Diagnostic Guide

Black Rot of Sweetpotato: A Comprehensive Diagnostic Guide

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Keywords: mycology, *Ipomoea batatas*, *Ceratocystis fimbriata*, pathogenicity testing**Disease:** Black rot.**Hosts:** Sweetpotato (*Ipomoea batatas*), morning glory (*Ipomoea* sp.) (de Beer et al. 2014), and carrot (*Daucus carota* subsp. *sativus*) (Stahr and Quesada-Ocampo, unpublished).**Pathogen:** Black rot of sweetpotato is caused by the fungal pathogen *Ceratocystis fimbriata* (Ellis and Halst.) (Halsted 1890). Although this is the original name of the pathogen upon first publication, multiple synonyms were introduced over time before returning to the original name. Formerly used synonyms for *C. fimbriata* include *Ceratostomella fimbriata* (J.A. Elliot), *Endocnidiophora fimbriata* (R.W. Davidson), *Ophiostoma fimbriata* (Nannf.), and *Spaeronaema fimbriatum* (Sacc.) (Clark et al. 2015; Webster and Butler 1967).**Taxonomy**Kingdom fungi, phylum Ascomycota, subphylum Pezizomycotina, class Sordariomycetes, subclass Hypocreomycetidae, order Microascales, family Ceratocystidaceae, genus *Ceratocystis*, species *fimbriata*. Current taxonomy can be found at MycoBank, www.mycobank.org.The name *C. fimbriata* has been used to describe fungi capable of infecting many different plants in multiple families. However, thorough research into the genetic relationship of fungi within the *Ceratocystis* genus and closely related genera has called for the name *C. fimbriata* to be restricted to isolates derived from sweetpotato or from the same phylogenetic species (de Beer et al. 2014; Harrington 2013).**Symptoms and Signs**Due to the soilborne nature of causal agent *C. fimbriata*, sweetpotato black rot starts in the field. However, during the growing season symptoms of black rot are not often observed, except intermittent lesions seen on storage roots at harvest if infected seed is used and/or the field had a strong disease pressure. According to the *Compendium of Sweetpotato Diseases, Pests, and Disorders*, reported field symptoms (not pictured) include stunting,

wilting, leaf chlorosis, and leaf drop (Clark and Moyer 2013). If the vine of an infected plant is pulled from the field prior to harvest, a lesion on the vine below soil level may be visible (Fig. 1). Active lesions will appear brown and necrotic (Fig. 1A), and black, globose perithecia with long necks should be observed protruding from the lesion surface (Fig. 1B). As the lesion matures, the infected tissue will become increasingly more necrotic and can cause the sweetpotato vine to split open (Fig. 1C). Although such splitting has been observed in greenhouse trials (Stahr and Quesada-Ocampo, unpublished), there has been no record of such advanced lesions in the field.

Postharvest, black rot of sweetpotato causes a hard rot in the sweetpotato storage roots (Clark and Moyer 2013). *C. fimbriata* is able to infect sweetpotatoes through healthy skin tissue, but infection preferentially takes place at lateral roots, lenticels, and wound sites (Lauritzen 1926; Stahr and Quesada-Ocampo 2020). Infected sweetpotatoes will exhibit shallow, circular lesions on the **FIGURE 1**Appearance of stem lesions on sweetpotato vines. **A**, Active lesions will appear brown to black in color on the sweetpotato vine. **B**, If black perithecia are observed, the globose base will be partially embedded in the vine tissue with the long necks of the perithecia protruding from the vine surface. **C**, Advanced lesions can cause the infected part of the vine to become completely necrotic and ultimately split open, but this has not yet been documented outside of greenhouse trials.[†]Corresponding author: L. M. Quesada-Ocampo; lmquesad@ncsu.edu**Funding:** This work was supported by the North Carolina Sweetpotato Commission and the United States Department of Agriculture (USDA) - Agricultural Research Service under project number NC02628.

