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RE-EMERGENCE OF PANAMA DISEASE (FUSARIUM WILT) AND SPECIAL THREAT POSED BY TROPICAL RACE 4

Randy Ploetz, Professor, Department of Plant Pathology, University of Florida, Tropical Research and Education Center, 18905 SW 280th Street, Homestead, FL 33031 USA. Telephone: 305-246-7000; Email: kelly12@ufl.edu.

ABSTRACT

Panama disease is the most important lethal disease of banana. The causal soilborne fungus, *Fusarium oxysporum* f. sp. *cubense* (Foc), is found in most banana-producing regions and is pathologically and genetically diverse. Races of Foc, which affect different groups of cultivars, have been useful for describing host reactions and new disease outbreaks. Races 1 and 2 are heterogeneous, whereas populations of the pathogen that affect the Cavendish subgroup are more homogeneous; they are separated into subtropical race 4 (SR4), which causes damage only where cold winter temperatures occur, and tropical race 4 (TR4), which causes damage in the absence of predisposing conditions. TR4 is decimating Cavendish monocultures in southern Asia and would affect 85% of the global production of banana were it disseminated more widely. TR4's competence under tropical conditions and the wide range of cultivars that it affects make it a serious threat to export and small-holder production worldwide.

This article summarizes the early history of, and research on, Panama disease, reviews its current status in different producing regions and recent research developments, and concludes with a discussion of TR4 diagnosis, interdiction, and control. Where TR4 has become established, it presents a most difficult management problem. There is an urgent need for innovative and useful research since the available management tactics are not very effective. If TR4 were to become established in the Western Hemisphere, radical changes would be needed in the American Cavendish-based export trades.

INTRODUCTION

Panama disease (fusarium wilt) is the most significant vascular wilt disease of banana (Ploetz 1990; Ploetz and Pegg 2000; Stover 1962). Simmonds (1966) ranked it as one of the six most destructive plant diseases. This notorious reputation stems from damage it caused in the first export trades, which were based on 'Gros Michel' (AAA). Extreme susceptibility to Panama disease, the use of infected suckers to establish new plantings, and the practice of monoculture doomed 'Gros Michel' and led to its eventual replacement by the Cavendish clones (Ploetz 2005; Stover 1962).

Panama disease was first reported in Australia by Bancroft (1876). He speculated that a fungus caused the disease and recognized that suckers that looked healthy could harbor the disease. Smith (1910) was the first to isolate the pathogen, which he called *Fusarium cubense*, and Brandes (1919) was the first to complete Koch's postulates. During the ensuing decades, almost all first reports of the disease in an area were on 'Gros Michel' (Stover 1962). Wollenweber and Reinking (1935) recognized that *F. cubense* was a variant of the common soilborne fungus, *F. oxysporum*. Soon after, their *F. oxysporum* var. *cubense* was renamed *F. oxysporum* f. sp. *cubense* by Snyder and Hansen (1940); it is referred to hereafter as Foc.

As the 'Gros Michel' era ended, Stover (1962): i) contributed new insights on the taxonomy, variation, and physiology of Foc; ii) helped describe Foc's interaction with banana; iii) characterized resistance and susceptibility in banana to this disease; and iv) studied the influence of edaphic factors on the pathogen and introduced flood fallowing as a means for cleansing contaminated soil. In several areas, Stover's results have been superseded by newer work, often with tools that were not available during his career. However, several of his conclusions have been corroborated, including:

1) Resistant genotypes of banana are the best tools for managing this disease (Jones 1994; Ploetz and Pegg 2000)
2) Soil treatments, such as flood fallow, are only temporarily effective (Herbert and Marx 1990)
3) Foc generally appears to have coevolved with its banana host in Southeast Asia (Ploetz 2006a,b; Ploetz and Pegg 1997); Simmond's (1966) hypothesis that strains of Foc could arise (be selected) from the native mycoflora in a new site have not been supported with experimental evidence

The transition by the trades from 'Gros Michel' to the Cavendish cultivars coincided with a dramatic reduction in the amount and types of research that were done on Panama disease (Ploetz 1990). Directly and indirectly, the disease changed the ways in which this multinational business produced and marketed its product. In addition to the massive replanting effort that this entailed, Cavendish fruit required different, far gentler measures for harvesting, handling, and shipping than were used for 'Gros Michel'.

