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Achieving sustainable cultivation of bananas

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Chapter 6

Towards sustainable management of Fusarium wilt of banana

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1 Introduction

The rapid growth of the banana industry in Latin America in the latter part of the nineteenth century and early part of the twentieth century was made possible through improvements in logistics such as the building of railways in Central America, rapid sea transport to North America on specialized boats called reefers and an expanding railway and commercial distribution network throughout the USA. This system allowed for large amounts of bananas to rapidly and effectively be shipped from plantations in the tropics to consumers in the temperate zones, first in North America and then to Europe. Early attempts to ship banana varieties from the tropics to consumers in the temperate zones had been disappointing due to a lack of temperature control and uneven and early ripening of the fruit of some banana varieties. Once these issues were brought under control, the banana industry build an effective supply chain based on a single banana variety, 'Gros Michel', with great success due to its high productivity in plantation settings, large fruit, thick skin, extended green life, slow ripening, excellent transportability and good taste. These favourable

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characteristics fuelled the development of a rapidly expanding monoculture of Gros Michel bananas grown in large-scale plantations near transport infrastructure in Latin America. Although ideal from a logistics and business perspective, enabling a constant supply and a consistent consumer experience, from a plant pathology perspective, it was a very high-risk strategy. The lack of genetic diversity in a crop grown in monoculture in large plantations over large areas is a prime example of how to create a high level of genetic vulnerability (National Research Council, 1972). The fact that genetic vulnerability is a real and major risk to food production is demonstrated by Fusarium wilt of banana (FWB), previously by the race 1 driven epidemic in Gros Michel in Latin America and currently by the dissemination of tropical race 4 (TR4).

2 The Fusarium race 1 epidemic in Gros Michel

FWB was initially caused by the so-called race 1, which originated in Southeast Asia (Ploetz and Pegg, 1997), and it has been hypothesized that causal agent(s) moved with asymptomatic bananas of the variety Silk from Asia to Jamaica sometime in the nineteenth century (Stover, 1962). From there, it slowly spread with contaminated planting material in the region, and the first major problems were noted in the Gros Michel plantations on the Atlantic coast of Panama and Costa Rica in the 1890s (Stover, 1962; Marquardt, 2001; McKenny, 1910). From this bridgehead, race 1 spread quickly to other banana-producing countries such as Suriname (1906), Trinidad and Tobago (1907), Cuba (1908), Guatemala (1910), Honduras (1916), Nicaragua (1919), Colombia (1929) and Venezuela (1930) in Central and South America (Ploetz, 2019) and started to have a devastating effect on the productivity of the large monoculture plantations of Gros Michel (Drenth and Kema, 2021; Marquardt, 2001; Ploetz, 2019; Soluri, 2005; Stover, 1962).

The massive destruction of the Gros Michel plantations led to various studies concerning the cause of the disease (Ashby, 1913), and a link was made to an earlier report by Bancroft (Bancroft, 1876), who first reported the disease from Australia and identified it as a Fusarium disease (Pegg et al., 1996). The epidemic caused havoc in plantations with the highly susceptible Gros Michel, and no effective control methods were identified despite large-scale efforts, such as flooding large plantations, to kill the fungus. Although this looked promising at first, the replanted fields very quickly succumbed to FWB again after replanting. Since no effective control methods were found, the banana companies at the time, and United Fruit Company in particular, saw one solution in moving to new areas, clearing the land and establishing new plantations. However, due to the classical problem of the lack of consultation of plant pathology expertise involved in critical decision making, they typically brought the disease with them in the planting material, equipment or soil and had to abandon these new plantations after a few years when they also collapsed due to FWB. This was a costly exercise that left a trail of economic, environmental and social destruction, and it has been estimated that over 40 000 ha of banana plantations had been abandoned by 1958 (Wardlaw, 1961). This shifting of cultivation and the need for clean land gave rise to corruption and political interference by the banana companies which turned the young democratic countries of Central America into what is often called 'banana republics' (Koeppel, 2008; Marquardt, 2001). It has been estimated that the FWB epidemic damage was over US$2.7 billion expressed in today's value (Ploetz, 2005), and this brought the Gros Michel-based banana industry to its knees in the late 1950s.

