Current state of Fusarium wilt of banana in the subtropics

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Abstract
Subtropically grown bananas have differential interactions with *Fusarium oxysporum* f. sp. *cubense* (*Foc*), causal agent of Fusarium wilt of banana (FWB), when compared with those grown in the tropics. The designation 'subtropical' race 4 (SR4) was assigned to *Foc* strains able to infect Cavendish (AAA) cultivars in the subtropics, but not in the tropics. 'Tropical' race 4 (TR4) gained prominence with the appearance and spread of a *Foc* strain that severely affects Cavendish bananas in both the tropics and subtropics. Recent surveys in Asia revealed TR4 as the predominant strain both in the tropics and subtropics, affecting not only Cavendish, but also many other cultivars. In many subtropical banana zones, *Foc* races 1 and 2, which complete the racial structure of *Foc*, are also found and cause severe losses in certain market-preferred dessert bananas. Environmental constraints increase the susceptibility of Cavendish bananas to SR4. However, the role of abiotic stresses in cultivar susceptibility to FWB needs to be better understood. It is not clear why some *Foc* strains only affect Cavendish in the subtropics, and what other factors, including pathogen virulence and microbial functional diversity, might be driving disease epidemics. Field experience suggests that optimum soil and water management strategies can reduce disease intensity, but targeted studies are needed to understand the virulence of different strains, the impact of fluctuating temperatures, soil pH, organic matter breakdown and soil microbial dynamics. Research findings on the epidemiology and management of FWB in Australia, Brazil, China, India and South Africa are discussed to propose priority areas for the development of improved disease management practices.

Keywords: Epidemiology; Panama disease; *Fusarium oxysporum* f. sp. *cubense*

INTRODUCTION

Banana is most commonly associated with the tropics where water is abundant and average temperatures range from 20-30°C. The crop, however, is also important in subtropical regions of Australia, the Middle East, China, India, South Africa, the Canary Islands, Turkey and southern South America, including southern Brazil, Argentina and Paraguay (Figure 1). In these countries, bananas are mainly grown for domestic markets, and the percentage of subtropical production may range from a small portion to almost all bananas grown in the country. In Australia, for instance, subtropical bananas account for only about 6% of national production sold on local markets (Hort Innovation, 2018), while in India and Brazil subtropical bananas represent more than 30% of the total production. In South Africa, China and the Middle East they represent 100% of the total production.

While geographically, the subtropics cover from 23.5° N or S and 40° N or S. Calberto et al (2015) defined subtropics by a temperature difference of more than 8° C between winter and summer temperatures and no more than three months with monthly temperature below 13° C (Figure 1). The summer season experiences higher solar radiation and longer days, while in the winter season days are short. In Australia and Brazil, the southern hemisphere climatic profile indicates that bananas potentially undergo heat stress between January to March in the summer and cold and water stress between June and August in the winter (Figure 2A and 2B). Yunnan and Guangxi in China, and Uttar Pradesh in India, considered the largest subtropical production areas in the two countries, have more severe winter temperature stress compared to Australia and Brazil (Figure 2C and 2D). Rainfall is generally more abundant in the summer season, while total rainfall varies greatly from site to site.

