Black Sigatoka: An Increasing Threat to Banana Cultivation

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Many of the millions who today enjoy bananas don't know of their colorful and varied history, or realize the wide range of human endeavor involved in their cultivation and in their long but rapid journey from the tropical plantation to the consumer's table (82). Before the 1880s, most Americans had never seen or eaten a banana, but very rapidly this fruit was transformed from a luxury and a novelty to the most widely eaten fresh fruit in the United States (46).

Bananas and plantains are one of the most important, yet poorly studied, crops worldwide (12,81). Modern bananas and plantains originated in southeastern Asia and the western Pacific regions, where their ancestors are still found in the natural forest vegetation (84). Cultivated bananas belong to the Eumusa section of the family Musaceae and are natural hybrids of *Musa*: *Musa acuminata* (genome A) and *Musa balbisiana* (genome B) (82,96,105,109). Today, bananas and plantains are cultivated in more than 100 countries throughout the tropical and subtropical regions of the world, although India, Uganda, Ecuador, Brazil, and Colombia account for 44% of the total production. They are grown on over 10 million hectares. Total production was estimated in 1998 at over 88 million metric tons, of which exports represented around 12 million metric tons (94). The remainder, over 85% of the production, is made up of a wide range of bananas, plan-

tains, and cooking bananas (Fig. 1) grown by small farmers and selected for specific eating and cooking qualities either for home consumption or local trade (81,94).

The export trade in dessert bananas from Central America and the Caribbean began in the mid-nineteenth century and developed rapidly after the introduction of refrigerated cargo ships. The trade was initiated with the triploid cultivar Gros Michel, which has been replaced by a small number of triploid dessert banana cultivars of *M. acuminata* belonging to the Cavendish subgroup, of which Grand Naine, Valery, and Williams are most common. Seventy-three percent of the world crop of plantains is grown and consumed in West and Central Africa. Currently, increasing quantities

of plantains are being exported to the United States and Europe (84).

On a banana plantation, plants can be seen at all stages of vegetative growth and fruit maturity year-round. Bananas in the tropics can be harvested any day of the year. The absence of seasonality in the production is an advantage, in that it provides continuity of carbohydrates in the diet and may represent a regular source of income (32). It also represents a disadvantage, because the plant is continually exposed to the effects of adverse environmental factors, pests, and pathogens.

Bananas and plantains are susceptible to a range of serious and debilitating diseases that have been an ongoing concern for growers of export bananas for much of the

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Fig. 1. Diversity of bananas, plantains, and cooking bananas typically found in most developing-country markets. Source: D. Mowbray and International Network for the Improvement of Banana and Plantain (INIBAP), with permission.

life of the industry. Initially, plantations were devastated by Fusarium wilt (also known as Panama disease), which resulted in the widely grown but susceptible cultivar Gros Michel being replaced by resistant cultivars from the Cavendish subgroup. The tropical race 4 of *Fusarium oxysporum* f. sp. *cubense* and the *Banana bunchy top virus* (BBTV) are currently regarded as serious threats to world banana production. Nevertheless, in spite of these and other diseases and pests, none has jeopardized the production of bananas as severely as the Sigatoka leaf spot diseases (11,32,76,84).

Etiology and Biology

Sigatoka, now usually referred to as yellow Sigatoka (Fig. 2A), was the most important foliar disease of bananas until the discovery and spread of black Sigatoka (23,50,76). Yellow Sigatoka is caused by *Mycosphaerella musicola* J.L. Mulder in J.L. Mulder & Stover, anamorph *Pseudocercospora musae* (Zimmerm.) Deighton, and takes its name from the Sigatoka Valley in Fiji where the disease reached epidemic proportions from 1912 to 1923. However, the disease was first described in Java in 1902 by Zimmerman (117). During the next 40 years, *M. musicola* became widespread, making it a classic, global disease epidemic (23,50,76).

Black leaf streak (Fig. 2B), caused by *Mycosphaerella fijiensis* Morelet, was also first described in Fiji, in 1963. However, it was widespread in the Pacific long before its discovery in Fiji (105). The anamorph was originally described as *Paracercospora musae* (Zimmerm.) Deighton; however, recently Crous et al. (18) sequenced

the rDNA of the internal transcribed spacer (ITS) region and showed that *Paracercospora* is synonymous with *Pseudocercospora,* and therefore, *Pseudocercospora fijiensis* (Morelet) Deighton is the correct name for the anamorph of *M. fijiensis*. Conidial morphological differences can still be used to separate the taxa at the species level (18). Black leaf streak was observed first in southeastern Viti Levu, just 60 km from the Sigatoka Valley, where yellow Sigatoka was first reported (83). Although black leaf streak was first reported in 1963, Meredith (66) noted that Trujillo and Goto (110) described a variant of ("the yellow") Sigatoka in the Hawaiian Islands that had been observed as early as 1958. They believed this variant was due to climatic factors or a different pathogenic strain of the fungus. However, their description is very similar to that described later for black leaf streak.

In Asia and Central America, where the two pathogens have coexisted, *M. fijiensis* eventually replaced *M. musicola* (11,23,66,104). However, whether or not one species dominates over another is a function of temperature. Yellow Sigatoka is normally observed under cooler conditions than black leaf streak (74,87). Mata et al. (64) found that germ tube growth of conidia of *M. musicola* was faster than that of *M. fijiensis* at 17°C, whereas *M. fijiensis* grew faster at higher temperatures. In Colombia, black leaf streak is the most important disease of bananas and plantain in the lowlands, but at 1,500 m in Lobo Guerrero, where the severity of black leaf streak is as severe as that observed on plantains in the lowlands, both pathogens coexist (S. Belalcazar, *personal communication*).

In 1976, a pathogen believed to be closely related to *M. fijiensis* was described from the Ulua Valley in Honduras, where a disease similar to black leaf streak had been observed since 1972 (77,101). The disease was called black Sigatoka to distinguish it from black leaf streak. This pathogen was named *Mycosphaerella fijiensis* var. *difformis* Mulder & Stover based on the presence of a stroma where conidiophores were formed, which is absent in *M. fijiensis*. The pathogen later spread to other banana-growing areas in Latin America (29,42,76,101) as well as to other banana-growing regions of the world (11,75; Fig. 3). Pons (80), on the basis of morphological characteristics, and Stover and Simmonds (105) determined that *M. fijiensis* and *M. fijiensis* var. *difformis* were synonymous. Molecular evidence from comparative studies of the ITS region of nuclear ribosomal DNA (rDNA) showed that *M. fijiensis* and *M. fijiensis* var. *difformis* did not differ in their nucleotide sequence (49). Although the name black leaf streak has precedence, we hereafter use the name "black Sigatoka" due to its prevalence in the literature and widespread usage in Latin America.

Black Sigatoka is considered the most damaging and costly disease of banana and plantain (11,42) because its control accounts for 27% of total production costs (101,105). It has been estimated that the disease causes greater than 38% yield loss on plantain (56), and even greater losses may occur on export bananas when control measures fail. The disease affects the leaves of banana plants, destroying the foliage very rapidly if control measures are not applied. Both growth and yield are

Fig. 2. Worldwide distribution of black Sigatoka (• = countries where black Sigatoka has been reported according to Carlier et al. [11] and Mourichon et al. [75]). Map courtesy of www.theodora.com/maps, with permission.

affected because of the reduction in the photosynthetic area (Fig. 4A and B).

