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Fusarial Wilt of Cavendish Bananas in Taiwan

Banana (*Musa* spp.) is a large, handsome, herbaceous plant native to Southeast Asia. Some species can reach heights of 8 m. In addition to the popularity of ripe banana fruit as a dessert, cooked green bananas are an important source of starchy food in some tropical countries. Also, fibers of banana plants are made into fabric or rough cordage. Banana fruit is one of the most important commodities of export trade in the world. In Taiwan, commercial cultivation of bananas is mainly for production of fresh fruit for local consumption and export to Japan.

The main commercial varieties of banana, including Gros Michel and Cavendish, are triploids of *M. acuminata* Colla (AAA) (9). Propagation is by planting the suckers that arise from the rhizome below ground. The treelike plant consists of the basal corm, a pseudostem of leaf sheaths, a terminal crown of leaves, and finally the true stem and inflorescence that arise in the meristem of the basal corm, traverse the pseudostem, and emerge through the foliar crown within a year after planting. The peduncle of the emerging inflorescence bends over to hang downward, and the seedless fruit develop from the inflorescence without fertilization (Fig. 1). In most countries, one or two suckers are permitted to grow to provide ratoon crops after harvesting. In Taiwan, however, most bananas are replanted every year to coincide with the spring export season and to reduce the risk of typhoon damage during the summer and fall.

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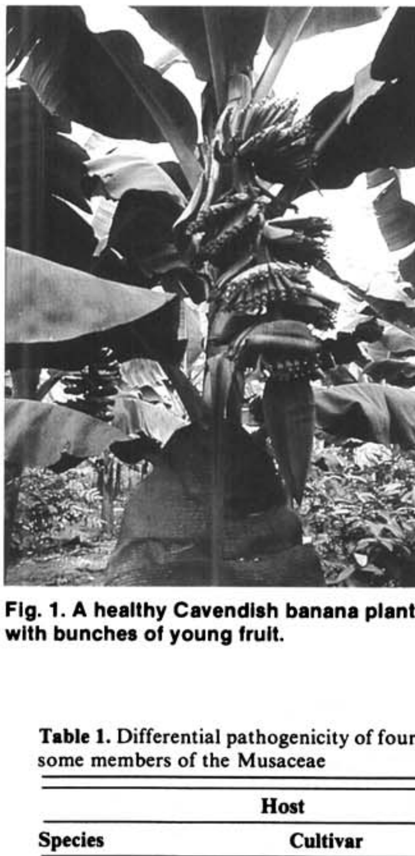

Fig. 1. A healthy Cavendish banana plant with bunches of young fruit.

History of the Disease

Fusarial wilt of banana, caused by *Fusarium oxysporum* Schlecht. f. sp. *cubense* (E. F. Smith) Snyder & Hansen, became epidemic in Panama as early as 1890 and thus has been commonly known as Panama disease (10). The disease is quite widespread in banana-growing regions of Asia, Africa, Australia, the South Pacific, and the tropical Americas. Fusarial wilt is one of the most catastrophic plant diseases of the world, destroying more than 40,000 ha of bananas in Central and South America over a period of 50 years.

Previously, only three races of *F. o.* f. sp. *cubense* were found on members of the Musaceae (Table 1). Races 1 and 2 cause wilt of bananas and race 3 attacks the wild *Heliconia* species (11). Race 1 is distributed worldwide and is most serious economically because it attacks Gros Michel, the favorite commercial banana cultivar for world trade in many

Table 1. Differential pathogenicity of four races of *Fusarium oxysporum* f. sp. *cubense* to some members of the Musaceae

Host			Pathogenicity[a]			
Species	**Cultivar**	**Genotype**	**Race 1**	**Race 2**	**Race 3**	**Race 4**
Musa acuminata Colla	Gros Michel	AAA	+++	–	– or +[b]	+++
	Cavendish	AAA	–	–	NT	+++
M. balbisiana Colla	···	BB	–	–	– or ++[b]	+++
M. acuminata × *M. balbisiana*	Silk	AAB	+++	–	NT	+++
M. acuminata × *M. balbisiana*	Bluggoe	ABB	–	+++	–	+++
Heliconia	···	···	– to +++[c]	–	+++	NT

[a] +++ = highly pathogenic, ++ = moderately pathogenic, + = mildly pathogenic, – = nonpathogenic, NT = not tested.
[b] Nonpathogenic or pathogenic, depending on isolate tested.
[c] Nonpathogenic or pathogenic, depending on species tested.

countries. For most banana-producing areas in tropical America, the disease has been under control since susceptible Gros Michel was replaced with the resistant Cavendish variety. Race 2 attacks only the hybrid triploid Bluggoe (ABB) and is endemic to Central America. A comprehensive monograph on fusarial wilt of bananas was published by Stover in 1962 (10). Since then, little of significance was published until a new race of the fungus appeared in Taiwan.