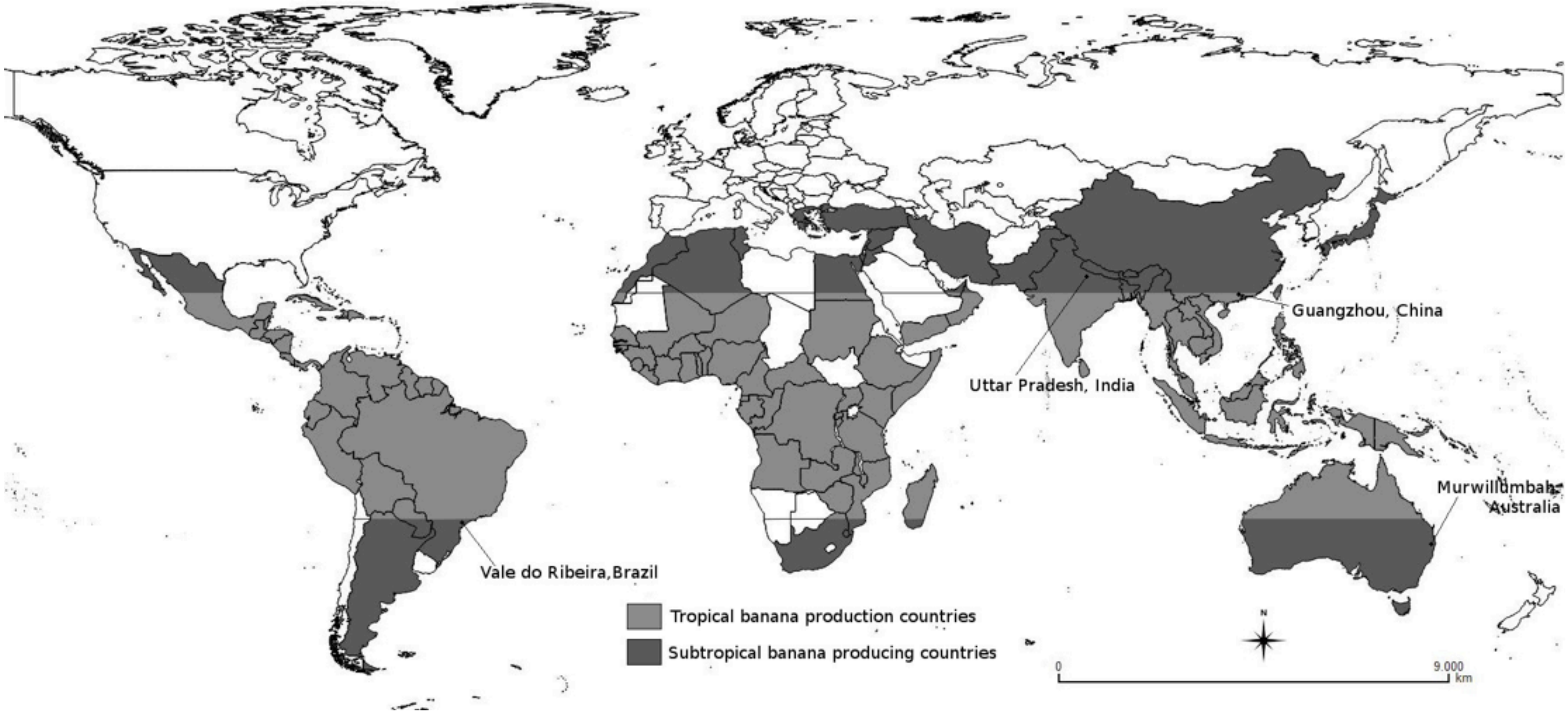

Figure 1. Banana producing countries in the tropics and the subtropics. Source (FAO, 2018).

Low temperatures are a major stress factor for subtropical bananas. Cavendish-type (AAA) cultivars are predominant in many subtropical banana production regions, although more cold tolerant Pome-types (AAB) cultivars are also grown (Lichtemberg et al., 2001). Cultivars such as Lady Finger and Prata (both AAB, Pome), Ducasse and Guangfen (both ABB, Pisang Awak) are important in the subtropics due to higher market prices and tolerance to environmental stresses in countries like Australia, Brazil, India and China. To avoid frost and reduce chilling impact, diverse practices are deployed – hill slope planting for air drainage, growing on slopes, protective screens and structures, timing of cultural practices like desuckering to target bunching during warmer periods and annual planting among others.

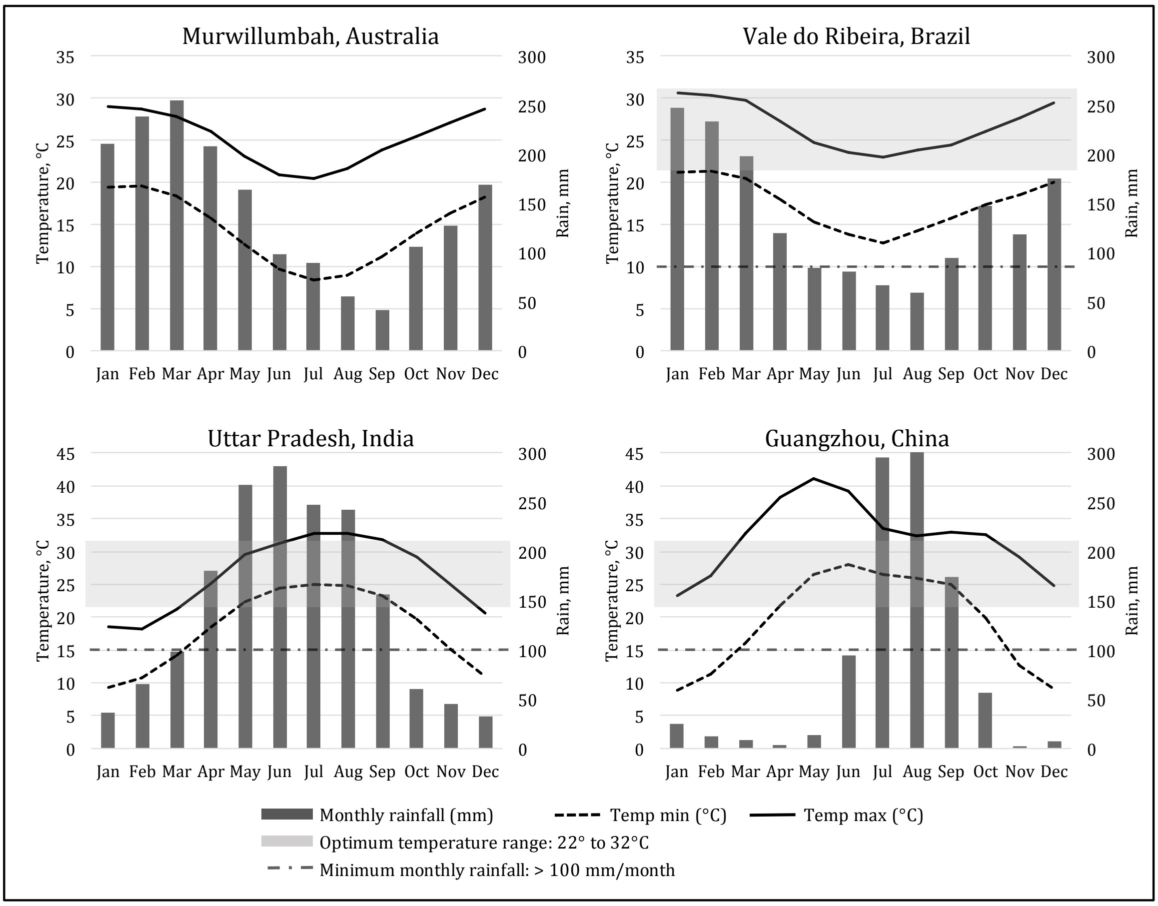

Figure 2. Average monthly rainfall, maximum and minimum temperature and cumulative rainfall in four different subtropical banana production regions in Australia, Brazil, India and China (Source of data: https://pt.climate-data.org/).

FUSARIUM WILT: A MAJOR CONSTRAINT FOR SUBTROPICAL BANANAS

Fusarium wilt of banana (FWB), caused by the soil-borne fungus *Fusarium oxysporum* f. sp. *cubense* (*Foc*) is a major constraint to banana production in the subtropics (Moore, 1995; Viljoen, 2002). The disease was first observed in subtropical Queensland (Bancroft, 1876), threatening banana production globally (Ploetz el al., 2015).

