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Management of Fusarium wilt of banana: A review with special reference to tropical race 4

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ABSTRACT

Banana (*Musa* spp.) is an important cash and food crop in the tropics and subtropics. Fusarium wilt, which is also known as Panama disease, is caused by *Fusarium oxysporum* f. sp. *cubense* (Foc). It is one of the most destructive diseases of this crop, and has a relatively wide host range. Its greatest impact was on the early 'Gros Michel'-based export trades. Resistant cultivars of the Cavendish subgroup were used to replace 'Gros Michel,' but are now succumbing to a new variant of the pathogen, tropical race 4 (TR4). Although TR4 is only found in the Eastern Hemisphere, it threatens global export and small-holder production of the Cavendish cultivars. Management of this disease is largely restricted to excluding the pathogen from non-infested areas and the use of resistant cultivars where Foc is established. The perennial production of this crop and the polycyclic nature of this disease hinder the development of other management strategies. Measures that are effective against annual or short-lived hosts of these diseases are usually ineffective against Fusarium wilt of banana. Effective biological, chemical and cultural measures are not available, despite a substantial, positive literature on these topics. Critical evaluations of, and realistic expectations for, these measures are needed. Better resistance is needed to this disease, especially that that is caused by TR4.

1. Introduction

Fusarium wilt is one of the most destructive diseases of banana (Ploetz and Pegg, 2000). The pathogen probably originated in Southeast Asia (Ploetz and Pegg, 1997; Ploetz, 2007; Stover, 1962; Vakili, 1965), but the disease was first recognized elsewhere. Bancroft's (1876) initial description from Australia was followed by reports from tropical America (Costa Rica and Panama in 1890) (Stover, 1962). A dramatic increase in the number of new records occurred in the early 1900s, most of which described damage in export plantations (Ploetz, 1992; Ploetz and Pegg, 2000; Stover, 1962). Currently, the disease is found in virtually all areas where banana is grown.

The importance and origins of the banana host are described in this review, especially as they relate to the impact of this disease. Genetic and pathogenic diversity is described in the causal agent, *Fusarium oxysporum* f. sp. *cubense* (Foc), as is the host × pathogen interaction. Remaining sections in the review are devoted to descriptions and evaluations of various disease management strategies. Effective, long-term management of Fusarium wilt of banana remains a challenge, due largely to the perennial host plant (Ploetz and Evans, in press; Ploetz and Pegg, 2000). Tactics for Fusarium wilt management on short cycle hosts (e.g. tomato or radish) are often ineffective over the multiple years that a banana crop is grown.

2. The banana host

Banana ranks among the world's most valuable primary agricultural commodities. In 2011, combined global production was about 145 million tonnes with a gross production value of US$44.10 billion (FAOSTAT, 2013). Bananas are the eighth most important food crop in the world and the fourth most important among the world's least-developed countries.

About 87% of the bananas that are produced worldwide are consumed by producers or sold in local or regional markets (FAOSTAT, 2013). Locally consumed bananas are significant staple foods in Africa, Asia and tropical America, and diverse cultivars are eaten raw, cooked and brewed (Karamura et al., 2012). The remaining 13% (worth US$8.9 billion in 2011) are sold in international markets (FAOSTAT, 2013). The exported fruit result in

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relatively high-paying jobs, valuable community services (e.g., schools, housing, and health facilities) and significant influxes of foreign currency in the producing countries. In 2009, banana was the most important export commodity produced by Ecuador, Costa Rica, Panama and Belize, and was ranked second or third in importance in Colombia, Guatemala, the Philippines, Honduras and Cameroon (FAOSTAT, 2013). Unlike the diverse, locally consumed bananas, those in export commerce are virtually all from cultivars of the Cavendish subgroup.

Banana originated in southern Asia and may have been one of the first domesticated crops (Perrier et al., 2011). Most cultivars are natural hybrids that were selected by early agriculturists. They are usually sterile, triploid, parthenocarpic and vegetatively propagated. Hundreds of cultivars exist (Perrier et al., 2011).

Only two of the recognized 50 subgroups of banana produce most of these fruit. The Cavendish subgroup is most significant, as over 40% of the global total comes from these cultivars (e.g. virtually all exported bananas plus 28% of those that are consumed locally), and the plantain subgroup, which is next in importance, is responsible for an additional 21%. Production figures are rounded out by heterogeneous collections of cooking cultivars (which are distinct from the plantains and total 24%) and dessert bananas (14%). Products of the banana breeding programs are relatively unimportant worldwide.

With minor exceptions, the edible bananas are hybrids of two diploid species, *Musa acuminata* (AA) and *Musa balbisiana* (BB) (Perrier et al., 2011; Simmonds, 1962; Simmonds and Shepherd, 1955). For example, the Gros Michel and Cavendish cultivars are triploid, pure *M. acuminata*, and AAA, whereas plantains are triploid, 2/3 *M. acuminata*, 1/3 *M. balbisiana* and AAB. The Linnaean binomials *Musa paradisiaca* (the AAB plantains) and *Musa sapientum* (the dessert banana, 'Silk' AAB) are invalid since they refer to interspecific hybrids (Stover and Simmonds, 1987).

