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Achieving sustainable cultivation of bananas

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Chapter 5

The past, present and future of Fusarium wilt of banana caused by Tropical Race 4

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1 Introduction

Fusarium wilt of banana (FWB) was and is a threat to global banana production. Previous epidemics were caused by Race 1 strains that decimated banana production in Central America, which was dominated by the then-major commercial banana variety Gros Michel (Ploetz, 2005a). Many contemporary varieties are vulnerable to Race 1 strains (Zuo et al., 2018; García-Bastidas, 2019; Martinez de la Parte et al., 2023). Therefore, resistance to Race 1 is a prerequisite for any new banana variety that comes to market, for instance in Brazil or East Africa, from the breeding programs of the Empresa Brasileira de Pesquisa Agropecuária (EMBRAPA) and the International Institute for Tropical Agriculture (IITA), respectively. Beyond resistance, methods of control have not sufficiently reduced the impact of FWB (Kema et al., 2021; Ploetz, 2015b). The replacement of Gros Michel by Cavendish varieties for the export markets provided a solution to the export banana industry which required major investments and changes to the logistic chain to ensure the delivery of marketable bananas in international markets (Ploetz, 2005b). Once these problems were solved through the packaging of the Cavendish bananas in cardboard boxes and changes in refrigeration during transport, followed by

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on-site ripening, Cavendish production steadily increased. The international banana production continued to grow and gradually developed into a monoculture landscape planted to the Race 1-resistant Cavendish cultivars such as 'Williams', 'Valery', and 'Grand Naine' wherever Race 1 resistance was required, not only in Central America but across the world.

The resistance in the Cavendish varieties to Race 1 turned out to be durable and has held up for over a century. The downside is that with every hectare added to the global dominion of Cavendish – now over 50% of all bananas produced these varieties or to the cavendish group? – the genetic vulnerability of contemporary banana production increases (Drenth and Kema, 2021). Cavendish was already affected by another strain of FWB in Taiwan in the late 1960s, but even after the dissemination of the causal agent that we nowadays know as Tropical Race 4 (TR4), the global industry considered this to be a far-away problem and little, if any, action was undertaken. More recent intercontinental spread of TR4 to the Middle East, Africa, and Latin America has been a wake-up call. The quest for solutions is on now, but after decades of neglect in research and development – demonstrated by little to no investments in plant breeding nor the identification of sources of resistance – it will take an immense effort to develop and deliver sustainable strategies. Meanwhile, Cavendish varieties, once the showstopper of FWB, now rapidly succumb in many areas due to the international and intercontinental dissemination of TR4. The introduction of TR4 in Mozambique is a good example. A 9000 ha farm was established by a group of investors to target the Middle-East market (van Westerhoven et al., 2023). Soon the required labor force was contracted from countries with industrial banana production, such as the Philippines. The exact origin of TR4 incursions in most countries, including Mozambique, is still unknown, but it is very likely anthropogenic and associated with the diverse workforce in the export-driven Cavendish production system (van Westerhoven et al., 2022). After a significant decline in production on infested farms, they are abandoned or at best turned into farms producing other crops. This, however, does not eliminate the causal agents of FWB. On the contrary, since bananas are no longer produced, the attention is reduced and TR4 continues to disseminate from these fields to other regions, threatening other banana varieties, including those that provide the staple food for millions of people in Africa's banana belt. The current expansion of TR4 demonstrates the overall failure of forward planning and quarantine to contain the pathogen and the inability to effectively manage it in the field. These strategies failed for Race 1 100 years ago and are currently failing for TR4. A point of difference is that the industry can now use clean tissue culture plants. The economically driven strategy of unlimited expansions to new un-infested areas failed in the Race 1 era and has already failed for TR4 in Southeast Asia and should not be repeated.

Instead, investments in research and development should turn the tide with science-based solutions and genetic improvement over time as is customary in other crops.

The genetic uniformity of global banana production facilitates the dissemination of diseases (Kema et al., 2021), requires massive fungicide inputs, and hits the global poor despite their diverse cropping systems. TR4 affects many more varieties than just the Cavendish clones as demonstrated in a study focused on Cuba (Martínez de la Parte et al., 2023; see also Chapter 4 in this book). Although smallholders grow a diversity of crops, which reduces the risk of disease outbreaks, the diversity among banana germplasm grown in Africa is very low. Additionally, awareness is also needed that traditional knowledge (Antonelli, 2023), despite its value, typically does not address novel introduced disease problems and does not suffice to feed rapidly growing populations in sub-Saharan Africa. Indeed, food security relies on a range of different crops and diversity within each crop, and the implementation of effective management practices based on solid data and proven strategies.

2 Past: origins, spread and biology

TR4 was first reported in Cavendish bananas in Taiwan in 1968 (Su et al., 1977). Since then, it has spread across Southeast Asia over a period of 50 years with limited documentation. In 2013, TR4 was reported for the first time outside Southeast Asia in Jordan and over the last decade has spread to 15 other countries in all major banana-growing regions of the world.

2.1 Origin of TR4

Whilst the first documented appearance of FWB-affected Cavendish was in 1968 in Taiwan (Su et al., 1977, 1986), the widespread presence in Indonesia suggests it originated there while anthropogenic factors have been involved in its dissemination across the archipelago and beyond (Maryani et al., 2018). Banana originates from Southeast Asia (Heslop-Harrison and Schwarzacher, 2007; Bakry et al., 2009; Donohue and Denham, 2009; Heslop-Harrison, 2011; Volkaert, 2011; Perrier et al., 2011; D'Hont et al., 2012; Li and Ge, 2017; Sardos et al., 2022). Hence, the highest level of inter- and intra-specific diversity of pathogens infecting *Musa* species – referred to in this Volume – originates from this area. Consequently, the highest level of diversity among banana-infecting *Fusarium* species – either pathogens or endophytes – is expected in Southeast Asia (van Westerhoven et al., 2024). Accumulated data confirm this hypothesis as the diversity of vegetative compatibility groups (VCGs); see (Puhalla, 1985; Ploetz, 1990) is larger in Southeast Asia than in any other region (Maryani et al., 2018). High levels of genetic diversity in this region are also confirmed by genomic data (van Westerhoven et al., 2024). Recent unpublished research has shown that TR4 is widely distributed across the Indonesian archipelago which indicates that TR4 is either a good disseminator or that demographic and anthropogenic factors are key for its local and global expansion, which seems to be confirmed by various studies (van Westerhoven et al., 2024; Ordóñez et al., unpublished). Since a substantial number of banana accessions is susceptible to TR4 (García-Bastidas, 2019), the chance for dissemination increases. Its spread throughout Indonesia may be connected to major internal migration in the past. For example, the occurrence of TR4 in the Papua province was confined to settlements of people originating from other Indonesian islands (Maryani et al., 2018). Other occurrences of TR4 in Southeast Asia seem to be associated with large industrial Cavendish plantations. Since susceptible banana varieties are grown worldwide and extensive traveling and exchange of farm workers and technical staff are common in the banana sector, the continuous spread of TR4 is predictable (Zheng et al., 2018).

