**Fusarium oxysporum f. sp. cubense** *(Foc)* is one of more than 100 *formae speciales* (special forms) of the *Fusarium oxysporum* species complex of pathogenic as well as non-pathogenic morphologically similar filamentous fungi. The *cubense* special form comprises the pathogenic strains that cause *Fusarium wilt* in cultivated bananas, as well as strains that affect species in the Musaceae and Heliconaceae families. However, it does not follow that the strains of *F. oxysporum* f. sp. *cubense* are necessarily related genetically[1]. *F. oxysporum* has no known sexual stage. Variation in the fungus is thought to result from mutations.

The pathogenic strains are commonly classified into four races that are meant to reflect differences in the cultivars on which they cause disease. In reality, there are more variants of the fungus than the number of races suggests. Progress in understanding the pathogen's diversity was made possible with the development of a method to classify *Fusarium oxysporum* strains into vegetative compatibility groups (*VCGs*), based on the ability of their hyphae to fuse and form stable heterokaryons (cells containing two distinct nuclei)[2]. Each VCG has its own characteristics in terms of aggressiveness and the banana cultivars that it attacks most readily. The VCG associated with tropical race 4 (TR4) — VCG01213/16 — was ranked as the greatest threat to banana production because of its lethal impact, wide host range and persistence in the soil[3].

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History

In 1876, the author of the first report of the disease, J. Bancroft, speculated that it was caused by a fungus. Unaware of Bancroft's work, a horticulturist at the Hawaii Agricultural Experiment Station also proposed in 1904 that a fungus caused the disease. The plant pathologist Erwin F. Smith became the first person to isolate the pathogen from banana tissues he had received from Cuba. He reported his results at the first meeting of the American Phytopathological Society held in Boston in 1908. Smith recognized that the fungus was in the genus *Fusarium* and named it *Fusarium cubense* because of its Cuban source. The study confirming that the fungus was indeed the causal agent was published in 1919. *Fusarium cubense* was recognized as a variant of *Fusarium oxysporum* and renamed *Fusarium oxysporum* f. sp. *cubense* in 1935.

Disease cycle

No sexual stage has been observed. Inside the plant, the fungus produces three types of asexual spores: microconidia, macroconidia and chlamydospores.

**Chlamydospores** are round, thick-walled resting propagules that are produced by the dying banana plant. Infection is initiated when they germinate in response to exudates from the roots and hyphae (long and branching filamentous structures collectively known as mycelium) penetrate the lateral roots.

Chlamydospores have a reputation for surviving for 30 years or more in soil, but it is more likely that the persistence observed in fields in which susceptible banana plants had not been grown for decades is the result of *Foc* living as endophytes and multiplying in alternative hosts, such as weeds. It has also been suggested that former fields of 'Gros Michel' that have been converted to Cavendish are still infective for susceptible cultivars because the *Foc* strains live as endophytes in the Cavendish cultivars.

**Microconidia** are one or two celled and oval- to kidney-shaped. They are the type of spore most frequently produced within the vessels of infected plants.

**Macroconidia** are four to eight celled, sickle-shaped, thin-walled and delicate. These spores are commonly found on the surface of plants killed by the fungus.

Australian scientists have established that 20 minutes in 65º C water is the minimum condition for killing *race 4* hyphae, microconidia and macroconidia in banana plant tissue, whereas chlamydospores require autoclaving.

It's still not clear how the fungus kills the plant. One hypothesis is fungus releases toxins into the plant, killing its cells. Another is that the fungus tricks the plant into killing its cells by triggering the natural process of programmed cell death that eliminates unwanted, damaged or used cells. The decaying plant tissues would then be used by the fungus as a food source.

The hypothesis is being tested in a banana that has been genetically modified to prevent the fungus from co-opting the plant's cell death pathways. Deprived of food, the fungus eventually stops growing and fails to colonize and infect the tissues of the transgenic plant.
Races

The pathogenic strains of *Foc* are classified into races based on the differential response of cultivars. Traditionally, four races are recognized, although certain situations suggest that more races may exist \(^\text{[16]}\). Extensive inoculation studies are needed to clearly define the various pathotypes, but these are expensive and time-consuming. The results may also be equivocal because of variability in growing conditions and/or in planting material. The race concept has been criticized for being an imperfect measure of pathogenic diversity and for not reflecting genetic relationships, but is nonetheless considered useful to describe host reaction and new disease outbreaks.

**Race 1**
Race 1 strains cause disease in *Gros Michel*, *Silk*, *Pome* and *Pisang awak* cultivars, among others.

**Race 2**
Race 2 strains prey on Bluggoe and closely related cooking cultivars.

**Race 3**
Race 3 strains were reported to affect *Heliconia* species, and to a lesser extent *Gros Michel* and seedlings of *Musa balbisiana*\(^\text{[17]}\). However, they have not been reported since\(^\text{[16]}\).