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surface of the root (Fig. 2A). Lesion color can range from brown, dark gray, greenish-black, to black depending on the sweetpotato cultivar and surface moisture (Clark and Moyer 2013). When conditions are favorable for sporulation, light gray mycelia will grow on the lesion surface, typically originating in the lesion center or at a wound site. Perithecia development will follow mycelial growth, and light-colored ascospore masses may be visible to the naked eye. However, diseased roots are often found after conditions are no longer favorable for sporulation or the sweetpotato has been washed on a packing line, which will cause the gray mycelia to subside and leave behind small black patches, which are remnants of sporulation structures (Fig. 2B). If the storage root is cut open, the tissue below a lesion will be black and necrotic (Fig. 2C), but the infection does not often internalize beyond the vascular tissue of the storage root (Clark and Moyer 2013). Finally, the fungus will produce a fruity odor, which is observed in both infected roots and when the fungus is grown in culture (Clark and Moyer 2013; Soares et al. 2000).

Host Range

C. fimbriata is known to infect many plant species in addition to sweetpotato, commonly producing canker and wilt diseases on woody hosts. Hosts of *C. fimbriata* include, but are not limited to, coffee (*Coffea* sp.) (Baker et al. 2003; Johnson et al. 2005), *Eucalyptus* spp. (Roux et al. 2000), fig (*Ficus carica*) (Harrington et al. 2011), taro (*Colocasia esculenta*) (Johnson et al. 2005; Mizukami 1951), hickory (*Carya* sp.) (Johnson et al. 2005), mango (*Mangifera indica*) (Baker et al. 2003; Harrington et al. 2011), and pomegranate (*Punica granatum*) (Li et al. 2016). Furthermore, in greenhouse settings *C. fimbriata* has been observed to infect tobacco (*Nicotiana tabacum*), soybean (*Glycine max*), and lettuce (*Lactuca sativa*) when plants were inoculated after wounding or at the seedling stage (Stahr and Quesada-Ocampo, unpublished). A summary of hosts can be found online in the Fungal Databases at the Systematic Mycology and Microbiology Laboratory, USDA-ARS (<https://nt.ars-grin.gov/fungalatabases/fungushost/fungushost.cfm>).

FIGURE 2

Diagnostic symptoms of sweetpotato black rot caused by *Ceratocystis fimbriata*. **A**, Dark and circular lesions form on the surface of the storage roots, usually centered around a wound, lenticel, or lateral root. **B**, Small black patches that are remnants of sporulation structures can often be observed in the lesion (arrows) and typically appear in the lesion center. **C**, Internally infected tissue will become black and necrotic, but necrosis does not typically extend beyond the vascular tissue.

Although the host list is extensive, host specialization among isolates has been reported (Baker et al. 2003). As research into the *Ceratocystis* genus continues and genomic tools advance, cryptic species in the *C. fimbriata* complex are being reclassified as new species. For example, previously classified *C. fimbriata* isolates from sycamore (*Platanus* spp.), cacao (*Theobroma cacao*), and almond (*Prunus* sp.) have now been reclassified as *C. platani*, *C. cacaofunesta*, and *C. destructans*, respectively (Engelbrecht and Harrington 2005; Holland et al. 2019).

Geographic Distribution

C. fimbriata has a large geographic range and has been documented on all cultivated continents. More specifically, *C. fimbriata* can be found in all places where sweetpotatoes are cultivated, including Asia (Li et al. 2016), Africa (Roux et al. 2000), and the Americas (Baker et al. 2003). Within the United States, *C. fimbriata* is most prevalent within the Southeast, and has been reported in the following states: North Carolina, Virginia, Georgia, Mississippi, Alabama, Louisiana, Arkansas, Missouri, and California (Scruggs et al. 2017). A summary of geographic distribution can be found in the Fungal Databases at the Systematic Mycology and Microbiology Laboratory, USDA-ARS, which includes geographic distribution by country (<https://nt.ars-grin.gov/fungalatabases/>). A detailed distribution map can also be found at <https://www.cabi.org/dmpd>, but it is not as current (1983).