Although the disease significantly reduces yield, the greatest loss probably occurs as a result of the premature ripening of fruit (Fig. 5), which can occur in the field and during transport and storage (62). Stover (99) demonstrated that simple defoliation or reduction in the photosynthetic area by mechanical means did not trigger the premature ripening that was noticed at levels of disease severity that did not affect yield or time of maturity. Stover suggested that it was very likely that some physio-logically active substance was translocated and induced these events. Research conducted at the Honduran Foundation of Agricultural Research (FHIA) found that early ripening occurred on fruit injected with crude extracts of *M. fijiensis* cultures, which also indicated that a specific substance or substances were related to early ripening (E. Ostmark, *personal communication*). Molina and Krausz (73) used crude extracts of *M. fijiensis* as a tool to evaluate host resistance to black Sigatoka. This preliminary study led to the discovery and identification of several phytotoxins produced by the fungus (98,107,111), although none was specifically associated with early ripening.

The pathogen establishes a 3- to 4-week biotropic relationship in leaves of susceptible cultivars after penetrating the stomata before any necrotic symptoms appear (40). Resistance of *Musa* species to *M. fijiensis* appears to be related more to postinfection activation of mechanisms such as the production of pathogen-related proteins (53) and phytoalexins (54) than to small changes in structure and preformed substances (40). Beveraggi et al. (4) reported that partial resistance in the cultivar Fougamou appeared to be partly linked to a pre-existing antifungal plant phenolic compound, while in the case of the highly resistant cultivar Yangambi Km 5, an active mechanism was induced following penetration of stomata by the fungus.

Symptomology

Although black Sigatoka was first described in 1964 (83), a detailed description of the symptoms was not published until 1969 by Meredith and Lawrence (67). Based on these observations, Fouré (20) redefined the symptoms shown during the development of the disease into six stages (Fig. 6), which are summarized in Table 1.

The first symptom, chlorotic specks, appears 14 to 20 days after infection. The period between the appearance of specks and the development of streaks and subsequently necrotic spots varies in length according to the cultivar and the severity of infection (23,42,65). Jacome and Schuh (42) found that symptom expression was delayed 7 to 14 days with shorter periods of leaf wetness (optimum at 18 h of leaf wetness after inoculation). In some areas, the first appearance of symptoms is correlated with the susceptibility of the cultivar (11; S. Belalcazar, *personal communication*). However, the length of the incubation period does not seem to correlate with overall resistance (20). On resistant cultivars, symptom development is very slow and may not progress to the spot stage (stage 4) until the natural senescence of the leaves (23,42,65). There is a stronger correlation of resistance/susceptibility with the latent period than with the incubation period (D. H. Marín and R. A. Romero, *unpublished data*).

Epidemiology

Conidia and ascospores both play roles in the spread of the disease. Conidia form under conditions of high humidity, especially if there is a film of free water on the leaves. They are formed during the development of the first stages of the disease (especially during dash [stage 2], streak [stage 3], and spot [stage 4]). The principal means of dispersal are rainwash and splash; conidia are not detached by wind. Conidia are associated mostly with local spread of the disease and are important
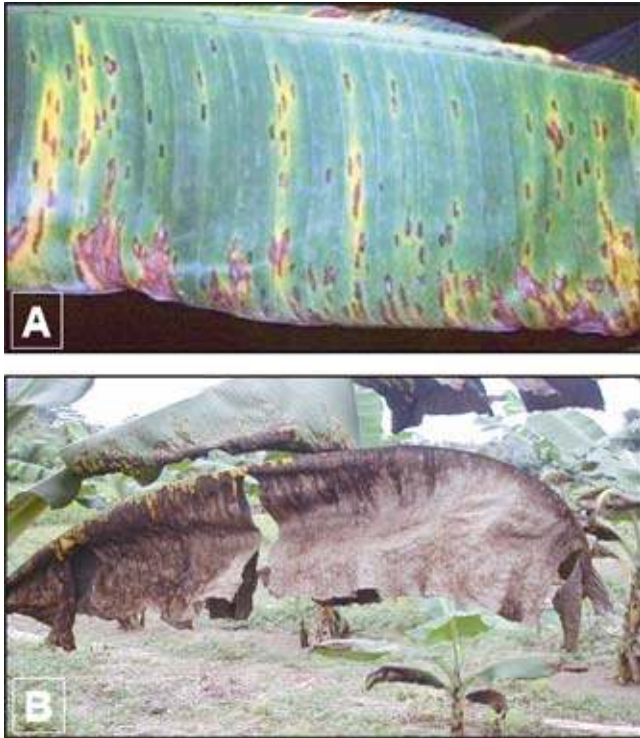

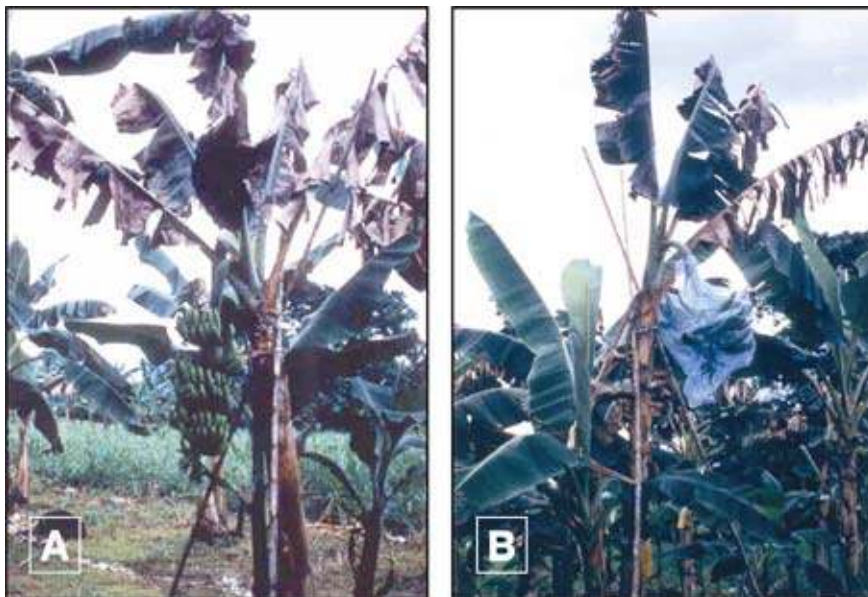**Fig. 3. Symptoms of A, yellow Sigatoka, and B, black leaf streak.**

Fig. 4. Severe defoliation of A, bananas, and B, plantains caused by black Sigatoka.

during periods of high humidity, frequent heavy dews, and intermittent showers. Because *M. fijiensis* produces relatively few conidia, ascospores are considered to be more important in the spread of black Sigatoka (26,101). However, Jacome et al. (44) stated that conidia are able to cause significant amounts of disease, and the disease symptoms are identical to the ones caused by ascospore infection. He indicated that conidia become more important during dry periods when disease development is delayed because of the presence of less conducive climatic conditions (44).

Ascospores are the primary means of dispersal over longer distances within plantations and into new areas, and are the usual means of spread during extended periods of wet weather (23,26,29,44, 62,69). Ascospores are produced in pseudothecia in mature lesions, which are common on the older leaves of the plant or in dead leaves lying on the ground. Meredith and Lawrence (67) reported that pseudothecia are produced on both sides of the leaf surface, but higher numbers are present on the adaxial surface. Conversely, Gauhl et al. (28) found that more pseudothecia and ascospores were produced on the abaxial leaf surface. Although Burt et al. (9) found that approximately 4.5 ascospores are released per pseudothecium, this number seems very low considering the high concentration of inoculum that is present in the air following rain (26). Ascospore release requires the presence of a film of water from rain or dew that imbibes the pseudothecia and results in the forcible ejection of the ascospores through the leaf boundary layer, where they are disseminated by air currents (69,101). Maturation of pseudothecia requires saturation of the dead leaf tissues for approximately 48 h (23,26,29,44,62,69). Under Hawaiian conditions, ascospore concentrations increased during the night, were highest about 0600 h, and decreased significantly during the day. On rainy days, peak concentrations occurred shortly after rain began. Seasonal increases in daily mean concentrations of ascospores are associated with increased rainfall and relative humidity (69). Gauhl (26), working with bananas, reported similar results under Costa Rican conditions. Whereas Meredith et al. (69) did not find evidence that ascospore production or release was affected by minimum temperatures, Gauhl (26) determined that there is a reduction in the production of inoculum during the drier (or less rainy) months of the year in the Caribbean zone of Costa Rica, which is also the season with the lowest temperatures (Fig. 7).

