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Pathogenicity of *Fusarium oxysporum* f.sp. *cabense* on bananas

Introduction

The genus *Fusarium* harbours numerous notorious soil-borne plant pathogenic fungi. This group of fungi diverged 91.3 million years ago and the pathogenic strains emerged with monoculture practices (Summerell et al., 2010; Gordon, 2017). One of the most economically important *Fusarium* species is *F. oxysporum* which is a species complex, consisting of 100 host-specific lineages, termed formae speciales (ff. spp.).

Panama disease on bananas (*Musa* spp.) is caused by *F. oxysporum* f. sp. *cabense* (FOC) which was first diagnosed in Australia in 1874 (Ghag et al., 2015a; Zheng et al., 2018). As banana cultivars are derived from *M. acuminata* (A genome) and *M. balbisiana* (B genome) species, banana varieties are either diploids or triploids (D'Hont et al., 2012; Janssens et al., 2016). The variety 'Gros Michel' (AAA) was the predominant cultivar grown for export which was highly susceptible to FOC Race 1 (R1). R1 spread across continents and led to a US\$2 billion loss in Gros Michel production in the 1950's (Ploetz, 2005). It was then replaced by the Cavendish (AAA) group of banana varieties which were resistant to R1. In 2011, global banana production reached 145 million tons, with the value of US\$ 44 billion (Dita et al., 2018). Although only 15% of the production enters the international market, 90% of it is made up of Cavendish varieties (Ploetz, 2015). A new pathogenic strain, Tropical Race 4 (TR4) of FOC emerged in 1967 in Taiwan. Since then, it was reported in the Philippines, Australia (Pegg et al., 1995), Papua New Guinea (Shivas and Philemon, 1996), China (Li et al., 2013a), Jordan (García-Bastidas et al., 2014), Mozambique (Ordonez et al., 2015), Pakistan (Ordonez et al., 2016). Within FOC, 33 genotypes and 20 Vegetative Compatibility Groups (VCGs) have been reported (Bentley et al., 1998; Fourie et al., 2009). The arrival of TR4 in Latin America threatens the future of global banana production.

The first symptoms of FOC infection include vascular discoloration of the roots and pseudostem. This leads to wilting of the basal leaves due to the shortage of water supply (Figure 1) (Swarupa et al., 2014). FOC reproduces asexually, producing macroconidia, microconidia and chlamydoconidia (Gordon, 2017). The latter can survive in the soil, on both dead plant material or non-host weeds up to 20 years (Dita et al., 2018). Banana breeding for disease resistance is challenged by the perennial nature of bananas, low female and male fertility and introducing new traits into a hybrid is virtually impossible (Dale et al., 2017).

Therefore, it is crucial to understand the pathogenicity of FOC and how it evades host-defences. This review briefly describes the 1) FOC infection process, 2) host-pathogen interactions, and 3) highlights the need for further research.

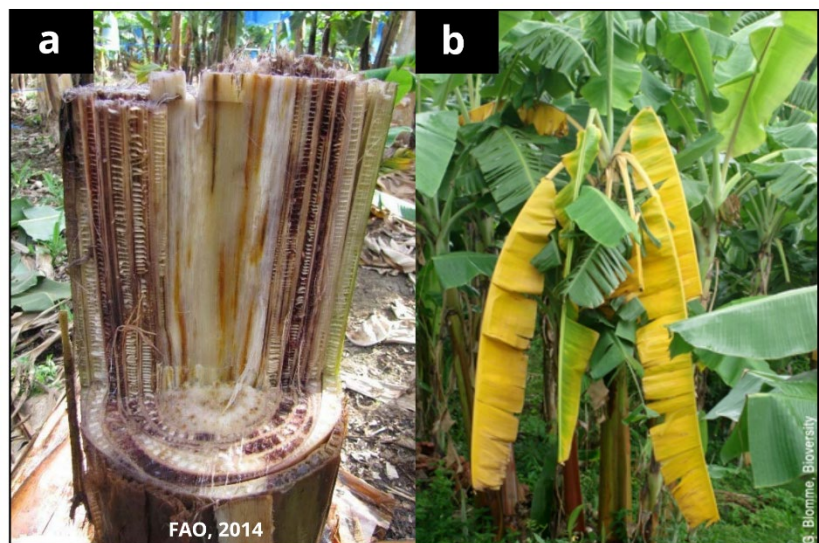


Figure 1. The soil-borne FOC enters the xylem, causes vascular discoloration (a) and leads to the wilting of banana basal leaves (b).

