Dissemination of Bananas in Latin America and the Caribbean and Its Relationship to the Occurrence of *Radopholus similis*

Bananas (*Musa* AAA) and plantains (*Musa* AAB) are important components of the human diet in almost every country of the world, either as a cooked food or fresh fruit. They are an excellent food source, and in some countries of the world (e.g., parts of Africa), they are the principal components of the diet. Bananas are a source of fiber, are low in sodium, and are the richest ready-to-eat source of vitamin B6 and potassium (7). They are the most widely consumed fresh fruit in the United States and are found year-round in supermarkets from the largest city to the smallest town. The average American citizen eats more than 10 kg of bananas yearly (24).

Over 76 million metric tons of bananas and plantains are produced worldwide each year, accounting for over 1.5 million jobs (43). Approximately 15% of bananas and plantains are grown for export. Exports are extremely important to the economies of many developing countries. For example, in Costa Rica, banana exports account for over one-half billion dollars (U.S.) in revenue, which is second only to tourism as a source of income.

Cultivated bananas are much improved over the "wild" progenitors that originated in Southeast Asia. Not only have bananas been improved by human intervention, but the crop has been spread by humans throughout the tropical growing regions of the world. As with many plant species moved by people, parasites and pathogens of bananas were moved along with them. Among the most important of these banana pathogens is the burrowing nematode, *Radopholus similis* (Cobb) Thorne.

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Table 1. Taxonomical classification of bananas according to Simmonds and Shepherd (57)

Genus	Genome ^a	Type	Subgroup	Common cultivars
<i>Musa</i>	AAA	Bananas	Gros Michel	Gros Michel
			Cavendish	Cocos Lacatan Dwarf Cavendish Valery (Robusta, Poyo) Grande Naine
<i>Musa</i>	AAB	Plantain	Plantain	False Horn French
<i>Musa</i>	ABB	Cooking bananas	Maia Maoli	Maqueño Bluggoe Pelipita

^a The designations A and B in the genome correspond to *Musa acuminata* and *M. balbisiana*, respectively. Bananas are natural hybrids of these two *Musa* species.

Fig. 1. Uprooting of banana plant with severe damage primarily caused by *Radopholus similis*.

Fig. 2. (A) *Radopholus similis* from carrot-disk culture. (B) Female showing stylet. (C) Banana roots showing nematode damage. Blackened areas are the result of the invasion of secondary fungi and bacteria. (D) Longitudinal section of a banana root showing discoloration of cortical tissue parallel to the stele.

We suggest, based on the evidence from the literature, that the dispersal of *R. similis* in the banana-production regions in Latin America and the Caribbean region occurred at least at three different times during the establishment of bananas in those regions. The first introduction probably occurred in the mid-1830s with the banana cultivar Gros Michel, the second in the 1950s with Cocos, a dwarf mutant of

Gros Michel, and the third and most important with Cavendish cultivars in the 1960s. Additionally, the nematode could have been dispersed with other *Musa* spp. and ornamentals (36,37,69) to the banana-growing areas.

Origin of Bananas

The plant named "banana" includes a large number of parthenocarpic clones

belonging to the genus *Musa* of the family Musaceae (47,68). The center of origin of the wild banana is Southeast Asia and the Pacific Islands extending from India to Papua New Guinea and including Malaysia and Indonesia (12,45,55,58).

Edibility evolved first in wild *Musa acuminata*. Taxonomic evidence indicates that the primary center where edibility evolved was the Malay Peninsula, possibly

including closely neighboring territories (56). Most cultivated bananas are derived from the species *M. acuminata* (genome A) and *Musa balbisiana* (genome B). Simmonds and Shepherd (57) designed a method of indicating the relative contribution of the two species to the different cultivated genotypes using the A and B genome designations (Table 1). Most of the commercial cultivars are triploids and belong to the AAA group. The three major groups under cultivation worldwide are: AAA, AAB, and ABB (56). Relatively few banana clones have moved from the center of origin in Southeast Asia, with the result that diversity of these plants declines from Asia to Africa to America (56).

Banana–Host of Many Nematode Species

Plant-parasitic nematodes are widespread and are the most damaging pests of bananas. Over 100 species have been reported on banana and plantain (8,20). Those nematode species involved in the destruction of the primary roots are the most detrimental to the crop. The disruption of the anchorage system results in uprooting and toppling of the plants (Fig.