Disease Outbreak in Taiwan

Cavendish is the most common banana variety in Taiwan. The first instance of fusarial wilt on this variety was observed in 1967 at Chiatung, in the main banana-producing area of southern Taiwan. In 1968, the number of infected plants remained very low and diseased plants were confined to the same orchard (Table 2). During the third year, however, the disease spread to surrounding fields and the number of affected plants increased from 27 to 5,536—a greater than 200-fold increase (Fig. 2). This caused great concern among the general public in Taiwan.

Emergency measures were put into effect by the government in 1970 to check further spread of the disease. When more than 10% of the plants in an orchard were infected, all banana plants in that orchard were to be dug up, cut into pieces, treated with lime, and buried 60 cm or deeper in the ground. When infection was less than 10%, each infected plant and the surrounding eight healthy plants were to be destroyed in the same manner. Transportation of suckers from infested areas to noninfested areas was prohibited. The government asked growers to convert infested banana orchards into rice paddies and offered monetary compensation.

Effective destruction of infected banana plants was the primary difficulty encountered in enforcing these quarantine measures. Digging up all banana plants, both healthy and diseased, was laborious and burying all tissues was impractical. Most growers just cut the diseased trunks into pieces and left the pieces on the ground, with the possibility of their being swept away by irrigation water and rain. Out of ignorance, a few of the growers even threw the diseased material into irrigation ditches. Surface water is considered one of the main means of dispersal because the disease usually first appeared close to ditches in previously noninfested areas. Occasionally, however, the disease appeared within an orchard with no irrigation connection to infested areas several kilometers away, suggesting that suckers were taken from the infested areas and planted in disease-free areas. Consequently, the emergency measures did not reduce spread of the disease and were discontinued in 1973.

The rate of increase in the area of infested banana fields started to decline in 1974 (Table 2). Although the disease appeared for the first time in 1978 in the central counties about 200 km from the disease center (2), the total area of infested fields has remained more or less constant since 1976. In 1983, about 1,500 of the 5,000 ha of banana plantations in Taiwan were infested and about one-half million trees were infected. This represents an increase of approximately 25% in infestation of banana plantations in 7 years, a relatively slight increase compared with the increase of over 45-fold during the 7 years prior to 1976 (Table 2).

The stabilization in total area of infested banana fields after 1976 appears to reflect the unique culture practices in Taiwan. The fields in which fusarial wilt appeared were converted to other crops the following years, and lands previously used for growing other crops were put into banana production. In the main banana-producing areas of Taiwan, bananas are replanted every season at about the same time in the spring. Thus, every year infected suckers and new infections will begin cycles of disease development with an outbreak late in the growing season. The number of banana trees infected annually in recent years probably represents the disease capacity under the cultural system and environmental conditions in Taiwan.

The Pathogen

Race identification. In 1972, Stover and Malo (12) reported that in pathogenicity tests done in Florida and Honduras, *F. o.* f. sp. *cubense* isolated from diseased Dwarf Cavendish obtained from Taiwan invaded suckers of Gros Michel but not of Dwarf Cavendish after 2.5 months. They concluded that the pathogen was race 1 rather than a new race and suggested that adverse growing conditions such as poor drainage caused the breakdown of resistance of Dwarf Cavendish.

Su and associates in Taiwan (13) also performed pathogenicity studies. Suckers of Cavendish and Gros Michel were inoculated with a pure culture of *F. o.* f. sp. *cubense* consistently isolated from diseased Cavendish bananas. Nine months after inoculation, both Cavendish and Gros Michel showed leaf yellowing and vascular discoloration similar to symptoms observed in the field. *F. o.* f. sp. *cubense* was reisolated from all experimentally infected plants. The incubation time used by Stover and Malo (12) was much too brief to demonstrate pathogenicity on Cavendish banana.