1. FOC infection process

The infection process of FOC in bananas can be visualised using green fluorescent protein (GFP) transformation and the use of confocal microscopy (Figure 2) (Li et al., 2011; Guo et al., 2015; Li et al., 2017; Warman and Aitken, 2018). FOC is a hemibiotrophic pathogen, with a saprophytic phase on the host (Ghag et al., 2014) and can lead to complete plant death in 17 days post infection (dpi). In brief, FOC penetrates the root epidermis via wounds (R1) or directly (TR4), colonises the root cortex while increasing the production of cell-wall degrading enzymes (CWDE), and then enters the xylem vessels (Dita et al., 2018). While TR4 can enter the epidermal and parenchyma cells, as well as the vascular tissues of roots in Cavendish varieties, R1 does not infect the Cavendish group (Guo et al., 2015; Li et al. and 2017). While FOC is able to survive on a non-host plant, the mechanism is unknown (Dita et al., 2018).

Pre-infection stages of FOC include spore germination (Deacon, 1996), which is constrained by fungistasis (e.g. root exudates required) (Ploetz, 2015) and adhesion to the host surface (Guo et al., 2012). Fungal growth and pathogenicity are controlled by G-protein complex (Guo et al., 2014), composed of α , β and γ subunits. The response of FOC's growth and virulence to environmental stresses involves two-component signalling pathways. Both R1 and TR4 have 20 putative histidine kinases, ~100 protein kinases and over 729 transcription factors (Guo et al., 2014) which are involved in FOC's pathogenicity.