Foc is a soil-borne pathogen that produces chlamydospores that persist in soil in the absence of the host. The fungus also survives in alternative hosts which it colonizes as a non-pathogenic parasite (Dita et al., 2018). Once banana plantations are infested with *Foc*, susceptible cultivars cannot be successfully replanted for decades (Stover, 1962). Once infected, banana plants show a progressive yellowing from older to younger leaves, necrosis in the xylem vessels and rhizome discoloration. Diseased plants fail to produce marketable bunches and eventually die (Stover, 1962; Ploetz, 2015).

Foc is a highly variable pathogen consisting of at least 24 vegetative compatibility groups (VCGs) and three races (Ploetz, 2006; Mostert et al., 2017). The races are defined by the pathogenic effect on differential host cultivars: *Foc* race 1 affects mainly 'Gros Michel' and 'Silk', race 2 affects bananas of the Bluggoe subgroup, and race 4 affects all cultivars in the Cavendish subgroup (Waite & Stover, 1960; Su et al., 1986). Race 4 is further divided into 'subtropical' race 4 (SR4) and 'tropical' race 4 (TR4) strains.

The designation 'subtropical' race 4 (SR4) was assigned to *Foc* strains able to infect Cavendish (AAA) cultivars in the subtropics, but not in the tropics, while 'tropical' race 4 (TR4) affect Cavendish bananas in both the tropics and subtropics (Ploetz, 2006; Buddenhagen, 2009). SR4 strains belong to a phylogenetic group that includes VCGs 0120/15, 0122, 0126, 0129/11, 01210 and 01219. Some of these VCGs (0120/15, 0129/11) occur in areas of subtropical banana production and cause disease in Cavendish under those conditions (Pegg et al., 1996; Viljoen, 2002). TR4 strains belong to a phylogenetic group that initially only included VCG 01213/16. However, recent studies based on SIX (secreted in xylem) genes profile suggest that strains belonging to VCG 0121 could be also considered as TR4 (Czislowski et al., 2017). Recent surveys in Asia revealed VCG 01213/16 as the predominant VCG both in the tropics and subtropics, affecting not only Cavendish but also many other cultivars (Li et al., 2013; Mostert et al., 2017). In addition, strains from VCGs traditionally designated as race 1 have also been reported as causing disease in Cavendish in the subtropics (Shivas et al., 1995; Thangavelu and Mustaffa, 2010).

Race designations in *Foc* and their relation with VCGs and environmental conditions are not particularly straightforward. Molecular studies have shown that clonal lineages of *Foc* are largely VCG-specific, but a correlation between these data and race designations is not always observed (Gerlach et al., 2000; Fourie et al., 2009).

More genetic data and deeper understanding of the *Foc*-banana interactions are being generated, but in the meantime, it is important to remember that TR4, which is more aggressive than SR4, also affects Cavendish in the subtropics. Therefore, proper diagnostic tools to discriminate these strains need to be in place both to avoid false alarms and needless eradication measures, in case of a SR4 strain, and to fail on early detection and containment of an eventual TR4 outbreak.

OCCURRENCE AND DISTRIBUTION OF POPULATIONS OF *Fusarium oxysporum* f. sp. *cubense* IN THE SUBTROPICS

Foc is widely distributed in the subtropics affecting different banana cultivars (Table 1). In Australia, race 1 (VCGs 0124 and 0125) is widespread throughout the entire east coast banana production area, and SR4 (VCGs 0120, 0129 and 01211) has been recorded from Bundaberg to Byron Bay (Bentley et al., 1998). In areas where race 1 inoculum pressure is high, growers have replanted Lady Finger with Cavendish cultivars. VCG 01220 is the only strain of the pathogen recorded in Western Australia and causes sporadic, minor losses of Cavendish bananas grown at Carnarvon during unfavorable growing conditions, especially waterlogging (Shivas et al., 1995).

FWB is widespread in most of the banana-growing states in India and threatens the livelihoods of local banana farmers. Disease incidence can be as high as 95%. Diversity studies indicated the presence of races 1, 2 and SR4 (VCGs 0124, 0125, 0124/5, 0128, 0129, 01211, 01212, 01214, 01217, 01218, 01220) as well as tropical race 4 (VCG 01213/16), which can affect a range of diverse cultivars (Table 1). Of these, VCGs 0124 and 01213/16 are considered the most important strains found in Uttar Pradesh, Gujarat, Madhya Pradesh and Bihar states where they affect dessert bananas, of which Cavendish cultivars comprise

52% of the total area planted and 64% of total production. The occurrence of VCG 0124 on Cavendish banana is unique to India.

Table 1. Banana cultivars and Vegetative Compatibility Groups (VCGs) of *Fusarium oxysporum* f. sp. *cubense* (*Foc*) present in different subtropical banana production countries

