Fusarium oxysporum* f.sp. *cubense (E. F. Sm.) W. C. Snyder & H. N. Hans, 1940 **Tropical Race 4 (TR4)**

Figure 1. A banana plant infected with *Fusarium oxysporum* f.sp. cubense Tropical Race 4 in Taiwan. Courtesy of Miguel Dita/Bioversity International, http://www.musarama.org/.

Synonyms

Fusarium cubense, Fusarium oxysporum, Fusarium oxysporum cubense, Fusarium oxysporum f. *cubense, Fusarium oxysporum Schlecht.* var*. cubense, Fusarium oxysporum* var*. cubense,*

Common Name(s)

Panama Disease, Panama disease of banana, Fusarium wilt, Fusarium wilt of banana, vascular wilt of banana

Type of Pest

Fungal pathogen

Taxonomic Position

Class: Sordariomycetes **Order:** Hypocreales **Family:** Nectriaceae

Reason for Inclusion in Manual

Suggested by CAPS community

Background Information

Panama disease, also known as Fusarium wilt of banana (*Musa* spp.), caused by the fungal pathogen *Fusarium oxysporum* f.sp. *cubense*, is one of the most notorious of all plant diseases. Although the pathogen probably originated in Southeast Asia, the disease was first reported in Australia in 1876 (Ploetz, 2000) and has since been found in all banana-growing regions of the world except for some of the countries bordering the Mediterranean Sea (PADIL, n.d.). Fusarium wilt is arguably the most significant vascular wilt disease of banana (Ploetz and Pegg, 2000). This notorious reputation stems from damage it caused in the first export trades, which were based on 'Gros Michel' (AAA) banana cultivars. Extreme susceptibility to Fusarium wilt, the use of infected suckers to establish new plantings, and the practice of monoculture doomed the 'Gros Michel' cultivar (Ploetz and Churchill, 2011). Fusarium wilt was responsible for the decimation of the export trades in Central and South America and the Caribbean. It has been estimated that about 40,000 hectares became unproductive over a period of 50 years, and the pathogen caused billions of dollars in economic damage (Ploetz, 2000). The industry was saved by changing to cultivars in the Cavendish subgroup (AAA genome), which were resistant to known strains (races) of this disease. However, Cavendish cultivars in plantations in subtropical Australia, the Canary Islands, South Africa, and Taiwan were also affected by *F. oxysporum* f.sp. *cubense* 'subtropical race 4'. More recently, Cavendish cultivars planted on a large scale in Southeast Asia are succumbing to *F. oxysporum* f.sp. *cubense* 'tropical race 4' (Ploetz and Pegg, 2000).

Pest Description

Fusarium oxysporum f.sp. *cubense* has been divided into races based on its pathogenicity on reference host cultivars. Among the most significant races of *F. oxysporum* f.sp. *cubense* pathogenic to edible banana, race 1 affects the cultivar 'Gros Michel'; race 2 affects bananas of the 'Bluggoe' sub-group; and race 4 affects all cultivars in the 'Cavendish' sub-group plus cultivars susceptible to races 1 and 2. Race 4 involves two subgroups, 'subtropical race 4' (SR4) and 'tropical race 4' (TR4), both of which are capable of causing disease on Cavendish and other cultivars. SR4 only affects bananas in the subtropics with predisposing factors such as cold temperature. TR4, however, can affect Cavendish plants with no predisposing factors in the tropics and subtropics. TR4 was recognized in the early 1990s and is responsible for serious losses of cultivars in the Cavendish subgroup in some areas of tropical Southeast Asia (EFSA, 2008; Ploetz and Churchill, 2011).

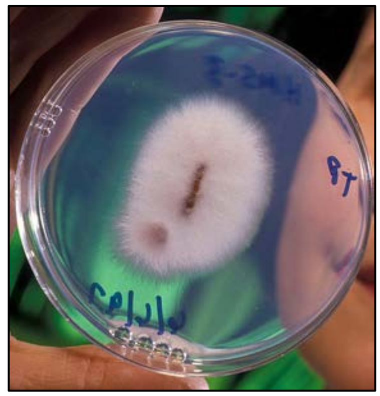

Figure 2. A plant-pathogenic strain of *Fusarium oxysporum* in culture. Photo Credit: Keith Weller, USDA-ARS.

Unlike subtropical outbreaks that affect cold-stressed Cavendish in Australia, the Canary Islands, and South Africa, TR4 affects Cavendish in the absence of predisposing factors such as cold winter temperatures. Originally found only in Southeast Asia, TR4 continues to spread in that region. In addition, it has recently been detected in the Middle East and Africa and for the first time in Australia (IPPC, 2013; García-Bastidas et al., 2014; DAF, 2015; Ordoñez et al., 2015).

