

**Panamerican Agriculture University, Zamorano**  
**Science and Agricultural Production Department**  
**Agricultural Engineering**



Special graduation project

**Epidemiology and management of *Fusarium oxysporum* f.sp. cubense**  
**tropical race 4: Literature Review**

Student

Dianna Christine Palma

Advisors

Carolina Avellaneda, Ph.D.

Julio Lopez, M.Sc.

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**Authorities**

**TANYA MÜLLER GARCÍA**

Rector

**ANA MARGARITA MAIER ACOSTA**

Vice President and Academic Dean

**ROGEL CASTILLO**

Department of Agricultural Science and Production Director

**HUGO ZAVALA MEMBREÑO**

General Secretary

## Content

List of Figures.....	5
List of Annexes.....	6
Abstract.....	7
Resumen.....	8
Introduction.....	9
Materials and Methods.....	11
Search Strategy.....	11
Inclusion and exclusion criteria.....	11
Literature Review.....	12
Geographical distribution.....	12
Taxonomy/Genetic Diversity.....	13
Dispersion.....	15
Biology/Ecology.....	16
Symptoms.....	18
Alternative hosts.....	20
Influence of climatic and soil factors.....	21
What are banana – producing countries doing?.....	22
Biological management.....	23
Chemical management.....	24
Resistant cultivars.....	25

	4
Conclusions.....	28
Recommendations.....	29
References.....	30
Annexes .....	41

**List of Figures**

Figure 1 Geographical distribution of <i>Fusarium oxysporum</i> f.sp. <i>cubense</i> .....	13
Figure 2 Life cycle of <i>Fusarium</i> wilt in banana .....	17
Figure 3 Infected plant vs healthy plant (internally).....	19
Figure 4 External symptoms (leaf wilting).....	19
Figure 5 Internal brown to red brick discoloration of the vascular system.....	20
Figure 6 Transgene expression cassettes and Southern analysis of selected transgenic lines.....	26
Figure 7 Comparison between the regular Cavendish vs the resistant transgenic lines in terms of symptoms.....	27

**List of Annexes**

Annex A Lineages based on phylogenetic inference and morphological observations.....	41
Annex B Alternative hosts of Foc TR4.....	42

### Abstract

Wilting in banana plantations caused by the fungus *Fusarium oxysporum* f.sp. *cabense* has generated massive losses over the years. So far, the fungus consists of 4 races, being race 1 the one that caused 100% losses to the Gros Michel variety and for this reason the Cavendish hybrid was introduced (not susceptible to race 1). Today this cultivar is threatened by race 4 (tropical or subtropical). There is no effective treatment to destroy this particular race. Currently, an integrated management is being implemented with different strategies adapted to all kinds of situations in the banana areas. For these measures to be effective, whether for prevention or management, it is important to understand the epidemiology of this fungus. This literature review compiled information in order to understand the evolution that the fungus has had over the years, emphasize the impact generated by climatic and edaphological factors and state the different prevention and management strategies such as biosecurity, chemical, biological and varietal control. Each of these points contributes to improved management. Based on the information collected, it was concluded that the evolution of *Fusarium oxysporum* f.sp. *cabense* influences the severity of the Foc R4T attack and the dispersal process should be a prioritized factor, as well as the management and prevention techniques for decision making.

*Keywords:* Epidemiology, Foc race 4, management, prevention, wilting banana.

## Resumen

Marchitez en plantaciones de banano causado por el hongo *Fusarium oxysporum* f.sp. *cubense* ha generado pérdidas masivas a lo largo de los años. Hasta el momento el hongo consta de 4 razas siendo la raza 1 la que causo pérdidas del 100% a la variedad Gros Michel y por esta razón se introdujo el uso de híbrido Cavendish (no susceptible a raza 1). Hoy en día este cultivar está amenazado por la raza 4 (tropical o subtropical). No existe un tratamiento eficaz para destruir esta raza en particular. Actualmente se está implementando un manejo integrado con diferentes estrategias adaptadas a todo tipo de situaciones en las áreas bananeras. Para que estas medidas sean efectivas, ya sea para la prevención o el manejo, es importante comprender la epidemiología de este hongo. Esta revisión de la literatura recopiló información con el fin de comprender la evolución que ha tenido el hongo a lo largo de los años, enfatizar el impacto generado por factores climáticos y edafológicos y presentar las diferentes estrategias de prevención y manejo tales como la bioseguridad, control químico, biológico y varietal. Cada uno de estos puntos contribuye a mejorar el manejo. Con base a la información recolectada, se concluyó que la evolución de *Fusarium oxysporum* f.sp. *cubense* influye en la severidad del ataque de Foc R4T y el proceso de dispersión debe ser un factor priorizado, así como las técnicas de manejo y prevención para la toma de decisiones.

*Palabras claves:* Epidemiología, Foc raza 4, manejo integrado, marchitez del banano, prevención.



## Introduction

The banana industry is one of the leading exploited crops worldwide. According to FAO's Banana Market Review 2019, global exports of bananas, excluding plantain, reached a new record high of an estimated 21 million tons in 2019, an increase of 10.2 percent compared with 2018, having one hundred and thirty-five countries involved in the banana industry (FAOSTAT 2018). In 2019, the leaders in banana production were India (largest producer of bananas worldwide (Thangavelu et al. 2019)), China and Indonesia with 30,460,000 tons, 11,998,329 tons and 7,280,659 tons respectively (kneoma 2019).

Although India is the largest producer, the majority of its production is for internal consumption, making Ecuador the largest exporter worldwide. In addition, The United States of America and European Union are the top importers of banana (Tridge 2021). Among the most cultivated subgroups of bananas worldwide, Gros Michel was the most commercialized due to its sweetness and richness. Up until the 1950's, it was replaced by the Cavendish since it was susceptible to strains of *Fusarium oxysporum* spp. Tropical race 1. Both subgroups derive from the diploid hybrids of *Musa acuminata* (A-genome) alone (Perrier et al. 2011).

Therefore, all plants springing from them are clones of the parent plant. Cultivars of Cavendish such as Grande Naine, Williams and Valery are the ones that currently dominate the international trade with approximately 47% of the total production (Thierry L 2015). Despite these common groups, there are also other cultivars which are exploited differently depending on the region and their morphological classification. They are usually classified by height and color of the pseudostem, nature of the leaves, color, form, and position of the stigma, type and orientation of the bunch, length of the peduncle, form, size, number, and curvature of the fruit and presence of seeds (INIBAP 1996), and even their disease and insect resistance (Ayala-Silv et al. 2008).