1; 20) and associated losses average approximately 20% per year (51).

Bananas, as most tropical crops, are characterized by polyspecific nematode parasitism. The burrowing nematode is widespread and is the most damaging species attacking most bananas, plantains, and cooking bananas (18,20,60). However, other nematode genera can be present in the same root system. Lesion (*Pratylenchus* spp.), spiral (*Helicotylenchus* spp.), and root-knot nematodes (*Meloidogyne* spp.) are usually associated with the crop. In spite of their importance in some areas, most research has focused on the burrowing nematode. Few studies have dealt with the interaction between nematodes in banana roots, probably due to the dominance of the burrowing nematode over the other species (18,20).

Damage caused by lesion nematodes is probably underestimated because of the similarity of the necrosis of root and corm to that caused by the burrowing nematode. *Pratylenchus goodeyi* is the most widespread and serious nematode in the African highlands and the major pest of Cavendish bananas in the Canary Islands. Banana is the only known host. *Pratylenchus coffeae* is distributed throughout the tropics and

has many hosts. In South and Central America, it appears to be more often associated with plantain than the Cavendish clones (17,19), but there is no evidence to suggest that any musaceous plant is a preferred host (19).

The spiral nematode, *Helicotylenchus multicinctus*, occurs in most regions where bananas are grown (18,38). In tropical areas where *R. similis* is present, the spiral nematode is of secondary importance (38). However, *H. multicinctus* may be numerically dominant to *R. similis* in localities where the species coexist (18). In subtropical areas where the burrowing nematode is rare or absent, *H. multicinctus* may be the major nematode problem of the crop. Severe decline of bananas caused by *H. multicinctus* occurs in Argentina, Cuba, Cyprus, Florida, Israel, Lebanon, and South Africa (38).

All banana cultivars are hosts of the root-knot nematodes (*Meloidogyne* spp.), which can cause considerable deformation and stunting of the roots. However, because they do not cause plants to topple, these nematodes are not thought to be as important as the more destructive lesion-forming species (17), which in mixed population are generally dominant (11,17).

Fig. 3. Life cycle of *Radopholus similis*.

Nevertheless, this situation is cultivar-dependent, and consequently, root-knot nematodes may dominate over the burrowing nematode (11). *Meloidogyne* spp. populations are probably suppressed by high populations of *R. similis* and *H. multicinctus*, which cause extensive root destruction (18). Root-knot nematodes are a problem in Taiwan, where they are the major nematode pest, and in some localities new to bananas where introduction of *R. similis* and *Pratylenchus* spp. has been avoided (17).

The Burrowing Nematode

R. similis was first described by Cobb (10) in 1891 from banana roots from Fiji (10,20). He described the new species in 1893 as *Tylenchus similis* (9,10,33,40,61) and indicated that females were not observed. In 1907, Cobb found both sexes infecting roots of sugar-cane in the Hawaiian Islands (9,10,33,40,61). Several years later, he received infected corms of Gros Michel from Jamaica and found additional specimens, which he used to publish a more complete description of the species in 1915 (10,33,60). Since then, *R. similis* has been found in most banana-growing areas worldwide (Fig. 2; 20). However, *R. similis* apparently is still absent in many banana-production countries, including Israel, the Canary Islands, Cape Verde Islands, Cyprus, Crete, Mauritius, the highlands of East Africa, and Taiwan (18,20). Most other species belonging to the genus *Radopholus* have been described from Australia and New Zealand. For this reason, *Radopholus* is considered indigenous to that area (34,53). A recent description of the distribution of *R. similis* is available (5).