The above focus on export bananas drew attention away from the impact of Panama disease outside the trades (Ploetz 1994). Diverse clones are attacked, many of which are as susceptible as 'Gros Michel' (Ploetz and Pegg 2000). Although these cultivars are still produced in diversified, multicropping situations, their intensive, monoculture production usually collapses (Ploetz 2006b). For example, only temporary production of 'Silk' (AAB) is possible in Brazil, Colombia, Venezuela, and other areas in tropical America. Continued production of this cultivar relies on new, virgin sites, as was required during the 'Gros Michel' era.

Since the Cavendish cultivars had been grown successfully for decades in the same soils that were used to produce 'Gros Michel', it had been presumed that future problems with Panama disease would be restricted to the above cultivars, at least in the Americas (Buddenhagen 1990). The illusion that the Cavendish clones were generally immune to Panama disease in the tropics was shattered in the early 1990s. Serious outbreaks of Panama disease developed in Sumatra and peninsular Malaysia in Cavendish plantations that had been planted for Middle Eastern and Japanese markets (Ploetz 2006b). In these and now several other locations in Southeast Asia, Cavendish has proven to be as susceptible as 'Gros Michel'.

A new variant of Foc, tropical race 4 (TR4), is responsible for the Asian outbreaks (Ploetz 2006a,b; Ploetz 2009). Unlike subtropical outbreaks that affect cold-stressed Cavendish in Australia, the Canary Islands, Cavendish in the absence of predisposing factors. Although it still has a restricted geographic distribution (Figure 1), TR4 continues to spread. Due to its wide host range, TR4 would impact 85% of the world's banana production if it were widely spread (Figure 2) (Molina et al. 2005; Ploetz 2009). TR4 poses a serious threat to the multibillion dollar export trade and the food stability and income of millions of poor farmers.

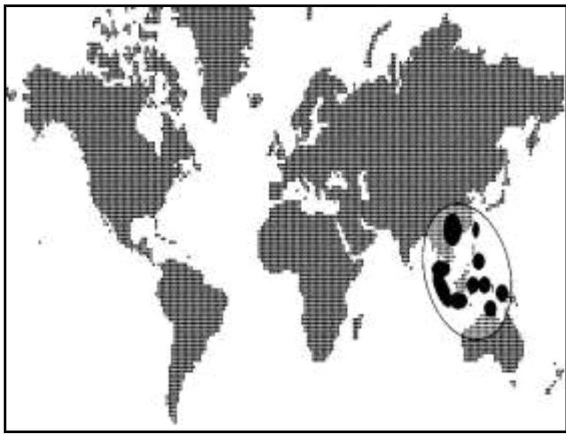

Figure 1. TR4 is found in blackened areas

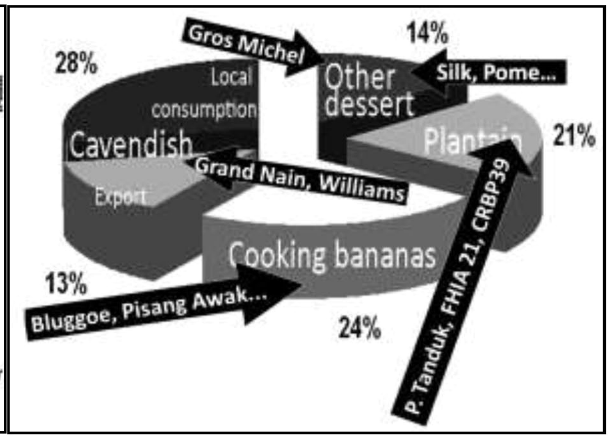

Figure 2. Cultivars that are affected by TR4

Fusarium oxysporum is a species complex of morphologically similar filamentous fungi (O'Donnell et al. 2009). It is comprised of mainly saprophytic strains, and contains plant pathogens that cause vascular wilts, rot, and damping off of hundreds of host species. Agriculturally and economically, it is the most important species in *Fusarium*. Over 150 special forms, formae speciales, of *F. oxysporum* are known, each of which has a unique host range of one or a closely related set of species (O'Donnell et al. 2009).