3 Infection and development of disease symptoms

Bananas are affected by a range of different plant diseases, of which FWB, also known as Panama disease, is one of the most important. Infection by the causal *Fusarium* spp. takes place in the secondary and tertiary roots (Wardlaw, 1961) which produce exudates that stimulate the germination of chlamydospores present in the soil (Ploetz and Pegg, 1999). The germ tubes of the spores penetrate the epidermal cells near the root tips and grow intercellularly along the elongation zone through the root cortex after which they enter the xylem vascular elements (Warman and Aitken, 2018). Once in the xylem, the fungus forms mycelium and microconidia to further colonize the xylem towards the rhizome. In resistant bananas, colonization is halted in the roots through the activation of a resistance response in the plant, preventing further ingress of the rhizome (Machardy and Beckman, 1981).

Once the fungus manages to move from the root into the rhizome, it can rapidly colonize the pseudostem through the formation of microconidia which are able to move quickly within the xylem vessels (Pegg et al., 2019; Trujillo, 1963; Machardy and Beckman, 1981). The upward movement of the fungus in the pseudostem is relatively quick, but the movement of microconidia upwards is restricted by perforation plates in the xylem. Recent research suggests that in addition to mycelial growth in the xylem, microconidia germinate, and their germ tubes facilitate passing through the perforation plates enabling recurrent conidia production for further upward movement (Warman and Aitken, 2018).

The pathogen acts more like a hemibiotroph during the early stages of infection, while it colonizes the vascular system in the pseudostem without causing external symptoms (Dita et al., 2018; Ploetz, 2019). However, at some stage, the plant starts to react to the invasion and tries to halt the fungus through the formation of gels, which enable the formation of phenolic compounds containing tyloses in an effort to contain the pathogen (Pegg et al., 2019). This process leads to the obstruction of the vascular system, which reduces the transport of water, resulting in the expression of external symptoms of water stress. Since bananas have a vascular capacity twice or thrice their need for growth, water stress symptoms only occur after significant progress of the disease and, hence, substantial reduction of water transport through the xylem vessels in the pseudostem (Beckman, 1990).

External symptoms of FWB include the formation of faint yellow streaks at the base of the petiole of the oldest leaf (Pegg et al., 2019) and chlorosis at the margins of the older leaves (Fig. 1a). These leaves eventually collapse at the junction of the petiole and the pseudostem, leaving a skirt of dead leaves draped around the plant (Fig. 1b). The pseudostem is also often split at the base (Fig. 1c). One of the most characteristic symptoms is the internal discolouration of the vascular system (Fig. 1d and e). Yellowish-to-brown and maroon-to-black lines may also be visible in the corm when cut (Fig. 1f). Discoloured vascular

Figure 1 Symptoms of Fusarium wilt in banana. (a) Yellowing and chlorosis at the margins of the oldest leaves; (b) leaves collapsed at the junction of the petiole and the pseudostem leaving a skirt of dead leaves draped around the plant; (c) splitting of the pseudostem at the base; (d) internal discolourations of the vascular system in the pseudostem; (e) close-up of vascular discolouration in the pseudostem; and (f) yellowish-to-brown and maroon-to-black lines in the corm when cut.

strands may also be visible in the rachis, and as a result of these combined symptoms affected plants rarely produce marketable bunches.

When the disease symptoms are fully expressed, and the banana plant is under significant water stress, the fungus also affects the parenchyma and the cortex and invades these tissues which are subsequently severely weakened. Here, large numbers of conidia and chlamydospores are produced and released into the soil when the plant collapses (Pegg et al., 2019). During the advanced stage of the disease, hyphae and sporodochia have also been observed protruding from stomata in the leaf sheaths, potentially providing an additional source of air and/or splash-borne inoculum (Warman and Aitken, 2018).

4 Efforts to manage Fusarium wilt of banana

4.1 Cultural control

The development of FWB in the field is to a large degree determined by the resistance level of the banana variety, the Fusarium race, and the environmental conditions prevailing in the plantation such as drought, flooding, heat stress and soil health, including microbial diversity and availability of nutrients as well as soil structure. Although the growth and proliferation of the pathogen occurs more rapidly under optimal conditions, the expression of FWB symptoms is accelerated under drought stress (Pegg et al., 2019). Drainage is important as wet soils and high rainfall have a negative effect on the production of bananas due to low oxygen levels in the soil, resulting in the death of root tips (Turner et al., 2007) and thus making them more prone to infection (Aguilar et al., 2000).