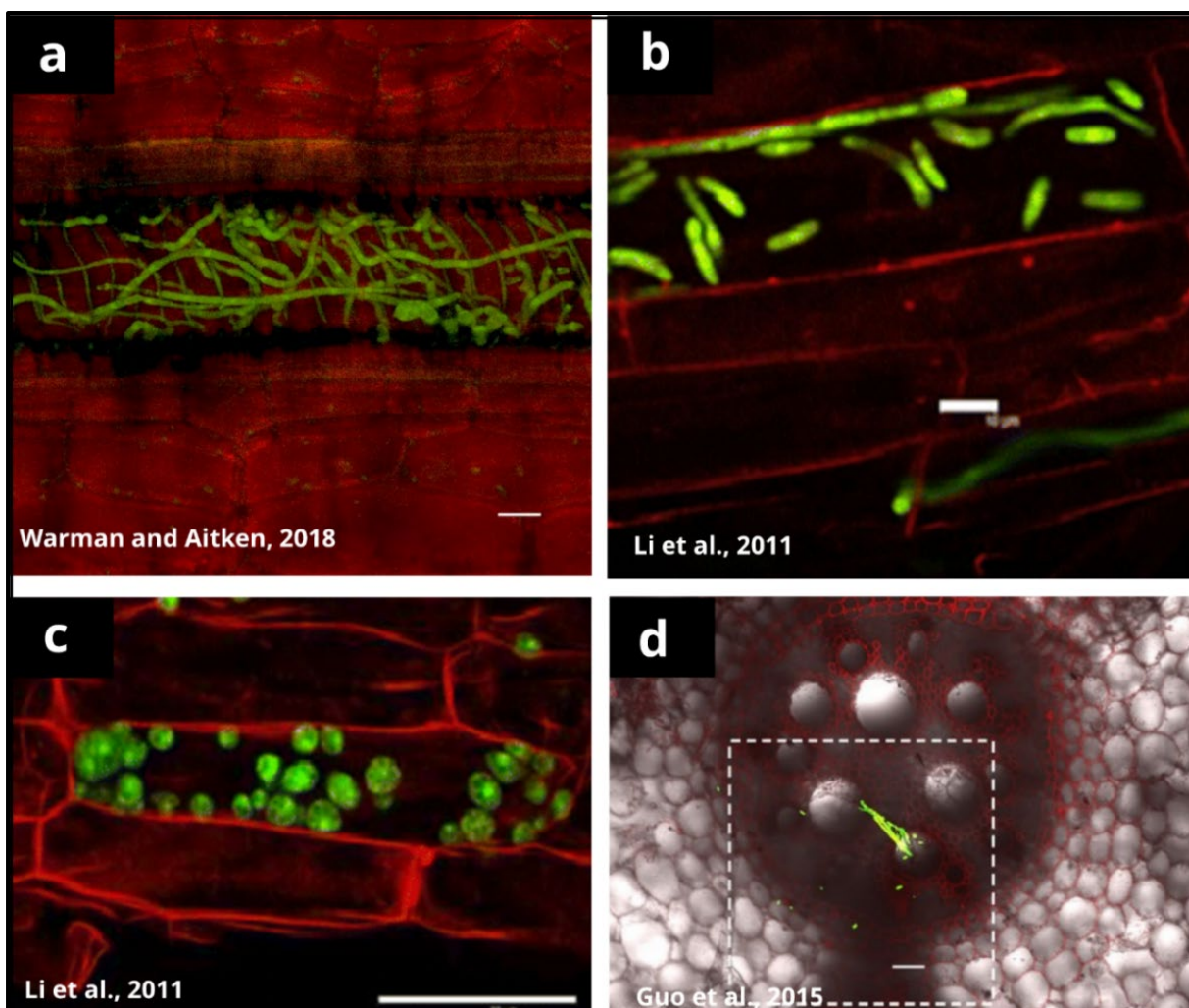


Figure 2. GFP transformation allows the visualisation of FOC infection within banana roots (Li et al., 2011). TR4 hyphae can enter the xylem vessel in the pseudo-stems of cv. Cavendish (a), produce microconidia inside epidermal cells (b) and chlamydospores in root cells (c). It can also produce conidia and hyphae in root xylem vessels (d).

2. Host-FOC interaction

Upon successful attachment to the banana plant, the plant innate immune defence system initiates the recognition of pathogen-associated molecular pattern (PAMP)-triggered immunity (PTI) and produces damage-associated molecular patterns (DAMP) (Fan et al., 2018). These PAMPs/DAMPs are recognised via pattern-recognition receptors (PRRs) which trigger genes to change the membrane Ca^{2+} flux (Swarupa et al., 2014), initiate mitogen-activated protein kinase (MAPK) cascades (Di Pietro et al., 2001; Ding et al., 2015) and strengthen the plant cell wall (Figure 3) (de Ascensao and Durbery, 2000; de Ascensao and Durbery, 2003; Van Den Berg et al., 2007).

FOC evolved to overcome banana PTI by secreting effector proteins (Czislowski et al., 2018) which can mask the presence of the pathogen, suppress host defence responses and induce transcriptional reprogramming of the host cell. These effectors are called *Secreted In Xylem (SIX)* proteins which function as avirulence proteins (Guo et al., 2014). While R1 has one copy of *SIX6*, TR4 has one copy of *SIX2*, *SIX6*, and *SIX8* proteins (Guo et al., 2014; Fraser-Smith et al., 2014). It was proposed that the horizontal gene transfer of *SIX* genes occurred between R1 or Race 2, and the ancestor of TR4 in the Indo-Malaysian region which could then infect cv. Cavendish (Ploetz and Pegg, 1997; O'Donnell et al., 1998; Czislowski et al., 2018).