Pathogen Isolation

C. fimbriata is a slow-growing fungus that can take at least 2 weeks to grow large enough to fully cover a standard 100-mm-diameter agar plate. As such, steps to reduce the risk of contamination from faster growing organisms should be taken when isolating *C. fimbriata* from any host tissue. Carrot baits and carrot agar (described in Figure 3 and Table 1, respectively) are considered selective for *C. fimbriata* (Moller and DeVay 1968) and as such are recommended for isolation, but they do allow for the growth of other microorganisms. Currently, no other selective or differential media for *C. fimbriata* exist, although potato dextrose agar and malt yeast extract agar (Table 1) are also commonly used for *C. fimbriata* propagation. Water agar should not be used for isolation or propagation of *C. fimbriata* because the fungus will not grow on this medium. Finally, *C. fimbriata* does not grow within sweetpotato

FIGURE 3

Use of carrot disc baiting for isolation of suspected *Ceratocystis fimbriata* isolates. **A**, Infected tissue should be placed in an internal cavity cut into one half of the carrot discs. **B**, The discs are reassembled and placed in a humidity chamber with damp paper towels to prevent the discs from drying out. **C** and **D**, Fungal mycelia will grow out of the carrot disc after 4 to 5 days.

tissue when kept at temperatures below 18°C (Stahr and Quesada-Ocampo 2020). Therefore, isolation from plant material that has been stored in a refrigerator or cold room for extended periods of time will have a lower success rate when compared with isolation from a sample stored at room temperature.

Isolation from storage roots. Storage roots should be surfaced sterilized by submersion in a 0.6% sodium hypochlorite solution for 5 min. Roots should then be thoroughly rinsed with sterile distilled water (SDW) and allowed to dry in a laminar flow hood. Using sterile technique, small triangular tissue samples should be cut from the edge of the suspected black rot lesion using a flame-sterilized scalpel. Tissue samples are then to be plated onto carrot agar amended with ampicillin and rifampicin (20 mg/liter each), with the inner side of the tissue facing down on the plate. Agar plates should be wrapped with Parafilm and incubated at room temperature (~23°C), with an approximate 12-h photoperiod. Very limited growth will be visible within the first 3 to 4 days; if prolific growth is observed during this period, it is most likely due to other fungal contaminants. After 5 to 7 days, the fungal colony should be large enough in size that the initial hyaline mycelia will have turned greenish-black. Being careful to avoid any other organisms that may be present, cut a 3 × 3-mm agar plug from the edge of the mycelial colony and transfer to a fresh plate. Transfer of the colony, in this manner, should be repeated until no secondary organisms are present. Once free of secondary organisms, allow the fungi to grow until perithecia producing tan-orange ascospore masses appear (~7 to 10 days). Because *C. fimbriata* is homothallic (Clark and Moyer 2013), singular ascospore masses should be of a single genotype. To obtain an axenic, single genotype culture, use a flame-sterilized scalpel, inoculation loop, or inoculation needle to grab a singular ascospore mass and transfer to a new plate. The ascospore masses are very sticky in nature and will adhere to a transfer tool when lightly touched.

Isolation from plant stems. Stem isolations are generally less successful than storage root isolations, because stem lesions in sweetpotato are less common, can quickly become necrotic, and often house saprophytic microbes. If an infection is suspected, gently remove the whole plant, including roots, and rinse free of any soil. Avoid cutting into or breaking the plant around the stem lesion, because it provides an entry site for sanitizer during surface sterilization, which may result in senescence of the causal organism. Once

free of soil, submerge the symptomatic area into a 0.6% sodium hypochlorite solution and surface sterilize as previously described. If the stem is large and sturdy, cut a small, triangular tissue sample from the edge of the lesion as previously described. If the stem is too small or fragile to cut a triangular tissue sample, simply make a thin cross section of the stem near the outer edge of the lesion. Plate triangular tissue sample or stem cross section onto amended carrot agar and proceed with the rest of the isolation as previously described.