Optimal nutrition and appropriate fertilizer use promote plant health and development, which is important to maintain productivity. The use of nitrogen fertilizers and the pH of the soil have notable effects on the development of FWB (Simmonds, 1966). It has been observed for a long time that disease problems are higher in sandy soils with low pH. Disease-suppressive soils in Latin America tended to have a neutral or slightly higher than neutral pH (Stover, 1962; Segura et al., 2022). Hence, adjusting the pH to close to 7 was often recommended. Different soil types have been reported to have an impact on the development of disease in Central America. These soils were labelled at the time as 'short life' and 'long life' soils, and although there is a difference in the development of disease, it is not sufficient to control FWB (Stover, 1962). The mechanism behind what are now called suppressive soils has been a point of debate for a long time, and it is hypothesized that several abiotic soil factors affect saprophytic soil microflora which play a role in the suppression of soil-borne diseases (Cook and Baker, 1983; Mendes et al., 2011; Segura-Mena et al., 2021; Teixeira et al., 2021; Taniguchi et al., 2023). Although the management of nutrients in a plantation has an influence on the rate of development of disease, it is clear that changes in the pH and soil nutrients are not able to control FWB (Pegg et al., 2019).

4.2 Fallowing and crop rotation

Fallowing, either bare fallow or flood fallow, was trialled extensively in Latin America to revive FWB-affected plantations. Where possible in tropical lowlands, flooding reduced the pathogen population significantly but at the same time also reduced the populations of most microorganisms in the soil, creating a biological vacuum which was often quickly recolonized by Fusarium after the flood fallow period. In all cases, the pathogen population re-merged quickly after replanting with susceptible Gros Michel plants (Stover, 1962). It is unclear whether these infections were the result of spores which had survived in the soil or whether the fields were replanting with asymptomatic but infected plant materials. At that point in time, tissue culture of banana plants was not available, and hence only suckers from other plantations were used. Later research in Taiwan showed that 30–40% of asymptomatic suckers taken from an infected field harbour the fungus (Su et al., 1986). The flooding of thousands of hectares of infested land had large ecological and environmental impacts but did not result in effective long-term control (Stover, 1962).

4.3 Crop rotation and intercropping

Crop rotation is often used as an effective tool to reduce the impact of soil-borne diseases. However, in the case of FWB, the intercrop must be chosen wisely as it has been shown that rotation with, for example, sugarcane did not reduce disease incidence, while paddy rice reduced disease incidence significantly (Su et al., 1986). The use of groundcovers such as pinto peanut has been shown to have a small effect on disease reduction in the field (Pattison et al., 2014). From a productivity point of view, crop rotation and intercropping improve soil health and structure while reducing the population numbers of slow-multiplying pests, such as nematodes. Intercropping and vegetating the inter-rows also significantly reduce runoff and soil erosion, yielding significant environmental and sustainability benefits (Pattison et al., 2014). However, these factors are not sufficient to reduce the long-term impact of aggressive strains of the polycyclic causal agents of FWB in perennial banana plantations with very limited options for crop rotation (Ploetz, 2015).

4.4 Chemical control

Several soil fumigants have been trialled in the past with limited success, including methyl bromide against the so-called subtropical race 4, which is another Fusarium lineage, in South Africa (Herbert and Marx, 1990). Although some success has been achieved with annual crops, no effective control has been achieved in perennial crops such as bananas. Some results have been documented from India with the application of the highly systemic fungicide carbendazim (Lakshmanan et al., 1987). However, this product has now been banned in many countries around the world due to exposure risk.

Despite much research and screening of large numbers of products, it has recently been concluded that Fusarium wilts are in general not successfully controlled through the application of fungicides (Pegg et al., 2019). Fungicides may, however, play a role in eradication programs where symptomatic plants are injected in conjunction with a herbicide such as glyphosate, which is used to kill the plant and prevent any regrowth from the corm. However, it has been observed recently that the use of herbicides gives rise to senescence of the plant tissue which stimulates rapid colonization and the production of chlamydospores in the senescing plant tissues, thereby potentially increasing the inoculum load (Warman and Aitken, 2018; Pegg et al., 2019). Further research is needed to look at effective ways to kill banana plants while killing the fungus to prevent the accumulation of inoculum.