**Race 4**
Race 4 was originally coined to designate the strains that attack *Cavendish* cultivars. Prior to the 1990s, symptoms of Fusarium wilt on Cavendish cultivars had been observed in the subtropical growing areas of Australia, Canary Islands and South Africa\(^\text{[18]}\), as well as in some tropical growing areas such as Jamaica and Guadeloupe. Circumstantial evidence suggested that the limited damage was due to predisposing factors: low temperatures in the subtropics and edaphic factors in...
the tropics\textsuperscript{[19]} . Originally classified as race 4, these pathogenic isolates were later reclassified as subtropical race 4 (\textit{STR4}) to distinguish them from the isolates that cause Fusarium wilt in the tropics in the absence of predisposing factors, which then became known as \textit{tropical race 4 (TR4)}.

The 01213/16 VCG (see Vegetative compatibility below) associated with TR4 was first identified in isolates from Taiwan at the end of the 1980s\textsuperscript{[12]} . In India, symptoms of Fusarium wilt have also been observed on the Cavendish cultivar ‘Grande Naine’ in the absence of predisposing factors, except that the VCG of the isolate (VCG0124) is associated with race 1 strains\textsuperscript{[20]} .

TR4 also attacks cultivars susceptible to races 1 and 2, and additional cultivars such as Barangan (Lakatan subgroup, AAA genome group\textsuperscript{[21]} ) and Pisang Mas. The wide host range of TR4 makes it difficult to diagnose outbreaks. For example, while a Cavendish with Fusarium wilt would immediately raise alarm, a Gros Michel infected with TR4 would not because the assumption would be it is infected with a race 1 strain.

For details on where TR4 has been found, go to the Musapedia page on TR4.

\textbf{Vegetative compatibility}

Vegetative compatibility is used to classify — into vegetative compatibility groups (VCGs) — isolates that share the same form (allele) of the genes that control the formation of an heterokaryon (a cell with two distinct nuclei)\textsuperscript{[2]} . Since alleles at each locus (the location of the gene on the chromosome) must be identical in order for isolates to be vegetatively compatible, isolates within a VCG are assumed to be clonally derived. On the other hand, since a mutation in one of those genes would make closely related isolates vegetatively incompatible, isolates that share a common ancestor could occur in different VCGs.

Each VCG is given a four to five digit code. The first three numbers refer to the \textit{forma specialis} to which the strain belongs, 012 in the case of the banana-specific f. sp. \textit{cubense}. The last number represents the order in which the VCGs were identified (0120, 0121, 0122 etc.). The race 1 isolate used to designate the first VCG0120 came from Australia\textsuperscript{[2]} . Some 24 VCGs have since been characterized worldwide.

The region with the greatest diversity of VCGs is Asia. A series of surveys documented 11 VCGs in the five banana-producing regions of mainland China\textsuperscript{[22]} , 3 VCGs and 4 isolates of unknown VCG in Indonesia's Lampung province\textsuperscript{[23]} , and 5 VCGs and 7 isolates of unknown VCG in Indonesia's West Sumatera province\textsuperscript{[24]} . A survey of 9 Asian countries reported 12 VCGs\textsuperscript{[25]} .

Tropical race 4 isolates belong to the VCG01213/16 complex, although other VCGs are also known to cause Fusarium wilt on Cavendish cultivars: the so-called STR4 strains that attack Cavendish bananas in the subtropics (0120, 0121, 0129 and 01211 in Australia; 0120 in South Africa and the Canary Islands and 0122 in the Philippines)\textsuperscript{[12]} . In India, VCG0124 isolates have also been extracted from Cavendish bananas exhibiting Fusarium wilt symptoms\textsuperscript{[20]} . In Latin America, VCG0124 isolates
are classified as race 1 because they infect Gros Michel but not Cavendish bananas.

References

25. Occurrence of various Vegetative Compatibility Groups (VCGs) of Foc in Asia, poster presented at the 10th International Congress of Plant Pathology held in China in 2013.

See also on this website

Photos on the symptoms of Fusarium wilt in the Musarama image bank
Video on the symptoms, transmission and prevention of Fusarium wilt in the Musarama video bank
News and blogs on Fusarium wilt:
  TR4 in Colombia
  Update on TR4 in Israel
  Zimbabwe authorizes passage of banana shipments from Mozambique
  Independent review of Biosecurity Queensland's TR4 programme
  TR4 confirmed in India
More stories...
Musapedia page on an INREF-funded research project managed by Wageningen University & Research Centre - Panama disease: Multi-level solutions for a global problem

Further reading

Diagnostic manual and links to presentations given at a 2014 FAO-CARDI regional workshop on the prevention and diagnostic of Fusarium wilt
Contingency plan (in Spanish) on TR4 for OIRSA countries
Fact sheet on Panama disease (8MB PDF) on the Plant Health Australia website
Fusarium wilt of banana laboratory diagnostics manual (1.8MB PDF) on the Plant Health Australia website
Datasheet on Fusarium oxysporum f. sp. cubense in CABI's Invasive Species Compendium
Panama disease: an old nemesis rears its ugly head, Part 1: The beginnings of the banana export trades Part 2: the Cavendish era and beyond

External links

Wikipedia page on Fusarium oxysporum f. sp. cubense
Website for the research projects on Fusarium wilt that are managed by Wageningen University & Research Centre: fusariumwilt.org
Banana Fusarium wilt in Africa website (under development)

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