Following the 'zig-zag model' (Jones and Dangl, 2006) of host-phytopathogen interactions, the plants evolved resistance (R) genes to recognise the effectors and respond by a secondary defence pathway. Numerous R gene candidates (RGCs) (Peraza-Echeverria et al., 2008), regions with nucleotide binding site and leucine-rich repeats (NBS-LRRs) (Pei et al., 2007) and non-expressor of pathogen-related genes 1 (*NPR1*) have been identified in bananas (Endha et al., 2008; Zhao et al., 2009). TR4 resistance has been found as transcriptional polymorphism of *RGC2* in wild banana (*Acuminata* ssp. *malaccensis*) (Peraza-Echeverria et al., 2008), *MdNPR1* gene in Dongguan Dajiao (*Musa* spp. ABB) (Zhao et al., 2009) and *MNPR1A* and *MNPR1B* genes in Cavendish varieties (Wu et al., 2013).

However, FOC has a great variety of pathogenicity mechanisms. It produces CWDEs including polygalacturonase (Dong and Wang, 2015) and exopolygalacturonase (Dong and Wang, 2011). FOC

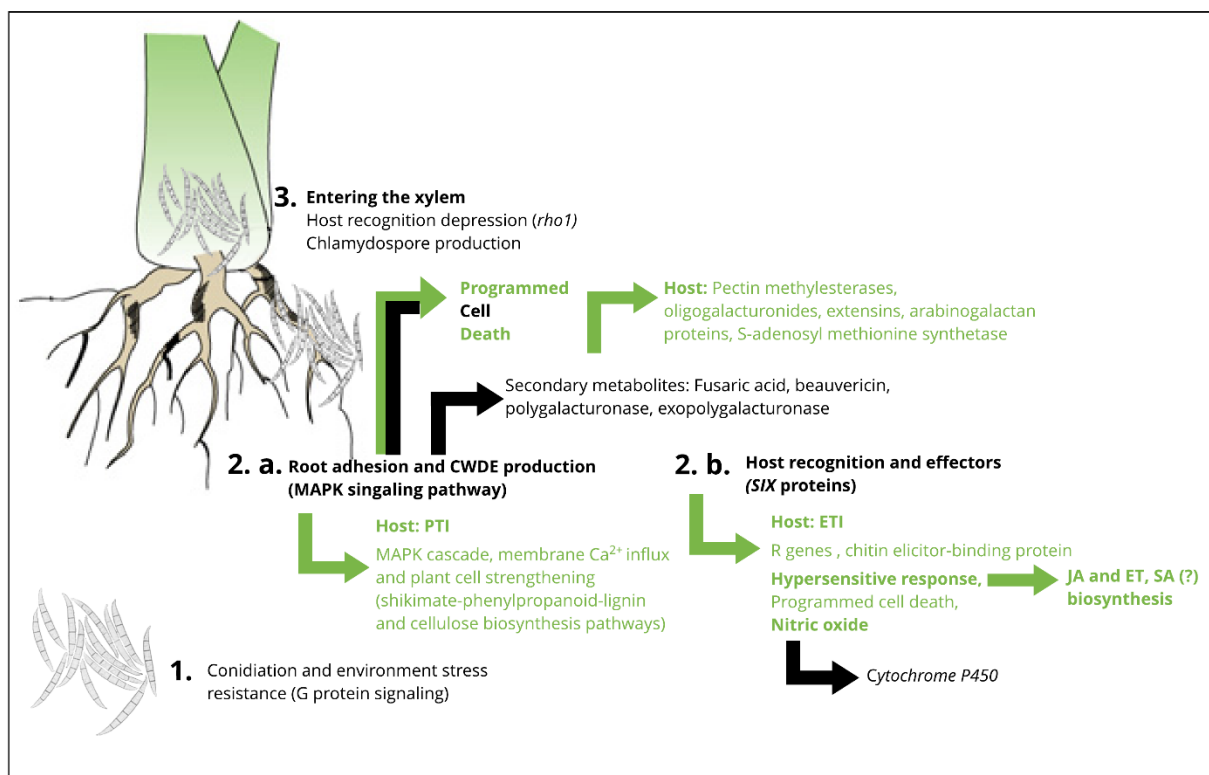


Figure 3. Infection processes of TR4 (black text) and host defence strategies (green text) in bananas. TR4 signalling pathways involved in infection are the G protein signalling, FMK1-controlled MAPK and pathogenicity-associated two-component signal transduction pathways (Guo et al., 2014 and 2015). In response, PTI and ETI are induced in bananas to protect plant cell walls, synthesise protective enzymes and plant hormones (Li et al., 2012).

also produces secondary metabolites including fusaric acid and beauvericin (Li et al., 2013c; López-Díaz et al., 2018) which suppress H⁺ pumping and cause K⁺ leaking in the plant cell. This process suppresses the mitochondrial oxygen absorption causing malic acid oxidation and leads to the reduction of plant cell viability.