Among the main phytosanitary limitations in the production of musaceae are Moko disease (*Ralstonia solanacearum*), Black Sigatoka (*Mycosphaerella fijiensis*) and specifically Fusarium wilt

(*Fusarium oxysporum* f.sp. *cabense*) (Dita et al. 2010; Zheng S-J et al. 2018) . Races of *Fusarium* have been evolving from the 1870's up until now, but they do not differ morphologically. There are four races of the pathogen, where race 1 (R1) attacks clones of the subgroups Silk (Banana Manzano, Musa AAB) and Gros Michel (Musa AAA). Race 2 attacks clones of the Bluggoe subgroup, and Race 4 with its tropical (R4T) and subtropical (R4ST) variants, attack all clones of the Cavendish subgroup (Moore N et al. 1995; Pérez-Vicente 2004; Dita et al. 2018). To date, no effective TR4 management methods and no alternative commercial banana clones resistant to the pathogen are known (Ploetz 2015b). Therefore, understanding the evolution the fungus has had from its first to most recent incursion, emphasizing the impact generated by climatic and soil factors and being able to implement the different prevention and management strategies against TR4 should be the major aspects to consider *Fusarium* knowledge.

## **Materials and Methods**

### **Search Strategy**

This study, using a systematic review method without meta-analysis, was carried out between March-May 2021. Articles relevant to Fusarium wilt in Musaceae were selected from recognized scientific bases such as Research gate, Pub Med, Science Direct, SciELO, and pages from the Food Agriculture Organization (FAO) to have reliable information with scientific value. Information was also obtained from the official phytosanitary organization web pages of countries like Costa Rica and Australia. Key words such as *formae speciale cubense*, race 4, management, epidemiology, and prevention were used to acquire the most specific and relevant information.

### **Inclusion and Exclusion Criteria**

In order to gather as much information as possible, articles were selected from scientific literature from 1962 to the present year (with an exception of one article from 1876), these articles being majority in English, followed by Spanish. The selected information came mainly from scientific bases, but information from gray literature was also included. Articles about race 1 were partially excluded.

## Literature Review

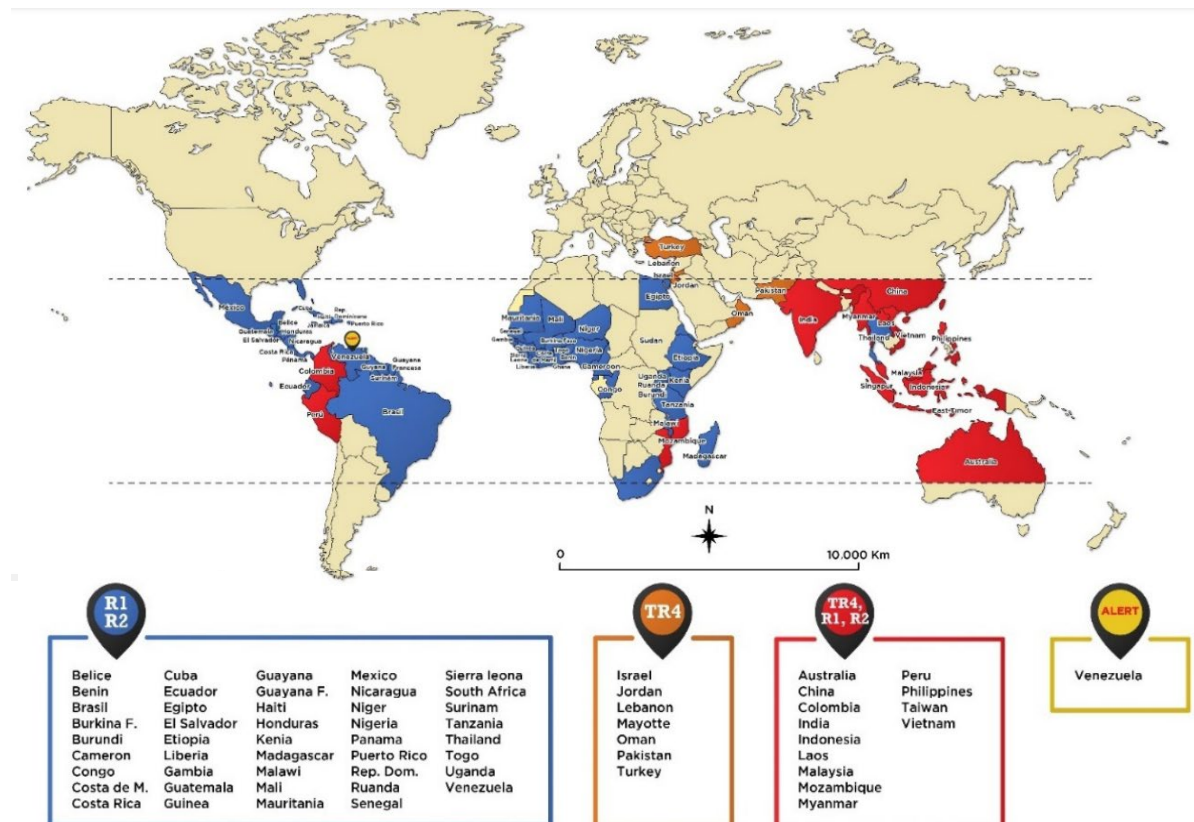
### Geographical Distribution

The Foc geographical regions vary slightly among Race 1 and 4 (Figure 1). The first incursion of Fusarium was reported in Southern Queensland in 1874 (Bancroft [date unknown]). In the early 1920s, there were reports of infected plantations in the Canary Islands, South and West Africa (1924) and Taiwan (Stover 1962; Viljoen 2002; Hwang and Ko 2004). The massive loss generated by Race 1 in the Gros Michel plantations (non-resistant) called for a substitution by a resistant breed, being this the Cavendish cultivars. However, Fusarium wilt evolved throughout the years into different races, one of which was destructive for Cavendish. Fusarium wilt caused by Tropical Race 4 first arose in 1967 in Taiwan, and due to the active movement of vegetative material, most likely infected, Indonesia followed on infected areas by Race 4 (Hong J.S 1986; Hwang and Ko 2004).