Pathogenicity on Cavendish was also demonstrated with a rapid method developed by Sun and Su (15) to determine differential pathogenicity of *F. o.* f. sp. *cubense* to banana plantlets derived from meristem culture. Again, the Taiwanese isolate—but not race 1—attacked Cavendish plantlets, although both isolates were capable of invading Gros Michel plantlets (Fig. 3). The Taiwanese isolate also attacked Silk (AAB), Bluggoe (ABB), and *M. balbisiana* Colla (BB) (Table 1). Since the Taiwanese

Table 2. Incidence of fusarial wilt on Cavendish banana in Taiwan from 1967 to 1976[a]

Year	Infested fields (ha)	Number of diseased plants
1967	0.27	1
1968	0.27	27
1969	25.41	5,536
1970	53.66	7,430
1971	130.51	16,195
1972	132.54	14,255
1973	446.20	145,771
1974	962.78	310,000
1975	1,070.88	460,000
1976	1,200.00	500,000

[a] Based on data provided by Taiwan Provincial Fruit Marketing Cooperative.

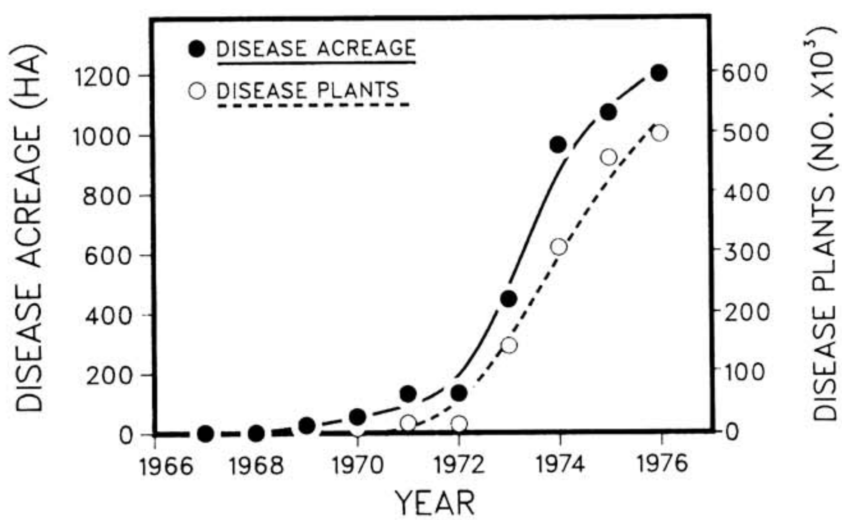

Fig. 2. Progress of fusarial wilt of Cavendish bananas during the first 10 years in Taiwan.

isolate differed from races 1, 2, and 3 in range of hosts within the Musaceae, the pathogen was designated race 4 of *F. o.* f. sp. *cubense* (13).

In principle, the morphological characteristics of races within the same forma specialis are indistinguishable.

Fig. 3. Symptoms on Cavendish plantlets derived from meristem culture and inoculated with *Fusarium oxysporum* f. sp. *cubense* isolates from diseased Cavendish bananas in Taiwan (right), Canary Islands (second from right), and Philippines (second from left); plant on left was not inoculated.

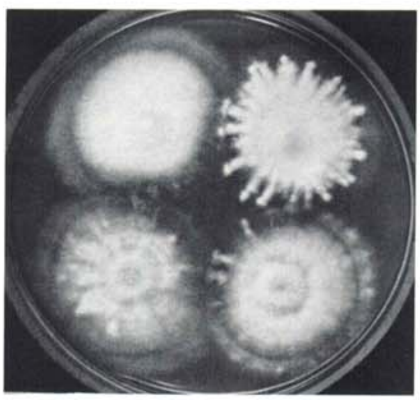

Fig. 4. Colony morphology of race 4 (upper right), race 1 (lower right), race 1 (upper left), and race 2 (lower left) of *Fusarium oxysporum* f. sp. *cubense* on K2 medium. The first two isolates were obtained in Taiwan and the last two, from R. H. Stover.

Fig. 5. Colony morphology of race 4 of *Fusarium oxysporum* f. sp. *cubense* from Taiwan (right) and Australia (left) on K2 medium.

Race 4 of *F. o.* f. sp. *cubense* from Taiwan, however, is unique in that it forms laciniate colonies on modified Komada's medium (K2 medium) distinct from colonies of races 1 and 2 (Fig. 4) (16). Six formae speciales of *F. oxysporum*, one saprophytic *F. oxysporum*, and three other species of *Fusarium* failed to form laciniate colonies on K2 medium. Every isolate of *F. oxysporum* obtained from more than 250 wilted Cavendish plants collected from different locations on Taiwan formed similar laciniate colonies (2,6,16). This may reflect the short history of the fungus in Taiwan and indicate that the race 4 isolates originated from a single mutation.