Country	**Region/State**	**Cultivars (Subgroup)**	***Foc* VCGs**
Australia	East Coast	Lady Finger (Pome AAB)	0120*, 0129*
		Cavendish (AAA)	01211*, 0124
		Ducasse (Pisang Awak ABB)	0125
	West Coast	Cavendish (AAA) only	01220
Brazil	Paraná	Nanica (Cavendish, AAA) Prata (Pome, AAB) Maçã (Silk, AAA)	0120, 0123, 0124, 0125, 0126, 0128, 01210, 01215
	Rio Grande do Sul	Prata (Pome, AAB) Nanica (Cavendish, AAA)	
	Santa Catarina	Prata (Pome AAB) Cavendish (AAA)	
China	Guandong	Brazilian (Cavendish, AAA)	0120/15, 0123
		Guangfen (Pisang awak, ABB) Dongguan Dajiao (Dajiao, ABB)	0126, 0124/22, 01213/16, 01220
	Guangxi	Brazilian (Cavendish, AAA) Guangfen (Pisang Awak, ABB) Dongguan Dajiao (Dajiao, ABB)	0123, 01213/16 01218, 01221
	Hainan	Brazilian (Cavendish, AAA) Guangfen (Pisang awak, ABB)	0123, 0124/22 01213/1601221
	Yunnan	Brazilian (Cavendish, AAA) Guangfen (Pisang awak, ABB)	0120/15, 01213/16, 01221
India	Assam	Athiakol (ND) Monthan (Bluggoe, ABB) Malbhog (Silk, AAB) Manohar (Pisang Awak, ABB)	0124, 0125, 0124/5, 0128, 0129, 01211, 01212, 01218, 01220
	Bihar	Grande Naine (Cavendish, AAA) Robusta (Cavendish, AAA) Monthan (Bluggoe, ABB) Manohar (Pisang Awak, ABB) Malbhog (Silk, AAB)	01213/16, 01220, 0124 0125
	Gujarat	Grande Naine (Cavendish, AAA)	0124
	Madhaya Pradesh	Grande Naine (Cavendish, AAA)	0124
	Uttar Pradesh	Grande Naine (Cavendish, AAA)	01213/16
South Africa	Kiepersol	Grande Naine (Cavendish, AAA) Williams (Cavendish, AAA)	0120
	Komatipoort	Grande Naine (Cavendish, AAA)	0120
	KwaZulu-Natal	Grande Naine (Cavendish, AAA) Williams (Cavendish, AAA)	0120

- VCGs associated to Fusarium wilt in Cavendish and considered as 'subtropical' race 4
- ND: not defined

In China, *Foc* is well established with 11 VCGs (0120/15, 0123, 0126, 0124/22, 01218, 01220, 01221, 01213/16) occurring in the Guangdong, Hainan, Fujian, Guangxi and Yunnan provinces (Li et al., 2013). Guangdong, formerly the province with the highest production of bananas, has the greatest *Foc* diversity, with VCG 01213/16 (TR4) being predominant. VCG 0120/15 (SR4) is also widespread in Guangdong and is present in Fujian and Yunnan, but not in Hainan province (Li et al., 2013). More isolates have been collected from different production areas of China for further investigation. VCG 0120/15 (SR4) is the only variant of the *Foc* present in South Africa (Visser et al., 2010), where it caused severe losses in Kiepersol, previously the primary banana production area in South Africa. More than half of the banana plantations in Kiepersol have now been replaced by other crops (Viljoen, 2002). The disease is also present in southern KwaZulu-Natal, where it is less damaging than in Kiepersol. *Foc* SR4 has been introduced into two other areas of the country in the early 2000s, Tzaneen and Komatipoort (Grimbeek et al., 2003), but has been stopped by early detection and proper containment efforts. The disease has not been reported from Levubu in the Limpopo province, which is a small area in northeastern South Africa that has been producing banana for decades (Viljoen, 2002).

In Brazil detailed studies on *Foc* VCGs are not yet available. Matos et al. (2009) reported eight VCGs (0120, 0123, 0124, 0125, 0126, 0128, 01210, 01215), but details of cultivars affected and geographic distribution were not reported Studies to better understand the diversity of *Foc* in the Brazilian subtropics are urgently needed as FWB is causing severe losses. For instance, in Northern Paraná (Santa Mariana, Urai, Assaí, Andirá) losses up to 100% are recorded each year in Silk plantations and in Corupá and the Ribeira Valley, losses in Prata can exceed 30%. Outbreaks of FWB in Cavendish bananas in the Brazilian subtropics are sporadic and associated with abiotic stress and poor management practices.

While *Foc* SR4 causes losses in Cavendish in the subtropics it is usually associated with periods of seasonal stress. Where *Foc* TR4 is present, this seasonal pattern is less marked (Table 1). In regions such as Guangdong, Hainan, Fujian, Guangxi and Yunnan (China) and Uttar Pradesh (India), *Foc* TR4 has caused yield losses up to 100% in Cavendish plantations.

EPIDEMIOLOGY AND FACTORS DRIVING DISEASE INTENSITY IN THE SUBTROPICS

There are no fundamental differences in FWB epidemiology between the tropics and subtropics other than those related to climate. General information on *Foc* epidemiology can be found in various reviews on the disease (Ploetz et al., 2015; Dita et al., 2018). In both the tropics and subtropics, the movement and use of infected planting material and poor quarantine practices have a prominent role in *Foc* dissemination. In fact, *Foc* TR4 was probably introduced into Laos, Myanmar and Vietnam with infected planting material from China (Zheng et al., 2018). Chinese companies setting up plantations in Laos, Vietnam, Myanmar and Cambodia frequently transport plant materials and equipment from infested areas in China across the border, thereby increasing the risk of disseminating pest and diseases. Spatio-temporal analyses of FWB in Silk banana plantations in Brazil also suggest the use of infected planting material as a primary means of *Foc* dissemination (Dita et al., unpublished). Once FWB is detected in a given location, *Foc* can potentially spread throughout the entire farm and epidemics may develop. The intensity of epidemics in space and time depends on biotic and abiotic factors, management practices, host resistance and pathogen aggressiveness. In the subtropics, winter temperatures play a significant role in disease development (Daniells 2010). A clear correlation has been demonstrated between FWB incidence and seasonal temperatures over a 2-year period in Kiepersol (South Africa), with the highest incidence occurring once temperatures increase after winter, and with disease incidence being the lowest in late summer (A. Viljoen, unpublished). A similar pattern has also been observed in the Ribeira Valley and Corupá (Brazil) with both Cavendish and Prata-type cultivars (Dita et al., unpublished). In fact, FWB in Cavendish primarily develops after severe winters and low rainfalls in these regions. Moore (1995) proposed that low winter temperatures affect the susceptibility of some Cavendish cultivars, as CO_2 assimilation efficiency and photosynthetic efficiency were lower for the susceptible Williams cultivar than the SR4-resistant 'Dwarf Parfitt' mutant 'DPM25' during winter (Smith et al., 2006).