To prevent host defences, TR4 expresses *rho1* gene to prevent host recognition in the xylem (Sutherlands et al., 2012). When host defence compounds are released against TR4, MFS transporter abundance is increased. To defend the plant cells, pectin methylesterases (PMEs) and oligogalacturonides (OGs) are released in response (Fan et al., 2018) which then induce plant defence signalling and hydrogen peroxide (H₂O₂) outburst. PME activities are higher in the roots of TR4 resistant cultivars in comparison to susceptible ones (Ma et al., 2013; Fan et al., 2017). Another host defence strategy is the formation of a network of extensins and arabinogalactan proteins (AGPs) (Wu et al., 2017) to create an impermeable barrier against TR4 hyphae and upregulating the shikimate-phenylpropanoid-lignin and cellulose biosynthesis pathways (Li et al., 2012). The accumulation of secretory proteins by the host in the endoplasmic reticulum (ER) can lead to plant cell death (PCD) and therefore the wilting of banana plants (Ghag et al., 2014). Transgenic lines expressing apoptosis-inhibition-related genes have been shown to lead to a decrease in disease severity by R1 (Paul et al., 2011; Ghag et al., 2014). While no progress has been made to discover TR4 genes responsible for apoptosis, a genome-wide analysis has identified TR4 autophagy-related genes (Wei et al., 2017).

While numerous high-throughput gene expression analyses have been carried out for banana roots (Wang et al., 2012; Li et al., 2012; Li et al., 2013c; Li et al., 2013c; Bai et al., 2013; Zhang et al., 2017; Niu et al., 2018), only Sutherland et al. (2013) and Guo et al. (2014) have conducted transcriptome analyses of TR4. Overall, more genes and pathways have been published about the banana immune system (Table 1) compared to the number of pathogenicity-related genes and pathways (Table 2.).

Table 1. Banana defence related genes, pathways and resistant varieties.

Banana plant	References
Root transcriptomes	Li et al., 2012; Wang et al., 2012; Li et al., 2013c; Bai et al., 2013
Digital Gene Expression Analysis	Niu et al., 2018
NPR1-like genes (<i>MNPR1</i> ; <i>MdNPR1</i>)	Endah et al., 2008; Zhao et al., 2009
Apoptosis-related genes (<i>MusaDAD1</i> , <i>MusaBAG1</i> , <i>MusaBI1</i> ; <i>API5</i> ; <i>Bcl-xL</i> , <i>Ced-9</i> transformation)	Paul et al., 2011; Ghag et al., 2014a; Dwivany et al., 2016
MaSERK1	Huang et al., 2010
Autophagy (<i>MaATG8s</i>)	Wei et al., 2017
Wound induced defence (Extensins, arabinogalactan proteins, pectin methylesterases)	Ma et al., 2013; Wu et al., 2017; Fan et al., 2017
Root cell wall-strengthening (<i>Catalase 2</i> , <i>PAE</i> , <i>PR-1</i> , <i>PR-3</i> , phenolics)	van den Berg et al., 2007; de Ascensao et al., 2003
Resistance genes (12 <i>Musa</i> RGAs; <i>RGA2</i> , <i>RGC1-5</i> ; <i>EF1</i> , <i>TUB</i> , <i>ACT1</i> , <i>ACT2</i> , <i>L2</i> , <i>RPS2</i> , <i>RAN</i> , <i>PR-4</i> ; <i>MaWRKY50</i>)	Peraza-Echeverria et al., 2008; Pei et al., 2007; Dale et al., 2017; Zhang et al., 2017; Niu et al., 2018
Chitinase production (<i>Chi1</i> , <i>Chi</i> , <i>RCC2</i>)	Subramaniam et al., 2006; Dwivany et al., 2016
<i>HSP90s</i> and melatonin	Wei et al., 2016
Photosynthesis-related factors	Dong et al., 2016
Phenylalanine ammonia lyase genes (<i>MaPAL1-4</i>)	Wang et al., 2016
Small interfering RNAs	Ghag et al., 2014b
Methyl jasmonate	Sun et al., 2013
Salicylic acid	Wang et al., 2015
Systematic acquired resistance (<i>MaNPR1A</i> , <i>MaNPR1B</i> , <i>PR-1</i> , <i>PR-3</i>)	Wu et al., 2013
Germplasm diversity	Li et al., 2015; Zuo et al., 2018
Genetic transformation (<i>Ace-AMP1</i> ; <i>MSI-99</i> : megalinin analogue; <i>PhDef1-PhDef2</i> : floral defensins; <i>Sm-AMP-D1</i> : seed defensin; Host-induced Gene Silencing Mediated Resistance)	Ghag et al., 2012; Mohandas et al., 2013; Ghag et al., 2014c, Ghag et al., 2014d