Geographical distributions of Fusarium not only provides a mapping tool, but also has influence on how aggressive the strains might be. The Asian Foc strain made its first strikes in Indonesia and Malaysia in the 1990s (Ploetz 2006). The incursions where afterwards more frequent: Northern Territory, Australia, 1997 (Moore N et al. 1995), Jordan (official report), Lebanon (García-Bastidas et al. 2014; Ploetz 2015a), and Mozambique (northern area) (Viljoen et al. 2020) in 2013 and 2016 respectively, and later from Israel in 2016 (Maymon et al. 2020). Since then the disease has spread throughout India, Pakistan ((Butler D 2013), ((Zheng S-J et al. 2018), Laos, Myanmar, Vietnam, and Cambodia (Zheng S-J et al. 2018) and Chinese provinces (Fujian, Guangdong, Guangxi, Hainan and Yunnan) (Hong J.S 1986; Qi YX. et al. 2008; Buddenhagen 2009; Li et al. 2013). Australia is well known for biosecurity measures to reduce dissemination, but had outbreaks in Queensland in 2015 (O'Neill et al. 2016). The American continent was TR4-free until 2019 with a case reported in the northern coastal region of La Guajira, Colombia (García-Bastidas et al. 2020). Recently, the Peruvian National Service of Agricultural Safety (SENASA) officially confirmed the presence of Fusarium Tropical Race 4 (TR4) (FAO 2021).

Figure 1

Geographical distribution of *Fusarium oxysporum f.sp. cubense*



Note. Taken from (Olivares et al. 2021)

### Taxonomy/Genetic Diversity

*Fusarium* wilt, also known as Panama disease, is a soil-borne fungus that attacks the vascular system of its host. *Fusarium oxysporum* has 106 *formae speciales* that are officially described, each with evolving races that vary depending on the host (Edel-Hermann and Lecomte 2019). In this case, *formae speciale cubense* affects primarily the Musaceae family. *Fusarium* wilting composes evolutionary lineages and races based on the pathogenicity in certain hosts. Races of *Fusarium* have been evolving from the 1870's up until now, but they do not differ morphologically. This evolution

includes four races in which the fourth Race has both tropical and subtropical populations/variants (Ploetz 2006).

Race 1, responsible for the massive loss on Gros Michel's plantations, also affects Maqueno (AAB), Silk (Manzano/Apple/Latundan), Pome (AAB), and Pisang Awak (ABB) (Ploetz 2005). Race 2 does not affect Gros Michel, but does cause problems to cooking bananas and plantains like Bluggoe (ABB) (Baimey et al. 2020). Race 3 has the least impact in the banana industry since it can only be hosted by *Heliconia* spp (tropical American banana relative) (Simmonds and Stover 1987). Contrary to this, Race 4 Foc is considered the most virulent group since it causes mortality on all Cavendish cultivars and also race 1- and race 2-susceptible varieties (S. K. Leong et al. 2010).

The main difference between the two variants of Race 4 is that SR4 causes disease in Cavendish only in the subtropics, while Foc TR4 is pathogenic under both tropical and subtropical conditions (Buddenhagen 2009; Mostert D et al. 2017). TR4 is more aggressive than STR4 (Ploetz 2006; Buddenhagen 2009). A further division to these variants is Vegetative Compatibility Groups (VCGs). Up until 2017, at least 24 vegetative compatibility groups (VCGs) that can affect *Musa acuminata*, *M. balbisiana*, *M. schizocarpa*, and *M. textilis* (Musaceae: Zingiberales; (Ploetz 2015b) were identified. Sub-Tropical race 4 has various VCGs, whereas Tropical race 4 has one re-known VCG (01213/16) conditions (Buddenhagen 2009; Mostert D et al. 2017) indicating its uniformity (O'Neill et al. 2016).

Several studies on clustering and subsequent phylogeographic relationship among isolates, revealed that the origins of related populations can be associated with that of the genetic relatedness. For example, isolates from Pakistan were closely related to those from the Philippines and those from Lebanon were genetically related to those from Jordan (Maymon et al. 2020). These studies do not provide information as the possible source of the strains but gives an idea as to how similar the different geographical strains are. In the case of Colombia, its isolates clustered with the representative isolate from Indonesia, evincing the possible source of incursion in South America (Maymon et al. 2020). In 2019, a phylogeny and genetic diversity study was done on the banana

Fusarium wilt pathogen *Fusarium oxysporum* f. sp. *cubense* in the Indonesian Centre of origin they were classified into nine major lineages as shown in annex 1 (Maryani et al. 2019) (annex 1).

### **Dispersion**

The major route of dispersion of this fungus is through its reproductive structures. Although these structures are main source of scattering, this process occurs in many ways. The distribution has more commonly been due to the introduction of new cultivars in growing areas (Stover 1962) or products from Musaceae-based material, meaning the movement of vegetative material due to anthropogenic activities (Pérez-Vicente 2004). The propagules can be move both short and long distances, not only by human activity (movement of contaminated plants, particles of soil in shoes, clothes, vehicles, etc) but also, contaminated water and substrates, movement of wild and domestical animals (including insects) and wind (Dita et al. 2018). In China, dissemination has been frequently by infected plant material and irrigation water from the river sources (Xu L. B et al. [date unknown]). Rotation of farm workers between plantations is also a common cause in neighboring farms (Viljoen et al. 2020). Natural phenomena like strong winds and severe flooding (runoffs) are hardly controllable and thus increasing further dispersal. In the case of plant material, higher emphasis is needed since an infected mother plant is able to transfer the structures to the suckers, which typically remain symptomless due to the long latent period of the disease (Stover 1962). Neighboring communities and sometimes a living campus for workers in the plantation can also contribute to farm-to-farm dissemination since domestic animals are considered vectors of the disease (Biosecurity of Queensland, 2016). In terms of wild animals, in this case insects the banana weevil borer, *Cosmopolites sordidus* (Germar; Coleoptera: Curculionidae), widespread in banana plantations, is the most important insect pest of bananas and plantains (Gold 2001) and also studies in Australia showed the presence of viable spores on their exoskeletons (Meldrum et al. 2013). Although nematodes (*Radopholus similis*) is not a vector, the wounds caused by the its penetration to the roots process

creates an easier entry for the fungus (increases intensity of the disease) (Dinesh B. M et al. [date unknown]; Somu 2012; Dita et al. 2018).

