Fusarium wilt or Panama disease of banana is widely regarded as one of the most destructive plant diseases in recorded history. It is caused by the soil-inhabiting fungus *Fusarium oxysporum* Schlecht f. sp. *cubense* (E. F. Smith) Synder & Hans (*Foc*). The disease was first recognized in Australia in 1874. Fusarium wilt has now been reported from all banana growing regions of the world except Papua New Guinea, the South Pacific Islands and some of the countries bordering the Mediterranean.

Fusarium wilt is a serious problem on many banana cultivars grown by smallholders for local consumption. These include Latundan (Philippines), maçã (Brazil), Pisang Rastali (Malaysia), Rastthali (India) which belong to the AAB ‘Silk’ subgroup; Lady Finger (Australia), Prata (Brazil), Virupakshi (India) which belong to the AAB ‘Pome’ subgroup and Chuoi Tay (Vietnam), Kayinja (East Africa), Kluai Namwa (Thailand) which belong to the ABB ‘Pisang Awak’ subgroup. Other locally important cultivars, such as those in the East African Highland subgroup (AAA ‘Mulika/Lujugira’) and Pisang Mas subgroup (AA ‘Sucrée’) have also been reported as susceptible in some environments. If the disease were to spread to the South Pacific, cultivars in the popular Pacific cooking banana subgroup (AAB ‘Maia Maoli/Popouliou’) would also be vulnerable as representatives have shown susceptibility in field tests. In addition, widely grown clones in the ABB ‘Bluggoe’ and AAA ‘Gros Michel’ subgroups are also susceptible.

Gros Michel was the basis of the early export banana trade in the Latin America/Caribbean region and it was the progressive decline of plantations of this cultivar due to Fusarium wilt in the 1940-50s that led to the adoption of cultivars in the AAA ‘Cavendish’ subgroup as the main export banana types. Cavendish cultivars have remained the mainstay of the world’s export industries to date. These types are also highly favoured for local consumption in countries such as Australia, China, Vietnam, India, Pakistan, Egypt and South Africa. Unfortunately, plantations of Cavendish cultivars in subtropical countries such as Taiwan, Spain (Canary Islands), Australia and South Africa are being increasingly attacked by Fusarium wilt. It is thought that plants in these areas are predisposed to systemic infection by certain strains of *Foc* by cold stress during winter. However, recent losses of Cavendish growing in export plantations in Malaysia, Sumatra and Java make it clear that other strains are quite capable of systemically infecting cultivars such as...
Valery, Grande Naine and Williams under tropical conditions. Although Cavendish growing in the Latin America/Caribbean region have not been reported as succumbing in large numbers, the world trade is again threatened by Fusarium wilt.

The classical and conspicuous external symptom of Fusarium wilt of banana initially appears as yellowing of the leaf margins of older leaves (this symptom may initially be confused with potassium deficiency, especially under dry or cold conditions). Yellowing progresses from the oldest to the youngest leaves. Leaves gradually collapse at the petiole or, more commonly, towards the base of the midrib and hang down to form a “skirt” of dead leaves around the pseudostem. In some cultivars, leaves of affected plants remain predominantly green until the petioles buckle and leaves collapse. The youngest leaves are the last to show symptoms and often stand unusually erect giving the plant a “spiky” appearance. Growth does not cease in an infected plant and leaves which emerge are usually paler in appearance than those of the healthy plant. The lamina of emerging leaves may be markedly reduced and exhibit wrinkling and distortion. Longitudinal splits may also develop in the pseudostem. A susceptible banana plant infected with Foc rarely recovers. However, poor growth of the clump may continue for some time and many infected suckers may be produced before the clump finally dies. No disease symptoms have been observed in fruit.

Infection occurs when the pathogen penetrates the roots of the banana plant. The fungus then invades the xylem vessels and, if not blocked by vascular occluding responses of the host, advances into the corm. Internal symptoms are characterized by vascular discoloration beginning with yellowing of the vascular tissues in the roots and corm which progress to form the continuous yellow, red or brown discolored vascular stands in the pseudostem and sometimes the bunch stalk.

As the plant dies, the fungus grows out of the xylem into the surrounding tissues, forming many chlamydospores which are returned to the soil when the plant decays. Foc is also able to colonize and persist in the roots of alternative hosts, including close relatives of the banana and several species of weeds and grasses, even though these plants remain symptomless under field conditions. The fungus can survive in soil for up to 30 years as chlamydospores in infested plant debris or in the roots of alternative hosts. Spread of the pathogen locally, nationally and internationally is most commonly by infected rhizomes or suckers and attached soil. Infected planting material may not exhibit symptoms. Foc can also be effectively spread in soil attached to implements or vehicles. From an isolated point of introduction in a disease-free plantation, Foc will spread slowly from plant to plant. If, however, spores are carried in surface run-off water or contaminate an irrigation reservoir, the disease can spread very rapidly, decimating a plantation within months if conditions are favorable.

Several factors influence the development of this disease. The banana cultivar is of primary importance and other factors such as drainage, environmental conditions and soil type also influence disease development. Suppressive soils, in which microbial populations suppress the pathogen population, were first described in...
the 1930s in Central America. Such soils have also been recorded in the Canary Islands, Australia and South Africa.

Research is currently underway to determine the pathogenic and genetic variation within Foc and the geographic distribution of variants. Before resistant cultivars can be deployed to combat this disease, the pathogenic and genetic diversity within and among populations of Foc needs to be assessed at local, national and international levels. Classical genetic techniques cannot be used to study the genetic diversity of this pathogen since no sexual stage has been found for Foc. Several analytical techniques have been applied to differentiate isolates of Foc. These include vegetative compatibility, volatile production, pectic enzyme and DNA analyses.