Ascospores are dispersed by wind; however, long-distance dispersal is limited to a few hundred kilometers due to their susceptibility to ultraviolet radiation (79). A consistent relationship between ascospore discharge and disease development has not been shown, thus limiting the usefulness of

spore trapping for disease forecasting (27,45).

Ascospores are deposited mainly on the lower leaf surface during the unfurling of a new leaf (Fig. 8A and B), producing a band pattern of infections on the side that is first exposed, which is a reflection of the increased spore deposition on the cylindrical candela leaf during its unfurling as opposed to the entire open lamina of the leaf.

Consequently, most infections occur on the abaxial surface of the leaves (23,29). Germ tubes take approximately 48 to 72 h to penetrate the stomata (3,101), although the fungus may grow epiphytically on the leaf surface for up to 6 days before actually penetrating the leaves (3). Successful infection is promoted by extended periods of high humidity and the presence of free water on the leaves (23,29,65). Maximum

Fig. 5. Premature ripening of banana fruit induced by a severe infection of black Sigatoka.

Fig. 6. Stages of disease development according to Fouré (20). Stage 2 is characterized by red-brown streaks on both sides of the leaf; in stage 3, streaks become wider and the color starts changing from red to dark brown; stage 4 is characterized by dark brown (lower) to black (upper) spots; in stage 5, a chlorotic halo develops around the black spots and lesions are slightly depressed; and stage 6 is characterized by lesions with whitish to gray centers that have a black border and are slightly depressed.

Table 1. Symptom description of *Mycosphaerella fijiensis* according to Meredith and Lawrence (67) and Fouré (20)

| Common name[a]	Meredith and Lawrence	Fouré	Description
Mark	…	Stage 1a	Depigmentation mark (whitish or yellow). Not visible in transmitted light. Only on lower surface.
Speck	Initial speck stage	Stage 1b	Red-brown speck on lower surface.
Dash/lesion	First streak stage	Stage 2	Red-brown streaks on both sides of the leaf.
Streak	Second streak stage	Stage 3	Wider streaks. Color starts changing from red to dark brown.
Spot	First spot stage	Stage 4	Dark brown (lower) to black (upper) spots.
Burn	Second spot stage	Stage 5	Black spot with chlorotic halo. Lesion is slightly depressed.
Necrosis	Third or mature spot stage	Stage 6	Center of spot dries out and becomes whitish to gray. Spot is surrounded by a dark brown to black border and further depressed.

[a] F. Wielemaker (115).
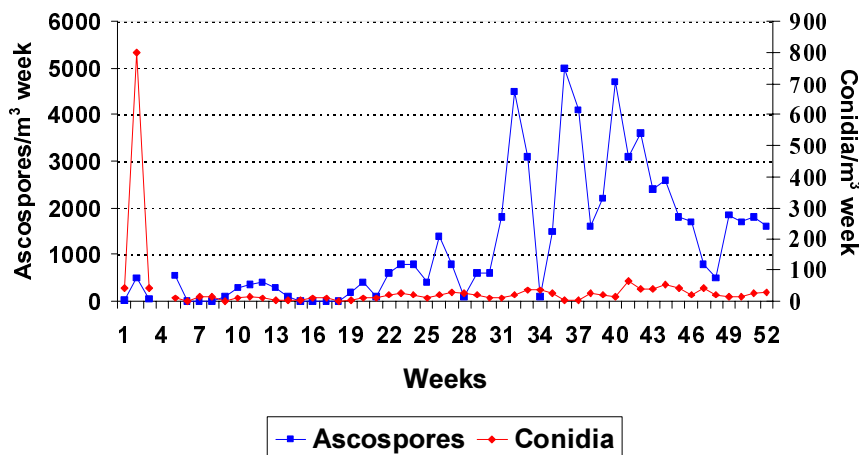
Fig. 7. Seasonal variation of ascospores and conidia captured using a Burkard spore trap located in an untreated plantain area in the Caribbean zone of Costa Rica. Source: Gauhl (26), with permission.
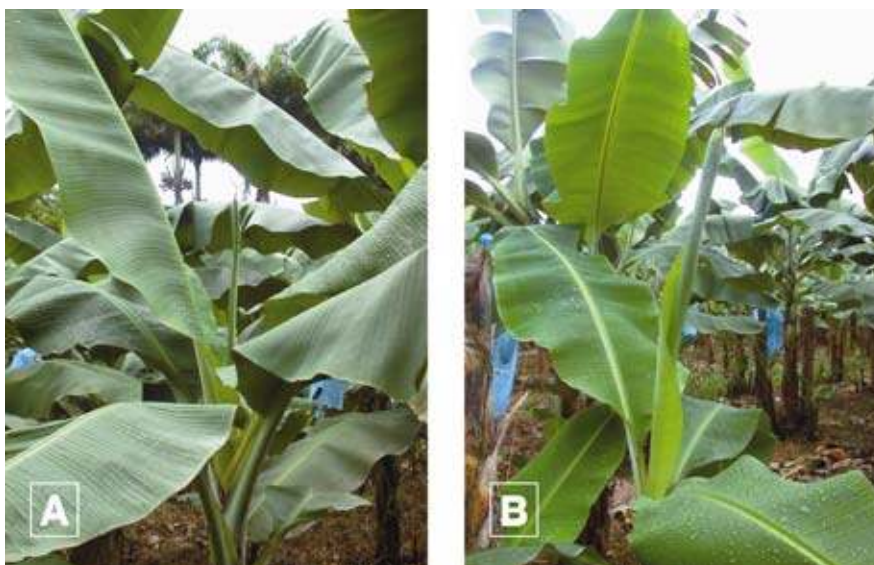

Fig. 8. A, Newly emerged (stage 2), and B, partially unfurled (stage 4) "cigar" or candela leaf.

germination occurs when there is free water present. Conidia germinate over a wider range of relative humidity (92 to 100%) than do ascospores (98 to 100%). The effect of temperature on germination can be characterized by a quadratic response function, with an estimated optimum of 26.5°C (44). Stover (102) observed maximum growth of ascospore germ tubes at 26 to 28°C after 24 h incubation. Jacome and Schuh (42,43) reported that older leaves were more susceptible; however, E. Bureau (*personal communication*) and Romero (86) observed that younger leaves are more susceptible (first to third) than older ones.

Incubation period. The time between infection and the appearance of symptoms varies according to weather conditions and plant susceptibility (68). In bananas, the time of leaf infection is estimated to coincide with the emergence of a new leaf from the apex of the pseudostem (101). Under very favorable conditions in Costa Rica, and with a susceptible host, the incubation period can be as short as 13 to 14 days, whereas during periods of unfavorable weather, the duration of the incubation period can extend up to 35 days (Fig. 9). Similar reports exist from Nigeria on plantains (72). During the rainy season, the incubation period was 14 days, but in the dry season it was 24 days. The duration of the incubation period also varies with the susceptibility of the cultivar to *M. fijiensis*. The incubation period was 26.2 and 25.1 days, respectively, in the cultivars FHIA 1 and FHIA 2, two tetraploid synthetic hybrids developed by FHIA, compared with 22.4 days in the susceptible cultivar Grande Naine (88).

After penetrating the leaf, the hyphae of *M. fijiensis* colonize adjacent cells for approximately 7 days without any evidence of disruption of the cells. The vegetative hyphae can emerge from stomata and grow on the surface of the leaf and penetrate adjacent stomata or produce conidiophores and conidia. This epiphytic growth allows the fungus to colonize adjacent leaf tissue, which results in rapid symptom development (26,101). *M. fijiensis* has a greater ability to penetrate several stomata than does *M. musicola,* which results in greater spotting than with the former pathogen (101).