### **Biology/Ecology**

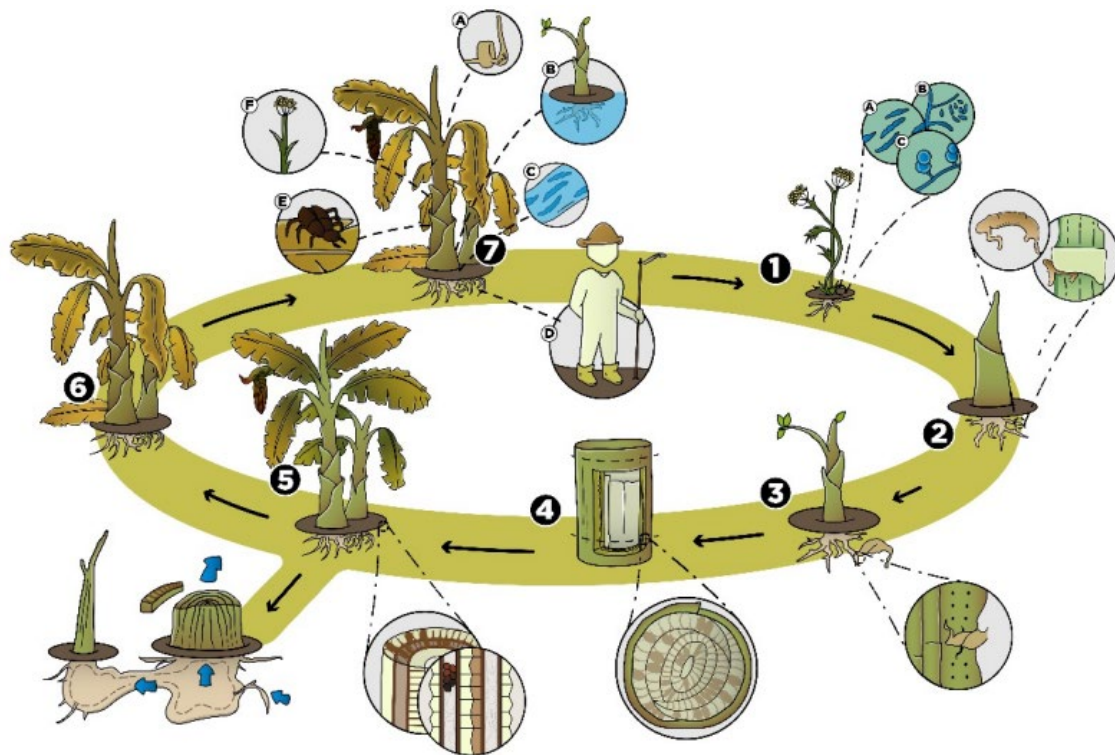
The optimum temperature for the development of *Fusarium oxysporum* is 25-28 ° C and the growth is inhibited when the temperature is close to 33 ° C and is not favorable below 17 ° C (Cook and Baker 1983). The colonization route of this pathogen is through the vascular pathways starting from the roots (Zhang L et al. 2018), and contrary to what is usually expected, the infection travels through the secondary or tertiary feeder roots, not the main root (Trujillo E. 1963). Its life cycle consists of three reproduction structures that represents certain aspects that make this fungus uncontrollable: macro and micro conidia and chlamyospores. The chlamyospore structures are of more relevant since they have the capacity of resisting any unfavorable condition (Stover 1962), and are able to survive in the absence of a primary host for decades, mainly because they form a thick-walled spore (Stover 1962); (Leslie and Summerell 2006). Consequently, there is a limitation in the establishment of new plantations. According to the study held in Mozambique about the occurrence and spread of Foc TR4, micro conidia were produced abundantly in false heads on short monophialides, and macro-conidia were produced sparsely in sporodochia. Single or pairs of chlamyospores were formed inside hyphae or macro-conidia after 10–14 days (Viljoen et al. 2020). In the actual process of infection, once penetration occurs and overcomes the first host barriers, the pathogen produces thickened hyphae and micro-conidia. The thickened hyphae then develop into chlamyospores in intra- and intercellular spaces (Li et al. 2011). Once the vascular system is infected, there is a Foc colonization of the rhizome (the most efficient form of infection), obstructing the mobilization of nutrients throughout the vessels, and therefore, becoming systemic, reaching the pseudostem (Li C et al. 2017). As the disease advances, the pathogen moves out of the vascular system to the adjacent parenchyma forming conidia and chlamyospores, which are released to the soil when the plant died (Baimey et al. 2020). Although they are called survival spores, they are not only produce



after the death of the plant, but also during the process of infection throughout the vascular system (Li et al. 2011). Figure 2 shows (1) Foc Spores (micro and macro conidia and chlamydo spores); (2) germination of the chlamydo spores; (3) colonization of the roots; (4) corm infestation; (5) development of wilt symptoms; (6) complete wilting of the mother plant; (7) pathogen dissemination: a. planting material; b. drainage water and runoff; c. irrigation water; d. workers; e. the weevil; f. weeds

**Figure 2**

*Life cycle of Fusarium wilt in banana*



Note. Taken from (Olivares et al. 2021); ((Ghag et al. 2015; Dita et al. 2018)

## Symptoms

There can be both symptomatic and asymptomatic plants (Figure 3). Throughout the infection process, the symptoms will more and likely occur between in 2-5 months after infecting the roots (Stover 1962). Overall, the pathogen penetrates the roots, obstructs vascular tissues, therefore hindering the movement of necessary nutrients from roots to the upper parts of the plants (Baimey et al. 2020). The first external symptom is usually the pale green streaks on the base of the petiole and the brown-reddish discoloration of the vessels under the epidermis of the petiole (Baimey et al. 2020). Thereafter, more symptoms that are visible appear. As the name suggests, wilting of the plant is the most notorious symptom observed. In addition, necrosis and rotting of roots, rhizome, and pseudostem vessels also occurs. The infected plant shows progressive yellowing of the leaves from older to younger (Viljoen et al. 2020); the oldest leaf sheaths can also show brownish streaks (Ploetz and Pegg 2000) (Figure 4). The leaf chlorosis, being one of the major observable symptoms, is suggested to be caused by the effect exerted by the phytotoxin called fusaric acid (FA) (Dong et al. 2012). The production of these toxins propels the secretion of gelatinous substances that end up causing the wilting and mortality of the banana plant (Guo L et al. 2014). In order to observe internal symptoms, a cross and longitudinal cut is required in the rhizome or pseudostem section (Figure 5). The typical observations are dark brown vessels, necrotic tissue, brown-reddish discoloration accompanied by sticky texture and rotten smell, but there are no internal symptoms in the fruits (Baimey et al. 2020).