Table 2. Pathogenicity-related genes and mechanisms of R1 and TR4.

R1 and TR4	References
Genome and transcriptome	Guo et al., 2014, Wang et al., 2017
Proteomics	Li et al., 2013c
Cell wall integrity (<i>FoOCH1</i>)	Li et al., 2014
Pathogenicity-associated genes (<i>Fga1</i> , <i>Fhk1</i> , <i>Fow2</i> , <i>Ste12</i>)	Guo et al., 2015
Avirulence genes (<i>SIX8a</i>)	Ploetz, 2015; Czislowski et al., 2018
Exopolygalacturonase	Dong and Wang, 2011
Host recognition suppression (<i>rho1</i>)	Sutherland et al., 2013
Host toxin production suppression (<i>chsV</i>)	Sutherland et al., 2013
Fusaric acid and beauvericin	Li et al, 2011; Li et al., 2013c; Portal et al., 2018; Ding et al., 2018
Oligogalacturonides	Fan et al., 2018
Plant cell wall degradation (<i>Snf</i> , <i>frp1</i>)	Sutherland et al., 2013
MAP kinase genes (<i>FoSlT2</i> , <i>FoMkk2</i> and <i>FoBck1</i>)	Ding et al., 2015
Nitrogen response pathway (<i>Cyp55</i>)	Sutherland et al., 2013
Conidia germination (<i>ERG6</i> , <i>ERG11</i> , <i>ERG13</i> , <i>ERG25</i>)	Deng et al., 2015
G-protein subunits (<i>FGA2</i> , <i>FGB1</i>)	Guo et al., 2016
bZIP transcription factor (<i>Foatf1</i>)	Qi et al., 2013

3. The future of TR4 control

This brief review has discussed the main mechanisms of FOC pathogenicity and banana defence mechanisms. There is no sustainable fungicide treatment against FOC (Nel et al., 2007) and while many biocontrol agents have been tested, mostly in pot trials (Getha et al., 2005; Nel et al., 2006; Xue et al., 2015; Wang et al., 2015; Fu et al., 2016), these agents are not economically sustainable for large-scale control. There are numerous pathogens infecting bananas, therefore multiple resistance gene stacking was previously proposed (Ghag et al., 2015b). While resistant somaclones have been developed in Taiwan (Hwang and Ko, 2004), tissue cultures have low adaptation rates and are costly in comparison to field-collected rooting tips (suckers) (Hamill et al., 1993; Alagumani, 2005). Should a new group of FOC resistant banana varieties emerge, it is likely that TR4 might again overcome banana defences by evolving new *SIX* proteins. As more studies have focused on banana responses to R1 and TR4 than on the pathogens themselves, further research is crucial to better understand TR4 chlamyospore production and germination and surviving on non-hosts in order to control TR4 in the field with affordable biocontrol methods.

Final word count: 1772

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