Latent period. Although conidia can be produced in lesions exhibiting early symptoms of *M. fijiensis* and contribute to the epidemic, the latent period is defined by the time the fungus starts to produce lesions with mature pseudothecia and ascospores, which are the main source of inoculum. Like the incubation period, the latent period also varies according to weather conditions, susceptibility of the host, and intensity of infections. Differences in the latent period from December 1993 to May 1995 for the susceptible cultivar Grande Naine, which is widely used for the fresh banana market, are shown in Figure 10. The latent period ranged from

25 days during the rainy season (June to December) to 70 days during the dry season at Guapiles, Costa Rica. When the weather is highly conducive for ascospore discharge and infection, many infections occur on the leaves. When infections are dense, they rapidly coalesce at a very early stage of development, accelerating the appearance of mature spots that are characterized by the presence of pseudothecia and ascospores (22). Under these conditions, leaves are rapidly and severely damaged.

The latent period also varies according to the level of resistance. For instance, the time from leaf emergence to first mature spot symptom under the same natural conditions for the cultivar Curraré, a cooking banana belonging to the subgroup plantain, was 44 days compared with 34 days for the cultivar Valery, a banana belonging to the subgroup Cavendish (26).

The term "disease development time" is widely used in the banana literature in the tropics to refer to the latent period, and it is defined as the time between infection and the formation of mature spots. Another common term used in the banana literature is "symptom evolution time" or "the transition period," which is the time from first symptoms to the appearance of mature spots (28). The symptom evolution time gives a good indication of how fast the disease is progressing on the leaves.

Chemical Control

Chemical control of black Sigatoka is achieved with the alternation of protectant (mancozeb or chlorothalonil) and systemic fungicides belonging to the benzimidazole, triazole, morpholine, and strobilurin (QoI) groups, applied either in oil or in an oil–water emulsion. The use of mixtures of mancozeb and the systemic fungicides is part of a strategy to delay or manage fungicide resistance.

Petroleum oil has been used for the control of Sigatoka leaf spot diseases since the 1950s in the French Antilles (33). Oil retards the development of initial stages of infection and, in combination with systemic fungicides, enhances the penetration of the systemic fungicide into the leaves (11). The rates of oil used range from 5 to 15 liters/ha. However, the accumulation of oil on the leaves reduces yield due to interference with gas exchange and therefore photosynthesis (Fig. 11; 41). The rate of oil used should be based on disease severity (Fig. 12), weather conditions, and the presence or absence of any significant fungicide-resistant population of the pathogen. When the severity of the disease is high, or there is a high proportion of isolates of the pathogen resistant to triazole fungicides, higher rates of oil are used to enhance fungicide performance. However, under dry conditions with high temperatures, the rate of oil should be reduced to avoid phytotoxicity, which appears as water-soaked streaks on the leaves.

The protectant fungicide mancozeb is available in formulations for use in an oil–water emulsion or in water. The protectant fungicide chlorothalonil, however, has to be applied in water alone because it is phytotoxic in the presence of oil.

Systemic fungicides used for the control of black Sigatoka provide better control than protectant fungicides. Systemic fungicides penetrate the leaf cuticle and inhibit the pathogen inside the leaf. On the other hand, protectant fungicides have to be deposited on the leaf surface prior to infection, where they act by inhibiting spore germination and penetration of the pathogen into the leaves. Therefore, because most infections occur in the lower surface during the unfurling of the new leaves, the effectiveness of protectant fungicides depends on how well the spray system used covers the lower surface of the leaves during unfurling and on the interval between applications.

Systemic fungicides have several attributes that make them more suitable for black Sigatoka control than protectant fungicides; however, they pose a risk because of the potential for resistance to develop in the pathogen population. Benomyl has been the most widely used ben-
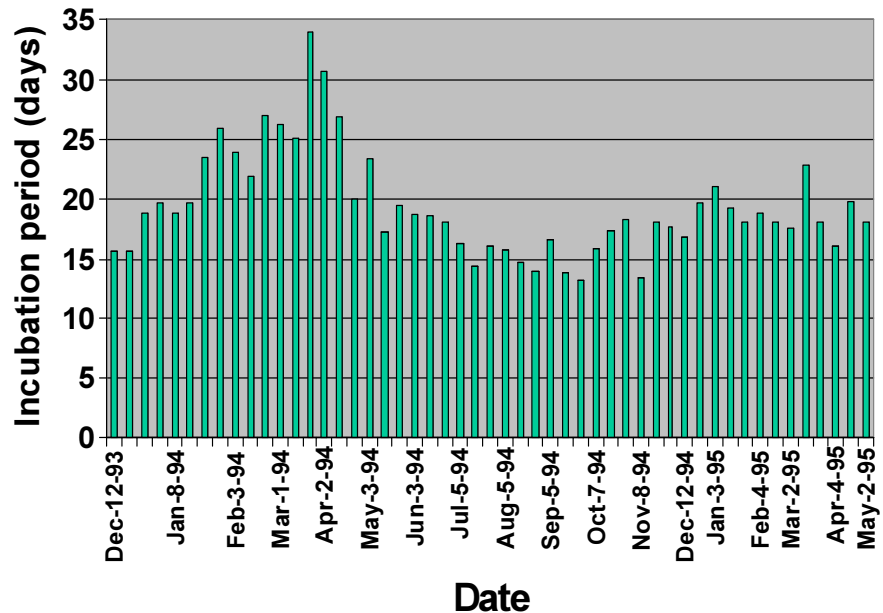

Fig. 9. Duration of incubation period of *Mycosphaerella fijiensis* on cultivar Grande Naine in Guapiles, Costa Rica, from December 1993 to May 1995. Each value corresponds to a mean of 10 leaves selected at stage 2 of the cigar leaf unfurling on the indicated date. Source: R. Romero and T. Sutton, *unpublished data*.

Fig. 10. Latent period of *Mycosphaerella fijiensis* in Grande Naine from December 1993 to May 1995 in Guapiles, Costa Rica. Each value corresponds to a mean of 10 leaves selected at stage 2 of the cigar leaf unfurling on the indicated date. Source: R. Romero and T. Sutton, *unpublished data*.
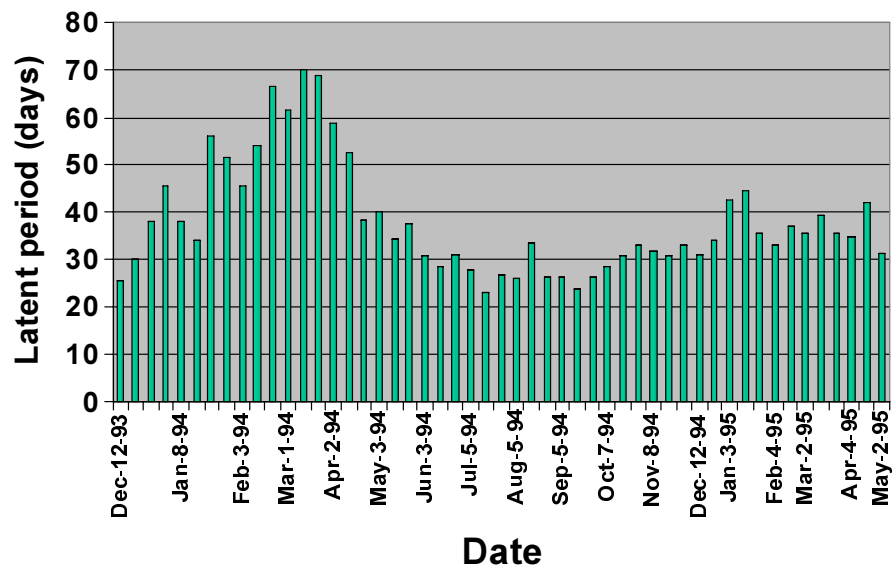
zimidazole fungicide for the control of black Sigatoka in Latin America. Tridemorph is the only member of the morpholine group currently registered for use in bananas; however, tridemorph has a limited ability to penetrate banana leaves (16). There are a large number of triazole fungicides registered for use in bananas for black Sigatoka control, all of which share the same mode of action (51).