4.5 Biological control

Despite significant efforts over a long period of time and many claims of efficacy of biological control agents in laboratory or glasshouse environments, none have achieved effective control of FWD under field conditions (Bubici et al., 2019). There are many knowledge gaps in the development and application of biological control agents, and although some may reduce the incidence of disease to a certain degree, none have shown to be able to reduce the disease incidence to economic insignificant levels. Biological control is sometimes seen as a component of an integrated management approach, which comprises numerous different practices which collectively result in a significant reduction of the inoculum load in the soil and the incidence of disease to such a degree that a banana variety susceptible to FWD can be grown in a plantation setting (Dita et al., 2018). However, data from multiyear field trials to support such claims are not available (Bubici et al., 2019). A common problem is that there are unrealistic expectations concerning the efficacy of biological control agents for a polycyclic disease in a perennial crop like bananas. These production systems leave very little room for less-than-perfect efficacy, as even a low incidence of disease can quickly grow into an unmanageable problem. Although the efficacy of biological control agents and soil amendments is often backed up by experimental data, this is commonly obtained using potted banana plants over a short period of time, such that the data have little, if any, relationship to the efficacy one would experience in the field for this polycyclic disease in a perennial crop with a lifespan of 5 years or more (Ploetz, 2015).

4.6 Exclusion

Due to the difficulty in managing FWB using chemical, cultural or biological control, there are only a few alternatives left. Experience over the last century has shown that there are presently only two effective ways to control the disease. The first is exclusion of the pathogen and the second is large-scale deployment of effective resistance.

Preventing the introduction of the pathogen relies on a range of different activities and strategies to be able to enjoy producing bananas in the absence of the pathogen. The benefits of not having a disease, called exclusion benefits, have been calculated for a number of banana diseases in Australia, including FWB caused by TR4 (Cook et al., 2015). The value of the concept of exclusion benefits is to highlight the importance of the obvious fact that a disease is easiest to manage if you do not have it. It reflects the economic benefits of the absence of disease and gives insight into the financial benefits of quarantine and exclusion methods. However, the age-old problem with exclusion approaches has always been a poor understanding of risk in many industries and deploying scarce resources to prevent problems not yet experienced by industry or consumers. The authors of this chapter have observed that every plant disease starts somewhere small and at that point is ignored as it is of no significance. A little more attention is paid when the disease starts causing problems at a regional level somewhere in the world, at which stage it is often classed as an emerging disease. At this stage, investment – if any – in the disease problem is still very low as it is considered not a major problem. Once the disease starts spreading to multiple locations, a bit more attention is paid to the disease in the form of meetings and raising awareness, but resources to study the mode of spread and epidemiology of the disease are hard to come by. The next stage is an invasion of the pathogen in a country with a major production base at which point more attention is paid and some resources are allocated to research focussed on finding ways to ‘manage’ the disease, while little to no attention is paid to the epidemiology and eradication of the pathogen. Only when a disease starts spreading in a major production area and has some serious impact on production, industries push the panic button and resources start to flow to solve the problem, at which point it is too late and the growers have to deal with the consequences of a pathogen like FWB. This scenario has played like a broken record again and again in almost all banana-growing countries with regard to almost all banana diseases with disastrous consequences with regard to FWB caused by race 1 in the past and by TR4 at present (Drenth and Kema, 2021).

Exclusion can be implemented at different levels such as continent, country, regions, individual plantations and blocks within a plantation. The best approach is to have exclusion strategies in place at all levels, but this is often difficult. Often the exclusion is active one level below from where FWB is.

The spread of FWB in Taiwan has been studied in great detail (Su et al., 1986) and used as a recent case study (Pegg et al., 2019). Since FWB is a polycyclic disease with many generations during the production cycle, the progress of its epidemic spread follows a sigmoid disease progress curve. Considering this, it is very important to keep the amount of available inoculum as low as possible to keep the development of the disease in the lag phase.