2.2 History of spread

The large-scale cultivation of the Race 1-resistant Cavendish bananas started when the Standard Fruit Company (now known as Dole) decided to deploy it in Central America in 1956, followed by the United Fruit Company (now known as Chiquita) in 1965. However, the first crack in its reputation already occurred in 1968 in Taiwan. There are no indications that the reemergence of FWB was taken very seriously beyond Taiwan, but gradually it was attributed to the so-called Tropical Race 4 (Ploetz, 1994). Eventually, Cavendish production in Taiwan was no longer profitable. This was largely due to TR4 (Su et al., 1977, 1986), but market developments – such as the production in the Philippines that gradually took over the export to Japan, South Korea, and even China (Qi, 2001) – also contributed to this decline. The export to China, first from the Philippines and later from Latin America, was also driven by the increasing magnitude of TR4 problems in China's national banana production. After initial reports of TR4 from Fujian – the province across Taiwan – banana production gradually intensified in Guangdong, the island of Hainan, and the southern provinces Guangxi and Yunnan, without any measures taken to limit the spread of pathogens thereby facilitating the ongoing dissemination of TR4 (Qi, 2001; Qi et al., 2008; Huang et al., 2016; Wu et al., 2019; Guo et al., 2015), which substantially reduced the national banana production volume. Meanwhile, TR4 had also been reported in the Philippines (Molina et al., 2008), Malaysia (Buddenhagen, 2007; Ong, 1996), Thailand (not official), and again later in Vietnam (Chittarath et al., 2018; Hung et al., 2017; Zheng et al., 2018), Laos, and Myanmar (Chittarath et al., 2018; Zheng et al., 2018). This dissemination took place over a period of 50 years (1968–2018) with relatively poor documentation, except for the last decade, which was largely due to the increasing impact of TR4 on Cavendish production and the switch from VCGs to the use of molecular diagnostics (Dita et al., 2010; Carvalhais et al., 2019) and genome sequencing (Ordóñez et al., 2015) enabling more accurate strain identification. TR4 was for decades mostly an 'Asian story', but since its identification in the Middle East, Africa, and Latin America, it has become a global issue (Kema et al., 2021). Indeed, its international and intercontinental spread have surpassed all quarantine and containment efforts, including the highly structured and legislation-anchored quarantine measures in Australia where it first appeared in the Northern Territory in 1997 but also hit the banana belt in Queensland in 2015. First on a single farm that subsequently was taken out of production, but in March 2023 cases on the seventh farm were reported in the region despite the introduction of intensive on-farm biosecurity measures. The only appropriate conclusion at this stage is that quarantine and FWB management in susceptible varieties such as Cavendish fail and hence lessons need to be learned on how to deal with the TR4 pandemic that threatens fruit and food production (van Westerhoven et al., 2022).

2.3 Biology

The biology of TR4 is not known to be different from other *Fusarium* strains infecting bananas (Martínez de la Parte et al., 2023; Kema and Drenth, 2023; see also Chapters 4 and 6 in this book). It produces micro- and macroconidia as well as chlamydospores (Maryani et al., 2018; Maryani, 2018). The external and internal symptoms caused by TR4 infections in Cavendish are indistinguishable from races causing FWB in other banana varieties (Fig. 1). Hence, FWB in Cavendish should raise an immediate alarm, albeit other genetic lineages can also incur FWB symptoms when predisposed to abiotic stress, such as drought and flooding (Pegg et al., 2019). These strains are referred to as sub-tropical Race 4, but they are genetically different, and belong to different VCGs (Bentley et al., 1998). The different races are defined by their ability to cause FWB in different banana varieties. Race 1 and Race 2 are limited to just a few banana varieties, while TR4 causes disease in the majority of banana accessions that were tested (Zuo et al., 2018; García-Bastidas, 2019; Martinez de la Parte et al., 2023). The occurrence and spread of TR4 have given rise to research into its epidemiology. For instance, its capacity to infect other hosts, such as weeds in banana plantations (Catambacan and Cumagun, 2022; Martínez de la Parte et al., 2023), has raised concerns about the efficacy of control methods. The ability to infect other hosts as an endophyte is likely not confined to TR4, but these aspects of the biology have simply not been thoroughly tested with Race 1 or Race 2 strains (Hennessy et al., 2005). Until now, anthropogenic factors have been considered the major drivers for the international and intercontinental spread of TR4 (Zheng

Figure 1 Fusarium wilt of banana (FWB). External and internal symptoms caused by Race 1 in Gros Michel (a, b) and by TR4 in Grande Naine (c, d). The causal agents of FWB cannot be distinguished by the symptoms they cause in banana plants.

et al., 2018). However, local spread is much more elusive. Once infected plants are present, and consequently, the surrounding soil is infested, and the labor-intensive practices in banana farms where each plant is visited multiple times during the production cycle of 9–12 months contribute to on-farm dissemination. Area-wide irrigation systems and extreme weather events – such as excessive precipitation and floods, as exemplified by typhoons Pablo and Yuka that hit Mindanao in 2012 and Perú in 2023, respectively – further contribute to the spread of TR4 (Nakasato Tagami et al., 2024). Contaminated water streams and rivers exacerbate TR4 dissemination (Salacinas, 2019; Acuña et al., 2022). The aerial spread of TR4 has been considered after sporodochia were observed on aboveground parts of the banana plant under