There are differences in the activities of the triazoles registered for use in bananas (35). Some compounds translocate faster than others in banana leaves. For example, propiconazole is translocated very rapidly toward the margins of the leaves, which can result in an infection pattern along the midrib during periods favorable for infection, whereas bitertanol is not translocated as rapidly and fewer infections occur along the midrib (11).

Two strobilurin fungicides are registered for use in bananas, azoxystrobin and tri-floxystrobin, both of which have a common mode of action (14). These fungicides display systemic activity on banana leaves and can be applied in an oil–water emulsion or in oil alone (11,36). Strobilurins inhibit ascospore germination, but germination, germ tube elongation, and mycelial growth of all individuals in a wild-type population are not completely inhibited.

Two fungicides with a mode of action that differs from the existing fungicides being used in bananas are expected to have full registration for the control of black Sigatoka in the near future. These are pyrimethanil, an anilinopyrimidine fungicide (70), and spiroxamine, a spiroketalamine fungicide (52).

Several compounds that activate the systemic mechanism of resistance in the plants also have been tested for the control of black Sigatoka. Of them, acibenzolar-S-methyl, is the most promising when applied every 35 to 40 days at the rate of 40 g a.i. ha^{-1}. Applications of acibenzolar-S-methyl retard spotting of the leaves, which results in less disease severity (55).

Application of fungicides on large banana farms for the export market is done by aircraft (Fig. 13), and on small farms growing fruit for the local markets, tractor-mounted or backpack sprayers are used. Aircraft are equipped with geographical positioning systems, which direct the pilot to the application targets. This technology avoids overlaps, missed paths, and over sprays (63). The total volume of spray suspension applied per hectare sprayed with these aircraft usually ranges from 12 to 25 liters ha^{-1}.

Early Warning or Forecasting Systems

Continuous growth of the host and favorable climatic conditions in most banana-growing regions, in addition to the action of the fungicides available for controlling the disease, provided the triggering mechanism for the development of an early warning system specific for Sigatoka diseases of bananas (8). The forecasting system for Sigatoka is based on the analysis of biological and climatic descriptors that target fungicide applications to specific periods when disease severity is starting to increase and environmental conditions are conducive for disease development (8,62).

The early warning system for black Sigatoka is an adaptation of the yellow Sigatoka warning system developed by Ganry and Meyer (25) and modified by Ganry and Laville (24) to use for controlling yellow Sigatoka in Cameroon. Ternesien (108) and Fouré (21) later improved Ganry and Laville's system. The latter system (21) is based on weekly observations of disease symptoms on young leaves of the plant, according to Fouré's symptom (stages) descriptions (20; Fig. 6). Arbitrary coefficients, based on incidence and severity of disease development, are used to calculate two variables: gross sum and state of evolution. Gross sum is based on the stage present and an arbitrary coefficient, which increases with the advance of the symptoms and the juvenility of the leaf. The state of evolution is calculated using the gross sum and the foliar emission period (21). Although threshold levels were initially suggested as a guide to spray timing, the fluctuation of these two variables was found to better define appropriate times to spray (8,62,115).

This forecasting system has been adapted and implemented in several countries in Latin America by national, private, and international organizations and initiatives (7,58–61,115; E. Bureau, *personal communication*; J. A. Guzman, *personal communication*). The system has also been simplified (15,57) as well as combined with climatic factors to develop a bioclimatic forecasting system for plantain (47).
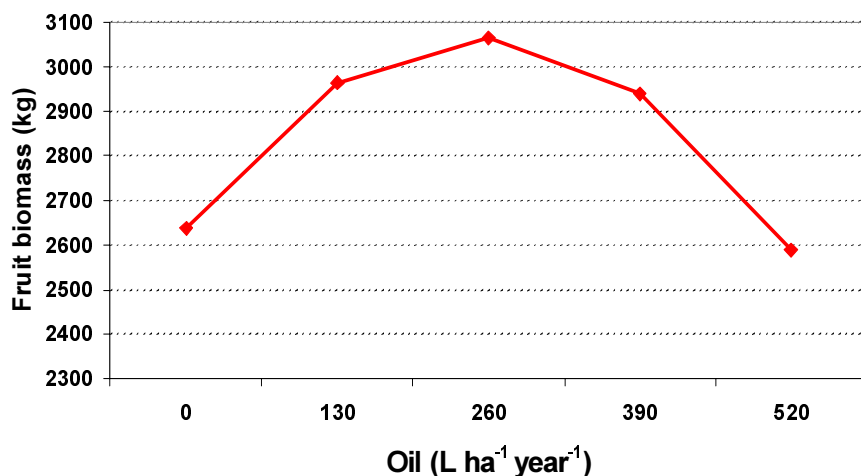

Fig. 11. Effect of oil rates (liters ha^{-1}) on fruit weight (kg per plot) of bananas. The rates of oil sprayed were accumulated within a 1-year period during four consecutive years from 1989 to 1992. Source: R. Romero and D. Marín (1993), *unpublished data*.

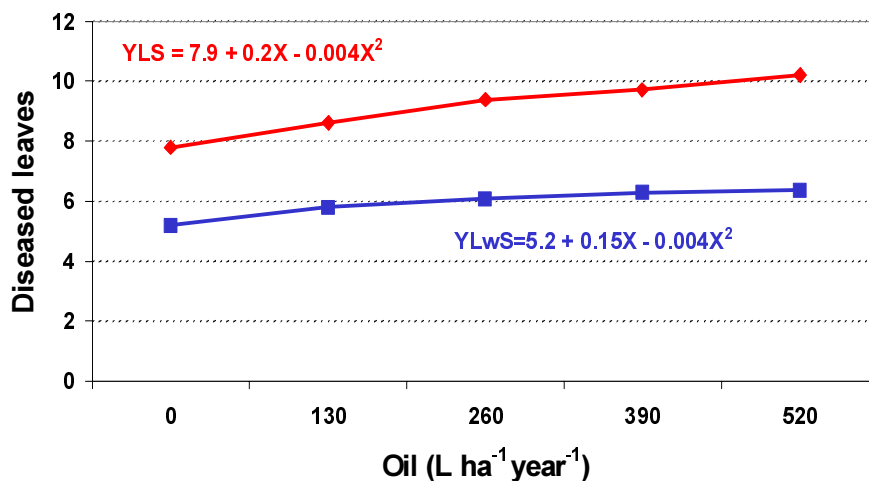YLS = 7.9 + 0.2X - 0.004X^2

YLwS = 5.2 + 0.15X - 0.004X^2

Fig. 12. Effect of oil rates (liters ha^{-1}) on youngest leaf with symptoms (YLwS) and youngest leaf with spots (YLS) of black Sigatoka. Rates of oil were accumulated within a 1-year period during four consecutive years. Source: R. Romero and D. Marín (1993), *unpublished data*.

In Central America, the commercial adaptation of the early warning system resulted in a significant reduction in the number of fungicide applications (62,115). However, various factors, including changes in weather patterns and reduced sensitivity to the demethylation inhibiting fungicides (DMI), has resulted in fixed systems (calendar schedules) replacing the biological forecasting system (115; D. H. Marín and R. A. Romero, *unpublished data*). Currently, some commercial programs still use the system to help make management decisions, but fungicide applications are no longer timed with it.