3. Fusarium wilt of banana

Simmonds (1966) described Fusarium wilt of banana as one of the most destructive of all plant diseases, due mainly to its impact on the 'Gros Michel'-based export trades. Until ca 1960, the export trades relied almost entirely on 'Gros Michel', which is highly productive but susceptible to race 1 of Foc. Monocultures of it that were used in export production facilitated the disease's rapid development and spread in the American and African trades, and the establishment of plantations with suckers that were infected with Foc hastened this process (Stover, 1962; Ploetz, 2005). As race 1-resistant Cavendish cultivars replaced 'Gros Michel', Fusarium wilt disappeared as a problem in export production (Buddenhagen, 1990).

The resistance of the Cavendish subgroup to race 1 has endured for decades, and large monocultures of these cultivars have remained in production in race 1-infested soils. Although the transition to Cavendish revitalized the trades, the risk of relying on a closely related set of clones was recognized by those who were familiar with the 'Gros Michel' history. In his evaluation of export production, Stover (1986) indicated that the trades were "… extremely vulnerable to a new disease, especially a tropical race of Fusarium wilt that could devastate the basis of the industry – the Cavendish varieties." Soon after his review, new plantations of Cavendish began to succumb to Fusarium wilt in Southeast Asia, and by the early 1990s it was apparent that a new race of Foc was responsible. Unlike the race that had affected Cavendish for decades in the subtropics ("race 4"), tropical race 4 (TR4) was competent in good soils in the tropics; it was the tropical race that Stover had feared. By the turn of the century, TR4 was recognized in a fairly wide area that included Australia (Northern Territory), China (Hainan, Guangdong, Guangxi), Indonesia (Halmahera, Irian Jaya, Java, Sulawesi and Sumatra), Malaysia (Peninsular and Sarawak), the Philippines and Taiwan (Ploetz, 2006a,b). The recent TR4 outbreaks in Jordan and Mozambique (Butler, 2013; Garcia et al., 2014) re-emphasized the threat it poses to global production (Ploetz, 2009; Ploetz and Churchill, 2011).

Fusarium wilt of banana is a typical vascular wilt disease. The pathogen infects roots of susceptible and resistant banana cultivars, but infection generally progresses into vascularized portions of the rhizome only in susceptible genotypes (Beckman, 1987, 1990). Tyloses, gums and gels are produced in xylem lumena in response to infection, but in resistant cultivars these host products are produced earlier and far more rapidly than in susceptible cultivars. Systemic infection of the pseudostem is blocked by these events in resistant cultivars, whereas the pathogen colonizes susceptible cultivars in advance of these host responses.

Affected xylem becomes reddish brown and is eventually plugged, thereby impeding water and nutrient transport. The oldest leaves wilt, die and can split at their base. Yellowing of leaf lamina is common, supposedly due to the actions of phytotoxins that are produced by the pathogen, although non-yellowing development of wilt symptoms is also known. Eventually, younger and younger leaves develop symptoms and the plant collapses.

3.1. Host range and variation in the pathogen

Musa acuminata, *M. balbisiana*, *M. schizocarpa* and *M. textilis* (Manila hemp) (Musaceae: Zingiberales) are affected. Other species can be infected by Foc (e.g. weed species in banana plantations), but do not develop disease symptoms (Hennesey et al., 2005; Waite and Dunlap, 1953). A recent report, which indicated a wide host range for Foc, utilized detached leaf assays and may not be reliable (Waman et al., 2013).

The pathogen is a genetically and pathogenically diverse fungus. Over 20 vegetative compatibility groups (VCGs), and diverse evolutionary lineages, AFLPs, DFGs, EKs, RAPDs and RFLPs are recognized in global populations of the pathogen (Bentley et al., 1995, 1998; Boehm et al., 1994; Fourie et al., 2011; Koenig et al., 1997; O'Donnell et al., 1998; Ploetz and Correll, 1988; Ploetz and Pegg, 2000). Traditionally, four races of Foc have been recognized (Stover, 1990; Stover and Buddenhagen, 1986; Stover and Simmonds, 1987). Race 1, which was responsible for the 'Gros Michel' epidemics, also affects 'Maqueño' (Maia Maoli - Popoulu subgroup, AAB), 'Silk', 'Pome' AAB and 'Pisang Awak' ABB. Race 2 affects ABB cooking bananas, such as 'Bluggoe' (ABB). Race 3, described as a pathogen of *Heliconia* spp. (tropical American banana relatives), had a minor impact on 'Gros Michel' and seedlings of *M. balbisiana* (Waite, 1963). Race 3 has not been reported since Waite's (1963) work and no voucher specimens for the pathogen exist. It is not considered below.