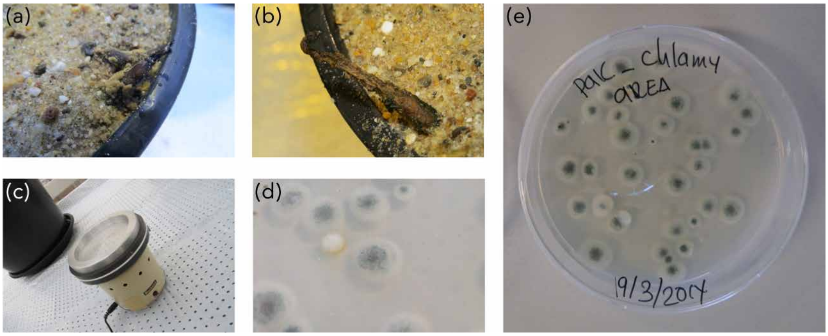

Figure 2 Artificially inoculated Cavendish bananas were subjected to aerial dispersal of Fusarium TR4 under greenhouse conditions. (a) and (b). During a severe infection, fungus covers exposed roots. (c) A sampling device for airborne spores that has a compartment for Petri dishes. (d) Details of a colony that tested positive for TR4 (arrowhead). (e) A Petri dish containing various fungal colonies including mycelium that tested positive for TR4.

greenhouse conditions (Fig. 2) and after the observed seed transmission of TR4 in greenhouse trials using *Setaria* as a model plant (Boggarapu, 2023). However, whether this mode of dissemination also plays a role under in-field conditions has not been elucidated.

3 Present: detection, epidemiology and control

The present situation regarding TR4 requires limiting further spread through improved control, and containment, supported by reliable detection, to distinguish TR4 from other *Fusarium* species occurring in bananas.

3.1 Detection

It is important to recognize that thus far there are no indications that *Fusarium* species in the *F. oxysporum* species complex regularly undergo sexual reproduction, despite the presence of mating-type alleles (Fourie et al., 2009; Leslie et al., 2006) and remnants of historical or occasional sexual reproduction (McTaggart et al., 2021; Fayyaz et al., 2023). The genetic diversity among *Fusarium* strains infecting bananas was elucidated upon after the discovery of VCGs (Puhalla, 1985; Correll et al., 1987; Correll, 1991; Leslie et al., 2006). It involved determining heterokaryon formation between strains after generating various nitrate non-utilizing (*nit*) mutants on a chlorate medium. Once plated in pairs, mutants that complement each other and produce abundant aerial mycelium are considered to belong to the same VCG and are therefore genetically similar. As a result, it was shown that the various *Fusarium* strains infecting bananas are frequently more closely related to species infecting other hosts than to each other. This has been used as an argument for their polyphyletic origin. Based on this, it was concluded that the host specificity within the *Fusarium oxysporum* species complex developed independently and multiple times (Baayen et al., 2000; Koenig et al., 1997; O'Donnell et al., 1998, 2004). Conducting VCG analyses is a time-consuming method to characterize fungal strains, and mutants are not always successfully generated thereby impairing genetic identification. Moreover, the number of VCGs among *Fusarium* strains infecting bananas is larger than in any other *F. oxysporum* species pathogenic on other hosts. For instance, *F. oxysporum* f. sp. *lycopersici* of tomato has only three VCGs (0030–0031 and 0035), and *F. oxysporum* f. sp. *melonis* comprises eight VCGs (0130–0138). Recent VCG analyses indicate that strains belonging to the previously called species *F. oxysporum* f. sp. *cubense* comprised over 26 VCGs, and various isolates belong to unknown VCGs, suggesting that the number of known VCGs is steadily expanding (Bentley et al., 1995; Katan and Di Primo, 1999; Moore et al., 1993; Ploetz, 2015a).

From all accumulated data, it was clear that, contrary to Race 1 and Race 2 strains, TR4 belongs to just one VCG: VCG01213 (Ploetz, 1994; Moore et al., 1993; Bentley et al., 1998). Using genomic analysis, it was shown that TR4 is a unique new lineage belonging to a new species named *F. odoratissimum* (Maryani et al., 2018). The various Race 1 strains belong to multiple VCGs and are also grouped into different species (van Westerhoven et al., 2024; Maryani et al., 2018). The polyphyletic origin of Race 1 and Race 2 complicates the development of molecular diagnostics. However, the genetic similarity of all TR4 strains – which are clones – facilitated the development of molecular diagnostics for TR4 (Aguayo et al., 2017; Ordóñez et al., 2019; Dita et al., 2010; Carvalhais et al., 2019; García-Bastidas et al., 2020a,b; Lin et al., 2013). These have been routinely used to diagnose TR4 and showed that it has spread to 15 countries in just 10 years since its first occurrence outside Southeast Asia in Jordan in 2014 (García-Bastidas et al., 2014; van Westerhoven et al., 2022).

3.2 Dissemination, phylogeography and epidemiology

Although it is known that Race 1 strains are commonly present around the globe (Fig. 3), the details of how they were disseminated in the past are unknown. Southeast Asia is the center of origin of bananas and hence is likely to also be the center of origin of most of its pathogens, due to the co-evolutionary processes taking place in these natural environments. The diversity within and between Race 1 *Fusarium* species (previously referred to as VCGs) is large (Ordóñez et al., 2015; van Westerhoven et al., 2024). It is logical to assume that the dissemination of these species has been facilitated by the transport of infected plant materials. People have taken cuttings or suckers from banana varieties to other areas, including long-distance travel. In addition, weather events such as excessive precipitation, typhoons, and floods may

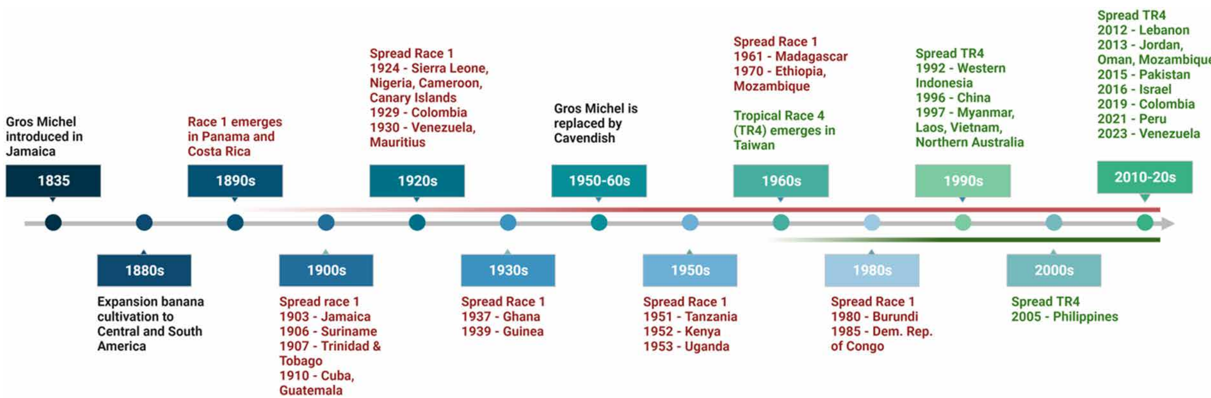

Figure 3 Timeline of the dissemination of Race 1 and TR4 in global banana production.