Lack of infrastructure, especially for irrigation, can increase periods of water stress on banana plants. Where irrigation exists, in the subtropical east coast banana production regions in Australia and in some properties in the Ribeira Valley in Brazil, water reservoirs for irrigation are located at the bottom of banana plantations planted on hillsides or slopes. Runoff water is then recycled upslope for irrigation. Initial detection of FWB led to some plantations abandoning irrigation, to reduce the risk of spreading the pathogen, exacerbating the environmental water stress and increasing disease symptom development on these farms. As in the tropics, mechanical damage caused by the banana weevil borer and nematodes, Ca deficiency and low soil pH can increase FWB in the subtropics. In Australia, banana fields with greater soil β-glucosidase activity had reduced expression of external FWB symptoms than soils with the similar *Foc* inoculum levels but a lower β-glucosidase activity, suggesting biological suppression of the fungus (Molina et al., 2015).

Studies to understand why *Foc* SR4 affects Cavendish cultivars only in the subtropics and not in the tropics and why R1 is less severe on Lady Finger in the tropics than the subtropics of Australia are required. The impact of low temperatures on pathogenicity of *Foc* SR4 and R1 strains during winter or between warmer and cooler growing regions of a particular country has received little attention in the past. Furthermore, understanding the impacts of winter temperatures on the competitiveness of antagonistic soil microorganisms and the overall function of the plant microbiome might help create a better understanding and assist management of FWB epidemics in the subtropics (Lakshmanan et al 2014). Subtropical regions where both *Foc* SR4 and *Foc* TR4 are present, such as Guangdong, Yunnan and northern India (Table 1), offer a good opportunity to study whether predisposing factors conditions for *Foc* SR4 also influence *Foc* TR4 in the subtropics.

Climate change is projected to increase land areas suited for banana production primarily in the subtropics and at higher altitudes in the tropics (Calberto et al., 2015). However, extreme weather events in terms of temperature, excess and lack of water and winds are projected to increase (Senevirantne et al., 2012; Thorton et al., 2014) with many negative implications for banana productivity. The weather extremes such as cold snaps, heat waves, droughts and heavy rainfall events, projected to increase with climate change, are associated with increased susceptibility of FWB. Extreme storms resulting in floods can also accelerate disease spread. Over the coming decades, the risk of FWB will increase, requiring improved and more crop management options to prevent greater losses.

MANAGEMENT OPTIONS AND CHALLENGES

Options to manage FWB in the subtropics may not differ from those recommended for tropical banana production. Pattison et al. (2018) proposed a set of practices to manage FWB considering three main scenarios: a) FWB is not present, b) FWB is detected (could be a quarantined strain or the expansion of strains already in country) and c) FWB is widespread (Figure 3). The seasonal fluctuations in subtropical banana production caused by low temperatures and / or low water availability, tend to limit grower's financial returns, also limiting their capacity to implement strategies to manage the disease.

Biosecurity and quarantine measures are required both in the tropics and subtropics. When FWB was first observed in the Kiepersol area in South Africa in the 1970s, growers tried to contain the disease by isolating newly infected areas and by disinfecting shoes and vehicles with copper oxychloride (Deacon, 1984). Copper oxychloride was later proven ineffective by Nel et al. (2007), and replaced with a commercial product based on didecyldimethyl-ammonium chloride. Currently, different products based on quaternary ammonia, together with a set of other biosecurity practices, are widely recommended and used in Australia (Biosecurity Queensland, 2016; Nguyen et al., 2018). Infected plants also need to be eradicated to reduce soil inoculum levels of *Foc* (Figure 3, scenarios B and C). The eradication method should be considered from an epidemiological and socioeconomic perspective (Biosecurity Queensland, 2016; Pattison et al., 2018). Once FWB reaches a point where eradication and other management practices are no longer viable (Figure 3, scenario D), the field will need to be replanted with resistant cultivars or even other crops.

Once banana growers have on-farm biosecurity practices in place they should consider management practices to suppress *Foc* and slow down the progress of disease. Disease progress has been slowed down by reduced and targeted nutrient inputs, particularly the avoidance of ammonium nitrogen, which may encourage disease development (Simmonds, 1966; Epp, 1987). Other disease suppressive practices include the use of ground covers, optimal and not excessive fertilizer applications, disease suppressive organic amendments and optimal irrigation with disease free water (Pattison et al., 2018). These practices may increase the establishment of organisms within the banana root, corm and pseudostem microbiome to compete with Foc. Case studies have shown that subtropical banana growers have slowed the development of FWB, by eradicating symptomatic plants and replanting the affected area with a ground cover like molasses grass (*Melinis minutiflora*) (Pattison et al., 2014; Wang et al., 2015; Fu et al., 2017). Groundcovers act to reduce run-off, erosion and the spread of disease propagules and to increase microbial competition with *Foc*, thereby slowing pathogen incidence and severity (Pattison et al., 2014; Rames et al., 2018).