Isolation with carrot baits. If isolation onto agar is unsuccessful, carrot baits can be used to attempt isolation. Carrot baits are also common when attempting isolation from non-sweetpotato hosts and possible insect vectors (da Silva et al. 2017; Harrington et al. 2011; Moller and DeVay 1968). To use a carrot bait, acquire a whole carrot and surface sterilize with sodium hypochlorite as done in prior isolation steps. Cut the carrot into 2-inch segments, and then half the segments into disks. On the interior surface of one disk, cut out a cavity large enough to contain a sample of infected tissue, insect, or whatever infected sample is being used (Fig. 3A). Under sterile conditions, collect the infected tissue sample (using either of the methods described above), and then place the infected tissue into the carrot cavity. Reassemble the carrot discs and place in a humidity chamber or deep-dish Petri plate (25 × 100 mm) with a damp paper towel (Fig. 3B). The baits should then be placed into an incubator set to 25°C. A 12-h photoperiod can be set, but *C. fimbriata* can successfully grow in the absence of light (Webster and Butler 1967). Incubate the carrot discs 5 to 10 days, while regularly checking moisture levels to ensure the carrot discs do not dry out or become waterlogged. After 4 to 5 days, mycelial growth

TABLE 1 Recipes for media commonly used for <i>Ceratocystis fimbriata</i> isolation and propagation	
Medium ^a	Per liter
Carrot agar	
Bolthouse Farms carrot juice	160 ml
Agar powder	16 g
Carrot broth	
Bolthouse Farms carrot juice, clarified via centrifugation	100 ml
Malt yeast extract agar	
Malt extract (2%)	20 g
Yeast extract (0.2%)	2 g
Agar (2%)	20 g
Potato dextrose agar	
Potato dextrose agar powder	39 g

^a Antibiotics can be added to any listed medium to control for bacterial contaminants. Rifampicin and ampicillin at 20 mg/liter each are recommended.

FIGURE 4

Morphological features used for identification of *Ceratocystis fimbriata*. **A**, Appearance of culture in carrot agar. **B**, Sexual ascospores given characteristic hat shape due to a gelatinous sheath forming a brim (arrow). **C**, Asexual spore types include cylindrical endoconidia and brown, globose chlamydospores. **D**, Black perithecia with globose base and long tapering neck. Scale bars have been included for size reference.

should be evident (Fig. 3C and D), and once perithecia have been produced the ascospore mass can be collected and plated to obtain a pure culture as previously described.

Pathogen Identification

Morphological characteristics are commonly used to confirm pathogen identity of suspected *C. fimbriata* isolates. In agar medium, cultures of *C. fimbriata* can range in color from black to brown to dark-olive green (Fig. 4A) (Morgan-Jones 1967; Webster and Butler 1967). Perithecia readily form on infected plant tissue and common agar media. These perithecia can be superficial or partially embedded in the growing substrate, are dark brown or black in color, and have a globose base with a long tapering neck from which hyaline, ostiolar hyphae protrude (Fig. 4D) (Clark and Moyer 2013; Engelbrecht and Harrington 2005). Asci are not visible, but single-celled hyaline ascospores are exuded in an extracellular matrix and form tan (Stahr and Quesada-Ocampo 2020), pink (Clark and Moyer 2013), cream (Clark and Moyer 2013; Engelbrecht and Harrington 2005), or orange (Stahr and Quesada-Ocampo 2020) colored masses depending on isolate and substrate. These smooth, elliptical ascospores (Fig. 4B) are key for identification because they possess a gelatinous sheath adhered to one side of the spore, leading to their characteristic hat shape (Clark and Moyer 2013; Webster and Butler 1967). Asexual spore types

(Fig. 4C) are also used for identification as subhyaline to hyaline, nonseptate, cylindrical endoconidia are typically produced in abundance on most substrates. Thick-walled, chlamydospores, also known as aleurioconidia (Engelbrecht and Harrington 2005), can also be produced. Chlamydospores are oval to globose in shape and range from pale to olive brown in color (Morgan-Jones 1967). Certain strains of *C. fimbriata* are also known to produce doliform endoconidia, but such a spore type has not been reported in sweetpotato-derived isolates (Webster and Butler 1967). Dimensions of perithecia and all spore types can be found in Table 2.