have contributed to regional dissemination. For TR4, very similar events may have contributed to its dissemination in Southeast Asia. However, its further international expansion has been monitored much more precisely since the development of the first molecular diagnostic (Dita et al., 2010) and upon its first occurrence outside Southeast Asia, as described by van Westerhoven et al. (2022). The most recent outbreak of TR4 has been reported in Venezuela, where it was found in three states (Aragua, Carabobo, and Cojedes), close to Lago Maracay – southwest of the capital Caracas – where many banana plantations are located (Hernández et al., 2023). This is the third reported occurrence in Latin America (Acuña et al., 2022; García-Bastidas et al., 2019) and underscores the failing quarantine strategies for TR4. Clearly, inadequate biosecurity strategies contribute to dissemination (van Westerhoven et al., 2024), such as exemplified in Mozambique, the Mekong delta, and Perú (Zheng et al., 2018; van Westerhoven et al., 2022, 2024), but it also underscores that excluding a soil-borne disease is extremely difficult, maybe even impossible. The first reported occurrence of TR4 outside Indonesia was in Taiwan (Su et al., 1977, 1986). The origin of that incursion seems to be related to a documented banana shipment from Sumatra to Taiwan (Buddenhagen, 2007). These plants may have been infected with TR4 and since then it started its regional, international, and intercontinental spread. Since virtually all further incursions have been closely monitored over the last two decades and many of the causal TR4 strains have been sequenced, it is known that TR4 is a single clone (Ordóñez et al., 2015). Therefore, forensic analyses are difficult as the number of mutations (1271 single nucleotide polymorphisms) is negligible (0.003%) compared to the entire genome size (46 megabases). However, bioinformatic tools enable the tracing of TR4 such as demonstrated in the Mekong Delta, where the occurences in Myanmar, Laos, and Vietnam is clearly linked to the TR4 strain that was described in the Southern Chinese province of Yunnan (Zheng et al., 2018). Chinese growers started banana plantations in the surrounding countries due to the increasing TR4 problems on their farms in China, while moving their equipment and bringing their personnel. It is likely that these processes contributed to the regional dissemination of TR4.

The use of disinfectants is widely recommended to prevent TR4 dissemination (Nel et al., 2007; Meldrum et al., 2013), but the procedures are often inadequate in practice. For example, Salacinas et al. (2022) showed that the efficacy of disinfectants toward TR4 requires an exposure time of 15 s, but recorded time-lapse data of real-world disinfestation stations were 3.42 (± 0.82) and 5.05 (± 3.08) s for footwear and tires, respectively. Hence, despite the good intentions, the practice fails and enables TR4 to survive. Since TR4 is soilborne, measurements of its distribution in soil have shown that propagules can be detected down to a depth of 1 m and can also be present in the irrigation water (Ploetz, 2015b). Apart from its capacity to grow as an endophyte in non-host plants, these epidemiological facts truly complicate the management of TR4 (Martínez de la Parte et al., 2024), and as Race 1 strains continued to spread after the introduction of Cavendish, TR4's dissemination will not stop after deploying resistant varieties (Fig. 3). *Fusarium* strains do not need bananas for survival, they easily survive as endophytes in non-host plant species.

3.3 Control and containment

The distribution of fungal propagules of *Fusarium* in the soil makes disease control unpredictable. Various methods have been used since the first FWB epidemic in Gros Michel, some of which are also being trialed to manage the epidemic in Cavendish. Inundation of whole fields through flood fallowing was a major effort to kill *Fusarium* in the soil (Stover, 1962a). Indeed, generating an anaerobic environment in the soil potentially kills all aerobic organisms. However, many beneficial microbes are also prone to destruction creating a biological vacuum. Inundation failed to control FWB in Gros Michel. Most likely, this was primarily due to the absence of biosecurity measures and the lack of tissue culture and hence, in many cases, asymptomatic infected new suckers were planted in the treated areas thereby restarting the epidemic (Stover, 1962b). However, inundation followed by planting tissue culture plants, which was developed in the 1970s (Ma and Shii, 1972), might be a strategy if followed by enriching the soil with antagonistic microbes after flooding. In practice, this can only be deployed in areas with flat fields and where sufficient water is available. An alternative to inundation is biological soil disinfestation. Initially, this method relied on the decomposition of biomass, ideally of plants from the *Brassicaceae* which produce glucosinolates that kill fungi and in particular *Fusarium* species (Messiha et al., 2007; Blok et al., 2000). Nowadays, various commercial products are available that induce anaerobic conditions and produce volatiles toxic to fungi during their decomposition under plastic. Under greenhouse conditions, these methods have proven efficacy, and field trials are also promising, but the method is expensive and requires substantial soil tilling. Overall, methods that generate anaerobic conditions are not specific and the lasting effects on the soil microbiome are unknown.

Rice hull burning is a method that is practiced in the Philippines and is derived from the control of the soil-borne Moko disease caused by the bacterium *Ralstonia solanacearum* (Molina et al., 2010). After chopping infected plants, a pile of rice hull is used to cover the remains of the plant and the corm and set on fire to smolder for days. Indeed, temperatures in the topsoil layer can go up to >300°C and consequently reduce the TR4 inoculum load, but measurements have also indicated that inoculum in deeper soil layers is unaffected. Variants of rice hull burning using wood or bamboo produce even higher temperatures but do not increase efficacy (Salacinas, 2019). Moreover, the entire process of burning requires substantial manual labor. Several workers are involved and consequently walk around infected plants, thereby potentially spreading the disease with their footwear. Experience has shown that rice hull burning does not stop the further spread of FWB (Fig. 4).