Keeping the inoculum as low as possible and preventing further spread of the disease can be managed in a number of different ways. The recent experience after the invasion of TR4 into North Queensland in Australia has been to destroy the initial plantation and take out of production the whole plantation at this initial stage of invasion. The next phase involved taking out of production whole blocks when an infection was found on a second plantation. The reason for removing whole blocks, and not only a small section, or circle, around symptomatic plants is that the absence of symptoms in a block does not mean the absence of disease. The incubation period of the pathogen in bananas is quite long, especially at low levels of inoculum. While in the past, neighbouring plants in a circle may have been removed within a certain distance of the infected plants, this approach does not make a lot of sense in modern plantations with mechanized traffic in the inter-rows with tractors and other machinery which will effectively increase the risk of moving the pathogen along the rows and not between rows. The exclusion approach described earlier has slowed the spread of TR4 in Northern Australia significantly.

The destruction of infected plants to prevent the further spread of the pathogen has not been investigated in great detail and in some cases has given rise to the spread of the pathogen. Early attempts involved burying infected pseudostems (Su et al., 1986), which turned out to be very labour intensive and ineffective. In some cases, growers in Taiwan disposed of affected pseudostems by throwing them in irrigation ditches and thereby exacerbating the problems. In other countries, methods used for control of the bacterial wilt disease Moko, such as rice hull burning, were recommended (Molina et al., 2010). These recommended methods were untested and, due to insufficient heat penetration at depth and the handling and movement of plant material, people and soil, have been shown to be ineffective (Ploetz, 2015; Ploetz, 2019; Salacinas, 2019).

It is interesting to note that after more than a century of FWB invasions in banana plantations involving three different races, no highly effective destruction methods have been developed and tested which could be used to contain the disease. In the past, benzimidazole fungicides, including benomyl and carbendazim, which are highly systemic, have been shown to have an effect in the field (Lakshmanan et al., 1987) but are banned in most countries around the world for health and safety reasons. Although several fungicides are quite effective at inhibiting the growth of *Fusarium in vitro*, such as prochloraz and propiconazole, they have shown to be ineffective under field conditions, most likely due to their lower level of systemic ability within the banana plant.

A local exclusion strategy is currently being implemented in North Queensland, Australia. In 2015, TR4 was detected on one farm on which the plants were eradicated and the whole farm was taken out of production to reduce the risk of further spread. Following this, a schedule of inspections on nearby or connected farms was implemented. This system relies on the early detection of infected plants through regular surveys and testing of plants showing even the slightest wilting symptoms. If testing yields a positive result, the plant and a certain number of surroundings plants or in some cases whole fields are injected with a herbicide to prevent further production of inoculum and release into the soil. The positive plant and its immediate neighbours are carefully cut up above soil level and placed in strong plastic bags to prevent inoculum release in the environment. The plants are not dug up to prevent disturbing the soil and erosion during heavy rain, but the rhizome is gouged out and urea is placed in the cavity to promote decomposition. Urea is then applied in a high dose to the affected area prior to covering it with a strong plastic sheet. Urea is added in a high dose to the soil (1 kg/m^2) and to the bagged plant material as urea produces volatile ammonia after hydrolysis by urease, an enzyme which is present in many soil-borne organisms, root tips of bananas and Fusarium itself (Sequeira, 1963). In addition to the short-term production of ammonia, the accumulation of nitrite has also been shown to have an antifungal effect (Löffler et al., 1986). This method has been used to slow the spread of TR4 in North Queensland with some success as after 6 years the disease has only spread a small distance to some neighbouring plantations (Pegg et al., 2019).

5 Why is Fusarium wilt of bananas so difficult to control?

The epidemic of Fusarium race 1 in Gros Michel and the TR4 epidemic in Cavendish have made it clear that effective control of FWB in susceptible cultivars in a large-scale monoculture plantation environment is not achievable using biological, chemical or cultural measures (Pegg et al., 2019). In some other crops, Fusarium wilt can be managed, which raises the question of what the biological as well as anthropogenic reasons are behind this apparent inability to manage FWB in bananas. In this regard, we like to make the following statements:

1. The ability of a very small number of spores to start an epidemic in a perennial banana crop;
2. The presence of a polycyclic disease in a perennial cropping system requires a very high level of efficacy of any control measure to be effective over the life of a banana plantation;