Four races of Foc are currently recognized. The term race is used less formally for this pathosystem since the genetic basis for susceptibility and resistance has not been characterized. The currently described races of Foc refer to strains of the pathogen which have been observed to be pathogenic to particular host cultivars in the field. Race 1 is pathogenic to cultivars in the AAB ‘Silk’ and ‘Pome’ subgroups and on AAA ‘Gros Michel’. Race 2 is pathogenic to ABB ‘Bluggoe’ and other closely related cooking bananas. Race 3 has been recorded in Honduras, Costa Rica and Australia on Heliconia species and has little to no effect on banana. Race 4 attacks AAA ‘Cavendish’ and all cultivars attacked by races 1 and 2. The current set of host differentials does not adequately assess the virulence which exists among populations of the currently designated races. It is not always possible to characterize populations of Foc using pathogenicity tests due to plant-environment interactions.

Vegetative compatibility is a technique based on asexual mechanisms which occur naturally in Foc that can be used in the laboratory to identify genetically isolated groups known as vegetative compatibility groups (VCGs). Strains of Foc which belong to the same VCG are genetically identical or very similar with respect to other characteristics and are, therefore, more closely related to each other than vegetatively incompatible strains. Vegetative compatibility analysis can be used to assess the diversity of strains of Foc within a given region and is much faster and more reliable technique than pathogenicity testing. Studies have shown a strong correlation between VCG and pathogenicity in Australia, but, since with Foc more than one race can occur within a VCG and there can be more than one VCG in each race, it is often difficult to use VCG for pathotype discriminations. Currently, twenty-one VCGs have been described for Foc and a pattern of distribution of these VCGs throughout the world is emerging. Recent studies show that fifteen of the twenty-one described VCGs have been recorded in populations of Foc in Asia, where Musa is indigenous.

As only asexual reproduction is involved in the population biology of this pathogen, genetic diversity can be measured by genotype diversity. This can be assessed by methods such as arbitrarily primed PCR (e.g. RAPD and DAF techniques) to generate DNA fingerprints. Using DNA fingerprinting, it is possible to determine the genetic relationships between different VCGs as well as isolates.
within each VCG. Molecular and genetic characterization which has been carried out to date places isolates of *Foc* into two distinct groups suggesting a biphylectic origin for this pathogen. These studies suggest that *Foc* and *Musa* coevolved in Asia to generate genetically diverse strains of the pathogen. However, additional studies are required to confirm the coevolution hypothesis.

Chemical control, flood fallowing, crop rotation and the use of organic amendments have not been effective in managing *Fusarium* wilt. It is now generally accepted that the only effective means of control is by host resistance. Natural sources of resistance exist in wild species and cultivars and in synthetic diploids developed by breeding programs. There are now four major conventional banana breeding programs and these are located in Honduras (FHIA), Brazil (EMBRAPA-CNPMF), Nigeria (IITA) and Guadeloupe (CIRAD-FLHOR). These programs have concentrated on using resistance in *Pisang Jari Buaya*, *Pisang Lilin* and *Musa acuminata* ssp. *burmannicoides* (Calcutta 4). Although it has not yet been possible to breed a Cavendish replacement because of fertility constraints, useful hybrids can be bred to replace AAB dessert and ABB cooking banana types. FHIA-01 (Goldfinger), a dessert banana from the FHIA breeding program with an acidic or “apple” flavor, has been identified as having resistance to race 1 and race 4 populations of *Foc* in Australia. Biotechnology, mutation breeding and somaclonal variations are also being used to produce resistant genotypes. Hybrids from breeding programs are to be tested in the field at selected sites around the world in the International *Musa* Testing Program (IMTP) organized by INIBAP with funds from UNDP.

Quarantine and exclusion procedures are effective in controlling the disease by restricting the movement of corms, suckers and soil that could be carrying *Foc* from infested to clean areas. The use of micropropagated planting material should be encouraged as this, if managed correctly, should be free from *Foc*. It is imperative that Cavendish attacking *Foc* populations recently recognized in Southeast Asia do not spread to other geographic locations, especially Latin America.

A method needs to be developed by which host-pathogen responses can be quickly and reliably ascertained in a growth cabinet or glasshouse environment. Pathogenic variability among genetically characterized isolates could then be determined. Epidemiological studies are also required to provide information on how different host genotypes and pathogen genotypes interact in the field in different geographical locations. A PCR-based detection system to identify pathotypes of *Foc* would be useful for screening plant material and identifying isolates in infested soil and diseased plants.

Continuing analysis of populations of *Foc*, particularly from Asia where maximum variability of host and pathogen are to be expected, will enhance our understanding of the genetic diversity of *Foc*. **Your help is needed.** INIBAP requests that specimens of vascular tissue from diseased plants be collected as is indicated in the diagram above. They should then be sent by airmail to Dr Natalie Moore (Plant Protection Unit, Department of Primary Industries, 80 Meiers Road, Indooroopilly, Q 4068, Australia) for analysis. Collaborators will be informed of results which will help national plant protection programs identify existing and potential problems.

The Department of Primary Industries (Dr N. Moore and Mr K. Pegg) and the Cooperative Research Centre for Tropical Plant Pathology (Dr S. Bentley) are two of INIBAP’s key partners in Queensland, Australia. INIBAP has supported research in Queensland on the genetic analysis of *Foc* isolates from Asia in association with ACIAR.