Biocontrol is another option for TR4 management, and many microbes produce compounds with *in vitro* efficacy toward TR4 (Nel et al., 2007; Lakshmanan et al., 1987; Davis et al., 1994; Yuan et al., 2012; Cao et al., 2005;

Figure 4 Rice hull burning is practiced in Philippines to manage Fusarium wilt of banana (FWB) caused by TR4. (a) Aerial photograph of a region on Mindanao that is struck with FWB. (b) Chopping of infected plants. (c) Chopped plant parts are covered with a heap of rice hulls that are set on fire to smolder for up to 3 days. (d) Open spots in a banana planation after practicing rice hull burning. However, FWB progresses through the plantation, see multiple rice hull burning attempts to stop the disease.

Saravanan et al., 2003; Kidane and Laing, 2010; Zhang et al., 2013). However, translation into effective commercial products for FWB management under field conditions has not been successful yet (See Bubici et al. 2019). Like the development of fungicides, it has to take into account aspects such as biological safety and the upscaling potential. The one-size-fits-all strategy that is often advocated with biocontrol, such as the almost mythical status of *Trichoderma* to control TR4 (Thangavelu et al., 2004), has hitherto not resulted in durable FWB management (Bubici et al., 2019). Also, plant volatiles have shown efficacy toward TR4, such as those produced by Chinese leek (Huang et al., 2012), but – again – field trials failed to show control at the plantation level. Mixed cropping is common in smallholder settings and backyard farming, and at a larger scale in agro-forestry landscapes, yet it does not exclude FWB (Fig. 5), but it may slow down its spread. Perennial plantation crops – such as banana, coffee, and cacao – are almost without exception monocultures, incompatible with crop rotation and mixed cropping as practiced in annual crops. However, the potential of cover crops is worth further investigation. For instance, plantations with *Arachis pintoy* as a cover crop showed a 20% lower disease severity (Pattison et al., 2014). Interestingly, this plant species can be infected by TR4 but recovered strains showed reduced pathogenicity on Cavendish bananas (Martínez de la Parte et al., 2024).

Management of foliar diseases in agriculture frequently relies on fungicide applications. Since Cavendish bananas are highly susceptible to black leaf streak disease – also known as Black Sigatoka disease – caused by *Pseudocercospora fijiensis*, the frequent use of fungicides to manage this

Figure 5 Fusarium wilt of banana (FWB) in an agro-forestry setting. (a) External symptoms of infected plant. (b) Internal symptoms, characteristic of FWB.

disease is a common practice in banana cropping (Chong et al., 2024: see also Chapter 4 in this book). However, it is often stated that FWB cannot be controlled with fungicides (Ploetz, 2015b). Indeed, TR4 and Race 1 strains are remarkably insensitive to single-target site fungicides, albeit sensitive to others (Cannon et al., 2022). However, the recently released Tymirium technology – based on succinate dehydrogenase inhibitors – has shown efficacy to TR4, and the commercial Vaniva® fungicide was recently released in the Philippines. This is a new development and time will show whether this will be a useful tool in the management of FWB.

Taken together, the history of the spread and failure of management of Race 1 in the Gros Michel era is currently repeated with TR4. This raises the question as to how TR4 can be managed. Contemporary management options for FWB are limited, and some options have been promoted that are not effective and have resulted in the continuous expansion of TR4 (van Westerhoven et al., 2024).

4 Future: preventative/curative disease control and breeding

If the current trend of TR4 dissemination continues and no effective disease control is implemented, the cultivation of Cavendish varieties will be further threatened (van Westerhoven et al., 2022). Therefore, it is necessary to consider whether FWB can be managed by novel disease control methods.

4.1 Preventative disease control

Presently, the best and cheapest strategy to manage TR4 is to exclude it (Cook et al., 2015). Prevention measures are mostly confined to exclusion, a combination of biosecurity practices aimed at restricting access to the plantation, farm layout with regards to access and water run-off, the use of disinfectants in foot baths, and tire dips combined with cleaning stations. To be efficacious, exclusion strategies should comprise well-coordinated nationwide prevention strategies. People and products entering countries should be assessed for the risk of carrying TR4 and excluded from certain areas to reduce the risk of introducing TR4 into new areas. In some countries, banners are used at airports and harbors to inform travelers about the risks of TR4 (Fig. 6). Ideally, disinfection mats to clean footwear are part of this strategy, but these are hardly used at any airport. Hence, introducing TR4 into a country with contaminated soils under footwear is an imminent risk. Also, the global circulation of containers and equipment to develop new plantations may facilitate the introduction of TR4 in uncontaminated areas as has happened in the Mekong region (Zheng et al., 2018) and Mozambique (van Westerhoven et al., 2022, 2023).

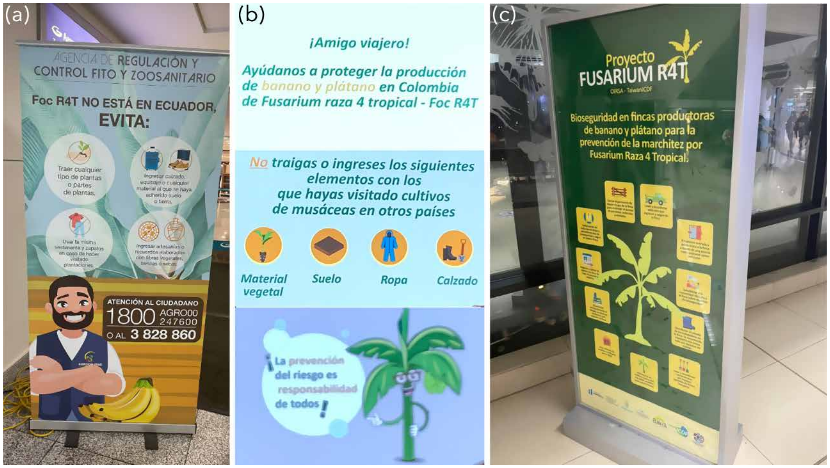

Figure 6 Travelers are informed about the risks of TR4 for banana production in Ecuador (a), Colombia (b), and Guatemala (c) at regional airports.