3 The inability to eradicate Fusarium from the soil once an infestation has taken place;
4 A very long period of time an infested field remains contaminated. It has been reported that even after 40 years the soil is still infectious due to the ability of the causal fungus to survive in the soil short term as conidia and long term as chlamydospores in dead plant tissues or as an endophyte in a wide range of grasses and weeds which then act as a reservoir of inoculum over many years (Pegg et al., 2019; Ploetz, 2015);
5 The relatively long incubation time which enables the fungus to multiply in the plant without any external symptoms, thereby escaping early detection;
6 The ability of the fungus to be present in asymptomatic suckers which may be used as planting material;
7 The inability of intercropping to significantly reduce the disease incidence;
8 The ineffectiveness of soil fumigants to reduce the inoculum load in the soil. The fungus is present in the xylem of the banana plant and chlamydospores are produced in large numbers high in the pseudostem. These spores are encapsulated in the decaying plant tissue, which often renders soil fumigation ineffective. In addition, the spores can survive at depth in the field and start a new epidemic which means that options such as soil fumigation, solarization, anaerobic soil disinfestation, chemical fumigation and biofumigation have typically not been effective;
9 Underestimation of the impact of this soil-borne disease. The often small and local initial infection is not dealt with effectively as it is seen as a manageable problem by some in the industry until it keeps growing and destroys the industry in whole regions or countries. Clearly, the lessons from the impact of the race 1 epidemic have not been heeded nor enacted upon, such that we are repeating history;
10 The lack of effective eradication strategies once an invasion has taken place;
11 The lack of genetic diversity and absence of resistance to race 1 and TR4 in large-scale monoculture plantations of first Gros Michel and then Cavendish, respectively. Combined with an industry supply chain focused on a single banana variety this leads to an extremely high level of genetic vulnerability to existing and emerging pathogens, spreading around the world at an ever-increasing pace; and
12 The underinvestment in research in pathology, genetics and breeding at a global level has given rise to last-minute disaster management after

the invasion of a new pathogen has taken place. Research with a much longer delivery horizon is required to stay ahead of the pathogens.

6 The solution that created a future problem

The race 1 epidemic in Latin America gave rise to research into managing FWB with the aim to continue to grow a susceptible variety such as Gros Michel. As remarked by the United Fruit scientist John Johnston in 1923 'after 20 years of study and treatment, using all the customary methods used in the practice of disease control, have failed to yield a solution to the problem of Panama disease' (Soluri, 2005). The lack of effective control options led to the ongoing spread of the pathogen and the banana producers continually moving to new land, resulting in great economic, environmental and social costs. Based on the results from soil-based experiments on previously abandoned plantations, the United Fruit scientist Dr Vining Dunlap started a series of experiments using flood fallowing in 1939. After he claimed some initial success with this method, extensive flood-fallowing operations commenced in Honduras and elsewhere on thousands of hectares (Soluri, 2005).

Since managing FWB in plantations had failed, the only option at hand was shifting the cultivation of Gros Michel to new un-infested land. This strategy bought some time but ultimately failed due to the inability to secure clean land, the continuous recurrence of FWB in these new plantations and the increasing costs of infrastructure. A resistant replacement was needed, and the banana industry was looking for a banana variety that is resistant to FWB, has a high yield, has a long green life of the fruit enabling long-distance transport and is acceptable to the consumer. The first modest trials with the variety 'Cavendish' took place by the Standard Fruit company in 1943, and although there was excellent resistance to FWB, the bunches did not ripen naturally and required temperature control and the use of ethylene gas to ripen properly. It took until 1956 before Standard Fruit made the decision to convert all of its production to Cavendish. Initial market acceptance was poor, prices were low compared to Gros Michel and the thin-skinned Cavendish bananas suffered badly from bruising during transport. Although already used since the 1930s, boxes were introduced, and the fruit was cut, de-handed, washed and cooled in the plantation in packing sheds prior to shipping to overseas markets where self-service supermarkets preferred this new boxed product. The United Fruit company followed Standard Fruit's move to Cavendish 3–4 years later due to the increased costs of finding new clean land to grow Gros Michel (Soluri, 2005).

Although this switch from Gros Michel to Cavendish stopped the FWB problem in the short term, the intrinsic vulnerability of growing a single clone in monoculture on a global scale was not addressed and no diversification took place. This led one of the leading banana researcher at the time, Dr Harry

Stover, to state that the banana industries 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' (Stover, 1986).