R. similis is a migratory endoparasite that is able to complete its life cycle entirely within the root (Fig. 2A and B). Penetration occurs mostly near the root tip, but nematodes can migrate along the entire length of the root (Fig. 2C). Females and all juvenile stages are infective, although males lack stylets and are probably non-parasitic (20). *R. similis* invades, feeds, and reproduces in cells of the cortex of the roots and corm (2,3,17,33). The nematode burrows between cortical cells, punctures cell walls with its stylet, and feeds on the cytoplasm, making cavities within the roots. As the cells are destroyed and the nematode migrates, cavities coalesce to form red-brown lesions (Fig. 2C; 2,3,37). Migration and egg-laying are governed by nutritional factors as females move away from the necrosis. Within the infected tissues, the females lay four to five eggs per day for 2 weeks. The eggs hatch after 8 to 10 days, and the juvenile stages are complete in 10 to 13 days (27); the life cycle is completed in 20 to 25 days at 24 to 32°C. As the nematode colony grows and expands its feeding area, a pink-red coloration extends parallel to the plant stele through the width of the cortical tissue (Fig. 2D; 2,3,33). The characteristic pink-red areas are infested with all stages of the nematode, whereas the blackened tissues are a result of the invasion by secondary fungi and bacteria (2,3,17,33). Microbivorous nematodes also become abundant in tissues, which are in the process of disintegration (33). The presence of fungi in nematode-induced lesions probably hastens the destruction of the roots and may contribute to toppling disease (Fig. 3; 20, 54,60).

Because bananas are traditionally propagated vegetatively by corms or parts of corms (often referred to as seeds), planting material is mainly responsible for wide-scale dissemination of the pest (20,32,33). The dissemination of *R. similis* is considered relatively recent, probably starting at the beginning of the nineteenth century (20). The wide distribution of burrowing nematodes is often correlated with the import of banana corms of the subgroup Cavendish (20).

Two morphologically indistinguishable host races of *R. similis* were first described by DuCharme and Birchfield (13). One race was shown to parasitize bananas but not citrus, whereas other race infected citrus and bananas. The banana race has been identified in most banana-growing areas of the world (Fig. 4), whereas the citrus race is known to occur only in Florida. Based on a number of biological, biochemical, and karyotype differences, the citrus race was elevated to a species level and renamed *R. citrophilus* (26). However, recent molecular and biological data indicate that *R. similis* and *R. citrophilus* may actually be the same species and therefore should be considered races of *R. similis* (29).

Recent molecular studies (14,21,22,27, 28,35) have revealed a high degree of genetic similarity among burrowing-nematode populations from different areas of the world. In a cluster analysis of random amplified polymorphic DNA profiles of mostly African *R. similis* populations, Falas et al. (14) found two separate clusters; however, a geographical relationship was not clearly evident. They suggested that

Fig. 4. Worldwide distribution of the burrowing nematode (*Radopholus similis*) associated with bananas (● = infected with *R. similis*).

knowledge of the origin of the planting material could help explain the genetic similarity among burrowing nematode populations. In contrast, Marin (35) found that the genetic relationship among Central American and Caribbean populations seemed to be associated with their geographic distribution. Aggressiveness of burrowing nematodes, a relative measure of their general damage potential without regard to resistance genes (52), varies among populations from different areas of the world (15,22,35,43,50); however, this character apparently does not correlate with the molecular similarity among these populations (35).

Although best known as a pest of *Musa* spp., *Piper nigrum*, *Saccharum* spp., and *Citrus* spp., *R. similis* also attacks many crops that are important in world commerce and subsistence agriculture, such as coffee and anthurium (39). Browning (6) suggested that pathogens of these and other crops did not evolve in agricultural systems but coevolved with them in natural ecosystems, a process which continues (6). The most important hosts for *R. similis* all share a common center of origin in the Indo-Malayan region (31). Vavilov (67) contended that parasites are more diverse in the center of origin of the hosts (cultivated and wild). Therefore, considering these factors (6,67), it is very likely that *R. similis* is indigenous to the Indo-Malayan area rather than to Australia, as has been suggested (34,53). Razak (44) suggested that *R. similis* is indigenous to Malaysia. Pattison et al. (41) suggested that *R. similis* was introduced into Australia, probably with infected planting material from Fiji.

Movement of Bananas to the New World

No exact dates can be assigned to the evolution and dissemination of edible bananas (Fig. 5). The essential events in Southeast Asia probably occurred millennia rather than centuries ago (56). From about the fifth to the fifteenth centuries, and perhaps earlier, the Indian Ocean was navigated by traders from Saudi Arabia, Persia, India, and Indonesia. Banana cultivars from Southeast Asia were distributed over the coasts of the Indian Ocean (12,45,62). The cultivars were a mixture of genomic combinations, including Red (AAA), Silk and Prata (AAB), Pisang Awak (ABB), and even AAs and ABs and some plantains (12).

