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May bananas go extinct? The epidemic of Panama disease. A review

Czy banany mogą „wyginąć”? Epidemia choroby panamskiej. Praca przeglądowa

Summary. Bananas are one of most popular fruits worldwide. Estimated export in 2020 reached a record high of 22.2 million tons, a 1.7% growth compared to 2019. They are cultivated in Asia, Africa, Australia, Latin, and South America. People value them for their taste, easy accessibility, low price, plenty of nutrients and vitamins, preparation versatility. They contain vitamins A, C, E, K and from B group, fibre, magnesium, phosphorus, calcium, and potassium. In some countries bananas and plantains are the basis of diet and are consumed daily, like rice or potatoes.
Unfortunately, these wonderful fruits may soon cease to exist. An illness called Panama disease caused by *Fusarium oxysporum* fungus is responsible for destroying 950,000 metric tonnes of crop yields annually. Previous variant of that disease almost caused a total wipeout of former mostly cultivated banana cultivar Gros Michel. In this work Panama disease history, biology, and prevention are reviewed.

Key words: banana, Panama disease, fungal disease prevention *Fusarium oxysporum* f. sp. *cubense*, *Fusarium* wilt

INTRODUCTION

Bananas are fruits grown in tropical regions and cultivated in more than 130 countries. Edible ones are of *Australimusa* and *Eumusa* series, which originated from the same genus. Majority of edible bananas are only of *Musa accuminata* or are hybrid of two wild diploid species – *M. acuminata Colla* and *M. balbisiana Colla*, and their consecutive diploid and triploid clones [Ordonez et al. 2015], which refer to A and B genomes. Bananas eaten by humans propagate asexually by rhizomes. In 1970s commercial production was popularized using tissue culture [Gowen 1995]. Bananas originated in India, Africa, and eastern part of Asia – Malaysia or Japan [Mohapatra et al. 2010]. Bananas are among most popular fruits in the world. In 2020, nearly 120 million metric tons were produced and 21.5 million were exported worldwide [FAO 2021], including Cavendish – most commonly traded variety. Annual production of Cavendish reached 50 million metric tons [Statista 2022]. Cavendish is also one of the most productive cultivars, characterized by productivity value of over 30 t/ha/yr. Banana plant is important not only as a food crop but is also used as a composting material [Ultra et al. 2005], an energy source through decomposition [Clarke et al. 2008], material for baskets, mats, tableware [Kambuou 2002], are required in social and religious rites in India [Mohapatra et al. 2010].

Panama disease (or Fusarium wilt) is a blight attacking banana perennial herbs. Soil-driven fungi *Fusarium oxysporum* f. sp. *cubense* (E.F. Sm.) W.C. Snyder & H.N. Hansen *(Foc)* are responsible for the infection. Its place in taxonomy is: Domain Eukaryote; Kingdom Fungi; Phylum Ascomycota; Class Ascomycetes; Subclass: Sordariomycetidae; Order: Hypocreales. Race 1 of *Foc* caused destruction of Gros Michel variety industry in Central America and the Caribbean in the 2nd millennium. Gros Michel cultivar was replaced by Cavendish cultivar, which is now the mostly exported banana variety. Cavendish and some varieties like plantains cultivated for local use are threatened by a new *Foc* type – Tropical race 4 (TR4). It is estimated, that about 80% of worldwide bananas and plantains is vulnerable to TR4. Tropical race 4 was spotted for the first time in Taiwan, in the late 1960s. *Foc* caused a substantial decrease in production, increase in production costs, bankruptcy among planters, loss of millions of dollars. In 2014 four hundred-million-dollar worth export industry was at risk in the Philippines. China, Mozambique, Ecuador, Oman, Jordan, Pakistan, Guyana, Suriname, Latin America and the Caribbean are also threatened. The disease is dangerous to large banana companies and to millions of locals as well. *Foc* is spread by planting material, water, soil, utilities, footgear and machineries and can persist in the ground for at least 20 years [Pérez-Vicente et al. 2014] or according to Cook et al. [2015] even more than 30 years.