Molecular confirmation for *C. fimbriata* should be used when possible. DNA can be extracted from a pure sample, and the internal transcribed spacer region and the translation elongation factor 1 α region of the genome can be amplified and sequenced. Primer names and sequences for these regions can be found in Table 3. The resulting sequences can then be compared against the full *C. fimbriata* genome (GenBank accession APWK000000000) using BLAST (Scruggs et al. 2017; Wilken et al. 2013). At this time, species-specific primers are not available.

Pathogen Storage

There are multiple options for maintaining cultures of *C. fimbriata* for long periods of time. First, because the fungus is slow growing (Webster and Butler 1967) and does not appear to lose

TABLE 2
Description of key morphological features used for identification of *Ceratocystis fimbriata*

Structure	Color ^a	Component	Dimensions ^a
Perithecia	Dark brown to black	Base	Width: 110 to 250 μ m Height: 120 to 250 μ m
		Neck	Base width: 28 to 40 μ m Top width: 16 to 24 μ m Length: Up to 900 μ m
	Hyaline to light brown	Ostiolar hyphae	Width: 2.2 μ m Number present: 7 to 16
Ascospores	Hyaline	Spore	Width: 3.5 to 5 μ m Height: 3.0 to 4.5 μ m Length: 5 to 7.5 μ m
Endoconidia	Hyaline to pale brown	Brim ^b Endoconidiophore	Tapering width: 0.5 to 0.1 μ m Width: 3 to 8 μ m Length: 35 to 172 μ m
	Hyaline to subhyaline	Spore	Width: 3 to 7 μ m Length: 7 to 37 μ m
Chlamydospores (aleurioconidia ^c)	Pale to olive brown	Conidiophore (aleurioconidiophore ^c)	Width: 4 to 7 μ m Length: 10 to 76 μ m
		Spore	Width: 6 to 16 μ m Length: 8 to 20 μ m

^a All color and dimensions have been compiled from multiple publications (Clark and Moyer 2013; Engelbrecht and Harrington 2005; Morgan-Jones 1967; Webster and Butler 1967). The largest published range in size for each structure component is shown.

^b Measurements taken with an electron microscope (Webster and Butler 1967).

^c Alternate nomenclature as used in Engelbrecht and Harrington (2005).

TABLE 3
Primer sequences to be used for molecular identification of *Ceratocystis fimbriata*

Region amplified	Reference	Primer name	Primer sequence
Internal transcribed spacer region	White et al. (1990)	ITS1-F	5'-CTTGGTCATTTAGAGGAAGTAA-3'
		ITS4	5'-TCCTCCGCTTATTGATATGC-3'
Translation elongation factor 1- α	Geiser et al. (2004)	ef1	5'-ATGGGTAAGGARGACAAGAC-3'
		ef2	5'-GGARGTACCAGTSATCATGTT-3'

virulence after serial transfer through artificial media compared with other fungi such as *Botrytis* spp. (Breen et al. 2016; Butt et al. 2006), *C. fimbriata* can be continually transferred through agar every 10 to 14 days for many months. However, if keeping and repeatedly transferring plate cultures is undesirable, mycelial plugs can be prepared for short- and long-term storage.

To prepare storage cultures, first procure carrot broth (Table 1), a 50% glycerol solution, and a mature *C. fimbriata* plate culture. Using sterile technique, cut five small (<5 mm) mycelial plugs from the edge of the *C. fimbriata* culture. Place the mycelial plugs into a 1.5-ml tube along with 500 μ l of carrot broth. Loosely close the tube to maintain limited airflow and allow an adjustment period of 3 to 5 days. If contamination is a concern, the adjustment period can be shorter, but recovery of storage isolates may be less successful. After the adjustment period, add 500 μ l of 50% glycerol solution to the tube and gently shake or vortex to mix. Place the tube on ice for 1 h before transitioning to a 4°C fridge for short-term storage (<1 year) or a –80°C freezer for long-term storage (>1 year). When recovering stored isolates, take steps to gradually warm the isolate before attempting plating. First, remove the tube from the 4 or –80°C and thaw on ice (for –80°C). Once thawed, hold the tube at room temperature for 1 to 2 h, or until the room temperature is reached. Finally, place the tube into a warm water bath, no hotter than 40°C, for an additional 1 to 2 h. Plate mycelial plugs onto room-temperature amended carrot agar plates. Growth should be observed within 3 to 5 days.