**Figure 3***Infected plant vs healthy plant (internally).*

Note. Taken from (Baimey et al. 2020)

**Figure 4***External symptoms (leaf wilting).*

Note. Taken from (Viljoen et al. 2020)

**Figure 5**

*Internal brown to red brick discoloration of the vascular system.*



Note. Taken from (Olivares et al. 2021)

It is important to highlight that Fusarium wilting can be confused with a common bacterial infection caused by *Ralstonia solanacearum*. Bacterial Moko in banana, contrary to Fusarium, affects from youngest to oldest leaves and it does affect the banana fruit.

### **Alternative Hosts**

Although pathogenicity of TR4 is on Cavendish cultivars, other plants may serve as a host, even without expressing symptoms (alternative hosts) (annex 2). Ornamentals and weeds (non-economic host) can be potential sources of inoculum, therefore making them boosters for the reestablishment of this disease (Hennessy et al. 2005); highly susceptible cultivars in the presence of high inoculum pressure may show external symptoms as early as 3 months after planting (Dita et al. 2018). According to Waite and Dunlap, *Paspalum fasciculatum*, *Panicum purpurescens*, *Ixophorus unisetus* (Poaceae), and *Commelina diffusa* (Commelinaceae) were alternative hosts of Race 1 in Central America (Waite and Dunlap 1953). In Australia, *Paspalum spp.* and *Amaranthus spp.*



(Amaranthaceae), where hosts for the SR4 strains. Whereas, *Chloris inflata* (Poaceae), *Euphorbia heterophylla* (Euphorbiaceae), *Cyanthillium cinereum* and *Tridax procumbens* (Asteraceae) were identified with TR4 strains in their roots in an affected area (Hennessy et al. 2005). None showed external symptoms similar to Fusarium wilting, suggesting that Foc may be able to survive as endophyte (symbiotic) in other hosts. Thus, it acts as a Fusarium inoculum reservoir (Dita et al. 2018). According to (Dita et al. 2018), proper weed management strategies should evaluate to possibly risk of also having an effect as Foc propagators. There are not official studies that can certainly state what reproduction structures are been held by these hosts. Can the use of herbicide or mowing weed management stimulate the production of chlamydospores and can chlamydospores originating from alternative hosts survive in the soil and infect banana plants again are questions that should be consider when managing this factor (Dita et al. 2018). Until now, the formae speciale cubense has only been proven to affect crops belonging to the Musaceae family. For example, Fusarium affecting passion fruit is indeed *Fusarium oxysporum*, but formae speciale passiflorae.

### **Influence of Climatic and Soil Factors**

Climatic and soil factors are vaguely taken into consideration when understanding the epidemiology of Fusarium wilting. Subtropical race 4 (FocSR4) strains are predisposed to cause an infection on plants that are grown in an uncondusive environment such as cool temperature, poor soil aeration, and under stress condition (Cumagun C.J 2012). In terms of climatic factors, natural phenomena is the major issue. Some Central American countries are highly susceptible to the hurricane and flooding seasons. In 2020, Hurricane Iota hit northern Colombia (TR4 plantations) and then continued its trajectory towards Belize. Therefore, the dispersal of Foc TR4 spores throughout Central America is highly possible either by gusts of wind or contaminated water from floods. Soil and its microbiome can be determinants for a suppressive characteristic. Soils with an active and functionally diverse microbiota are presumed to have a higher suppressive capacity towards Fusarium Wilting (Sparks 1996). Soil and microbiome can either create Foc-suppressive environments in the soil

or by hinder host penetration and colonization (Dita et al. 2018). A suppressive activity leads to lower or no levels of the pathogen. In Hainan, (Xue C et al. 2015) found *Bacillus* spp, *Rhizobium*, *Bhargavaea*, *Pseudolabrys*, and *Sinorhizobium* to be bacterial groups suppressing Foc. The soil structure can also influence Fusarium incidents. According to (Simmonds and Stover 1987), a well-drained (low levels of compactation) and aerated soil improves radicular development and therefore reduces Fusarium wilting. In the Canary Islands, high clay content soils had a higher suppressive rate (Domínguez et al. 2001).

### **What are Banana – Producing Countries doing?**

As of to date, there is no effective control against TR4. However, there are many management strategies been implemented by banana-producing countries. The main action of free- TR4 plantations is to prevent the entry of the fungus by enhancing rigorous biosecurity measures. Australia is the leading country on biosecurity measures for Foc TR4 regarding the investments, implementation and further research. Fusarium wilt Tropical Race 4 research program endeavors to build on short-Term advances in biosecurity research, by investigating mid- and long-term Strategies that would allow banana growers to profitably produce bananas in an integrated system in the presence of Fusarium wilt (Pattison et al. [date unknown]). They have in-farm biosecurity procedures and several options for a post-incursion that ranges from plant destruction, use of bio-controls to options for farming on infected land (Pattison et al. [date unknown]). Overall, their surveillance and tracing, diagnostics, compliance, engagement, communications, and financial supports have led to a successful TR4 management. However, these measures do not guarantee a 100% Foc TR4 free. All countries have their regulatory instruments that rule in decision making related to phytosanitary issues. In Mozambique, they restricted the movement of vegetative material from infected farms, reduced access points (gate control/fence), proper disinfection of footwear, vehicles and equipment and held awareness programs for farm workers and neighboring communities (Viljoen et al. 2020). One of the most effective disinfectant in sterilizing the farming tools, equipment, and footwear is quaternary