HISTORY OF FUSARIUM WILT

Papers suggest that *Fusarium* wilt has its origin in South-East Asia [O'Donnel et al. 1998, Ploetz 2000] however, the oldest characteristic comes from Australia [Bancroft 1876]. *Foc* was also found in Central America in 1890 [Ashby 1913], Cuba [Smith 1910], Trinidad [Rorer 1911], Puerto Rico [Fawcett 1911] and Jamaica since 1903 [Ashby 1913, Smith 1910], Caribbean Islands in 1925 [Stover 1962]. From the start of the 20th century the disease started to spread quickly, mainly on large company grounds, due to export of infected but symptomless rhizomes or suckers [Ploetz and Pegg 2000]. Problem of TR1 was disregarded after 1950, when more resistant Cavendish was presented [Pérez-Vicente and Dita 2014]. Stover [1962] suggested how *Foc* epidemics originated, clamming as follows: „a) the wilt probably evolved on several susceptible varieties of edible bananas in the India-Malayan area; b) susceptible variety Silk (Apple AAB) was present in the Caribbean in 1750, while Gros Michel (AAA) was not introduced until early 1800's and was not extensively planted before 1850; the wilt was already present in some areas where Silk was planted before Gros Michel introduction; c) during the rapid expansion of Gros Michel in the Caribbean between 1890 and 1910, lands formerly infested with diseased Silk were planted with Gros Michel. It has been estimated that between 1890 and the mid-1950s, more than 40,000 ha of Gros Michel were destroyed”. TR4 originated at the beginning of 1990’s in Malaysia and Indonesia [Masdek et al. 2003, Nasdir 2003], then moved to southern-eastern regions of Asia and Australia in less than ten years [Pérez--Vicente and Dita 2014].

PANAMA DISEASE SYMPTOMS

There are two types of *Foc* disease – „yellow leaf syndrome” and „green leaf syndrome” [Stover 1962, Pérez-Vicente 2004]. „Yellow leaf syndrome” might be mistaken for a potassium deficiency, because of similar symptoms – old leaves outlines turn yellow, progressing from old to new leaves. Then leaves subside, sag and hang down around the pseudostem due to necrosis. „Green leaf syndrome” is similar to yellow leaf syndrome, but leaves do not change color before collapsing and bending. In both cases new leaves show the symptoms last, often continue to grow, but in a pale shade, until the whole plant collapses. Fruits are unaffected [Dita et al. 2013]. The blight is most visible in the place where the stele meets the cortex [Niwas et al. 2022].

The reason for withering is heavy water stress caused by lack of permeability of mesh plates of the xylem vessels and pathogen attacks like mycelia clogging, intoxication, and plant defense mechanism e.g., gum and tylose secretion or vessel shrinkage [Beckman 1990].

Once infected, plants are not likely to recover. When it happens, growth is very slow and new suckers are produced sick. Internal symptoms include: vascular tissue of the roots and rhizomes turn yellow, pseudostem’s vascular strands turns yellow, red, or brown, petioles’ vessels may turn red. When a banana plant dies, *Foc* continues to develop. After fungus grows out from the xylem, it produces numerous chlamydospores, which stay in the ground as the plant rots. The blight lasts in the secondary host roots e.g., plants comparable to bananas or various weed species, however mentioned plants do not suffer from the disease. All *Foc* races show same symptoms on *Musa*, thus different races cannot be distinguished just by observation [Stover 1962, Ploetz 1990, Ploetz and Pegg 2000, Dita et al. 2013].

Foc might be mistaken for Moko, the bacteria wilt caused by *Ralstonia solanacearum* race 2, because of somewhat similar symptoms although, both may be easily differentiated with closer analysis [Pérez Vicente and Dita 2014].

NOMENCLATURE OF *FUSARIUM OXYSPORUM*

Fusarium oxysporum fungal species is an anamorphic, filamentous, and morphologically undifferentiated complex. It includes saprophytes, antagonists and pathogens to plants, animals and human [O’Donnell and Cigelnik 1999]. In the case of agriculture and ecology, this is the most meaningful taxa in *Fusarium* [Ploetz 2006b]. *Fusarium oxysporum* species can also attack not only banana plants e.g., *F. oxysporum* f. sp. *batatas* may affect tobacco too [Pérez-Vicente and Dita 2014].

MORPHOLOGY AND ANATOMY OF *FOC*

Fusarium oxysporum f. sp. *cubense* hyphomycete [Niwas et al. 2022] fungus is a teleomorph. According to Stover [1962] the fungus is asexual and haploid, hence its population structure is believed to be mostly clonal [Fourie et al. 2009, Groenewald et al. 2006]. For reproduction and dispersion, it produces macroconidia, microconidia, which are generated in sporodochia, and chlamydospores [Fourie et al. 2011]. Macroconidia are of 27–55 × 3.3–5.5 µm, numerous, curved like a sickle with an ability to straighten, have slender walls, and have 3–5 septa. Apical cell is of crescent, thin shape. Basal cells resemble feet. Macroconidia are grown in individual phialide in hypha. Microconidia are of 5–16 × 2.4–5.5 µm, mostly septa deprived, of oval, elliptic, or kidney shape and generated largely in false heads in short monophialides. Chlamydospores are of 7–11 µm in diameter, are developed in hyphae or conidia, individually, by two, or in chains. Mycelia grown on potato-dextrose-agar (PDA) may resemble hair or cotton, form remote or numerous colonies and are of white, pink, light purple, or, in some circumstances, black and red color [Stover 1962, Ploetz 1990, Pérez-Vicente et al. 2003].