Resistance of *M. fijiensis* to Fungicides

Benomyl resistance in *M. fijiensis* was first reported in Honduras in 1977 after 2 or 3 years of continuous use (100), and resulted in significant losses (106). However, benomyl continued to be used in most Central American countries because resistance was not widespread. Between 1987 and 1990, the availability of benomyl, tridemorph, and propiconazole, each of which has systemic activity and provides postinfection control, provided the opportunity for the use of the early warning system in Central America, previously described in this article. Approximately six treatments of each of these systemic fungicides were sprayed in rotation each year from 1988 to 1991, which resulted in satisfactory control of black Sigatoka. However, in 1991, the first evidence of widespread resistance to benomyl in Costa Rica was reported (1) after approximately 10 years of use, although Rodríguez and Jiménez (85) reported first changes of sensitivity to this fungicide in Costa Rica as early as 1985. Between 1991 and 1992, resistance to benomyl was suspected as the main cause of unsatisfactory disease control, and the product was withdrawn from the control programs, which motivated an increase in the use of propiconazole (90). High levels of benomyl resistance were found in several farms in Costa Rica in 1995, 3 years after benomyl was removed from the control programs, indicating that

benomyl-resistant individuals persisted in the pathogen population. The ability of benomyl-resistant strains of *M. fijiensis* to survive in the population in the absence of benzimidazole use is evidence that acquisition of resistance to benzimidazoles did not result in a loss of fitness. When the aggressiveness of benzimidazole-resistant isolates was compared with benzimidazole-sensitive isolates of *M. fijiensis*, the former caused more disease severity than the sensitive isolates. However, because the benzimidazole-resistant strains were obtained from fields with a history of fungicide use,

Fig. 13. Turbo thrush aircraft spraying fungicide over a banana plantation for controlling black Sigatoka.
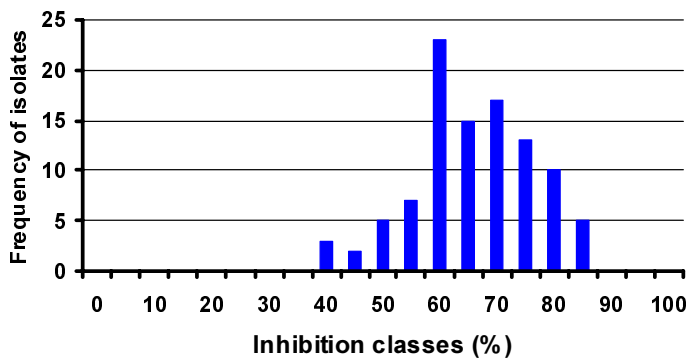

Fig. 14. Sensitivity distribution of germ tube growth inhibition of a wild-type population of ascospores of *Mycosphaerella fijiensis* at an azoxystrobin rate of 1.0 µm ml⁻¹. Source: R. Romero, *unpublished data*.

Table 2. Comparisons of EC_{50} of propiconazole-less sensitive isolates and propiconazole-sensitive isolates among triazole fungicides (R. A. Romero, M. Guzmán, and A. Jiménez, *unpublished data*)

Fungicide	I[a]	No.	Mean EC_{50} (µg ml⁻¹)	*t* value (unequal variances)	SD	Range of EC_{50} Min.	Max.	Rf[b]
Propiconazole	R	39	0.1255		0.1491	0.0020	0.5000	
	S	39	0.0047	5.06**	0.0029	0.0001	0.0130	26.7
Fenbuconazole	R	39	0.02026		0.0055	0.0010	0.3442	
	S	39	0.00298	1.96	0.0014	0.0006	0.0060	7.0
Difenoconazole	R	39	0.01703		0.0516	0.0010	0.3240	
	S	39	0.00909	1.72	0.0014	0.0001	0.0066	5.9
Tebuconazole	R	39	0.01713		0.0399	0.0030	0.2570	
	S	39	0.00293	1.17	0.0148	0.0001	0.0900	1.9

[a] Isolates: R = propiconazole-less sensitive isolates; S = propiconazole-sensitive isolates.
[b] Rf = resistance factor.

whereas sensitive strains originated from areas with no history of fungicide use, definitive conclusions about the increased aggressiveness of the benzimidazole-resistant strains of *M. fijiensis* could not be made (90). Resistance of *M. fijiensis* to benzimidazoles also developed in the 1980s and early 1990s in Belize, Guatemala, and Mexico, and in the late 1990s in Panama, Colombia, and Ecuador.

Propiconazole was the first demethylation inhibiting fungicide widely used commercially on bananas in Central America, although flusilazole and hexaconazole had been used in Belize. Following its introduction in 1987, a maximum of six applications of propiconazole was commonly used. After the withdrawal of benomyl from the control programs, however, the number of applications of propiconazole used per year increased to 8, and in some instances, to 10 (89). Unlike resistance to benzimidazoles, in which the phenotypes express high levels of resistance to any dose of the fungicide, the buildup of resistance to DMI fungicides in *M. fijiensis* proceeds gradually, and phenotypes express a large range of sensitivities (89). Thus, the definition and detection of isolates less sensitive to propiconazole is more complex compared with the benzimidazoles. Consequently, the unsatisfactory control of black Sigatoka observed in 1992 and subsequent years in several farms in Costa Rica was not immediately associated with a loss of sensitivity of the pathogen population to propiconazole due to the absence of initial baseline sensitivities to the fungicide (89).

In a study conducted in 1994, the sensitivity of a population of *M. fijiensis* treated with propiconazole since 1987 was compared with a population obtained from backyard plants and small-scale farms that had no history of fungicide use and were isolated from the main banana production area. A significant shift in sensitivity to propiconazole was detected in the two

populations of *M. fijiensis* with a history of propiconazole use compared with the population where fungicides had not been used. The sensitivity ratios between the mean (EC_{50}) for isolates from the two fungicide-treated populations and the mean EC_{50} of the untreated population were 6 and 7.5, which are considered high and reflect the poor control of black Sigatoka observed between 1992 and 1993 on these farms (89). This conclusion is supported by similar sensitivity ratios associated with unsatisfactory control of apple scab (6,19,39,97).

All DMI fungicides are cross-resistant; however, the degree of cross resistance varies for the different DMIs. Table 2 shows a comparison of EC_{50} values of a group of 39 isolates of *M. fijiensis* collected from farms that had received sprays of propiconazole for about 8 years and showed reduced sensitivity to this fungicide, and a group of 39 isolates from a population with no history of fungicide use, to values for three other triazole fungicides that had not been widely used for controlling the disease at that time. Although there is a significant difference in EC_{50} values between propiconazole less-sensitive isolates and propiconazole-sensitive isolates, the difference between these two group of isolates is of much lower magnitude for the other triazoles tested than for propiconazole, and the differences are not statistically significant. The values of the resistance factors are also a good indication of the differences in the degree of cross resistance among these triazoles.

Currently, DMI resistance is widespread in the most important banana producing areas of Central America (R. A. Romero, *unpublished data*). However, in spite of the widespread resistance to DMIs that has resulted in lower efficacy of these fungicides, they continue to be used and still constitute important products for the control of the disease when shorter intervals

between applications are used or when they are applied in mixtures with mancozeb or tridemorph with up to 10 to 12 liters of oil per hectare. Additionally, successful use of DMIs in the presence of a resistant population of *M. fijiensis* relies greatly on maintaining low inoculum levels through the use of sanitation practices, as described later in this article.