Race 4 of Foc affects race 1 and race 2 susceptible cultivars in addition to the Cavendish cultivars (Stover and Simmonds, 1987; Su et al., 1986). Before the outbreaks in Southeast Asia, Cavendish cultivars had only been affected in the subtropics (Canary Islands, South Africa and Australia) (Ploetz et al., 1990), presumably due to disease-predisposing low temperatures in these areas (Moore et al., 1993). The assumption that race 4 in the subtropics was an artifact of environment was supported by the presence race 4 isolates in the subtropics in the same VCGs (0120 and 0124-0125) of race 1 isolates in the tropics (Ploetz and Pegg, 2000). Isolates of "subtropical race 4" are also found in VCGs 0129 and 01211. In contrast, a unique population of the pathogen, VCG 01213-01216, affects Cavendish in the tropics (Ploetz, 2006a,b). Unlike subtropical race 4, TR4 is competent in the absence of cold temperatures or other predisposing factors (Ploetz, 2006b). Although subtropical race 4 does not affect Cavendish in the tropics, TR4 does so in the subtropics.

3.2. Epidemiology

Fusarium wilt of banana is a "polycyclic" disease. Vanderplank (1963) suggested that Fusarium wilt of cotton developed from discrete pockets of soilborne inoculum over the course of a single season, and was thus "monocyclic" (there is one cycle of infection). However, multiple cycles of infection occur in banana plantations that are affected by Fusarium wilt of banana. Devastating losses can eventually develop even when very small amounts of the pathogen infest fields and the disease initially raises little concern. For example, the first outbreaks of TR4 in China and the Philippines were not taken seriously, but slowly developed into destructive and uncontrollable problems (Buddenhagen, 2009).

Stover (1962) indicated that Foc survived for decades in infested soil, and that banana-free rotations were ineffective measures for managing the disease in most soils; production of 'Gros Michel' was usually impossible in previously affected plantations. Chlamydospores of Foc in dead host material play a role in its survival, but its persistence for long periods is probably due to its ability to infect non-host weed species. In studies in tropical America and Australia, Foc was isolated from the roots of diverse grasses and other weed species in banana plantations that were affected by race 1 and TR 4 (Hennessy et al., 2005; Waite and Dunlap, 1953). The ability of Foc to survive in the absence of its banana host is a significant factor in the management of this disease.

Foc is disseminated in diverse ways (Stover, 1962). Infected suckers are most efficient. After the infectious nature of this disease was demonstrated by Brandes (1919), the trades instituted rigorous selection schemes in which suckers for new plantations were taken only from disease-free portions of fields, and those that exhibited vascular discoloration were discarded (Stover, 1962). In many cases, suckers were also washed and treated with fungicides or biocides. Nonetheless, cryptically infected suckers made it past inspectors into new fields. Before tissue-culture plantlets became available (see below), it was virtually impossible to establish pathogen-free plantations. However, even after it was possible to produce clean planting material, secondary contamination of plantations by Foc was common. For example, TR4-affected Cavendish plantations were routinely established with tissue-culture plantlets.

Foc is also disseminated in soil, which indirectly contaminates things in and around plantations but is also used to grow plantlets prior to field establishment (Buddenhagen, 2009). Surface waters are easily contaminated, and the use for irrigation of water from contaminated rivers or ponds is especially dangerous. Furthermore, Foc is moved on contaminated tools, farm equipment, clothes and footwear (Stover, 1962).

Any or all of these avenues can facilitate Foc movement in and around a given plantation, and other means may be possible. Recently, Meldrum et al. (2013) detected TR4 on the exoskeletons of the banana weevil, *Cosmopolites sordidus*, and suggested that the insect could be a vector or disease predisposing agent. Aerial dissemination of Foc may be possible since macroconida/sporodochia of the pathogen are produced on artificially inoculated plants in greenhouse experiments (Miguel Dita and Gert Kema, personal communication). Other formae speciales of *F. oxysporum* move in this manner, especially in greenhouses (Elmer, 2012a; Timmer, 1982). The recent transcontinental jumps in the distribution of TR4 suggest that something other than sucker transmission was responsible in these range expansions. Although these outbreaks may have resulted from something as simple as muddy boots of plantation workers from Southeast Asia, other means could be responsible. Better understandings are needed for the long-distance dissemination of this pathogen.

3.3. Management

There are limited options for managing Fusarium wilt of banana. The perennial nature of this pathosystem and the corresponding polycyclic nature of the disease has complicated the development of long-term measures (Ploetz, 2007). Moreover, poor resistance exists in important groups of banana and technical hurdles confront those who would improve disease-susceptible cultivars. For example, extremely poor fertility in the Cavendish subgroup constrains its improvement via conventional breeding (Aguilar Morán, 2013). The improvement of this crop has been a significant problem for as long as improvement programs have been in existence (see 3.3.5. Resistance) (Ortiz, 2013).