RACE DIVERSITY

Races in regard to *Foc* have been in use since 1950s [Stover 1962]. They are defined by ability to infect specific reference varieties. Due to troublesome breed designations, additional methods of distinguishing genetic diversity were introduced. Vegetative compatibility group (VCG) tests were used to classify *Foc* into 24 distinctive VCGs: VCG0120 through VCG0126 and VCG0128 through VCG01224 [Ploetz 2006a, Bentley et al. 1998, Kistler et al. 1998]. DNA markers showed, that *Foc* originated from different, not related progenitors but has similarities in structure and physiology through convergence, meaning some VCGs are more closely related to *F. oxysporum* f. sp. compared to other VCGs [O'Donnel et al. 1998, Baayen et al. 2000, Fourie et al. 2009]. Strains of different VCGs affect different banana varieties hence, races were introduced. Another reason for the affinity to certain cultivars may be a horizontal gene transfer between the *F. oxysporum* complex [Ma et al. 2010]. Generally, the origin of *Foc* shows a strong dichotomy determined as types or clades [Groenewald 2006]. The present epidemy is caused by VCG01213-01216, commonly called Tropical Race 4 (TR4) [Ploetz 2006a, Niwas et al. 2022]. Race 4 includes two „sub races": sub-tropical race 4 and tropical race 4. The first one shows inferior effect on economy, afflicting mainly plants exposed to stress factors, primarily cold [Hwang and Ko 2004].

BIOLOGY AND ECOLOGY

Germination of *Foc* chlamydospores is induced by close presence of banana roots. Contagion happens as an answer to primary and secondary root exudate [Li et al. 2011]. The process of infection occurs as follows: firstly, chlamydospores sprout, secondly hyphae stick to epidermis and percolate it. Next mycelia travel through the cortex to the xylem vessels. There fungus generates microconidia and toxins, which travel further the upstream in the sap, branching to near vessels and creating fungal structures anew [Li et al. 2011]. *Foc* develops in 9–38°C, with the best temperature range of 23–27°C [Pérez et al. 2003]. The blight is the mostly active in warm and wet months but the most crucial factors are the plant's resistance to the pathogen, *Foc* pathotype, inner and surface drainage, environment, and soil type. Low pH ground favors the growth of the fungus. On the other hand, using nitrates instead of ammonia and fortifying the soil with calcium slows infection [Peng et al. 1999, Nel et al. 2007]. They are endophytic *Fusarium oxysporum* cultures capable of restraining the *Foc* in greenhouse condition. Unfortunately, the method needs to be used with others to be effective [Forsyth et al. 2006].

HOSTS OTHER THAN GENERA *MUSA*

Chloris inflata sin *Chloris barbata* (purpletop Chloris) [Hennessy et al. 2005], *Commelina diffusa* (spreading day flower), *Ensete ventricosumi* (Ensete) [Wardlaw 1972], *Euphorbia heterophylla* (wild poinsettia), *Tridax procumbens* (coat buttoms) [Hennessy et al. 2005, CABI 2007], *Panicum purpurenscens* [Pérez-Vicente and Dita 2014].

SPREADING

Foc is most likely to propagate, if plants are close to one another, thus suggesting plant-to-plant dispersal of the fungus [Meldrum et al. 2013]. *Foc* is also likely to spread through planting material, infected plant parts – e.g., contaminated but asymptomatic suckers [Hwang and Ko 2004], soil and water, and probably by windy and rainy weather, floods, and by insects [Pérez-Vicente et al. 2014], especially banana weevil borer Cosmopolites sordidus (Coleoptera: Curculionidae), which travels underground [Gold et al. 2001, Meldrum et al. 2013]. Another way of transmitting the *foc* is low sanitary attention. *Foc* is confirmed to spread by soil carried by native fauna, e.g. with an assistance of nematodes which help *Foc* penetrate root and corm and on boots and machinery of the planters [Niwas et al. 2022]. It is possible for *foc* to spread from infected to blight-free areas due to soil shift by transport or water movements [Pérez-Vicente et al. 2014].