ammonium compound (Nel et al. 2007). These programs included symptoms, early detection and containment of new outbreaks, which involves routine scouting and the appropriate isolation of newly infested field sites. A proper risk analysis for Foc TR4 is needed in case of incursions and if there is a case, affected plantations are fenced off (ditches around it to stop the flow of contaminated waters) and there is restricted access under quarantine conditions only (Maymon et al. 2020). Various methods can be used in the identification of TR4, but they all depend on economic factors, locations of certain laboratories and the appropriate equipment. The identification starts by collecting pseudostem samples (pseudostem strands) collected from symptomatic plant (Viljoen et al. 2020). To do this process surveys are usually performed to collect information on the location, variety and planting history was obtained (Viljoen et al. 2020). Some farms follow a certain transect strategy like zigzag and even use GPS coordinates for each plant sample. Thereafter, samples are mobilized to laboratories for a proper identification. The processes can be DNA molecular analyses, sequence analyses (Dita et al. 2010) (O'Neill et al. 2016), Pathogenicity assays (Viljoen et al. 2020), Subsequent principal component analyses (PCA) and hierarchical clustering (Maymon et al. 2020), morphological and VCG identification (Nelson et al. 1983). After a confirmation, there should be a proper disposal of infected material. One of the major problems in the management of TR4 is the monocrop system used for banana, making the entire plantation susceptible (Dita et al. 2018). The Cover crops practiced has been use more since it improves soil-health (control weeds and nematodes, prevent soil erosion, and to reduce the intensity within the FW field (Charles 1995; Fongod A et al. 2010; Duyck et al. 2011; Djigal et al. 2012; Pattison et al. 2014; Tardy et al. 2015). Other strategies consist of biological soil disinfestation, and compound-supplemented soil in their banana plantations (Baimey et al. 2020).

### **Biological Management**

Biological management is one of the most recent methods use globally. Microbiome plays a crucial role when it comes to suppressing FW intensity. According to (Bubici et al. 2019), *Pseudomonas* spp. Strains controlled up to 79%, *Trichoderma* spp. Strains up to 70%, and *Bacillus* spp , being the less

effective, with a 42-55% of *Fusarium* wilting. Fluorescent pseudomonads are among the most effective rhizosphere bacteria, because in addition to disease control, they exert beneficial effect on plant growth promotion (Kloepper et al. 1980). In India, a medicinal plant (*P. betle* L.) extract exhibited the highest antifungal activity against the tested plant pathogen *Foc*, (Mohammed A.M et al. 2011). Antifungal activity reduces mycelium growth under both greenhouse and field conditions (Akila et al. 2011). On the other hand, some organisms can be used as bio-indicators, being *Gammaproteobacteria* an indicator species of healthy banana plants (*Foc* TR4 free) in Nicaragua and Costa Rica (Köberl et al. 2017).

### **Chemical Management**

A proper irrigation and fertilization is very important in the management of FW (Waterlogging and acidification of nutritive solutions are generally avoided, and monthly treatments with zinc sulfate recommended) (Hecht-Buchholz 1998). In 1990, Herbert and Marx conducted a treatment with carbendazim and potassium phosphonate, in which only potassium phosphonate showed some effectiveness against *Foc* (Herbert and Marx 1990). However, their results were inconsistent and according to Lakshmanan's study, the disease incidence was reduce up to 13.5% of the rhizome of cv. "Rasthali" at the time of harvest by injecting 2% carbendazim (Lakshmanan et al. 1987). Thereafter, studies with prochloraz and propiconazole showed some inhibition in mycelial growth and the use of benomyl and the demethylation in a root dip treatment controlled up to 80.6% of symptoms (Nel et al. 2007). Soil amendments also affects chemical strategies. Studies showed that *Fusarium* infection as NO<sub>3</sub> commonly decreases the severity of the disease. In contrast, NH<sub>4</sub> shows the opposite effect (Ploetz 2015b). Soil should have an adequate amount of phosphorus since it promotes root growth and therefore, improves FW management (Dita et al. 2018). In greenhouse conditions, Silicon (Si) application reduce FW symptoms (Fortunato et al., 2012a). The addition of CaCO<sub>3</sub>, Ca (OH)<sub>2</sub> or CaSO<sub>4</sub> to the soli can reduce the germination of chlamydospores and FW severity in banana without changing



soil pH (Peng 1999). Overall, overdose or deficiency of a nutrient can hinder the intensity of Fusarium wilting (Mur LA. J. et al. 2017).