Susceptible banana cultivars can usually be grown only if pathogen-free propagation materials are used in pathogen-free soil. Tissue-culture-derived plantlets are the most reliable source of clean material. Although they are more susceptible to Fusarium wilt than traditional banana seed pieces (Smith et al., 1998), they should be used to propagate this crop whenever possible. In subsistence agriculture or other situations in which their expense may be an issue, tissue-culture plantlets can be used to initiate disease-free nurseries to produce pathogen-free conventional seed pieces (Lule et al., 2013).

3.3.1. Quarantine and exclusion

In pathogen-free regions, effective quarantine and exclusion are essential. Foc cannot be eradicated from soil once it is infested, and exclusion of the pathogen from noninfested plantations can be very difficult once it moves into a region.

Regional awareness and contingency programs have been created in the Western Hemisphere to ensure that stakeholders are informed about the symptoms and potential impact of TR4 (Pocasangre et al., 2011). Similar plans should be developed in the Indian subcontinent and non-affected areas in Africa and the Middle East. When TR4 arrives in new areas, early recognition and delineation of the affected areas are desirable. To that end, an IGS-based diagnostic that was developed for TR4 would be useful (Dita et al., 2010).

3.3.2. Biocontrol

In a review on the biological control of Fusarium wilts with nonpathogenic *F. oxysporum*, Fravel et al. (2003) indicated that "The difficulty in controlling Fusarium wilt has stimulated research in biological control of Fusarium wilt independently of the recent concern for environmental protection." Although this quote describes the rationale for research on Fusarium wilt of banana, their article had only one reference on biocontrol agents for Fusarium wilt of banana (Gerlach et al., 1999).

There have been very few field studies in which long-term biocontrol efficacy has been investigated for Fusarium wilt of banana (Ploetz, 2004). Although diverse microbes had been tested by the early 2000s, most of the published work resulted from *in vitro* assays or short-term greenhouse studies (Cao et al., 2004; Getha and Vikineswary, 2002; Mohandas et al., 2004; Pan et al., 1997; Sivamani and Gnanamanickam, 1988; Thangavelu et al., 2001, 2003, 2004; Saravanan et al., 2003). At the time, field studies were uncommon and only one clearly reported results in the field; in it, the best treatment of Sivamani and Gnanamanickman (1988) resulted in an 18% annual loss. If this rate was compounded over 5 years (longer banana plantation life times are common), 63% of the plants would be lost (Ploetz, 2004).

In the decade since biocontrol work on Fusarium wilt of banana was last reviewed (Ploetz, 2004), the above trends have continued, as few field studies have been reported and most publications describe only lab and greenhouse research (Borges et al., 2007; Fishal et al., 2010; Forsyth et al., 2006; Lian et al., 2008; Mohandas et al., 2010; Nel et al., 2006a,b; Sun et al., 2011; Thangavelu and Jayanthi, 2009; Thangavelu and Mustaffa, 2012; Ting et al., 2010; Wang et al., 2013; Weber et al., 2007; Wu et al., 2013; Zacky and Ting, 2013). In two exceptional situations, field results were reported: the best treatment of Thangavelu and Jayanthi (2009) resulted in a nonsustainable incidence of 20% after 8 months, and in another study, promising greenhouse treatments failed in the field; in it, Belgrove et al. (2011) noted that "… neither the nonpathogenic *F. oxysporum*, *P. fluorescens*, nor combinations thereof reduced Fusarium wilt development significantly."

The success rates for biocontrol efforts with other Fusarium wilts are comparable to those published for Fusarium wilt of banana. However, annual losses of 10–20% that might be tolerated in a short-term crop are not sustainable in a perennial crop (Ploetz, 2004). Unfortunately, noncritical evaluation of results for Fusarium wilt of banana is common, as is the use of short-term studies on this disease to indicate that effective management is possible in long-term commercial production. In the first cycle of a banana crop, the planting-to-harvest interval is typically 14–18 months. Thus, if fruit production for at least one cycle is the goal of producers in Foc-infested soils, it is clear that cost-effective biocontrol measures for this disease have not been developed (Thangavelu and Mustaffa, 2012). Tactics that could be used to forestall biocontrol failures in the field will require better understandings of these interactions and realistic evaluations of their efficacy.

3.3.3. *Chemical measures, fungicides*

Limited or questionable efficacy has been associated with various chemical measures. Nel et al. (2007) tested root dips of diverse benzimidazole, demethylation inhibitors, phosphonate and strobilurin fungicides in *in vitro* and greenhouse experiments. No applications or results in the field were reported. Although they speculated that pretreatment with fungicides might enhance the performance of biological treatments, as was reported by Elmer and McGovern (2004) for Fusarium wilt of cyclamen, work on this possibility has apparently not been conducted for Fusarium wilt of banana.