Distribution of race 4 outside Taiwan. In 1977, R. H. Stover sent *F. o.* f. sp. *cubense* isolates from diseased Cavendish plants in the Canary Islands and Philippines to Taiwan for identification. These isolates caused typical fusarial wilt symptoms on Cavendish plantlets and were therefore identified as race 4. Recently, race 4 of *F. o.* f. sp. *cubense* was reported in Australia and South Africa (7,8).

Fig. 6. A diseased Cavendish banana plant with conspicuous yellowing symptoms on the lower leaves.

Fig. 7. Longitudinal section through a diseased rhizome of Cavendish banana plant showing extension of vascular discoloration from mother corm (left) to daughter sucker (right).

Race 4 isolates from Australia, Philippines, and the Canary Islands all formed laciniate colonies on K2 medium. Their laciniate appearance was not distinct, however, and the laciniate fringes differed in shape and size from those of Taiwanese isolates (Fig. 5). This suggests that race 4 of *F. o.* f. sp. *cubense* occurring in other countries did not originate from Taiwan and that independent mutations may have occurred in different regions during approximately the same period.

Symptoms and Development of the Disease

In southern Taiwan, Cavendish suckers are planted from April to May, and the first symptom, yellowing of lower leaves, usually begins to appear in October. The color stands out so conspicuously that the disease has been called "yellow leaf disease" locally (Fig. 6). The number of plants with the yellowing symptom increases greatly after the emergence of the inflorescences in December, and disease incidence reaches a maximum in February and March when harvest of banana fruit begins (13).

Yellowing begins along the leaf margins and advances toward the midribs. Brown spots of various shapes and sizes appear on the yellow leaves, and the petioles turn brown and buckle. Eventually, the whole drooping leaf turns dark brown. Yellowing and buckling progress from older to younger leaves, and the entire plant dies. Frequently, the pseudostems split longitudinally just above the soil level. Occasionally, outer leaf sheaths of infected plants separate from the pseudostems and collapse, and the trees appear thinner than uninfected ones.

When the pseudostem and rhizome of an infected plant are cut longitudinally, the vascular tissue shows reddish or brownish dots and streaks. As the disease progresses, the discolored vascular strands become more numerous and more deeply stained. Discoloration also occurs in the parenchyma below the soil line, around the infected vascular strands. This is due to secondary invasion by saprophytes that eventually cause the tissue to become dark brown and black. Infection sometimes passes into young suckers through their attachment to infected parent rhizomes, as indicated by connecting discolored vascular strands (Fig. 7).

Dissemination and Survival of the Pathogen

As already mentioned, surface water and planting material are two major means for long-distance dispersal of the disease in Taiwan. During periods of heavy rainfall, spores of the pathogen and infected tissues on the ground are liable to be carried in surface drainage water into irrigation ditches and transported to noninfested areas via the irrigation system. Therefore, the disease usually appears along the edges of the irrigation ditches in previously noninfested areas.

Approximately 30–40% of suckers obtained from rhizomes of diseased Cavendish plants are infected (13). Occasionally, suckers obtained from infested areas have been used to plant new fields, thus becoming sources for new infestations. Further spreading of the disease within newly infested areas usually results from cultural practices, such as plowing before replanting and hoeing after planting.

Race 4 of *F. o.* f. sp. *cubense* survived more than 3 years in the fields in the absence of bananas (Table 3). When soil was covered with water, however, the population dropped to a nondetectable level within 4 months (1). Amendment of soil with urea was also very effective in reducing the pathogen population, but similar treatments with sugarcane leaves, rice straws, green manure, or compost were ineffective (14).

When roots from 25 species of weeds and eight species of rotation crops grown on pathogen-infested areas were plated on K2 medium, *F. oxysporum* with laciniate colonies similar to those formed by race 4 of *F. o.* f. sp. *cubense* was isolated from the following weeds: *Cyperus iria* L., *C. rotundus* L., *Gnaphalium purpureum* L., and *Fimbristylis koidzumiana* Ohwi. Isolates from these weeds were able to cause wilting of Cavendish plantlets in greenhouse tests and were therefore considered to be race 4 of *F. o.* f. sp. *cubense*. Also, race 4 from Cavendish banana infected roots of these four species of weeds without causing visible symptoms. This suggests that in the absence of banana, race 4 may be able to perpetuate itself on roots of certain weeds in the field. Roots of rotation crops and other species of weeds tested were not infected (14).