Pathogenicity Tests

Inoculum for pathogenicity tests can be prepared in two ways, depending on desired spore type. Mixed spore suspensions containing endoconidia, chlamydospores, and the highly infectious ascospores can be obtained from 10-day-old *C. fimbriata* cultures grown on carrot agar by adding a 5% Tween-20 solution to the plate. Once 1 to 2 ml of the Tween solution is added, spores can be gently dislodged using a rubber scraper or spatula and carefully massaged against the agar to separate the ascospore masses. The spore suspension should then be

recollected from the plate, the concentration determined using a hemocytometer, and the suspension diluted with SDW to a working concentration of 5×10^3 spores/ml (Stahr and Quesada-Ocampo 2020). If mixed spore suspensions are undesirable due to the difficulty of separating ascospore masses, primarily endoconidial suspensions can be prepared by flooding 7-day-old *C. fimbriata* cultures, grown on malt yeast extract or potato dextrose agar, with 10 ml of SDW and scraping with a rubber spatula. The spore suspension can then be filtered through four layers of sterile cheesecloth and rinsed with an additional 5 ml of SDW. The spore suspension concentration should then be determined using a hemocytometer and diluted to a working concentration of 2×10^5 spores/ml (Baker et al. 2003).

Currently, there are no known resistant sweetpotato cultivars to *C. fimbriata* (Scruggs et al. 2017), so commercially available varieties such as Covington in North Carolina or Beauregard in Louisiana can be used for pathogenicity testing. If unfamiliar with disease signs and symptoms, varieties with lighter skin colors are recommended over purple-skinned varieties, because lesions will be easier to observe with the naked eye. Pathogenicity should be tested on the storage roots, which can be acquired from a local market or packing house. Roots should be surface sterilized as described previously, to prevent other common and faster growing pathogens such as *Rhizopus* or *Fusarium* from skewing the results. Common to many postharvest pathogens, *C. fimbriata* will preferentially infect at wound sites (Stahr and Quesada-Ocampo 2020); thus, storage roots can be wounded to promote infection. If not wounding roots, it is recommended to perform pathogenicity tests with a larger sample size because infection through healthy skin tissue is less common (Lauritzen 1926; Stahr and Quesada-Ocampo 2020). If wounding, wounds can be made with either a toothpick to produce a small puncture wound or a handheld wounding tool (Collins et al. 2018) to produce three evenly spaced punctures on the sweetpotato (Fig. 5). Roots, wounded or not, should then be soaked in either the mixed spore suspension or the endoconidia suspension for 20 min with periodic gentle agitation. After soaking, place roots into sterile plastic containers and maintain a relative humidity of 80% or greater. Methods to maintain relative humidity within the plastic containers will vary depending on container dimensions and number of roots per container but can typically be managed by adding small Petri plates containing SDW or damp paper towels to the containers (Scruggs and Quesada-Ocampo 2016). Store the containers in a dark growth chamber or incubator at 29°C for a maximum 3-week period. If the isolate tested is pathogenic, lesion development and/or sporulation will be observed within 14 days of inoculation, with lesion development occurring as early as 4 days post-inoculation and sporulation as early as 7 days postinoculation. A variety of measurements can be taken to determine the virulence and aggressiveness of the isolate, including incidence of lesion development and sporulation, and lesion and sporulation area diameters taken at the end of a 3-week period or taken periodically every 2 to 4 days (Stahr and Quesada-Ocampo 2020).

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FIGURE 5

Optional wound sites to be used for pathogenicity testing. **A**, Small singular puncture wound produced by a sterile toothpick. **B**, Slightly larger but more shallow set of puncture wounds produced by **C**, a handheld wounding tool. This tool was assembled from a piece of stainless steel, a drawer handle, and three 4-mm self-drilling screws spaced 3.8 cm apart.

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