Injections of fungicides into plants have also been tested. In India, Lakshmanan et al. (1987) reported that rhizome injection with 2% carbendazim (Bavistin 50 WP) protected 'Rasthali' for one crop cycle. However, injection with carbendazim and several other fungicides had no effect in South Africa (Herbert and Marx, 1990). In Australia, pseudostem injections with 20% potassium phosphonate gave some control on 'Williams', but results were erratic (Pegg, unpublished), perhaps due to the reduced sensitivity of *F. oxysporum* f. sp. *cubense* to phosphonate at phosphate concentrations that occur naturally in the banana plant (Davis et al., 1994).

Soil fumigation, which was a standard treatment for many Fusarium wilt diseases, was tested against Fusarium wilt of banana by Herbert and Marx (1990). They reported a nine-fold reduction in disease incidence on 'Williams' 26 months after soil was treated with methyl bromide. However, fumigated areas were eventually re-invaded by the pathogen, and continued production was not possible.

Nel et al. (2007) reported that Sporekill (Poly dimethyl ammonium chloride), which killed conidia of Foc in 30 s, and Jik (Sodium hypochloride) and Prazin agri (Polymeric biquanidine hydrochloride and quaternary ammonium compound), which killed conidia in 5 min, could be used to disinfest tools, farm equipment and shoes. These products were more effective disinfestants than copper oxychloride and Farmcleanse (Quaternary ammonium compound), which had been used in banana plantations in, respectively, South Africa and Australia.

3.3.4. *Cultural measures*

Mixed plantings in small-scale or subsistence agriculture, in which diverse banana cultivars are grown with other crops, often develop more moderate losses than if they had been planted in monocultures (Stover, 1962). Thus, when high yields of a single cultivar are not the objective, it may be possible to produce susceptible clones on a small scale. In contrast, monoculture production of susceptible cultivars is difficult in infested areas.

3.3.4.1. Physical measures. Rice hull burning (heat sterilization of the soil) has been recommended in the Philippines and Indonesia (Molina et al., 2010). Rice hulls are mounded on top of an affected mat and burned, supposedly generating sufficient heat to kill the pathogen. No data on the efficacy of this treatment are available. Recently, previously healthy plants in treated plots were observed in the Philippines (Fig. 1). During rice hull burning, it is probable that the insulating capacity of soil restricts lethal heat to the top few cms of soil.

In the previously discussed work of Herbert and Marx (1990), solarization reduced disease incidence for one cycle only when it was combined with methyl bromide fumigation; the impact of solarization alone was not significant. In another study in Indonesia, a 6-month delay in symptom development was reported after solarization for 10 months (Hermanto et al., 2012).

In 1939, Dunlap used flood fallow to rejuvenate Foc-infested soil (Stover, 1962). His success was followed by an intense use of flood fallow by the United Fruit Company from 1945 to 1955. It was predicated on the assumption that 5 years of production could be obtained in treated sites before disease incidence reached 50% (a much more lenient standard than would be applied in export production today). Flooded soil was rapidly recolonized by the pathogen, and as the associated costs for labor, machinery and engineering increased and flood fallow became uneconomic, this practice was discontinued. Nevertheless, this measure had been widely used and had the added benefits of eliminating the Moko disease pathogen, *Ralstonia solancearum*, and the burrowing nematode, *Radopholus similis*, from infested soil (Stover, 1962).

Fig. 1. A TR4-disease focus on Mindanao in the Philippines in which rice hull burning has been used as a management tool. The affected mat in the upper left of the disease focus illustrates ineffectiveness of this measure.

3.3.4.2. *Soil amendments.* The impact of nitrate (NO_3) and ammoniacal (NH_4) nitrogen are well documented on Fusarium wilts of annual hosts (summarized by Elmer, 2012b). In general, NO_3 decreases the severity of these diseases, whereas NH_4 increases them. Although no publications were found on the impact of N fertilization on Fusarium wilt of banana in the field, results from *in vitro* and hydroponic experiments led Zhang et al. (2013) to suggest that high levels of NH_4 could inhibit penetration of banana roots by Foc. That these results conflicted with the typical increase in severity of Fusarium wilts by NH_4 was not discussed.

Another element that is not considered as a typical plant nutrient, silicon (Si), has been studied for disease suppression (Datnoff et al., 2007), although virtually all of the studied host plants have been annuals and most of the diseases have been foliar. Banana is an accumulator of Si (Henriet et al., 2006), which significantly increases the possibilities that it would impact Fusarium wilt. Nevertheless, the supporting data are weak. Fortunato et al. (2012a,b) reported physiological responses of susceptible and resistant banana cultivars to race 1 in 40 and 60-day pot studies, but presented scant evidence for disease reduction and no results from the field. Likewise, even though Kidane and Laing (2010) indicated that their work "… demonstrated that the combined application of biocontrol organisms, silicon and mulching can provide an effective control option for banana growers dealing with Fusarium wilt in their plantations" they only reported results from pot studies in the greenhouse. Their field data were limited to plant growth measurements (no disease or yield data were provided). Finally, Jones et al. (2011) reported a "modest but significant decrease in *Fusarium* wilt" in pot studies, but no field data.