PREVENTION

Boots, gear, and truck wheels need to be constantly disinfected mainly using formaldehyde and quaternary ammonium formulations [Nel et al. 2007, Meldrum et al. 2013].

To naturally prevent *Foc* spread, crop rotation is used. In Guangzhou, China, a region strongly affected by the blight, Chinese leek (*Allium tuberosum*) and banana are sown alternately [Zhang et al. 2011]. Other crop rotation techniques are maize-banana and more effective pineapple-banana [Niwas et al. 2022].

Another natural way to fight off the disease are organic amendments e.g., fertilizers containing opponent microorganisms to *Foc* or microorganisms supporting banana herbs [Fu et al. 2017]. Most promising supporting bacteria are plant growth promoting rhizobacteria (PGPR) [Niwas et al. 2022].

Supporting banana plants with an addition of silicone (Si) provides them with natural barrier, mitigating the symptoms. Silicone most likely accumulates in the banana leaves, preventing pathogen from penetrating the plant [Fortunato et al. 2012].

Borax (H_3BO_3) at 500 ppm was found effective in inhibiting the growth of *Foc* followed by zinc sulphate addition in *in vitro* and field conditions [Niwas et al. 2019].

Application of phyto-hormones e.g., methyl jasmonate (MeJA) boosts plants immunity to several infections including *Fusarium* wilt and regulates interactions between plants and microbes. The use of MeJA stimulates banana herbs to more intensive enzyme utilization and lowers the amount of H_2O_2 and malondialdehyde (MDA) after inoculations against *Foc* TR4 [Sun et al. 2013].

Bio-control agents (BCAs) are found useful in *Foc* prevention. Soil fortified with *Trichoderma harzianum* successfully restrains Panama disease harmfulness at the similar level as fungicide carbendazim. Also, *streptomycetes* derived from banana roots inhibits growth of *Foc* [Xue et al. 2015]. Moreover, use of artificial inoculation to tissue cultured banana plantlets is an effective way of soothing the symptoms and boosting the plant development [Paparu et al. 2004, Jie et al. 2009].

It is possible to develop blight-resistant banana varieties using breeding programmes and genetic engineering. Various techniques are used such as particle bombardment, sonication assisted vacuum infiltration of the apical meristem, or utilization of multiple bud clumps followed by *Agrobacterium*-mediated gene transformation. Proteins resembling thaumatin are promising options for genetic engineering of wilt-proof plants [Mahdavi et al. 2012].

The most promising and non-invasive methods so far are universally recognized selection and selection programmes for wilt tolerance or resistance [Buddenhagen 2009]. A novel technique is being tested consisting of greenhouse and field tests, providing fair information of blight response to the evaluated genotypes of banana [Li et al. 2013].

Innovative breeding techniques regarding *Fusarium* wilt immune clones are being developed. Shoot tip cultures were proven to be immune to *Foc* races 1 and 4 bred *in vitro* while fortified with fusaric acid and fungal crude filtrates. Unfortunately, since banana plants are bred asexually, any breeding programmes are difficult to accomplish. However, some *Foc* resistant clones have been engineered using somaclonal techniques [Israeli et al. 1995, Wu et al. 2013].

CONCLUSIONS

Panama disease is a serious problem faced by food producers, food scientists, local, and worldwide people. The blight spreads easily, is difficult to contain, and causes irrevocable damage. Considering the multiple role of bananas – food, income, trade, and cultural aspects, banana plants are worth protecting. On the other hand, such severe disease as *Fusarium* wilt needs to be well examined to find effective ways to prevent and oppose it now and in the future. One of the most promising ways of fighting off the blight is genetic engineering however, many people protest against it. In such case, better topic understanding and proper education is required.

Considering the effort to prevent Panama disease, it seems possible to save the bananas from extinction. However, many methods presented in this work require specialized tools, skills, or expertise. Bananas are mostly cultivated in the developing counties, where access to such technology is limited or people are skeptical about methods like genetic modifications. To sum up, it theoretically seems feasible to protect bananas from extinction, however considering the lack of resources, severity of Panama disease, and prejudice to genetic modification methods, not immune banana varieties are likely to extinct.

SUGGESTED LITERATURE

To learn more about *Fusarium* wilt sampling, the authors suggest: „Protocol for sampling *Fusarium* wilt or Panama disease by *Fusarium oxysporum* f. sp. *cubense* infected plants and tissues" by N. Moore, QDPI or adaptation by L. Pérez-Vicente and A. Batlle.

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