Fusarium oxysporum f.sp. *cubense*, a soilborne hyphomycete, is one of more than 100 formae speciales (special forms; abbreviated f.sp.) of *F. oxysporum* that cause vascular wilts of flowering plants. The *F. oxysporum* complex contains pathogenic and saprophytic strains that cannot be distinguished morphologically. Colonies grow 4-7 mm/day on Potato Dextrose Agar (PDA) at 24°C (75°F), with slight to significant aerial mycelium (Fig. 2), and white to purple

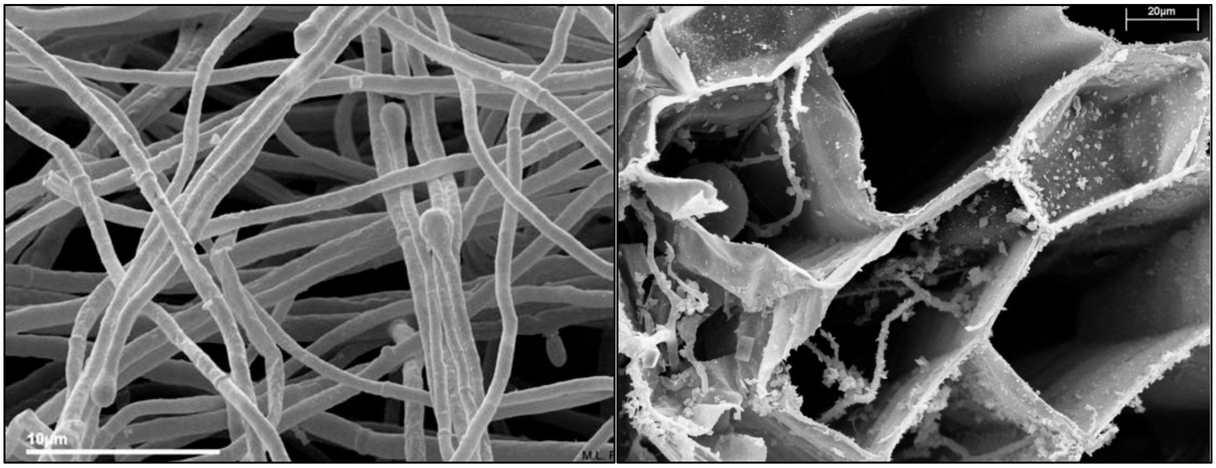

Figure 3. Left: Scanning Electron Microscopy (SEM) photo of the mycelium of *Fusarium oxysporum* f.sp. *cubense*. Right: SEM of the fungus invading the cortex of a banana root. Courtesy of Mônica Lanzoni Rossi, CENA http://www.musarama.org/.

pigmentation. Sporodochia are tan to orange, and sclerotia are blue and submerged. Micro- and macroconidia are produced on branched and unbranched monophialides. Microconidia are 5-16 x 2.4-3.5 µm, one- or two-celled, oval- to kidney-shaped, and are borne in false heads. Macroconidia are 27-55 x 3.3-5.5 µm, four- to eight-celled and sickle-shaped with foot-shaped basal cells. Terminal and intercalary chlamydospores are 7-11 µm in diameter, usually globose and are formed singly or in pairs in hyphae or conidia. *Fusarium oxysporum* f.sp. *cubense* has no known teleomorph (Ploetz, 2000; Ploetz, 2006).

Biology and Ecology

The disease cycle begins with the entry of the pathogen into the potential host via the root tip (Fig. 3). Substances produced by the host, in the region behind the zone of elongation of the root meristem, elicit a pathogen response which results in the germination of chlamydospores. The germinated hyphae then infect the lateral roots and progress to invade the xylem vessels. Further spread of most initial infections is usually stopped in the xylem by the vascular occluding responses of the host, which include the formation of gels, tyloses, and the collapse of vessels. In susceptible cultivars, some of these infections advance ahead of these defense mechanisms. Microconidia are formed in the xylem vessels and are spread through the vascular system of the plant, streaming to new sites where they germinate. Hyphae are then produced, and this begins the invasion at this new site, thus repeating the cycle. In resistant varieties, the initial pathogen-induced occlusion reaction is further enhanced by the production of phenolic compounds, which lignifies these obstructions and limits the pathogen to the infected vessels; no further colonization of the xylem vessels occurs (PADIL, n.d.).

Figure 4. Advanced disease symptoms of tropical race 4 affecting Cavendish banana clones at the Coastal Plains Banana Quarantine Station, Northern Territory, Australia: (a) Banana plant showing typical symptoms of Fusarium wilt, yellowing, necrosis and collapse of leaves (notice that leaves form a skirt around the base of the plant). (b) Cross section of pseudostem showing the dramatic vascular discoloration. Photographs courtesy of the University of Queensland (Dr. Juliane Henderson).