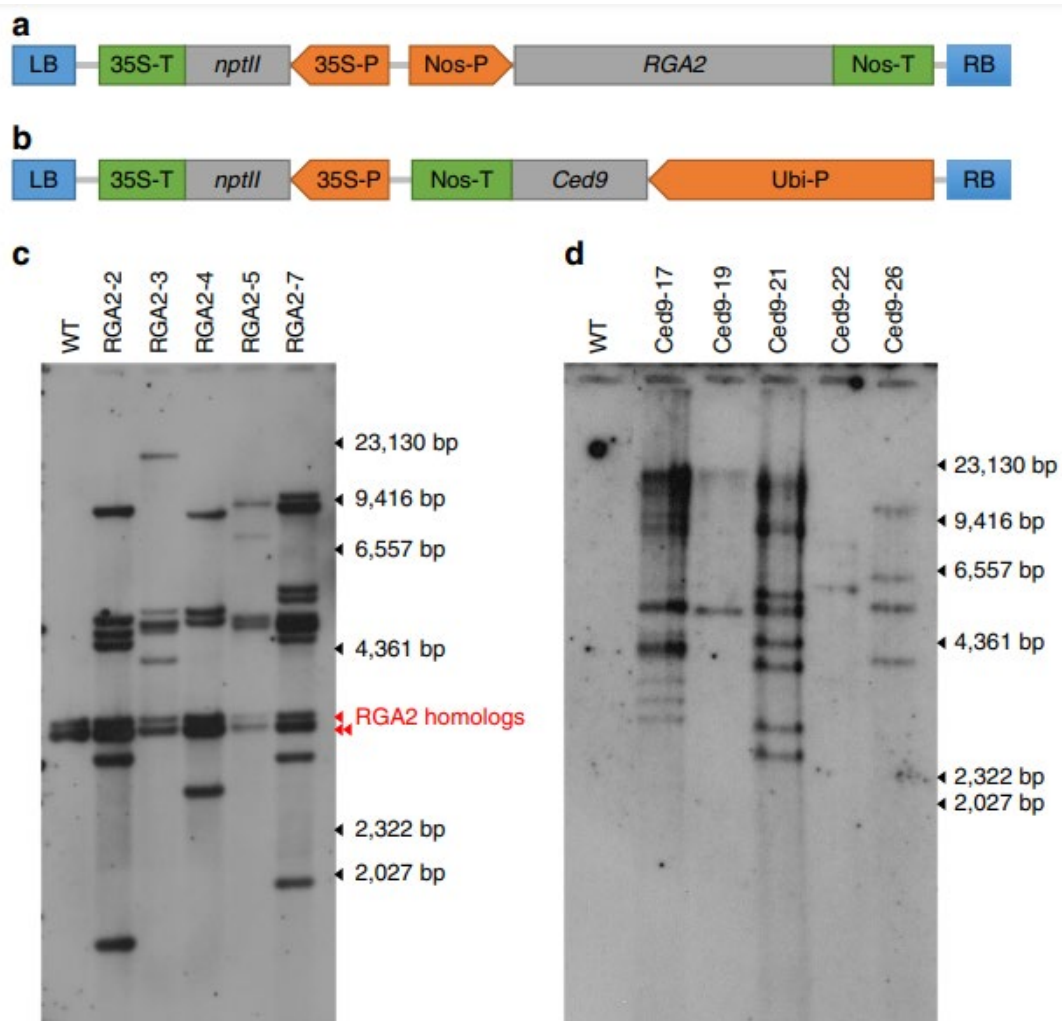
### **Resistant Cultivars**

Cavendish plantations are soma-clonal, thus making it very susceptible to even the smallest outbreak. Breeding programs are one of the most promising and effective way to manage Foc TR4 since it can replace susceptible cultivars with resistant varieties and is the most viable option for growers to continue growing banana in infested fields (Uazire et al. 2010). Planting of Foc-tolerant or Foc-resistant cultivars accompanied by cultural practices help to improve the disease incidence and increase the crop (Haddad et al. 2018). In Mozambique, a resistance evaluation was carried out on five Cavendish banana clones, being GCTCV-119 soma-clone the most resistant followed by GCTCV-218 (Viljoen et al. 2020). There is still not an official Foc TR4 resistant cultivar, but further research found a vital route in the resistance process. An official funding alliance was published this year in order to use gene-editing CRISPR (Clustered Regularly Interspaced Short Palindromic Repeats) technology to create a non-genetically modified variety of Cavendish, also resistant to TR4 by activating the expression of the RGA2 gene (Alan 2021). It was a 3-year field trial where two lines of transgenic Cavendish were used in the Northern Territory of Australia where TR4 is endemic. One transformed with RGA2, a gene isolated from a TR4-resistant diploid banana, and the other with a nematode-derived gene, Ced9 (Figure 6). Ced9 had five lines (Ced9-17, 19, 21, 22, and 26), which contained between one and many transgene copies with no endogenous homologs identified; both remained disease free (Dale et al. 2017) (Figure 7). According to Professor Dale, the active resistance gene called RGA2 was found in wild banana from Indonesia. In his research, by adding the gene to the Cavendish cultivars, it generated five RGA2 transgenic banana lines: RGA2-2, 3, 4, 5, and 7. The results showed that RGA2-3 was the most resistant banana since its RGA2 gene was about 10 times more active than the others. Yet, RGA2-2, 4, and 5 also had a high resistance. Figure 6 shows A. RGA2 and B. Ced9 expression cassettes. LB, left border; RB, right border. Determination of transgene copy

number in C. RGA2 and D. Ced9 transgenic banana lines by Southern blot analysis. Genomic DNA from WT, RGA2 and Ced9 lines was digested with HindIII and XmaI, respectively. DNA molecular weight marker II (Roche) reference is indicated on the right hand side.

**Figure 6**

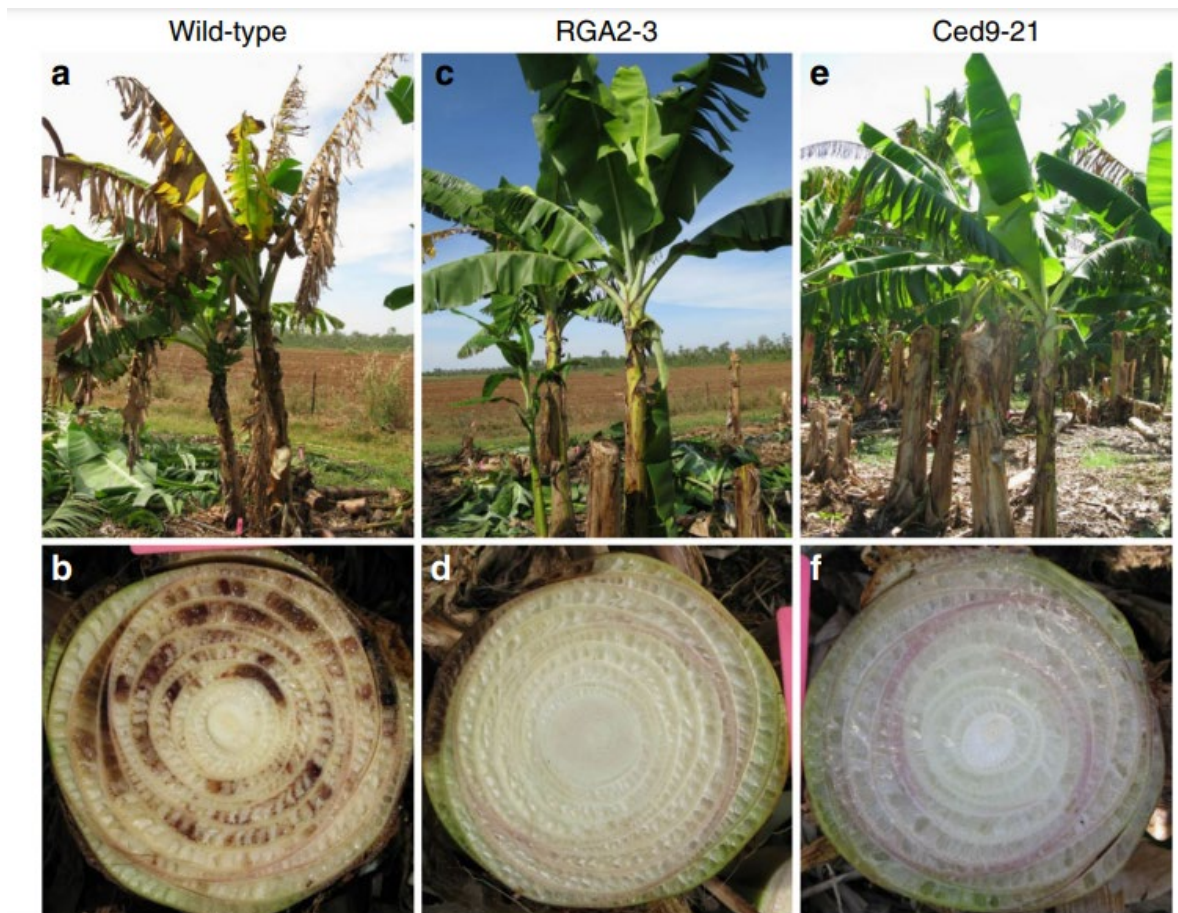
*Transgene expression cassettes and Southern analysis of selected transgenic lines.*