Foc affects primarily banana and plantain, but other banana relatives are also susceptible (Ploetz 2006b). Diverse characters have been used to study variation in Foc (Boehm et al. 1994; Groenwald et al. 2006; Moore et al. 1993; Stover 1962). Significant progress to understand the population biology of Foc resulted after the development of a straightforward method for determining vegetative compatibility groups (VCGs) in the late 1980s (Ploetz and Correll 1988; Puhalla 1985), and over 20 VCGs of Foc have been reported to date (Ploetz and Pegg 2000).

"Race" has been used to classify strains of Foc since the mid-1900s (Stover 1962). Pathotypes ("races") that affect different groups of banana cultivars are not nearly as well defined as are races of some other plant pathogens (pathosystems in which a gene-for-gene interaction are known are the best examples). Races 1 and 2 of Foc are heterogeneous, and numerous clonal lineages and VCGs have been identified in each (Ploetz and Pegg 2000). Although they are imperfect measures of pathogenic diversity in Foc, race designations are useful when describing host reactions and new disease outbreaks.

Three races of Foc are conventionally recognized on banana: 1, 2, and 4 (race 3 was described for isolates of Foc that affected *Heliconia* spp. (Waite 1963)). Race 1 was responsible for the epidemics on 'Gros Michel', and also affects 'I.C.2' (AAAA), 'Silk' 'Pome' (AAB), 'Pisang Awak' (ABB), and 'Maqueno' (AAB). Race 2 affects cooking bananas, especially those in the Bluggoe subgroup (ABB). And race 4 affects race 1- and race 2-suscepts, cultivars in the Cavendish subgroup and diverse additional cultivars, such as 'Pisang Mas' (AA) (Ploetz and Pegg 2000).

The Cavendish cultivars are affected mainly in the eastern subtropics. For decades, losses have occurred in subtropical Australia, the Canary and Madeira Islands, and South Africa (Ploetz 1990). In these areas, race 4 is comprised of isolates in VCG 0120-01215, and to a lesser extent in Australia, VCGs 0129 and 01211 (Ploetz and Pegg 2000). Cavendish is also affected in Taiwan (Hwang and Ko 2004), and previous reports indicated that this was related to the subtropical outbreaks, even though production areas in Taiwan have relatively warm winters and are technically in the tropics (Kaohsiung, 22°S latitude, is south of the Tropic of Cancer) (Ploetz 2006b). In hindsight, damage in Taiwan may have been due to TR4.

Cold winter temperatures in the subtropics are thought to predispose Cavendish to race 4. For example, photosynthesis of 'Williams', a Cavendish cultivar, was reduced by 75% during the winter in Queensland, Australia (Moore et al. 1993). Damage also occurred on Cavendish in the tropics, but it was uncommon and also associated with predisposing factors (Ploetz 1994). Pockets of damage occurred on Cavendish on Guadeloupe (17°S) after ash from a volcanic eruption lowered soil pH, and in Jamaica (18°S) in low-lying and poorly drained soils above 700 m in elevation.

In summary, prior to the 1990s Cavendish succumbed in exceptional situations but performed well in good soils in the lowland tropics. Since these cultivars had resisted Panama disease for decades in the same soils in which 'Gros Michel' was devastated, it appeared that the 'Gros Michel' populations of Foc were incapable of mutating to virulence on Cavendish (Buddenhagen 1990).

The Special Threat Posed by Tropical Race 4 (TR4). The recent outbreaks of TR4 have been alarming. Isolates of TR4 are in VCG 01213-01216, a unique population that was originally identified in Taiwan in 1990 and is now known to define TR4 (Ploetz, 2006a,b). TR4 has also been reported in Australia (Northern Territory), China (Hainan, Guangdong, and Guangxi), Indonesia (Halmahera, Irian Jaya, Java, Sulawesi, and Sumatra), Malaysia (Peninsular and Sarawak), and the Philippines (Mindanao) (Molina et al. 2005; Molina 2009).