The next step after country border exclusion is to assure the exclusion at the farm level. This requires the exclusion of all non-essential people and movement on the plantations and the implementation of clean and dirty zones, footwear exchange stations, and disinfection units at each entry of a farm. Traditionally, packing stations are centrally located in banana plantations, and hence, trucks drive through plantations to deliver inputs and pickup packed fruit. A good biosecurity strategy is to use only on-farm equipment for transportation inside the farms. This includes motorcycles for personnel, cars, trucks, and tractors. Clearly, this requires a redesign of farm layouts with sufficient space for parking vehicles, frequent on-farm bus transportation, dedicated on-farm vehicles of every kind, and trucks and drivers having to wait outside the farm gate for deliveries and pickups. The development of zones is far more effective than the costly and time-consuming business trying to thoroughly clean and disinfect any vehicle entering a farm. The same is true for footwear where boot exchange stations are far more effective than footwear and disinfection stations, where people and equipment need to be exposed to disinfectants for a certain amount of time (Salacinas et al., 2022). These activities should supplement fencing off plantations to avoid unauthorized access. In addition, plantations are often not continuous, and different sections are connected, either by roads, rivers, or irrigation canals. A key issue arising here is that these measures involve expensive infrastructure and different working practices. It is also important to realize that these procedures need to be implemented prior to the arrival of TR4 on a plantation. Experience has shown that most plantation owners are reluctant to invest in measures preventing TR4 from arriving, and consequently, once this happens it is too late to implement such measures. Moreover, the efficacy of these measures is higher once implemented in a sector-wide fashion, which further complicates the prevention of TR4.

Once a plantation is infested in a particular area, it is important to delay further spread to other fields. For that purpose, aerial surveys have been explored to proactively identify suspect spots in plantations (Nakasato Tagami et al., 2024). This high-throughput method can map entire farms, regions, or countries and does not require farm entry for personnel to manually inspect farms, which can be a bottleneck. All farm data, geographical and logistical details, and aerial images, from airplanes, drones, or satellites, are loaded into a platform for inspection. The resolution of these images is usually 5–7 cm to identify suspect spots enabling subsequent on-farm inspection to sample and investigate TR4 presence. The frequency of such inspections is key; hence aerial surveys only pay off if they start prior to the arrival of TR4, and surveys are repeated over time at regular intervals and the subsequent inspection activities are streamlined to ensure that suspected areas or plants are identified in a timely manner. Currently, most TR4 incursions have been notified too late and FWB was already widespread and out of control. For instance in Perú, FWB was first observed in Chira Valley Cavendish plantations in April 2021 (Acuña et al., 2022) and by June 8, 2023, a total of 207 cases were reported (Nakasato Tagami et al., 2024). This expansion of TR4 is tightly connected to the production system in the Chira Valley, which is unique as it comprises 8.000 smallholder farm settings of on average one ha and two dozen larger plantations making up a total area of 10.000 ha that are all connected through a generic irrigation system from the Poechos Reservoir in the Sullana province close to the Southern border of Ecuador. The aforementioned aerial survey mapped the entire region, identified suspect open areas that were subsequently sampled, and confirmed the presence of TR4 (Nakasato Tagami et al., 2024). Genomic sequence data suggest that the incursion in Perú is independent of an earlier incursion in Colombia (Reyes-Herrera et al., 2023).

Dissemination by water is a key element of TR4 epidemiology. The tropical storm Pablo in 2012 moved the front of TR4-driven FWB to an unanticipated area in Mindanao in the Philippines, thereby increasing the indirect impact of this storm. Clearly, this impact was only observed after banana plantations were recuperated and many plants simultaneously started suffering from FWB. There is substantial anecdotical information on watershed and FWB dissemination, e.g. in the Pearl River basin of Guangdong (Molina et al., 2005) and the Mekong Delta (Zheng et al., 2018), and the aforementioned rapid dissemination of TR4 in Perú is linked to the shared irrigation system that supplies the entire banana region. Molecular diagnostics have also detected TR4 propagules in water, thereby supporting the important role of water dissemination (Salacinas, 2019). Various methods have been implemented to disinfect water for small-scale use such as in foot baths and vehicle wash-down stations (Nguyen et al., 2018; Nel et al., 2007). However, these systems are not suitable for large-volume irrigation systems where only water sourced from deep wells is safe to use, while decontamination of river water and reservoirs requires the implementation of UV-C systems that are currently being tested. In conclusion, prevention methods can be improved but require substantial investments and coordination at a national and regional scale prior to the arrival of the pathogen. These investments nevertheless pay off over time as unlimited TR4 infestations result in rapidly decreasing production volumes and eventually a non-profitable sector.

4.2 Curative disease control

In many crops, innovative cultivation methods have contributed to the yield and quality of produce. For instance, the increase in tomato production has been equally attributed to breeding efforts and to innovation of cultivation methods (Noordam, 1987; Welleman and Verwer, 1983). Tomatoes were lifted off the soil and are now produced on a substrate of rock wool or other components such as cocoa peat. Similar trends have occurred in berry and kiwi production (Schwab, 2020). Disease control, nutrition, and irrigation have modernized plantation cropping, and innovative post-harvest processes have made bananas available in the most remote places. However, in-field banana cropping has barely changed over the last century (Kema and Drenth, 2018). Rotation schedules, which are difficult to implement in perennial plantation crops, and cultivar diversification have not been practiced, albeit other varieties have been available. Clearly, market forces and economic reasons have dominated the arguments for this century-long status quo.

Fungicides have proven to be a cornerstone for disease management of black leaf streak disease in banana cultivation but for FWB management the first commercial fungicide has only been released recently in the Philippines. As mentioned by Drenth and Kema (2023, Chapter 6), biocontrol has put forward great promises, but few successes in banana production. There are numerous reports of microbes affecting fungal growth in the laboratory (Yadav et al., 2021; Thangavelu et al., 2004; Ploetz, 2015b; Mohandas et al., 2004; Kloepper et al., 2004; Jie et al., 2009; Getha et al., 2005; García-Bastidas et al., 2022), but the efficacy lacks under field conditions (Bubici et al., 2019). Nevertheless, contemporary research into the microbiomes of soils and plants provides intriguing leads for biocontrol (Tao et al., 2023; Martínez de la Parte et al., 2024). Notwithstanding these promising recent developments, the described and proposed options for improved disease control are remarkably similar to those that were unsuccessfully advocated and practiced in stopping the previous FWB epidemic in Gros Michel monocultures (Stover, 1962b). Therefore, new FWB-resistant banana varieties are required to manage TR4 in the current era.