The strobilurin fungicides were introduced in the banana market in Central America in the late 1990s. Azoxystrobin was introduced in 1997, trifloxystrobin was introduced between the years 2000 and 2001, and pyraclostrobin will be commercially available in 2003. These compounds have a good efficacy against *M. fijiensis*. When azoxystrobin was first introduced, up to six applications per year was recommended. Monitoring of sensitivity of populations of *M. fijiensis* to strobilurins was initiated in 1998 at the beginning of their commercial use, utilizing in vitro tests. In large banana operations, the monitoring method used to detect shifts in sensitivities of *M. fijiensis* to strobilurin fungicides was based on the inhibition of germ tube growth. Strobilurin fungicides inhibit spore germination and mycelium growth. Ascospores were discharged into petri dishes with water agar amended with the respective dose of the fungicide, and their germ tube lengths were measured after 48 h. The relative growth inhibition was calculated with respect to germ tube growth on nonamended medium. Germ tube growth inhibition is then compared with a population of *M. fijiensis* with no history of strobilurin use. The distribution of sensitivities of *M. fijiensis* according to germ tube growth inhibition for a wild-type population of the pathogen at a concentration of azoxystrobin of 1.0 µg ml^{-1} is shown in Figure 14. Note that a range of sensitivities expressed resembles the characteristic response observed with DMI fungicides. At this rate of fungicide, there are individuals in the same population with only 40% germ tube growth inhibition and individuals with 90% inhibition, which is similar to that observed with the DMI fungicides. Although these studies were conducted before the importance of including the alternative oxidase inhibitor salicylhydroxamic acid (SHAM) in the medium was understood (78), they did provide a basis for detecting the dramatic shift in sensitivity that was observed in some farms in 2002. Using the technique described above, a frequency distribution of ascospore germination was constructed for the fungicide trifloxystrobin using four populations originating from banana farms with a history of 2 years of strobilurin use and one wild-type population (Fig. 15). Two populations from banana farms showed a significant departure from the sensitivity of the wild type and the other two populations of the pathogen from farms subjected to strobilurin use and pro-
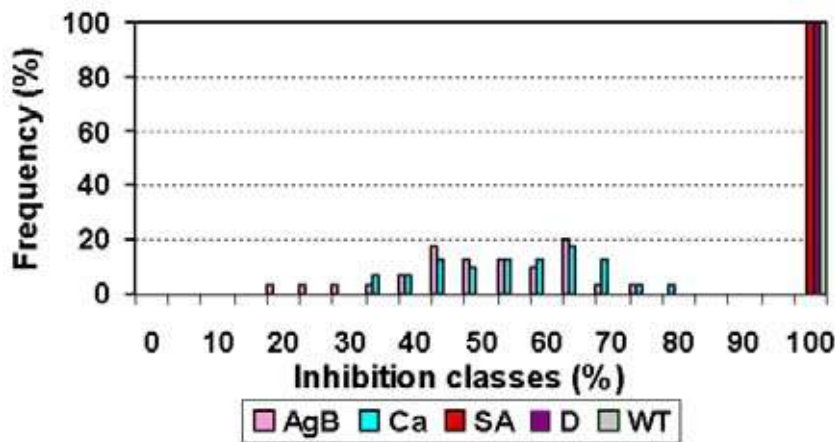

Fig. 15. Distribution of sensitivities according to germ tube growth inhibition of four populations of *Mycosphaerella fijiensis* from banana farms treated with strobilurin fungicides and from one population (WT) with no history of fungicide use. Source: R. Romero, *unpublished data*.

vide strong evidence for a shift in sensitivity of populations of *M. fijiensis* in banana plantations in Costa Rica.

To further examine the occurrence of strobilurin resistance in *M. fijiensis* in Costa Rica, samples of populations of the pathogen from various farms were assessed for the presence of the mutation G143A in the cytochrome b protein. This point mutation has been found in isolates of *M. fijiensis* associated with high levels of strobilurin resistance collected from an experimental farm in Costa Rica (13), and is known to cause high levels of resistance in several pathogens (95). Table 3 shows the frequency of the G143A mutation found in four populations of *M. fijiensis*, including a wild type, and the proportion of ascospores with germ tube growth >150 μm at 10.0 μg ml^{-1} azoxystrobin. The mutation G143A was not found in the wild-type population, and the proportion of ascospores with germ tubes growing at >150 μg ml^{-1} was zero. On the other hand, the mutation G143A was detected at frequencies ranging from 1 to 11 in the farms where resistance to strobilurins was suspected. Similarly, in these farms, the proportion of isolates with germ tube growth >150 μm was high, especially in farms 2 and 3. These results indicate that the mutation G143A was present in field isolates of *M. fijiensis* from banana farms that had received four to six applications of strobilurins per year for the previous 2 years. However, the proportion of individuals with germ tube growth greater than 150 μm was higher than the frequency of the mutation G143A found in the same populations. The causes of this apparent disparity between the frequency of the G143A mutation and the proportion of less sensitive isolates based on germ tube growth inhibition is still not resolved and could be related to the induction of the alternative oxidase pathway or to the existence of more than one mechanism of resistance to the strobilurin fungicides in *M. fijiensis*. A second target site mutation at position 129 (F129L) has been identified but has not been reported in *M. fijiensis* (2).

Biological Control

In general, biological control of black Sigatoka is extremely challenging because of the polycyclic nature of the disease, the presence of plants of all ages, and the unfurling of highly susceptible leaves every 6 to 12 days. Biological control of *M. fijiensis* has received little attention because of the availability of highly effective fungicides as well as the limited interest and financial support to find alternative methods of control. However, the development of strains of *M. fijiensis* less sensitive or resistant to systemic fungicides and the increasing demand for environmentally safe control measures has increased the interest in finding alternatives for the control of black Sigatoka over the past decade.

Bacteria are the main group of microorganisms that have been tested for biological control of *M. fijiensis*. Jiménez et al. (48) isolated 225 ephiphytic bacteria from banana leaves and evaluated them for activity against *M. fijiensis*. Only 12 isolates showed efficacy in vitro, and just one isolate (*Pseudomonas* sp.) provided better control than chlorothalonil under greenhouse conditions.

Pseudomonas spp. selected for biological control have been difficult to establish in the phylloplane; therefore, the search for a biological control agent has focused on species of *Bacillus* which have a greater potential to colonize the foliar surface and form resistance structures which aid in surviving adverse environmental conditions. However, M. Guzmán and R. Villalta (*unpublished data*) evaluated the biological efficacy of a commercial strain of *Bacillus subtilis* and found that it provided very little control.

Two isolates of *Serratia marcescens* have shown good antagonistic activity against *M. fijiensis* under laboratory conditions (Fig. 16). These bacteria provided slightly better control than propiconazole in a greenhouse trial. When evaluated under field conditions, they provided control similar to that of a fungicide program consisting of the alternation of propiconazole, tridemorph, and mancozeb (31). These results are contrary to those obtained by Miranda (71), who did not observe effective disease control using the same isolates in addition to three other strains of *Bacillus* spp.

Selection of microorganisms for the control of black Sigatoka has also focused on bacteria capable of secreting cell wall hydrolitic enzymes such as chitinases and gluconases. González et al. (30) isolated 120 chitinolytic bacteria from banana leaves from areas with high and low disease severities and found the highest frequency of isolates in areas with low disease severity.