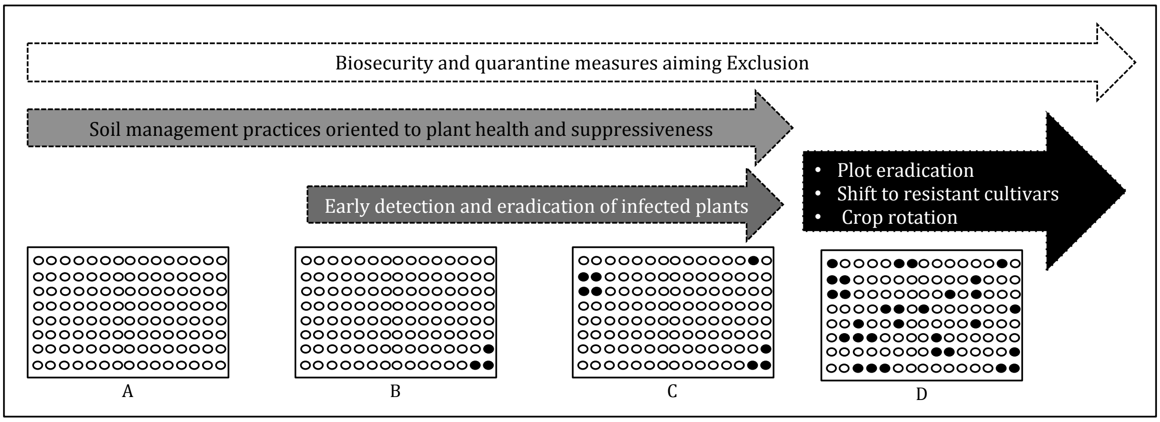

Figure 3. Different scenarios of the occurrence of Fusarium wilt of banana (FWB) in a banana plantation and major recommended management practices. A. FWB is not present. B. The first incursion of FWB was recently detected. C. The disease is established at low levels with a patchy distribution. D. The disease is evenly distributed at high levels of incidence. White and black circles represent healthy and FWB-infected plants, respectively (Modified from Pattison et al. 2018 and Dita et al. 2018).

The planting of resistant banana cultivars is the most effective approach to manage FWB. However, such cultivars need to be acceptable to local markets and should adapt well to prevailing environmental conditions. *Foc* SR4-resistant Goldfinger (FHIA-01) introduced into South Africa and packed together with Cavendish bananas generated negative consumer response and a momentary decline in demand for dessert bananas. Due to the unavailability of a replacement for Cavendish bananas in South Africa, growers in Kiepersol are replacing their bananas with avocados and macadamias.

Mutation breeding was used successfully to generate 'DPM25' with resistance to SR4 FWB, (Smith et al., 2006), but the commercial success is still to be determined. Mutation breeding can be used to develop new cultivars where fewer options for cultivar substitution exist. However, subtropical regions where a diversity of banana cultivars are grown and consumed may have a greater chance of developing or selecting more resistant banana cultivars. However as was the case of Gros Michel, the replacement of one cultivar by another may be mandated not solely by the consumer acceptance, but by the availability of a resistant cultivar.

The extreme events associated with climate change will further challenge subtropical banana growers' ability to manage Fusarium wilt and demand increased investment. In Brazil, hurricane Catarina caused huge losses due to heavy rains and strong winds in 2004 (McTaggart-Cowan et al., 2006). In Australia, growers in the east coast subtropical production zone have experienced several intense rainfall and wind events, e.g. ex-tropical cyclones Oswald, 2014 and Debbie, 2017. Climate modeling predicts greater frequency of extreme climatic events (CSIRO and BoM, 2015).

CONCLUDING REMARKS

In subtropical regions, banana growers have been dealing with different strains of *Foc* for over a century. Subtropical banana growers typically have fluctuating production cycles, limited available resources and supply domestic markets. Environmental constraints such as extreme cold temperature and frosts lead to production on steep and sloping land, imposing additional restrictions on disease management options. Changes in soil and water management, like groundcovers, optimal irrigation and careful use of nitrogen fertilizer have allowed production to continue. The increase in climate variability and extreme weather events, however, places additional stresses on banana plants and on these growers.

As *Foc* TR4 continues to spread globally, it imposes a far greater threat to subtropical banana production around the world. Quarantine and biosecurity to prevent the spread of the disease to unaffected areas are doubly important where grower resources for disease management are limited. For scientists, studies of SR4 present a unique opportunity to understand the interaction of abiotic factors with the banana plant and the soil and plant microbiome in the expression of FWB. Studies in zones with co-occurrence of SR4 and TR4 are especially important and will provide insight into the management of FWB with the increasing extreme weather events with climate change. Therefore, floods, drought and unfavorable environmental conditions, which impose additional stress on the plants in subtropical production, need to be managed for the efficacy of FWB management practices.

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Literature cited

Bancroft, J. (1876). Report of the board appointed to enquire into the cause of disease affecting livestock and plants. Votes and Proc. 3, 1011-38.

Bentley, S., Pegg, K.G., Moore, N.Y., Davis, R.D., and Buddenhagen, I.W. (1998). Genetic variation among vegetative compatibility groups of *Fusarium oxysporum* f. sp. *cubense* analyzed by DNA fingerprinting. Phytopathology 88 (12), 1283–93 https://doi.org/10.1094/PHYTO.1998.88.12.1283.

Biosecurity of Queensland. (2016). Panama Disease Tropical Tace 4: Biosecurity Standards and Guidelines. Queensland: Department of Agriculture and Fisheries. Available online at: http://abgc.org.au/wp-content/uploads/2015/03/Biosecurity-standards-and-guidelines.pdf

Buddenhagen, I. (2009). Understanding strain diversity in *Fusarium oxysporum* f. sp. *cubense* and history of introduction of 'Tropical Race 4' to better manage banana production. Acta Hortic. 828, 193-204 doi: 10.17660/ActaHortic.2009.828.19.

Calberto, G., Staver, C., and Siles, P. (2015). An assessment of global banana production and suitability under climate change scenarios. In Climate change and food systems: global assessments and implications for food security and trade, Elbehri, A. ed. (Rome, Italy: Food Agriculture Organization of the United Nations), p.264-291. Available online at: http://www.fao.org/3/a-i4332e.pdf.

CSIRO and BoM. (2015). Climate Change in Australia – Projections for Australia's NRM Regions (Melbourne, Australia: CSIRO and Bureau of Meteorology), pp.216. Available online at: http://www.climatechangeinaustralia.gov.au/media/ccia/2.1.4/cms_page_media/168/CCIA_PROJECTIONS_TECHNICAL_REPORT.pdf.