Bananas and plantains were present in Africa before the arrival of the Portuguese in the fifteenth century. It is likely that they entered Africa from Indonesia-Malaysia, rather than from India, by way of Madagascar and/or the east coast around the tenth century (23,45,46,56,62). However, the cultivars of the upland of East Africa and of low tropical Africa are broadly different (30,56). It is believed that the sweet bananas (AA and AAAs) were introduced into East Africa very early from Arab settlements (30). Later, in or after the seventh century, cooking bananas (AAB and ABBs) were introduced into Madagascar from southern Borneo. From there, they were moved northward through the Zambies Valley, and then westward along the Congo to the west coast (30). West Africa has mainly cooking bananas, although some small, sweet AA and AAA clones are grown. Mainly dessert bananas are present in East Africa, including Egypt (30).

The Portuguese first explored the coast of Guinea from 1469 to 1474 and took bananas from there to the Canary Islands in the late fifteenth century (23,30,45,47,62). However, exactly when bananas reached the Canary Islands is still unclear and somewhat controversial (25). Simmonds (56) and Hernández (25) provided evidence that they arrived in Gran Canaria in the year 1402, whereas Rodríguez (47), Hernández (25), and Langdon (30) reported 1482. Because the Portuguese first explored the coast of Guinea in 1469 to 1474, it is likely that bananas were introduced late in the 1400s rather than earlier in that century as stated by Simmonds (56) and Hernández (25). Hernández (25) also considered the possibility that bananas came from the Philippines, which were under Spanish dominion.

In 1516, Friar Tomás de Berlanga brought a banana plant to Hispaniola, currently Dominican Republic, from the Canary Islands (16,30,45,47,55,62,68). It has also been suggested that bananas were introduced by the Portuguese into the New World via the Cape Verde Islands (1,4,66). Simmonds (55) stated that the clone brought by de Berlanga was unidentified. However, Langdon (30) claimed that the banana introduced by Father de Berlanga was known as "Dominicos," which today is a common name for a plantain belonging to the French group. The first clones identified in the New World were the "silk fig" (Apple Banana, *Musa* AAB) and the French plantain (*Musa* AAB), which were present in the West Indies in the seventeenth century (55).

Father de Berlanga also planted bananas in the Monastery of San Francisco, where

Fig. 5. Spread of bananas from the Indo-Malay region to the rest of the world.

they flourished (47). Then they were taken to Cuba in 1529, to Mexico in 1531 by Vasco de Tuerroa, and to Costa Rica in 1541 by Diego Guadierrez. When Father de Berlanga was made bishop of Panama, he also took banana plants with him (47).

Although hypothesized, there is little evidence of pre-Columbian presence of bananas in the New World (56,68). This hypothesis is based on the findings of leaves resembling those of bananas in pre-Colombian deposits in South America. However, these leaves may belong to another plant closely resembling the banana plant (68). There also are reports from studies in pre-Columbian graves in Peru of finding not only banana leaves but also seedless banana fruit that belonged to the old species *Musa paradisiaca*, today known as the plantain group (*Musa AAB*) (1,66). According to Fernandez de Oviedo (16; originally published in 1535 to 1537), bananas were not known in the New World before 1516, at which time they were brought to Santo Domingo by Father de Berlanga.

In contrast, Langdon (30) assembled evidence that bananas were "fruits of the land," meaning that they were already present when the Spaniards arrived. He presented evidence of banana plants in Puerto Rico, Mexico, Costa Rica, Panama, Colombia, the Guianas, Brazil, Ecuador, and Peru, from 1535 to 1556. He suggested that

bananas have been a major food crop in both Polynesia and tropical South America for more than 2,000 years and provided evidence for the link between the two regions (30). Von Loesecke (68) stated that the fruit probably was introduced from the Pacific by the first migrations of Polynesians about the time of Christ. Other researchers have concluded that bananas from the Maia Maoli group (popoulu type) could have been taken from the Pacific to Ecuador around 200 B.C. (12,30).

When the Amazon was explored, just 24 years after the banana arrived in Hispaniola, bananas were found under cultivation along the river. Because it is unlikely that bananas could have been disseminated so quickly from Mexico to Brazil, on the Atlantic side of South America (1,4,66), it has been hypothesized that these tropical plants were brought to the New World before Columbus by West Africans who shared their environment with these plants (1,4,66).