The principal means of *F. oxysporum* f.sp. *cubense* spread is by asymptomatic infected suckers or rhizome pieces used for planting. The organism can also spread by contaminated soil attached to planting material or farm machinery and by water running through infested soil. However, these means are of more significance in terms of local spread (Ploetz and Pegg, 2000). *Fusarium oxysporum* f.sp. *cubense* may remain viable in soil for decades. Reports of viability for 20 years in soil are common, and extreme reports of 40 years have been indicated (Ploetz et al., 2015b). The recent identification of several weed hosts of TR4 (Hennessy et al., 2005) suggests that these hosts may also play a role in the survival and spread of the pathogen.

Symptoms/Signs

Yellow and wilted leaves are typical symptoms of Panama Disease/ Fusarium wilt (Fig. 1, 4). The yellowing typically progresses from the older to the younger leaves. The yellow leaves may remain erect or collapse at the petiole and hang down along the pseudostem. Collapsed leaves may form a skirt around the base of the plant (Fig. 4a). Splitting of the pseudostem at the base of the plant may also occur (Fig. 5) (PADIL, n.d).

Figure 5. A split pseudostem in a banana tree affected by Fusarium wilt. Courtesy of Miguel Dita/Bioversity International, http://www.musarama.org/.

The first internal symptom, a reddish brown discoloration of the xylem, develops in feeder roots, the initial sites of infection. Vascular discoloration progresses to the rhizome, is most prominent where the stele joins the cortex, and ultimately proceeds up to and includes large portions of the pseudostem (Fig. 4). On plants that are more than 4 months old, the oldest leaves yellow or split longitudinally at the base. Eventually, younger and younger leaves wilt and collapse until the entire canopy consists of dead or dying leaves (Ploetz, 2006).

Banana suckers that are less than about 4 months old do not develop visible symptoms of Panama Disease. The fruit of the banana plant also does not show any specific disease symptoms (PADIL, n.d.).

Pest Importance

Fusarium oxysporum f.sp. *cubense* TR4 represents the worst threat to sustainable banana production worldwide and, due to its wide host range, would impact about 60% of the world's banana production if it were widely spread (Ploetz, 2015a, personal communication). The great fear is that TR4 would devastate export bananas and bananas grown by smallholders if it spread to the Americas and Africa. TR4 poses a serious threat to a multibillion dollar industry and the food stability and income of millions of poor farmers (Ploetz and Churchill, 2011).

Banana is an important crop in Hawaii and Puerto Rico. In 2013, it was grown commercially on 900 acres in Hawaii, and total production was 7,300 fresh tons at a value of $13 million (USDA-NASS, 2015). In 2012, over 5 million banana trees were grown on 1,828 farms in Puerto Rico, and the total value of the harvest there was over $12.1 million (USDA, 2012).

Fusarium oxysporum f.sp. *cubense* is listed as a harmful organism in the following countries: Colombia, French Polynesia, Honduras, New Caledonia, and Peru. In addition, *Fusarium oxysporum* f.sp. *cubense* is listed as a harmful organism in the following countries: China, Costa Rica, Ecuador, Honduras, Morocco, Pakistan, Samoa, South Africa, South Korea, and Vietnam (PExD, 2015). There may be trade implications with these countries if this pathogen becomes established in the United States.

Known Hosts

Major Hosts: *Musa* spp. (banana, plantain).

Other hosts: *Chloris inflata* (purpletop rhodes grass), *Cyanthilium cinereum* (little ironweed), *Euphorbia heterophylla* (Mexican fireplant), *Tridax procumbens* (coatbuttons) (Subramanian, 1970; Hennessy et al., 2005; Ploetz, 2006).

Known Vectors (or associated insects)

Fusarium oxysporum f.sp. *cubense* is not known to be transported by a vector.

Known Distribution

Africa: Mozambique. **Asia**: China (Hainan, Guangdong, Guangxi), Indonesia (Bali, Halmahera, Irian Jaya, Java, Sulawesi and Sumatra), Malaysia (Peninsular and Sarawak), the Philippines, and Taiwan. **Middle East**: Jordan, Lebanon, Oman, Pakistan. **Oceania**: Australia (Queensland, Northern Territory) (Dita et al., 2010; Ploetz and Churchill, 2011; IPPC, 2013; García-Bastidas et al., 2014; DAF, 2015; Ordoñez et al., 2015).

Pathway

Banana suckers that are less than about 4 months old do not develop visible symptoms of Panama Disease/ Fusarium wilt. The lack of visible symptoms on suckers has assisted in the movement of the pathogen to new regions through the movement of these asymptomatic suckers to new areas as planting material (PADIL, n.d.).