Czislowski, E., Fraser-Smith, S., Zander, M., O'Neill, W. T., Meldrum, R. A., Tran-Nguyen, L. T. T., et al. (2017). Investigation of the diversity of effector genes in the banana pathogen, *Fusarium oxysporum* f. sp. *cubense*, reveals evidence of horizontal gene transfer. Mol. Plant Pathol. 19, 1155–1171. doi: 10.1111/mpp.12594

Daniells, J., 2010. Fusarium wilt of banana–an integrated approach to disease management. Tree & Forestry. Sci Biotechnol 2, 50-55.

Deacon, J.W. (1984). Panama disease of banana in South Africa. Horticultural Science 1, 29-31.

Dita, M., Barquero, M., Heck, D., Mizubuti, E.S.G., and Staver, C.P. (2018). Fusarium wilt of banana: current knowledge on epidemiology and research needs toward sustainable disease management. Front. Plant Sci. 9, 1–21 doi: 10.3389/fpls.2018.01468.

Epp, MD. (1987). Somaclonal variation in bananas: A case study with Fusarium wilt. Banana and Plantain Strategies (Cairns, Australia: ACIAR Proceedings 21) pp. 140-150.

FAO. (2018). Food and Agriculture Organization of the United Nations. FAOSTAT Statistics Database. Available online at: http://www.fao.org/faostat/en/#home.

Fourie, G., Steenkamp, E.T., Gordon, T.R., and Viljoen, A. (2009). Evolutionary relationships among the vegetative compatibility groups of *Fusarium oxysporum* f. sp. *cubense*. Applied and Environmental Microbiology 75, 4770–4781 DOI: 10.1128/AEM.00370-09.

Fu, L., Penton, C.Y., Ruan, Y.Z., Shen, Z.Z., and Shen, Q.R. (2017). Inducing the rhizosphere microbiome by biofertilizer application to suppress banana Fusarium wilt disease. Soil Biology and Biochemistry 104, 39-48 DOI: 10.1016/j.soilbio.2016.10.008.

Gerlach, K.S., Bentley, S.,Moore, N.Y., Pegg, K.G, and Aitken, E.A.B. (2000). Characterisation of Australian isolates of *Fusarium oxysporum* f. sp. *cubense* by DNA fingerprinting analysis. Australian Journal of Agricultural Research 51, 945–53 DOI: 10.1071/AR99172.

Grimbeek, E.J., Viljoen, A., and Bentley, S. (2001). First occurrence of Panama disease in two banana-growing areas of South Africa. Plant Disease 85: 1211-1211 DOI: 10.1094/PDIS.2001.85.11.1211B

Hort Innovation. (2018). Australian Horticulture Statistics Handbook 2016/2017 - Fruit. (Sydney, Australia: Horticulture Innovation Australia Limited), pp. 116. https://horticulture.com.au/wp-content/uploads/2018/03/Hort-Stats-2016-17-Fruit-web.pdf

Lakshmanan, V., Selvaraj, G., Bais, H.P., 2014. Functional Soil Microbiome: Belowground Solutions to an Aboveground Problem. Plant Physiology 166, 689-700.

Li, C.Y., Mostert, G., Zuo, C.W., Beukes, I., Yang, Q.S., Sheng, O., Kuang, R.B., Wei, Y.R., Hu, C.H., Rose, L., Karangwa, P., Yang, J., Deng, G.M., Liu, S.W., Gao, J., Viljoen, A., and Yi, G.J. (2013). Diversity and distribution of the banana wilt pathogen *Fusarium oxysporum* f. sp. *cubense* in China. Fungal Genomics & Biology 2 DOI: 10.4172/2165-8056.1000111.

Lichtemberg, L.A., Malberg, J.L. and Hinz, R.H. (2001). Suscetibilidade varietal de frutos de bananeira ao frio. Revista Brasiliera de Fruticultura 23(3): 568-572

Matos, A.P., Silveira, J.D.S., Ferreira, D.M.V., Cordeiro, Z.J.M., and Trocoli, R.O. (2009). Characterisation of isolates of Fusarium oxysporum f. sp. cubense into vegetative compatibility groups in Brazil. In: Global Perspectives on Asian Challenges. ISHS/Promusa Banana Symposium. ISHS/Promusa, 39. http://www.promusa.org/tiki-download_file.php? fileId=106&display.

McTaggart-Cowan, R., Bosart, L.F., Davis, C. A., Atallah, E. H., Gyakum, J. R., and Emanuel, K. A. (2006). Analysis of Hurricane Catarina (2004). Mon. Wea. Rev. 134, 3029–3053 https:// doi.org/10.1175/MWR3330.1.

Molina, A.B., Hermanto, C., Pattison, T., Subandiyah, S., Winarno and Sukarman. (2015). Integrated crop production of bananas in Indonesia and Australia. Final Report. (Canberra, Australia: Australian Centre for

International Agricultural Research), pp.133. Available online at: http://banana-networks.org/Bapnet/files/2018/01/AS-C34B31-TERMINAL-REPORT-final.pdf.

Moore, N.Y. (1995). Fusarium wilt of banana: pathogen variability and host-pathogen interaction. PhD thesis, The University of Queensland, pp.152

Mostert, D., Molina, A. B., Daniells, J., Fourie, G., Hermanto, C., Chao, C. P., et al. (2017). The distribution and host range of the banana Fusarium wilt fungus, *Fusarium oxysporum* f. sp. *cubense*, in Asia. PLoS ONE. 12:e0181630. doi: 10.1371/journal.pone.0181630

Nel, B., Steinberg, C., Labuschagne, N., and Viljoen, A. (2007). Evaluation of fungicides and sterilants for potential application in the management of Fusarium wilt of banana. Crop Protection 26, 697-705 DOI: 10.1016/j.cropro.2006.06.008.