From the sixteenth to the nineteenth century, the Portuguese and the Spaniards carried bananas all over tropical America. Dutch, British, French, and German traders also played a role in the distribution of the Gros Michel and the Cavendish group to West Africa, Latin America, and the Caribbean (12). Gros Michel and Dwarf Cavendish were introduced early in the nineteenth century, and several other clones

were introduced to Dominica via Kew Botanical Garden in 1902 (55).

Although bananas were introduced very early in the history of America, it is unlikely that *R. similis* was introduced at the same time. The fact that *R. similis* is absent in the Canary Islands (20) supports this hypothesis, because these islands were an important point of commerce for trade between America and the Old World.

Introduction of Gros Michel (*Musa AAA*)

Gros Michel appears to be native in Burma (currently Myanmar), Thailand, Malaysia, Indonesia, and Ceylon (currently Sri Lanka), but it is absent from or was recently introduced to the Philippines, New Guinea and the Pacific, Africa, and the New World. In the New World, Gros Michel first appeared in Martinique (Fig. 6) early in the nineteenth century (45,47,55). Kervégan (1935), cited by Simmonds (55), suggested that a naval officer introduced it to the botanical garden at St. Pierre.

Although the exact date is unknown, the banana industry became established after the introduction of Gros Michel to Jamaica around 1835 from Martinique by Jean Francois Pouyat (45,47,55,62). Forty years later, Gros Michel was distributed widely in Central America and the Caribbean area, and adopted for the banana trades (55).

Fig. 6. Introduction of banana cv. Gros Michel from Southeast Asia.

Commercial plantations in Central America and Cuba are believed to originate from the plant brought to Jamaica (45).

Colombia made the first import of Gros Michel banana suckers from Jamaica in 1892, and Surinam made the first import in 1904 (47). Gros Michel was grown almost exclusively in Almirante, Panama. Infections of banana by *R. similis* apparently were widespread, and uprooting was abundant. However, the symptoms associated with *R. similis* infection of Gros Michel

and Cocos banana roots and corms were not described until 1957 (33).

Introductions of Gros Michel to the Pacific Islands were made around the turn of the century: from Jamaica to Fiji in 1891 (via Kew, England), to Hawaii in 1903 (via Nicaragua), and to Australia in 1910 (43,50). There is no information about the introduction of Gros Michel to Fiji, previous to the introduction made from Jamaica, about the time Cobb made his observations on *T. similis*. Although no cultivar was

mentioned during Cobb's visit to Fiji in 1890 to 1891, it is possible that the first specimens of *T. similis* observed were associated with Gros Michel plants imported from Jamaica.

The introduction of *R. similis* to the New World probably occurred with the introduction of Gros Michel. The Gros Michel group has a moderate level of resistance to burrowing nematodes (49), which may have allowed this pest to go almost unnoticed at that time. Initial nematode screenings in Central America found that *R. similis* was present on Gros Michel (33,63). Additionally, Cobb received infected Gros Michel corms from Jamaica to complete his description of *T. similis* in 1915 (10,61).

Introduction of Cocos (*Musa AAA*)

The history of the Central American banana industry is largely the history of the United Fruit Company (55,58). Before 1958, nematodes were of no concern to the banana industry. Banana growers traditionally cultivated Gros Michel, which resisted the damaging effects of nematodes. In the mid 1950s, a mutant of Gros Michel, known as Cocos, was distributed to all United Fruit Co. plantations (Fig. 7; Guatemala, Honduras, Costa Rica, Panama, Dominican Republic, and Turbo, Colombia, and possibly to Nicaragua and Ecuador). The Cocos cultivar was found in Finca Cocos in Puerto Armuelles, Panama. Because Cocos was more wind-resistant than Gros Michel, it became the latter's replacement. Unfortunately, seedbeds in Puerto Armuelles were contaminated with *R. similis*, and hundreds of thousands of infected seeds were distributed throughout

Fig. 7. Distribution of banana cv. Cocos in Central and South America.

Fig. 8. Dissemination of the banana Cavendish cultivars from Southeast Asia to the rest of the world.

the plantations of United Fruit Co. (52; C. Stephens, *personal communication*).