3.3.4.3. *Disease suppressive soils.* Disease suppressive soils are soils in which a virulent pathogen does not cause typical levels of disease on a susceptible host. These situations are contrasted with soils in which disease predisposition occurs (i.e. where a normally avirulent pathogen causes disease on a predisposed, normally resistant host). For example, the "disease-conducive" pockets of soil that Peng et al. (1999) studied in Carnavon, Australia were areas in which water logging and/or drought predisposed Cavendish to damage by normally nonvirulent populations of race 1 in the VCG 0124/0125 complex; areas in these fields in which disease did not develop were not suppressive, but lacked disease-predisposing conditions (Pegg et al., 1995; Ploetz and Pegg, 2000).

In general, disease suppressive soils are classified by the length of time that production can be maintained (Alvarez et al., 1981; Chuang, 1988; Stover, 1962, 1990). Volk (as reported by Stover, 1962) classified disease-conducive "non-resistant" soils (later called "short-life" soils) as those in which plantations were abandoned 5–10 years after they were first planted. In contrast, plantations in "resistant" soils (later called "long-life" soils) remained in production for more than 20 years.

Stolzy and co-workers (reviewed by Toussoun, 1975) associated disease suppression with chemical and physical factors and found the closest association between suppression and soils in which montmorillonoid clay was found. Later, Stover (1990) recognized examples of suppressiveness in several different areas, and mentioned specific attributes of some of these soils. He concluded that the mechanisms for suppressiveness were unknown, but were probably biologically based.

There has been much recent interest in soil health in banana production, and soil structure, permeability, mineral content and microbial attributes have been recognized as key components of "healthy" soils (Pattison and Lindsay, 2006; Turner and Rosales, 2005). Undoubtedly, plantation productivity and the response to some pathogens (especially nematodes) is enhanced in healthy soils. However, there are no examples of suppressiveness to Fusarium wilt of banana being created in, or transferred to, formerly conducive situations. Greater understandings of Fusarium wilt-suppressive soils would be needed before this desirable trait could be reproduced.

Table 1
Response of important banana cultivars/genotypes to tropical race 4 of Fusarium wilt.

Genome	*Subspecies* or subgroup	Cultivars/ genotypes[a]	Response to tropical race 4 (TR4)[b]
AA	*M. a.* ssp *malaccensis*	'Pahang'	S/R (Kema et al. pers. comm.)[c]
AA		'Sucrier'	S (Daniels et al., 2011; Molina et al., 2010)
AA		'Pisang Jari Buaya'	SS (Walduck and Daly, 2007) R (Huang et al., 2005)
AA		'Rose'	R (Huang et al., 2005)
AAA	Cavendish	'Grand Nain', 'Williams', 'Ambon hijau'	VS (Molina et al., 2010; Walduck and Daly, 2007) XS (Huang et al., 2005)
AAA	Lujugira-Mutika	numerous	?[d]
AAA	Gros Michel	'Pisang embung'	XS (Huang et al., 2005) S (Walduck and Daly, 2007)
AAA		'Red', 'Green Red'	VS Walduck and Daly 2007
AAA		'Lakatan'	XS (Molina et al., 2010; 2011; Walduck and Daly, 2007)
AAA		'Ibota Bota'	XS (Huang et al., 2005)
AAB	Plantain	Numerous	?[d]
AAB	Pome	'Improved Lady's Finger'	VS (Huang et al., 2005; Walduck and Daly, 2007)
AAB	Maia-Maoli	Several	VS (Walduck and Daly, 2007)
AAB		'Silk'	VS (Molina et al., 2010)
AAB		'Mysore'	VS (Huang et al., 2005) S (Walduck and Daly, 2007)
ABB	Bluggoe	Bluggoe	XS (Huang et al., 2005)
ABB		Pisang Awak	S (Walduck and Daly, 2007)
ABB		Saba	?[d]
AAA	Somaclone	'Formosana' (GCTCV218)[e]	S (Walduck and Daly, 2007)
AAA	Somaclone	GCTCV119[e]	SS (Huang et al., 2005; Walduck and Daly, 2007)
AAAA	Bred hybrid	FHIA 2 ('Mona Lisa')[f]	R (Huang et al., 2005)
AAAA	Bred hybrid	FHIA 17[f]	VS (Walduck and Daly, 2007) XS (Huang et al., 2005)
AAAA	Bred hybrid	FHIA 23[f]	VS (Walduck and Daly, 2007) XS (Huang et al., 2005)
AAB	Bred hybrid	FHIA 25[f]	R (Huang et al., 2005; Walduck and Daly, 2007)
AAAB	Bred hybrid	CRBP-39[g]	SS (Huang et al., 2005)
AAAB	Bred hybrid	FHIA-01 (Gold finger)[f]	SS/R (Walduck and Daly, 2007) R (Huang et al., 2005)
AAAB	Bred hybrid	FHIA 18[f]	SS/R Walduck and Daly, 2007 R (Huang et al., 2005)
AAAB	Bred hybrid	FHIA 21[f]	MS (Huang et al., 2005)
AAAB	Bred hybrid	SH-3640 (High Noon)[f]	VS (Walduck and Daly, 2007) XS (Huang et al., 2005)
AABB	Bred hybrid	FHIA 3[f]	SS (Huang et al., 2005)

[a] Cultivar names are the most common internationally recognized synonym of a given clone. With the exception of 'Sucrier,' which is used as a dessert banana, the other AA diploids in this table have been used primarily as parents in breeding programs.