Measures for Disease Control

Disease resistance. In a selection program to determine if a resistant segregant could be obtained from the local commercial variety, more than 3,000 suckers from healthy Cavendish bananas grown in severely diseased banana fields were planted in an infested field augmented with a large amount of diseased tissue. After 1 year, plants with wilt symptoms were discarded and the remaining healthy ones were multiplied by transplanting their daughter suckers in the same field. At the end of the second year, any clones with infected members were discarded and the remaining healthy ones were multiplied again. At the end of the fifth year, eight clones seemed to possess some resistance because none of their offspring showed disease symptoms. At the end of the sixth year, however, members of these eight clones were infected. The program was subsequently discontinued.

The Taiwan Banana Research Institute has a collection of about 150 banana cultivars from all over the world. All existing commercial cultivars tested are susceptible to race 4 of *F. o.* f. sp. *cubense* (6).

Crop rotation. In southern Taiwan, farmers usually grow two crops of rice and one crop of vegetables annually. Under this cropping system, the fields are flooded for about 5 months of the year. Since flooding is detrimental to the survival of race 4 of *F. o.* f. sp. *cubense* in soil (1,14) and since flood fallow has been shown to be an effective method for controlling fusarial wilt of bananas in tropical America (10), crop rotation with paddy rice was considered a possible control measure. Field tests showed that rotation with paddy rice for 1 and 3 years reduced the disease incidence from 40% to 12.7 and 3.6%, respectively (Table 3). Disease incidence was not decreased when infested banana fields were rotated with sugarcane or sunflowers for 3 years. In other tests, the disease incidence was decreased from 20% to 0% in certain areas after a 2-year rotation with paddy rice (4). Rotation with paddy rice is currently a common practice for farmers in Taiwan to reclaim the infested banana fields for banana production.

Disease-free propagating material. Because suckers obtained from wilt-infested areas are important sources of inoculum, suckers for planting must be obtained from disease-free areas. This is becoming increasingly difficult because of the widespread nature of the disease. A meristem culture technique was consequently developed for mass propagation of pathogen-free banana plantlets for commercial planting (5). Plantlets originating from meristem culture became well established under field conditions and gave rise to mature plants with uniform growth and normal fruit yield (Fig. 8). The harvest period was shortened from the usual 3 months to 1.5 months because of the uniform growth of plantlets. Plantlets are also cheaper and easier to propagate and transport than suckers. In recent years, more and more banana growers have begun using meristem culture plantlets to establish their fields.

Progress and Prospects

Although none of 40,000 Cavendish plants grown from suckers showed any visible difference in morphology, about 3% of Cavendish plantlets derived from meristem culture were variants (3). Variation included plant size, color of pseudostems and leaves, and shape of leaves and fruit. Because of the high frequency of variation among Cavendish

Fig. 8. Mature Cavendish banana plants grown from plantlets derived from meristem culture.

Fig. 9. Parental Cavendish banana plants (left rows) and morphological variants resistant to race 4 of *Fusarium oxysporum* f. sp. *cubense* (right rows) in an infested field.

Table 3. Effect of crop rotation on incidence of fusarial wilt of Cavendish banana

Rotation crop	Rotation period (years)	Number of suckers planted	Average wilt incidence[a] (%)
Rice	1	791	12.7
Rice	3	682	3.6
Sugarcane	3	1,051	54.8
Sunflower	3	716	52.0

[a] Average wilt incidence before rotation was about 40%.

plantlets derived from meristem culture, the plantlets were tested recently for resistance to race 4 of *F. o.* f. sp. *cubense*. Of 17,979 plantlets planted in infested soil in the greenhouse, 45 were free from infection after 4 months. Eighteen of these surviving plants remained healthy 1 year after being transplanted in a heavily infested field. All 18 plants were morphological variants with inferior fruit quality (Fig. 9). Screening plantlets derived from meristem culture of various commercial cultivars is still in progress.

Because bananas in Taiwan are replanted every year, local commercial varieties propagated by suckers are being tested again to determine if a segregant can be obtained that will tolerate disease for just 1 year, rather than for 6 years, as previously attempted.

Banana breeding is very difficult because most cultivated bananas are triploids that rarely produce seeds. This difficulty may be overcome by new technology, however. Even if the approaches mentioned cannot produce commercially acceptable resistant clones, desirable resistant traits will be identified in the process. With the rapidly advancing biotechnology in the areas of somatic hybridization through protoplast fusion and genetic transformation, such resistant traits will be useful in the future for the development of new somatic hybrids and genetically engineered bananas that are commercially acceptable and disease resistant.

Acknowledgment

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