4.3 Breeding

For FWB management, there is one outstanding and almost century-long example of success: the cultivation of Cavendish bananas in areas infested with Race 1 demonstrating outstanding and durable resistance to FWB caused by Race 1 strains. It is therefore remarkable that despite the success of resistance, so little has been invested in understanding the basis of this remarkable resistance in Cavendish to Race 1 strains. Only recently, the genetic basis of this resistance has been explored (Ahmad et al., 2020), and breeding bananas is not any longer seen as a senseless endeavor, prone to failure (Kema and Drenth, 2020). Several breeding efforts have delivered improved varieties with resistance to black leaf streak disease and other constraints (Bakry and Horry, 2016; Bhagwat and Duncan, 1998; Buddenhagen, 1990; Heslop-Harrison, 2011; Menendez and Shepherd, 1975; Ortiz et al., 1995; Persley and De Langhe, 1987; Pillay and Tenkouano, 2011; Shepherd, 1994; Silva et al., 2001; Stover and Buddenhagen, 1986; Vuylsteke, 2000). Notwithstanding these successes, contemporary breeding programs have not released varieties matching the yield and fruit quality of Cavendish bananas (Ploetz, 2015b). However, the development of genomics enables modern breeding techniques, and molecular tools have opened immense opportunities to circumvent hitherto experienced obstacles in banana breeding.

The advent of tissue culture drastically changed banana cultivation. Millions of healthy banana plants are produced every year and distributed globally to start new or recuperate existing plantations. Previously, the multiplication through suckers was the main driver of the FWB Race 1 epidemic in the 1900s. One of the aspects of tissue culture was the observation of off-types caused by somaclonal variation. Most of these variants are discarded, but some had attractive phenotypes, such as reduced tallness resulting in Dwarf Cavendish. Other variants showed a better tolerance to abiotic stress or had better bunch characteristics (Roux, 2004; Roux et al., 2004, 2008; Jain and Maluszynski, 2004; Novak et al., 1990, 1995; Khayat et al., 1998; Khayat and Ortiz, 2011). These observations stimulated a process to select somaclonal variants with improved disease resistance, for instance at the Taiwan Banana Research Institute (TBRI). This resulted in a cultivar called Formosana which was reported to have improved resistance to TR4 (Molina et al., 2011), and through the years other variants – collectively known as Giant Cavendish Tissue Culture Variants, GCTCVs – have been developed and tested in TR4-infested soils. The experience with these clones, however, has been inconclusive. Contrary to agronomical disadvantages such as longer cycling times, tall stature, and poor bunch characteristics, there have been reports of higher sugar content. Cultivation of some of these clones – such as GCTCV219 – revealed that there are many synonyms and hence it is sometimes difficult to ensure that reports are discussing the same germplasm. Nevertheless, some of the GCTCV clones showed a remarkable reduction of FWB compared to controls (Hwang, 1990; Hwang and Ko, 2004; Ploetz, 2015b; Van den Berg et al., 2007). These observations were unfortunately reported and advertised as 'resistance' or 'tolerance' (Molina et al., 2011; Hwang and Ko, 2004; Ploetz, 2015b). Hence, many growers whose farms suffered from FWB caused by TR4 adopted these clones and continued production. Within a short period of time, these clones however started suffering from FWB and increasing the inoculum levels, underscoring that reduced susceptibility or tolerance to TR4 is not a solution. The perennial nature of the crop, combined with the soil-borne nature of FWB, does not enable reduced susceptibility to durably control TR4. The recommendations to grow these variants also resulted in reduced awareness and quarantine measures enabling the further spread of the disease. Thus, in conclusion, the GCTCV clones have done more harm than good and indirectly contributed to the further dissemination of TR4 (van Westerhoven et al., 2022).

It is well known that Cavendish clones can be cultivated in soils that are infested with Race 1 strains and such a level of resistance is required for any new germplasm with resistance to TR4 to solve the current FWB crisis. Mutation breeding may play a role and interesting approaches, such as a novel transposon-based mutation strategy, have been developed which have yielded promising results (Khayat, 2020). Another method to induce mutants is through chemicals or radiation. The International Atomic Energy Agency (IAEA) has invested in mutation programs over the years (Roux, 2004; Roux et al., 2004, 2008; Novak et al., 1995), but the program has not resulted in new germplasm that can withstand FWB.

In conclusion, mutation breeding has made valid contributions to banana improvement and may hold promise for disease resistance. However, for FWB, the complete resistance of Cavendish vs. Race 1 is the ultimate benchmark. Everything that does not meet this level of resistance falls short – such as the aforementioned GCTCV clones – and may contribute to the continued dissemination of the disease.

Plant transformation has enabled genetic engineering in bananas (Wang et al., 2021). Disease resistance has been an important target for banana improvement but The Achilles' heel of banana transformation for disease resistance is the ultimate lack of understanding of the genetic basis of disease resistance. Thus far not a single gene has been functionally tested to prove the genetic control of Race 1 in Cavendish (Ahmad et al., 2020). Once a series of genes conferring resistance to FWB is identified and characterized, genetic engineering attempts can be much more focused and do not have to rely anymore on genes from other plant species. This will avoid at least one aspect of objection to genetic engineering: the use of genes from other plant species. Although resistance to TR4 is currently considered to be vital, any new banana variety should also have resistance to Race 1 strains. Therefore, the improvement of Cavendish is a common strategy in contemporary genetic improvement strategies. Contrary to resistance to Race 1, the only identified gene for resistance to a fungal pathogen in banana is *RGA2*, which provides complete resistance to TR4. Dale et al. (2017) managed to identify and clone the *RGA2* gene and transferred it to the Cavendish cv. Williams. Subsequent greenhouse and field trials have shown the required level of resistance, similar to the donor species *Musa acuminata* ssp. *malaccensis* (D'Hont et al., 2012). Subsequent work should focus on the identification and characterization of more resistance genes in banana, which requires substantial screening for resistance in the widest possible suite of germplasm (García-Bastidas, 2019) to support any improvement strategy, whether genetic engineering or breeding for resistance.