[b] To enable comparisons among different sets of data, ratings from some studies were converted to a uniform scale, where: XS = extremely susceptible; VS = very susceptible; S = susceptible; MS = moderately susceptible; SS = slightly susceptible; R = resistant.

[c] Seedling progeny of 'Pahang' segregate for TR4 response (Kema pers. comm.).

[d] ? = unclear reactions for these subgroups/cultivars.

[e] GCTCV = Giant Cavendish Tissue Culture Variants from the Taiwan Banana Research Institute (Hwang and Ko, 2004).

[f] Hybrids bred at the Fundación Hondureña de Investigación Agrícola (FHIA) in Honduras.

[g] Hybrid bred at the Centre Africain de Recherches sur Bananiers et Plantains (CARBAP) in Cameroon.

3.3.5. Resistance

In Foc-infested soils, resistant cultivars have been the only consistently effective tool for managing this disease. Resistant cultivars exist for several different kinds of banana, but are needed in other situations (Buddenhagen, 1990).

3.3.5.1. Pre-existing genotypes. Xu et al. (2011) conducted a cost analysis for the use of different banana genotypes. They indicated that profitable markets existed for race 1- and TR4-resistant cultivars in China. Which cultivars would be most profitable depended on whether plantations were infested with Foc, what race was found in infested fields, and market preferences. In infested soils in which lower rents were charged but fewer cultivars could be grown, they recommended replacing susceptible cultivars with other crops or resistant cultivars. Shorter rotations (3–5 years) and flexibility in which cultivars would be produced were necessary in Foc-infested soil.

3.3.5.2. Products from conventional breeding programs. The first banana breeding program, which began in Trinidad in 1922, was succeeded by several others (Ortiz, 2013). Each of the breeding programs has faced enormous challenges. Primitive diploids that have been used as parents by the breeding programs usually have very poor agronomic and fruit traits, and introgression of disease resistances that they possess into advanced lines can take several generations. The polyploid nature of the crop; long generation times from planting to seed production; the large size of this plant and the corresponding need for large areas for hybrid evaluation; genetic abnormalities that exist in many parental lines; the need for final products to be parthenocarpic and sterile; and the low fertility of cultivars that need improvement are additional hurdles that impede progress (Lorenzen et al., 2013; Ortiz, 2013).

There is a critical need for TR4-resistant bananas that meet standards imposed by local and export markets (Ploetz and Evans, in press). Unfortunately, many of the world's important bananas are susceptible, and other important bananas have unclear responses to TR4 (Table 1). Although the reactions of plantain hybrids suggest that the plantains may be vulnerable, only preliminary results are available (Molina et al., 2010; 2013). To date, no information has been published for the Lujugira-Mutika subgroup (East African Highland Bananas). Information is needed on the susceptibility of cultivars in these important subgroups.

Currently, tolerance to TR4 is found in several bred hybrids, especially those developed by the program at the Fundación Hondureña de Investigación Agrícola (FHIA) in Honduras (Rowe and Rosales, 2000) (Table 1). The FHIA hybrids have been widely deployed, and are especially important in Cuba where they are grown without significant inputs of fertilizers and fungicides (Alvarez, 1997; Alvarez and Rosales, 2008). Unfortunately, only some agronomic, post-harvest and organoleptic standards are met by TR4-tolerant hybrids from FHIA and other improvement programs. For example, the high-yielding dessert clones 'FHIA-01' and 'FHIA-02' had lower pulp-to-peel ratios, were not as sweet, and had lower overall consumer acceptance than the Cavendish cultivars, 'Grand Nain' and 'Williams' (Dadzie, 1998). Therefore, they could not be used as replacements for the Cavendish clones in export production.

The acceptance of products from the breeding programs is more probable in non-export, smallholder situations in which post-harvest attributes are less important, or where less than excellent taste might be tolerated (e.g. in subsistence circumstances). Nonetheless, their adoption by local producers still depends on local uses and preferences, and hybrids that would be readily accepted in one area might not be used in another (Nowakunda and Tushemereirwe, 2004; Dzomeku et al., 2007; Gaidashova et al., 2008; Njuguna et al., 2008; Uazire et al., 2008). Understanding these requirements is key to the successful deployment of clones that would tolerate TR4.

