries and seedling hypocotyls of *Coffea arabica* causing dark sunken anthracnose lesions.

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