TR4 is distinguished from subtropical race 4 because it is genetically distinct and damages Cavendish in the tropics in the absence of predisposing conditions (Ploetz 2006b). Research is needed to better define the host ranges of the two patho-types. Although they are similar, some clones, such as 'Pisang Lilin' (AA), are affected only by TR4, and the reaction of other clones that are affected in the tropics, such as 'Pisang Berangan' (AAA), is not known in the subtropics since they are not produced there. Alternatively, the tropical response of other clones that are affected by subtropical race 4 in the subtropics is not known [e.g., 'Yangambi Km 5' (AAA), 'FHIA-03' (AABB), and 'FHIA-23' (AAAA)]. Based on the reaction of 'Pisang Tanduk' and

'FHIA-21' (see papers in Molina et al. 2005), it appears that TR4 affects the AAB plantains, and nothing is known about the reaction of the important East African Highland cultivars to TR4. Additional work is needed to clarify the response of these important clones to TR4.

RECENT RESEARCH ADVANCES

Although Snyder and Hansen's name is still used to designate this pathogen, research over the last decade indicates that it is represented by at least three phylogenetically distinct taxa (Fourie et al. 2009; Koenig et al. 1997; O'Donnell et al. 1998; Ploetz 2006; Taylor et al. 1999). The phylogenies of these populations have been investigated with cDNA and DNA sequence work (Fourie et al. 2009; Koenig et al. 1997; O'Donnell et al. 1998; Ploetz 2006; Taylor et al. 1999). These studies did the following: i) identified several clonal lineages within the taxon; ii) delineated relationships within Foc and among the Foc VCGs; iii) demonstrated that some of the clonal lineages of Foc were more closely related to other formae specials of *F. oxysporum* than to other lineages of Foc; iv) suggested that one of the lineages, defined by VCG 01214, may have evolved in Africa, outside the Southeast Asian homeland of banana; and v) indicated that recombination between VCGs 0124/0125 and 01212 probably occurred (it is unclear whether this is historic or ongoing, and whether sexual or parasexual mechanisms have been involved). The significant genetic differences that are evident among the VCG 01214, VCG 0120 and VCG 0124 clades indicate that they are phylospecies, genetically related groups of individuals that are related by descent (O'Donnell et al. 1998).

MANAGING PANAMA DISEASE

Effective disease management relies on avoidance, exclusion, and eradication of the causal agents; protection of, or development of resistance in, the host plant; and treatment of affected plants (Ploetz 2007). Aspects of these principles are discussed as they relate to TR4.

Avoidance. The importance of using disease-free planting materials cannot be overstated, and any measure or legislation that would produce disease/pathogen free materials and disseminate them to growers would be useful (Diekmann and Putter 1996). Banana suckers can harbor bacteria, fungi, nematodes, and viruses, and it is in and on them that many economically important pathogens are moved and established. Thus, tissue-culture plantlets should be used whenever possible. Since Foc is moved effectively in infected suckers, these traditional seedpieces should never be moved internationally.

Exclusion. Excluding pathogens from production areas can be difficult, but is a most cost-effective disease management strategy (Palti 1981). The early detection and accurate identification of pathogens are often important first steps in exclusion, and the certification of pathogen-free status and safe movement of germplasm rely on their success. Recently, an accurate molecular diagnostic method was developed to identify TR4 (Dita et al. 2010). It is being refined/adapted for use with plant and soil samples (Dita, personal communication), and could potentially assist exclusion, eradication and management efforts.

Quarantines can be an important first line of defense against the movement of important pathogens, and most countries have lists of forbidden or restricted pathogens and host plants.

Unfortunately, these rules are not always enforced effectively and there are many examples of destructive agents moving despite quarantines. The spread of TR4 in Asia is an example of the continued movement of an important problem despite general awareness in the region of the extent and seriousness of a problem.

Eradication. If pathogen exclusion has failed, a different set of strategies is needed. These measures are diverse, always more expensive than pathogen exclusion, and are seldom effective. The investment of ca. $1 billion to eradicate citrus canker in Florida is an extreme example of the expense of an unsuccessful effort to eliminate a pathogen (Gottwald et al. 2002).