3.3.5.3. Non-traditional improvement, mutation breeding. Somaclonal mutants, the so-called Giant Cavendish Tissue Culture Variants (GCTCV), have been developed for over 3 decades in Taiwan (Hwang and Ko, 2004). Somaclones with enhanced tolerance to TR4 are recurrently selected in TR4-infested fields, and several are now widely tested or used, especially in Southeast Asia. However, they are not completely resistant and can usually be grown for only one or two cycles in TR4-infested sites. Conversion to, and production of, these somaclones by the trades would be costly and would radically change export production norms given the need to replant frequently. Poor finger and hand architecture for the somaclones further complicates their use by the export trades. Despite these deficiencies, the GCTCVs are currently the best TR4-tolerant alternatives for the exported Cavendish clones.

3.3.5.4. GMOs. Genetic transformation of banana has become relatively commonplace, and disease resistance is one of the most sought-after traits (Remy et al., 2013). There are convincing arguments for using genetic transformation to create resistant genotypes, especially when targets, such as Cavendish-like export bananas, are difficult to improve via conventional breeding (Aguilar Morán, 2013). When and whether GMO bananas will be accepted in the marketplace is not clear. However, even if GMO bananas were accepted there are still significant technical challenges to creating cultivars that resist TR4 or other races of this pathogen in the field.

A range of transgenes have been tested, but only short-term results from greenhouse or incubator experiments are usually reported. For example, no results are available from race 1 field trials (Subramaniam et al., 2006; Paul et al., 2011; Ghag et al., 2012), and field results for TR4 tolerance are often absent (Hu et al., 2013; Mahdavi et al., 2012; Yip et al., 2011). In a single paper published 9 years ago, two of 51 Cavendish transformants that expressed the human lysozyme (*HL*) gene fruited in a TR4 field trial (Pei et al., 2005). Whether subsequent work with these or similar lines has been conducted is not known. Long-term field results for GMO bananas are needed to demonstrate promise that they might offer when combatting this disease.

4. Discussion

Fusarium wilt of banana caused an estimated US$2 billion in losses during the 'Gros Michel' era (Ploetz, 2005). Given the current annual value of export production and the great importance of Cavendish for small-holders, it is possible that TR4 will eventually cause even greater losses. To date, few figures are available. In Cavendish plantations in Indonesia, Taiwan and Malaysia, Hermanto et al., 2011 and Peng et al., 2013 estimated losses of USD$121 million and USD$253 million, respectively (as cited in Aquino et al., 2013). In China and the Philippines, where far greater production of Cavendish occurs and greater losses have occurred, monetary losses are surely higher but no estimates are available.

The ultimate impact of TR4 will depend on when it is disseminated to other banana-producing regions, and whether effective control measures are available once this occurs. Only two of the world's top 10 exporters and only one of the nine nations in which banana is a top three export commodity are currently affected by TR4. Clearly, continued movement of TR4 will only increase the damage it has already caused.

In the context of this special issue of Crop Protection, differences are emphasized between Fusarium wilt of banana and other Fusarium wilts that are covered herein. The causal agents, host × pathogen interactions, epidemiologies and control strategies for the different Fusarium wilts are quite similar. However, the perennial host and polycyclic nature of Fusarium wilt of banana make its management a great challenge (Ploetz, 2007). The huge volumes of soil that would require treatment over long periods of time underscore the implausibility of protective or therapeutic control. For example, Smith (as quoted by Stover, 1962) recognized that "… the impossibility of …" fungicidal management "… on a commercial basis barely needs consideration…." And the importance and susceptibility of the Cavendish subgroup highlight the need for resistant, productive genotypes (Ploetz and Evans, in press).

Despite a considerable body of literature which indicates that diverse measures can be used to manage this disease (see Thangavelu and Mustaffa, 2012), there are actually few effective options. Unfortunately, most of the control measures that have been reported have not been tested in real world situations in field environments. Unrealistic expectations are common. Where Cavendish cultivars would be grown in TR4-infested areas it will be necessary to produce other crops, GCTCV somaclones, or resistant cultivars, such as those described by Xu et al. (2011). These are generally undesirable alternatives, since productivity and market acceptance for the somaclones is lower and low productivity or small markets exist for the other cultivars. Clearly, resistance is needed for Cavendish and other susceptible cultivars (Buddenhagen, 1990; Ortiz, 2013; Ploetz and Evans, in press).

5. Conclusions

Fusarium wilt is one of the most destructive diseases of banana. A newly recognized variant of the pathogen, TR4, threatens global production of Cavendish and other important genotypes. Although TR4 is restricted to the Eastern Hemisphere, its recent range expansion into Africa and Western Asia indicates that further movement is possible. The great concern is that it will eventually move into other unaffected areas, including the Indian subcontinent and the Americas.

Despite decades of research, there are still few effective options for managing this disease. Resistant cultivars are the best tools in affected areas, but they are scarce, nonproductive, or commercially unacceptable. Better resistance is needed to this disease.

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