Nguyen, T., Tran-Nguyen, L., Wright, C., Trevorrow, P., and Grice, K. (2018). Evaluation of the efficacy of commercial disinfectants against Fusarium oxysporum f. sp. cubense Race 1 and Tropical Race 4 propagules. Plant Disease. doi: 10.1094/PDIS-03-18-0453-RE.

Pattison, A.B., Molina, A.B., Chao, C.P., Viljoen, A., and Lindsay, S.J. (2018). Integrating management practices to support banana production in the presence of Fusarium wilt. Acta Hortic. 1196, 129-136 DOI: 10.17660/ActaHortic.2018.1196.15.

Pattison, A.B., Wright, C.L., Kukulies, T.L., and Molina, A.B. (2014). Ground cover management alters development of Fusarium wilt symptoms in Ducasse bananas. Australasian Plant Pathology 43: 465-476 DOI: 10.1007/s13313-014-0296-5.

Pegg, K.G., Moore, N.Y., and Bentley, S. (1996). Fusarium wilt of banana in Australia: a review. Aust J Agric Res 47, 637–650 https://doi.org/10.1071/AR9960637.

Ploetz, R. C. (2006). Fusarium wilt of banana is caused by several pathogens referred to as *Fusarium oxysporum* f. sp. *cubense*. Phytopathology 96, 653–656 doi:10.1094/PHYTO-96-0653.

Ploetz, R., Freeman, S., Konkol, J., Al-Abed, A., Naser, Z., Shalan, K., et al. (2015). Tropical race 4 of Panama disease in the Middle East. Phytoparasitica 43, 283–293. doi: 10.1007/s12600-015-0470-5.

Rames, E.K., Pattison, A.B., Czislowski, E., and Smith, M.K. (2018). Soil microbial community changes associated with ground cover management in cultivation of Ducasse banana (*Musa* sp. ABB, Pisang Awak subgroup) and suppression of Fusarium oxysporum. Australasian Plant Pathology 47, 449-462 doi: 10.1007/s13313-018-0578-4.

Seneviratne, S. I., Nicholls, N., Easterling, D., Goodess, C. M., Kanae, S., Kossin, J., Yali Luo, Y., Marengo, J., McInnes, K., Rahimi, M., Reichstein, M., Sorteberg, A., Vera, C., and Zhang, X. (2012). Changes in climate extremes and their impacts on the natural physical environment. In Managing the risks of extreme events and disasters to advance climate change adaptation. Field, C.B., Barros, V., Stocker, T.F., Qin, D., Dokken, D.J., Ebi, K.L., Mastrandrea, M.D. Mach, K.J., Plattner, G.-K., Allen, S.K., Tignor, M. and Midgley, P.M., eds. (Cambridge, UK and New York, USA: Cambridge University Press and IPCC). p.109-230.

Shivas, R.G., Wood, P.M., Darcey, M.W., and Pegg, K.G. (1995). First record of *Fusarium oxysporum* f. sp. *cubense* on Cavendish in Western Australia. Australasian Plant Pathology 24, 38-43 https://link.springer.com/article/10.1071/APP9950038.

Simmonds, N.W. (1966). Bananas, 2nd edn (London, UK: Longmans), pp.512.

Smith, M.K., Hamill, S.D., Langdon, P.W., Giles, J.E., Doogan, V.J., and Pegg, K.G. (2006). Towards the development of a Cavendish banana resistant to race 4 of Fusarium wilt: gamma irradiation of micropropagated Dwarf Parfitt (*Musa* spp., AAA group, Cavendish subgroup). Australian Journal of Experimental Agriculture 46, 107-113. doi: http://dx.doi.org/10.1071/EA04175.

Stover, R. H. (1962). Fusarial wilt (Panama disease) of bananas and other *Musa* species. (Kew, Surrey, England: Commonwealth Mycological Institute), pp.117.

Su, H., Hwang, S., and Ko, W. (1986). Fusarial wilt of Cavendish bananas in Taiwan. Plant Dis. 70, 814–818 doi: 10.1094/PD-70-814

Thangavelu, R., and Mustaffa M. (2010). First report on the occurrence of a virulent strain of Fusarium wilt pathogen (race-1) infecting Cavendish (AAA) group of bananas in India. Plant Disease 94, 1379-1379 DOI: 10.1094/PDIS-05-10-0330

Thornton, K., Ericksen, P.J., Herrero, M, et al. (2014). Climate variability and vulnerability to climate change: a review. Global Change Biology 20, 3313-3328 https://doi.org/10.1111/gcb.12581.

Viljoen, A. (2002). The status of Fusarium Wilt (Panama disease) of banana in South Africa. South African Journal of Science 98, 1-4.

Visser, M., Gordon, T.R., Fourie, G., and Viljoen, A. (2010). Characterization of South African isolates of *Fusarium oxysporum* f. sp.*cubense* from Cavendish banana. South African Journal of Science 106, 44-49 DOI: 10.4102/sajs.v106i3/4.154.

Waite, B. H., and Stover, R. H. (1960). Studies on Fusarium wilt of bananas: VI. Variability and the cultivar concept in *Fusarium oxysporum* f. sp. *cubense*. Can. J. Bot. 38 985–994. doi: 10.1139/b60-087.

Wang, B., Li, R., Ruan, Y., Ou, Y., Zhao, Y., and Shen, Q. (2015). Pineapple–banana rotation reduced the amount of Fusarium oxysporum more than maize–banana rotation mainly through modulating fungal communities. Soil Biol. Biochem. 86 77–86. doi: 10.1016/j.soilbio.2015.02.021

Zheng, S.J., García-Bastidas, F.A., Li, X., et al. (2018). New geographical insights of the latest expansion of *Fusarium oxysporum* f.sp. *cubense* Tropical Race 4 Into the Greater Mekong Subregion. Front Plant Sci 9 https://doi.org/10.3389/fpls.2018.00457.