Pathogen eradication is usually very difficult, and there are no known examples of the successful eradication of a soilborne fungal pathogen in a newly infested area. Eradicating Foc would be especially difficult. Foc survives for decades in infested soil due to its formation of resilient chlamydospores and infection of alternative weed hosts that do not develop symptoms, but perpetuate the pathogen in the absence of a banana host (Waite and Dunlap 1953). Soil disinfestants (e.g., flooding and methyl bromide-chloropicrin fumigation) have been shown previously to be ineffective since Foc can rapidly recolonize treated soils as a facultative saprophyte (Herbert and Marx 1997; Stover 1962).

Protection of healthy plants and treatment of diseased plants. Although diverse chemical, physical, and biological measures have been used against plant diseases, they have had a very limited impact on Panama disease. Fusarium wilts are favored in acidic soils, but serious outbreaks of Panama disease are known in calcareous soils (e.g., pH = 7.5 – 8.2 in South Florida) (Ploetz et al. 1999). There are no effective chemical pesticides that protect banana from Panama disease or allow diseased plants to be effectively treated. For Foc, physical barriers, such as fences, that would be used to restrict inoculum movement, would need to be effectively maintained for a very long time. Although they have received considerable attention, biological control measures for Panama disease that are effective for more than several months have not been developed (Ploetz 2004). Likewise, minimal information has come from "soil health" research. Given the exceedingly complex soil environment and the perennial, polycyclic nature of Panama disease, it is unreasonable to expect soil health strategies to have a very significant impact against this problem.

Resistance. Resistance to disease can be a formidable disease management tool, and genetic resistance obtained via conventional breeding has been responsible for some of the most important advances in production agriculture during the last century (Simmonds and Smartt 1999). Although susceptible genotypes may be useless against foliar diseases that progress rapidly, they can be used for years against slow-developing soilborne diseases before they need to be replaced or replanted. For example, this has been the manner in which TR4 has been managed in Taiwan (Hwang and Ko 2004). Somaclonal variants of 'Giant Cavendish' that have moderate tolerance to TR4 are used for one or two cycles before production is discontinued. Fields are then flooded and/or fallowed to rice before being replanted. These shortened production schemes are more expensive than traditional multi-ratoon schemes and would require radical changes if they were to be adopted in the Americas.

Field evaluation of important cultivars from Latin America and Africa (e.g., plantain and the highland bananas) in countries where TR4 is already present (e.g. Asia) should contribute to increased preparedness in TR4-free countries. Under controlled conditions, germplasm needs to be identified that resists TR4 and which could be used in improvement programs.

TR4 diagnosis, interdiction and control. Given the importance of TR4, the desire to keep the pathogen out of noninfested production areas and the need to detect early outbreaks, recent research has focused on a rapid and reliable diagnostic procedure. Although some reported techniques have not been selective (e.g., Groenwald et al. 2006; Lin et al. 2009), a new PCR diagnostic reliably detects only strains in VCG 01213-01216 (Dita et al. 2010), and is being adapted/refined for use in soil and infected plant material (Dita, personal communication).

Obviously, keeping TR4 out of noninfested areas is a high priority. Action plans, similar to that which has been developed for Tropical America (Ploetz 2008; Pocasangre et al. 2009), should be developed for Africa and areas in Asia that remain free of TR4. Where TR4 is established, it will be necessary to institute new, holistic measures and to accept some losses due to this disease. In addition to using tolerant cultivars, single production cycles (treating the crop as an annual rather than perennial), intercropping, fallowing with nonhost crops, flooding, and the use of silicon or other soil amendments may be useful. Research is needed to identify which measures are most effective.

SUMMARY

Diseases of clonal perrenial crops are among the most difficult management challenges in tropical agriculture (Ploetz 2007). There is an urgent need for innovative and useful research on TR4 since the only available management tactics are not very effective. No effective chemical control measures exist and disease resistance is limited. Biological control efforts have only been moderately successful for annual hosts of fusarium wilts, and there has been no example of the successful use of this approach for a perrenial crop such as banana (Ploetz 2004). Soil health approaches, wherein diverse biotic and abiotic factors are manipulated to directly or indirectly improve plant health, are also in vogue but have offered little real promise for managing this difficult problem. Measures must be taken to exclude TR4 from the Western Hemisphere. Education and a heightened awareness of the nature and seriousness of this threat are needed among quarantine personnel, producers, and those in international commerce.

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