7 The rise of Fusarium wilt in bananas caused by tropical race 4

It is of interest to note that since Stover's statement the vulnerability of Cavendish plantations is under the spotlight again. Before this statement was made, plantations of Cavendish in Taiwan were already succumbing at an alarming rate to FWB caused by a new strain of the fungus (Su et al., 1977; Su et al., 1986) which soon started spreading in Southeast Asia and was devastating newly established Cavendish plantations in Indonesia and Malaysia and given the designation Tropical Race 4 (TR4) (Pegg et al., 1993). Soon after, this new race was found in China (1996), Northern Australia (1997), Philippines (2005) before it was found further afield in the Middle East (Lebanon, 2012), Africa (Mozambique, 2013) and Latin America (Colombia, 2019; Peru, 2021; Venezuela, 2023) (Drenth and Kema, 2021; Viljoen et al., 2020; van Westerhoven et al., 2022). Unfortunately, this time no clear replacement variety is waiting in the wings. At present, investments are being made to revive breeding programs and into novel techniques to engineer disease resistance which are undergoing field testing and are awaiting consumer acceptance (Dale et al., 2021).

8 The strong arm of resistance

The resistance of Cavendish against race 1 is durable. It has endured and has never been broken through mutations in race 1 strains, despite the huge selection pressure. Hence, resistance against FWB is extremely stable and durable. It is not the versatility of Fusarium which is causing the current problems, but the emergence and spread of a new strain that may have been existing for quite some time in the centre of origin (Ordonez et al., 2015; Maryani et al., 2019). In effect, it is now known that the strain affecting Cavendish may be considered a new species, *Fusarium odoratissimum* (Maryani et al., 2019). In the centre of origin, new pathogenic strains are expected to evolve and be able to successfully colonize the seeded wild bananas growing throughout the jungles of Southeast Asia. It has been hypothesized that this arms race with the host maintains sexual recombination in fungi under the red queen hypothesis originally stated in 1973 (Van Valen, 1973). Although it was long believed that FWB-causing Fusarium fungi are reproducing strictly asexual, recent research using multiple genome comparisons has shown that mating types are present and that sexual reproduction occurs within many phylogroups of Fusarium (McTaggart et al., 2021). Conclusions concerning the mode of reproduction are often based on fungi collected during disease outbreaks which significantly skew the data in favour of asexual reproduction while ignoring the process of sexual reproduction which most likely created these clones in the first place (Drenth et al., 2019).

Breeding of bananas started a century ago in 1922 in Trinidad and was aimed at creating a Gros Michel resistant to FWB (Wardlaw, 1961). At present there are 12 banana breeding programs around the world (Smith and Pillay, 2021), and different breeding objectives, strategies and approaches are being used from conventional breeding strategies involving evolutionary approaches (Amorin et al., 2021), reconstructive approaches (Bakry et al., 2021) as well as unconventional approaches involving somaclonal selection (Khayat, 2021), private and public genetic modification efforts (Dale et al., 2021).

Somaclonal variation has also been extensively exploited in bananas and has given rise to shorter-stature plants, improved fruit quality and higher productivity. The continuous selection of somaclones of Cavendish in many subsequent rounds has also given rise to clones with reduced susceptibility to TR4. The Taiwan Banana Research Institute has had some success with this approach, and several Giant Cavendish Tissue Culture Variants (GCTCV) clones have been produced over the years, such as GCTCV 218 (Formosana) and GCTCV 219 (Hwang and Ko, 2004). However, these plants are often taller and have a longer crop cycle and some have poor bunch characteristics. Although they are less susceptible to TR4, they still succumb to the disease and may in effect make it worse long term by multiplying the amount of available inoculum in the soil. In the belief that they have solved the problem, growers stop active removal of infected plants and continue business as before, which worsens the situation. As such, these somaclonal variants may at best produce a short-term solution to the problem. The other point to make here is that banana growers have to be careful that no planting material is taken for propagation from these as the fungus may still invade this material and thus may lead to the further spread of FWB and in effect make the problem bigger instead of smaller.

The race 1 epidemic in Latin America stimulated foundational breeding programs (Smith and Pillay, 2021) (Martínez de la Parte, 2023, Chapter 4, this volume). First, breeding started in Trinidad at the Imperial College of Tropical Agriculture where wild bananas were crossed with Gros Michel (Wardlaw, 1961). The United Fruit Company started its own breeding program in Honduras in 1959, and after a significant amount of pre-breeding among several diploid bananas several varieties were bred. However, acceptance of varieties from these programs has been minimal. Other breeding programs started after the introduction of black leaf streak disease in Africa.