Note. Taken from (Dale et al. 2017)

**Figure 7**

Comparison between the regular Cavendish vs the resistant transgenic lines in terms of symptoms.



Note. Taken from (Dale et al.2017)

### **Conclusions**

The evolution of this pathogen does influence the severity of the attack, since even the origin of the reproduction structure can determine how aggressive the strain can be on different cultivars and under the different conditions that had been part of making the races more damaging than the previous one.

The dispersion process is the mayor problem when it comes to control, since there is not only anthropogenic scattering, but also natural phenomena that is hardly control and yet, it is the least consider factor in the decision-making.

Various management techniques are adjustable and efficient in the prevention and management of the fungus worldwide including fungicides applications. However, the number one strategy is implementing rigorous biosecurity measures.

In order to control fungus dispersion and pathogen control, weed and host plant management is essential.

### **Recommendations**

Integrate strategies that are adaptable for the region and create alliances among banana producers to have a more effective control over the incidence of Foc TR4/ STR4.

Increase campaigns to raise awareness of the impact of this fungus on banana plantations (economic losses).

Work along with national and international phytosanitary authorities to have the appropriate procedures according to regulatory instruments established by the country of origin.

Adapt the recommendations above to the most recent information regarding Foc TR4.

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## Annexes

## Annex A

*Lineages based on phylogenetic inference and morphological observations.*

Foc Lineage	Fusarium Taxa	Etymology	Geography and host	Pathogenicity
Foc Lineage L1	<i>Fusarium odoratissimum</i>	strong odour associated with older cultures	Kutai Timur, East Kalimantan, Musa sp. var. Pisang Kepok (ABB)	Gros Michel (AAA) and Cavendish (AAA).
Foc Lineage L2	<i>Fusarium purpurascens</i>	purple pigmentation which was observed when cultivated on potato dextrose agar	Kutai Timur, East Kalimantan, Musa sp. var. Pisang Kepok (ABB).	Gros Michel (AAA)
Foc Lineage L3	<i>Fusarium phialophorum</i>	Elongated phialidic collarettes observed in culture.	Tanah Bumbu, South Kalimantan, Musa sp. var. Pisang Awak (ABB).	Gros Michel (AAA)
Foc Lineage L4	<i>Fusarium grosnicheli</i>	Association with the banana variety Gros Michel.	Bogor, West Java, Musa acuminata var. Pisang Ambon Lumut (AAA).	Gros Michel (AAA)
Foc Lineage L5	<i>Fusarium duoseptatum</i>	microconidia are frequently 2-septate	Kapuas, Central Kalimantan, Musa sp. var. Pisang Kepok (ABB).	Gros Michel (AAA)
Foc Lineage L6	<i>Fusarium tardichlamyosporum</i>	delayed chlamyospore production observed in this species	Sikka Flores, Musa acuminata var. Pisang Barangan (AAA).	Gros Michel (AAA)
Foc Lineage L7	<i>Fusarium cugenangense</i>	Cugenang, the location where this species was collected in Indonesia	Cianjur, West Java, Musa sp. var. Pisang Kepok (ABB).	Non-pathogenic on Gros Michel (AAA) and Cavendish (AAA).
Foc Lineage L8	<i>Fusarium hexaseptatum</i>	Six conidial septa observed in its macroconidia.	Sukabumi, West Java, Pisang Ambon Kuning (AAA).	Gros Michel (AAA)
Foc Lineage L9	<i>Fusarium tardicrescens</i>	slow growth rate in culture	N/A	N/A

(Maryani et al. 2019)

## Annex B

Alternative hosts of *Foc* TR4.

Type of Plant	Family	Species	Reference
Ornamental	Heliconiaceae	<i>Heliconia caribea</i> <i>Heliconia latispatha</i> <i>Heliconia chartacea</i> <i>Heliconia collinsiana</i> <i>Heliconia crassa</i> <i>Heliconia rostrata</i> <i>Heliconia marie</i> <i>Heliconia vellerigera</i>	Pittaway, Nasir et al. 1999 EPPO. PQR Database  Ploetz, R.C, 2000
	Cannaceae	<i>Canna indica</i>	Waman, Bohra et al. 2013
	Araceae	<i>Aglaonema pictum</i>	Waman, Bohra et al. 2013
	Zingiberaceae	<i>Hedychium oronarium</i>	Waman, Bohra et al. 2013
Crop	Musaceae	<i>Musa sp.</i> <i>Musa schizocarpa</i> <i>Musa textiles</i> <i>Musa acuminata</i> <i>Musa balbisiana</i>	Pegg, Moore et al. 1996 Ploetz 2006 Ploetz 2015 EPPO. PQR Database
Weed	Commelinaceae	<i>Commelina diffusa</i>	Hennessy, Walduck et al. 2005 Waite, B, 1953
	Poaceae	<i>Choris inflata</i> <i>Ixophorus unisetus</i>	
	Asteraceae	<i>Tridax procumbens</i>	
	Euphorbiaceae	<i>Euphorbia heterophylla</i>	
Grass	Poaceae	<i>Paspalum fasciculatum</i> <i>Panicum purpurascens</i>	Hennessy, Walduck et al. 2005 Waite, B, 1953 Pittaway, Nasir et al. 1999

(Olivares et al. 2021)