Table 3. Frequency of isolates with germ tubes >150 μm at 1.0 μg ml^{-1} of azoxystrobin and the frequency of the mutation G143A for a wild-type population and from four populations of *Mycosphaerella fijiensis* from farms subjected to six strobilurin applications a year for the period 1998 to 2000

Farm	Frequency of ascospores with germ tube growth >150 μm[a]	Frequency of gene G143A
Wild type	0	0
Farm 1	5	1
Farm 2, cable 24	38	3
Farm 2, cable 16	41	11
Farm 3	58	11

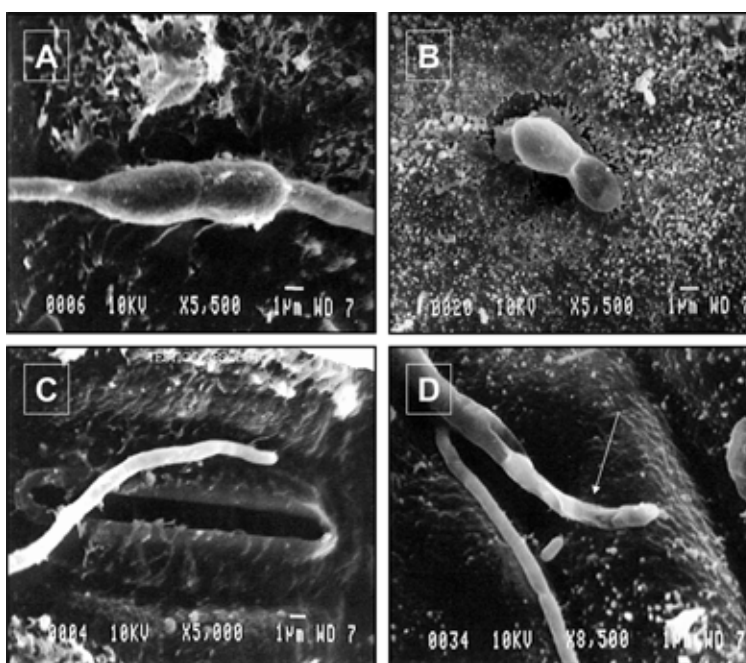[a] Based on measurements of 320 ascospores per site. Data courtesy of Syngenta.

Fig. 16. Effect of antagonistic bacteria on *Mycosphaerella fijiensis* growth. A, Normal germination of an ascospore. Both germ tubes are capable of infecting the plant. B, Germination of the ascospore inhibited by biocontrol agent. C, Normal growth of mycelium and penetration through stomata. D, Mycelium growth altered and infection process stopped by the biocontrol agent. Source: R. González, with permission.

Although little research has been done on the biological control of black Sigatoka, it is unlikely that a biological control agent or agents will be found that will provide a similar level of control to conventional fungicides. However, they may be useful, especially where fungicide resistance is a problem. From the research that has been conducted so far, it is clear that any future use of biocontrol agents in the management of black Sigatoka must be part of an integrated disease management program (5,37).

Other Control Measures

Even though chemical control remains the most important tool for managing black Sigatoka, cultural methods play an important role in reducing conditions for the development of the disease (62). For example, the reduction of inoculum levels on the farm is one of the most important cultural practices used to help in managing the disease. Sporulating tissue is removed from the leaf as soon as it reaches the mature stage (Fig. 17). This practice is commonly known as deleafing (Fig. 17A), detipping, or "surgery" (Fig. 17B), depending on the tissue excised (11,62). Removal of these lesions is very important because this tissue decomposes once it is removed, thereby reducing the inoculum (11), which translates into improved disease control (10). Spores can be produced in necrotic tissue remaining on the plant for up to 22 weeks, while leaves on the ground produce

a reduced amount of inoculum, and the infectious period is reduced by half (D. H. Marín and R. A. Romero, *unpublished data*). Additional practices such as the application of urea and other products to the excised tissue lying on the ground can accelerate tissue decomposition and reduce inoculum density (34).

The reduction of relative humidity in the field also aids in the management of black Sigatoka. An efficient drainage system, which rapidly removes superficial and underground water, and proper plant distribution both facilitate drying and help reduce the relative humidity (11,62). In banana producing regions where irrigation is needed, undertree or drip irrigation is preferred to an overhead system, which wets the leaves and provides free water on the leaf surface, which is necessary for ascospore germination (115).

Improving general plant health through an adequate nutrient supply and efficient weed and nematode management is also part of the integrated approach for the management of black Sigatoka (62).

Resistant cultivars are the only practical method of control for small-scale and subsistence growers, who often cannot afford chemicals. All bananas grown for the fresh market belong to the Cavendish subgroup and are highly susceptible to black Sigatoka. Conventional breeding of Cavendish bananas is not possible because of the female sterility of all cultivars in the group.

In contrast, breeding plantains and other cooking type bananas, which are widely used for small growers for local markets and as a food staple, has been successful. Several tetraploid hybrids with resistance to black Sigatoka have been developed by FHIA (91) and the banana breeding program from IITA in Nigeria (112,113). Hundreds of hectares of the FHIA hybrids are grown in Cuba (L. Perez-Vicente, *personal communication*) and in smaller growing regions in many other countries around the world.

Other international breeding programs aiming to develop resistant cultivars of both dessert and cooking bananas exist in Brazil, Cameroon, and Guadeloupe (11,23). Genetic transformation of bananas to confer resistance to black Sigatoka is being attempted as efficient transformation methodologies are developed (17,92,93). However, there is no information available on any significant level of resistance being achieved by this technology.

The Future of Integrated Management of Black Sigatoka

New trends in global trade will have an important influence on disease control measures due to public concern on environmental issues. Therefore, safer fungicides, drift, buffer areas, and hazardous waste management, among others, are important issues in the development of new strategies for controlling black Sigatoka.

Future disease management programs will continue to focus on an integrated crop management program that includes cultural as well as improved chemical controls. Because of the high susceptibility of the cultivars on which banana export is based, chemical control will continue as the keystone for the management of black Sigatoka. Because conventional breeding programs are unlikely to produce a suitable export banana cultivar to replace Cavendish cultivars, a potential alternative would be the development of a genetically modified Cavendish cultivar with resistance to black Sigatoka. However, public concern about genetically modified food in North America and Europe may hinder the development of this alternative.

Since 1987 there has been an active working group of banana industry representatives participating in the Fungicide Resistance Action Committee (FRAC; information available online), through which guidelines for the use of systemic fungicides with risk of developing resistance have been developed and implemented. These guidelines have included antiresistance strategies such as limiting the number of applications of the fungicide at risk, rotation and or alternation of fungicides with different mode of action, the use of a protectant fungicide as a companion, and periods 3 months or longer during a 12-month period during which the at-risk

Fig. 17. Field inoculum reduction by removal of diseased tissue through A, deleafing, and B, detipping and surgery.

fungicide is not used. These strategies have been accompanied by intensive monitoring to detect shifts in sensitivities of the pathogen to the different systemic fungicides. Mixtures of systemic fungicides with different modes of action have not been evaluated on bananas but should be investigated, not only for their efficacy, but also from the resistance management perspective.

Historical use of systemic fungicides, especially in Costa Rica, has shown that a shift in sensitivity or appearance of resistance strains of *M. fijiensis* occurs just a few years after commercial introduction of the fungicides. These shifts have been documented for the benzimidazoles (85,90), triazoles (89,103), and more recently, for the strobilurin fungicides (38,95,116). Significant shifts have not been observed with morpholines in Costa Rica, in spite of their early introduction and use soon after the identification and spread of black Sigatoka in 1980.

The widespread resistance of populations of *M. fijiensis* to the systemic fungicides available for use in bananas provides compelling evidence that chemical control strategies for black Sigatoka should be based more on protectant than on systemic fungicides. A protectant fungicide program assisted with systemic fungicides provides the possibility of satisfactory control of the disease through time and space. However, protectant fungicides require more frequent application during the rainy season to provide adequate protection during continuous periods favorable for infection. Enhancement of the fungicide mixtures considering oil type and rate, fungicide partners, and reduced-drift adjuvants is also essential for maintaining a good chemical control strategy. Additionally, spraying systems, both ground based and aerial, including complementary equipment such as electronic flying flagman systems, automatic flowmeter controllers, and constant pressure nozzles, require continuous improvement to assure adequate deposition of the fungicide mixtures.

Essential components of integrated crop management programs that minimize the likelihood of severe epidemics must include drainage maintenance and construction, proper fertilization, and nematode and weed control, among others. Additionally, internal inoculum management, through the elimination of sporulating tissue by deleafing, detipping, and "surgery", is a key component of improved disease control. Chemical treatment of diseased tissue on the ground, to accelerate tissue decomposition and reduce inoculum density, may become important in the future. Additionally, new fungicides and biological controls, in combination with compounds that promote/enhance self-defense mechanisms (55,114), are needed to develop new strategies for the management of black Sigatoka.

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