There have been shipments of *Musa* spp. plant material from the Philippines (3), China (17), and Malaysia (32) since 2004. There have also been shipments of *Musa* spp. plant material to Hawaii (3) and Guam (1) from Thailand. There were also 12 shipments of *Musa* spp. plant material from Israel to Puerto Rico, totaling 159,000 plant units. Israel borders Jordan, a country known to have TR4 (AQAS, 2015). It is unclear whether or not the plant material in these shipments was grown from tissue culture. Tissue-culture plantlets do not pose a risk to the spread of TR4 (Ploetz, 2015a, personal communication; Ploetz et al., 2015b). Based on the units reported (plant units, kg), however, it is unlikely that all of this material was from tissue culture.

In addition to these shipments, there were 7 interceptions in Hawaii of *Musa* spp. plant material intended for propagation from the Philippines since 2004 (AQAS, 2015).

Potential Distribution within the United States

Bananas are grown commercially in Hawaii and Puerto Rico (USDA, 2012; USDA-NASS, 2015). These tropical regions are most vulnerable to establishment of *F. oxysporum* f.sp. *cubense* TR4.

Musa spp. are also present in Florida and parts of Alabama, Louisiana, and Texas. *Cyanthilium cinereum* (little ironweed) is present in southern Florida. *Tridax procumbens* (coatbuttons) is present in Florida and the southern tip of Texas (BONAP, 2014).

Survey

Approved Method for Pest Surveillance (AMPS)*:

The approved survey method is a visual screening for symptomatic host material.

There are several races of *Fusarium oxysporum* f.sp. *cubense.* The symptoms are similar for all races. Tropical race 4, however, affects the "Cavendish" banana cultivar, which is resistant to other races of this disease. Surveys for tropical race 4 should only occur in "Cavendish" banana cultivars.

*For the most up-to-date methods for survey and identification, see Approved Methods on the CAPS Resource and Collaboration Site, at https://caps.ceris.purdue.edu/approved-methods.

Literature-Based Methods:

Visual symptoms of Fusarium wilt are well described (Ploetz, 2006; EFSA, 2008; Ploetz and Churchill, 2011; PADIL, n.d.). Symptomatic material is collected for molecular analysis and diagnosis. Pronounced yellowing symptoms of Fusarium wilt are easy to observe in the field. However, very early symptoms are more difficult for the untrained eye to detect. Evidence of Fusarium wilt is vascular discoloration in the lower pseudostem or in the rhizome (CABI, 2014).

Key Diagnostics

Approved Method for Pest Surveillance (AMPS)*:

Morphological for species-level identification.

The race of most pathogens is generally determined by inoculation of host differentials. Molecular methods are available in the literature to distinguish tropical race 4 (Dita et al., 2010; Dita et al., 2013; Peng et al., 2014).

*For the most up-to-date methods for survey and identification, see Approved Methods on the CAPS Resource and Collaboration Site, at https://caps.ceris.purdue.edu/approved-methods.

Literature-Based Methods:

In general, strains of *F. oxysporum* f.sp. *cubense* cannot be distinguished morphologically. Previously, TR4 could only be identified using pathogenicity tests and with vegetative compatibility groups (VCG) (Ploetz, 2006). Dita et al. (2010) have developed a PCR diagnostic for TR4 that can also be used for detection in symptomatic plants. This was a major breakthrough in diagnostics for this pathogen. Dita et al. (2013) have since utilized a nested PCR (originally developed in Dita et al. (2010)) that is more sensitive and can detect TR4 in symptomless host plants and in soil.

Peng et al. (2014) have developed a real-time fluorescence loop-mediated isothermal amplification (RealAmp) assay that is highly sensitive and can detect *F. oxysporum* f.sp. *cubense* race 4. This assay can be completed with the use of a portable fluorescent reader and no expensive reagents. However, it does not distinguish between TR4 and SR4.

Easily Confused Species

This fungus causes wilting symptoms in hosts but may be confused with other banana diseases. Symptoms of Fusarium wilt of bananas can be mistaken for Moko disease, caused by *Ralstonia solanacearum* race 2. The two can be distinguished if the plant has fruit. Fusarium wilt does not affect fruit, but Moko disease, blood disease, and Xanthomonas wilt all cause an internal dry rot symptom clearly visible if the fruit is cut.

Symptoms similar to those caused by Fusarium wilt - such as leaf yellowing - may be caused by other biotic and abiotic factors, including water stress. Care should be taken to avoid attributing such yellowing to Fusarium wilt by examining the plant for other external and internal symptoms, such as vascular discoloration (CABI, 2014).

There are three known races of *Fusarium oxysporum* f.sp. *cubense* that affect banana (races 1, 2, and 4). Race 4 is the only race known to affect the Cavendish banana cultivar, which is resistant to other races of this pathogen (Ploetz, 2006).

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