The combination of a tropical crop cultivated by subsistence farmers and by large companies for export, the sterility of the existing varieties and the standardization of the supply chain since the 1960s focussed on Cavendish has led to stagnation on the variety improvement front and a lack of research funds for genetics and pre-breeding. Products from breeding programs make up a very small percentage of global production, and both Gros Michel and Cavendish did not arise from breeding programs but are very old landraces, identified at least 200 years ago, but potentially a lot longer, by Asian farmers in tropical rainforests. If breeding is to be successful, novel genetic approaches and wild banana germplasm need to be explored and investigated in much greater detail.

9 Conclusion

The expansion of large plantations to produce bananas for export based on a single variety, first Gros Michel, followed by Cavendish over the twentieth century, combined with increases in travel and trade and movement of plant material has given rise to the global spread of pathogens such as Yellow Sigatoka and Black leaf streak disease and FWB caused by race 1 and more recently by TR4 (Drenth and Kema, 2021). Due to the uniformity of the banana crop in most parts of the world and the lack of diversification, an extreme level of genetic vulnerability has been created which now risks derailing the global banana industry.

Over the last century, several major banana diseases, either originating from the centre of origin or new encounter pathogens, such as Moko in Latin America, have invaded many banana-growing regions around the world and have added significant costs, in the form of labour and agrochemical inputs, to the production of bananas (Soluri, 2005). However, unlike some of the other pathogens such as bacterial wilts (Blomme et al., 2017) and foliar diseases such as Black leaf streak (Guzman et al., 2019), there are no effective short- or long-term solutions to dealing with FWB in perennial banana plantations. Hence, the only effective options are exclusion and/or resistance. Exclusion has been effective for a significant amount of time to contain race 1 and TR4 to areas close to its centre of origin, but the overall lack of concerted action prior to the arrival of the disease has resulted in the spread of TR4, first within Asia, then to Australia, the Middle East, Africa and recently to Latin America. Now that the FWB TR4 pathogen has established itself in all banana-growing continents, it will continue to spread locally following the bridgehead effect (Drenth and Kema, 2021; Lombaert et al., 2010).

The impending spread of TR4 must be slowed down as at present no effective resistance exists in market-acceptable banana varieties. The lack of well-characterized germplasm and research in genetics and pre-breeding by industries and large producing and consuming countries has become very evident. The conservatism across the industry and its auxiliary stakeholders is remarkable, considering the impact of past plant disease epidemics in bananas (Drenth and Kema, 2021) and the global importance of the crop. Compared to other crops of similar economic significance, banana truly can be considered as an orphan crop when it comes to the genetic research effort.

An overview of genetic improvement in bananas has recently been published (Smith and Pillay, 2021). In addition to genetic improvement through classical plant breeding methods (Amorin et al., 2021) and reconstructive hybridization approaches (Bakry et al., 2021), other approaches are currently being explored such as mutagenesis and selection for resistant somaclonal variants (Khayat, 2021), as well as identifying and inserting resistance genes into Cavendish using a genetic modification approach through insertion of a resistance gene (Dale et al., 2021) or gene editing (Wang et al., 2020). All these public and private approaches are warranted to overcome the current TR4 pandemic.

10 Where to look for further information

- A good introduction and background to bananas and their production and fusarium wilt in bananas can be found at the Promusa website: https://www.promusa.org/Fusarium+oxysporum+f.+sp.+cubense.
- A series of research articles on the spread of fusarium wilt, epidemiology, detection and control options has recently been published as an e-book: Kema, G. H. J., Drenth, A., Dita, M., Jansen, K., Vellema, S. R. and Stoorvogel, J. eds. (2021). *Fusarium wilt of Banana, a Recurring Threat to Global Banana Production*. Lausanne: Frontiers Media SA. doi: 10.3389/978-2-88966-484-9. https://www.frontiersin.org/research-topics/7653/fusarium-wilt-of-banana-a-recurring-threat-to-global-banana-production#articles.
- Wageningen University hosts a website which provides insights and links to much of the current Fusarium research in bananas: https://fusariumwilt.org/index.php/en/about-fusarium-wilt/.

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