The most recent shift in genetic engineering is undoubtedly revolving around CRISPR/Cas9-based technologies. In banana, Tripathi et al. (2019) were the first to apply it for the inactivation of banana streak virus, which is endogenous in *M. balbisiana* germplasm and is a major hurdle in banana breeding. This technology holds great potential to engineer FWB resistance once resistance genes have been identified. Dale et al. (2017) reported that *RGA2* is also present in Cavendish, but it is not or hardly expressed. CRISPR/Cas9 is a tool that may be able to modulate that expression to render such edited Cavendish bananas resistant to TR4. The rapidly increasing body of genomic data in banana research, both of host and pathogens, may provide leads for FWB resistance. However, CRISPR/Cas9 should not be regarded as a panacea for disease resistance in banana as most likely transfer of genes through hybridization is required to introgress suitable target genes from the wider *Musa* germplasm into suitable varieties.

Breeding bananas is fraught with difficulties (Kema et al., 2021). Currently, there are about 12 banana breeding programs around the world (Smith et al., 2021), which focus on regional markets in Latin America and Africa, for dessert bananas and plantains. Others also focus on dessert bananas for international markets. There are several reasons why banana breeding is challenging such as parthenocarpy, sterility, and the triploid nature of most edible bananas (Amah et al., 2021). A classical – so-called evolutionary breeding – approach was used to try and improve Gros Michel in the first banana breeding program at the Imperial College of Tropical Agriculture in Trinidad that commenced in 1922. The same strategy is also being followed by the breeding program at the Fundación Hondureña de Investigación Agrícola (FHIA) in Honduras. Screening of some lines of this program has shown that FHIA banana and plantain hybrids perform better than many other varieties to TR4, but none were truly resistant (García-Bastidas, 2019; Martínez de la Parte et al., 2023). The EMBRAPA program essentially follows the same strategy and frequently releases new varieties for the domestic market in Brazil (Silva et al., 2001). The IITA and its partners have developed a breeding program for East African Highland Bananas over the last decade, which has adopted a range of innovative genomic tools to accelerate conventional breeding (see https://breedingbetterbananas.org/). The breeding program at the Centre de coopération Internationale en Recherche Agronomique pour le Développement (CIRAD) follows a different strategy through a reconstituting approach. Here, fertile diploids are improved and eventually used in 4x/2x crosses to generate seedless triploids. This approach has the advantage that wild germplasm can be used to enrich the breeding gene pool and that plenty of seeds are being generated. All evolutionary and reconstructive conventional breeding programs listed by Smith et al. (2021) are based in universities or institutions. It is remarkable that thus far commercial breeding companies have not invested in banana breeding, although the FHIA program was initiated by the United Fruit Company in 1959 but is now a governmental endeavor. Recently, a number of commercial start-ups in the United Kingdom (Tropic Biosciences), the United States (Nature Source Improved Plants), and The Netherlands (Yelloway) have emerged that target the development of disease-resistant bananas.

A thorough and reproducible screening method is a key element in breeding for resistance, irrespective of the breeding strategy used. To achieve this, germplasm is first screened under standardized greenhouse conditions prior to evaluation in the field. These analyses are crucial and cannot be conducted on-site in most regions because TR4 is not present in the countries where these breeding programs are based, or it is not allowed to use infested areas as trial sites for quarantine reasons. Another bottleneck is the narrow genetic base of cultivated bananas used to improve varieties. Access to the widest possible genetic diversity in Southeast Asia is essential to achieve genetic gain in banana breeding. Furthermore, genetic studies on the inheritance of resistance to the major diseases and pests are essential to target genes conferring resistance. This information is generic and can be used by any of the aforementioned banana improvement strategies. Therefore, contemporary research programs should focus on discovery research to unveil the genetic basis of required traits of bananas for the future as a foundation for diversification away from Cavendish. Banana is among the last major edible crops where tremendous genetic gain can be potentially achieved, provided we are using a plethora of strategies and increase the critical mass of research that is required for progress.

5 Conclusion

Looking into the future, it is tempting to ask, what is next? Another new race causing FWB? Further dissemination of TR4 within currently affected countries and to other countries is inevitable. But will new resistant varieties, able to grow unimpeded in TR4-infested plantations, come to market in time? We have seen some false dawns with the introduction of so-called ‘tolerant’ varieties which did not solve the problem and contributed to further dissemination of the pathogen. Hence, authorities may have to play a role in the testing and recommendation of new germplasm. This is common practice in many other crops and countries to transparently inform growers and to prevent the reoccurrence of major plant diseases.

What happens once another new *Fusarium* race or species surfaces? All relevant germplasm must be formally tested with such a variant. At present, it takes years before such information is available and it is often not comprehensive. Is there a danger of new pathogenic variants? Yes, there is, but there is an important difference. Now there are collections of sequenced *Fusarium* strains, hence new seemingly pathogenic variants can be rapidly characterized. Based on that information, existing and new germplasm can be proactively tested for resistance. Moreover, once there are signs of reduced resistance of new germplasm under field conditions, strains should be isolated, sequenced, and tested. Overall, the banana research community has grown, companies are more aware, and new companies are founded with well-trained committed individuals. Hence, the risk of surprises has reduced, and the awareness of global plant disease epidemics is much higher in our more connected world. New incursions of TR4 and other plant diseases are noticed and communicated rapidly. This chapter has provided suggestions on how to act once that happens and above all, what should be done to prevent it. Collective action is required, and thorough, reliable prevention and quarantine measures should be practiced. New promising germplasm is under development and exciting new management options based on disinfection technology, innovation in banana cultivation, biological phenomena, and microbial consortia are being developed. The combination of new insights and technologies will help to better control TR4 and other banana diseases that have spread around the world over the last century (Kema et al., 2021). A well-resourced and connected research community is needed, supported by national and international legislation on plant health, using a comprehensive and rigorous research approach, grounded in genetics and breeding and addressing the various needs of the crop along with rigorously tested and validated disease control options to secure the production of this major food crop and the world’s favorite fruit.

6 Where to look for further information

- Global Alliance Against TR4; https://iica.int/en/global-alliance.
- World Banana Forum: https://www.fao.org/world-banana-forum/en/.
- Wageningen University: https://www.wur.nl/en/dossiers/file/banana-cultivation.htm.

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