Cocos Farm, the site where the original Cocos plant was found in Armuelles in 1948, was sampled in 1958, and no *R. similis* infestation was detected (63). From Cocos Farm, the cultivar was moved to Palo Blanco and from there to Zapatera and Jobo Farm. The site in Zapatera was probably the origin of the infestation of Cocos in Armuelles. The Gros Michel growing in those areas was also infected with this nematode (63). Cocos was introduced to Honduras from Armuelles in 1955. The seedbeds were established at Guaruma 2, and all plantings used as a seed source were infected (63).

The burrowing nematode was found in all divisions of the United Fruit Co. surveyed in the late 1950s (63). With exception of Tiquisate (Guatemala) and Esquinas (Costa Rica) districts, the occurrence was limited to the Cocos cultivar. So this pathogen apparently was transported along

with the planting stock of the Cocos cultivar. In Tiquisate and Esquinas, the nematode was also found in Gros Michel (63). Thus, the second dissemination of *R. similis* occurred with the spread of Cocos. The source of contamination was, very likely, a Gros Michel plant.

Dissemination of Abaca (*Musa textilis*) and Ornamentals

A collection of abaca, also known as Manila hemp, also was brought to the Botanical Garden in Lancetilla, Honduras, from Panama in 1928 (48). However, the original source of abaca planting material is not documented. The establishment of abaca plantations in Central America during 1941 and 1942 was done with plant material from Lancetilla (48). If abaca was infected with *R. similis* during the seed reproduction at Lancetilla, it is likely that planting of this *Musa* sp. also contributed to the dissemination of the burrowing nematode in Central America. However,

there is no documented evidence to support this hypothesis.

R. similis have been introduced to other regions with different host plants, such as ornamentals (36,69), including species belonging to the genus *Musa* (69). Therefore, it is also possible that burrowing nematodes were introduced to banana-growing areas with ornamental plants.

Dissemination of Cavendish Cultivars (*Musa* AAA)

The first and best known introduction of dwarf Cavendish (Chinese banana) was made by Charles Telfair from southern China to Mauritius in 1826 (Fig. 8). In 1829, some plants were sent to Barclay of Burryhill in England. Later the Duke of Devonshire purchased one plant for his private gardens at Chatsworth. From there, the missionary John Williams took suckers to Samoa in 1838, and then the clone was spread to Tonga and Fiji in the 1840s, and from Tahiti to Hawaii about 1855. Austra-

Fig. 9. (A) Young fruit and floral bud of banana cv. Grande Naine. (B) Bagged fruit of Grande Naine prior to harvest.

lia and New Guinea probably received this clone from the same source (43,45,55).

In 1884, dwarf Cavendish was imported and planted in Bath Gardens, St. Thomas. In 1909, the Robusta cultivar, also known as Valery, was brought into Jamaica from Guatemala and was planted in South Manchester (47,55). However, how Robusta reached Guatemala is not documented.

Lacatan, another Cavendish cultivar, was already grown in the Imperial College in Trinidad in 1933. The stock plants were obtained from the Trinidad Department of Agriculture and apparently came from the Philippines (Fig. 8) via Costa Rica (5). Lacatan was introduced to Jamaica from Trinidad about 1926 (47).

Except for the Standard Fruit Company in La Estrella, Costa Rica, and the Aguan, Honduras, only the United Fruit Co. grew bananas in Central America before the 1960s (C. Stephens, *personal communication*). When United Fruit Co. converted to

the Cavendish types because of their resistance to Panama disease in 1958 to 1959, a shipload of Lacatan corms, heavily infected with *R. similis*, was brought to Changuinola, Panama, from Jamaica. Much of Changuinola was planted with this infected material, and production decreased rapidly (33; C. Stephens, *personal communication*).

The United Fruit Co. had a small banana breeding program in Panama in the 1920s. The program was started from cultivars brought from Cuba, Panama, and Costa Rica. The amount of germplasm was augmented by material collected from 1921 to 1927 by D. A. Reinking from French Indochina, the Philippines, Malay States, Siam, Sumatra, Java, Celebes, New Guinea, Halmahera, Banda, Australia, Burma, and India. Later, the program was terminated, and the collection was transferred to Lancetilla, Honduras. A new cultivar, Valery, was brought by Reinking

from the Botanical Garden of Saigon (Fig. 8). Valery, which is resistant to Fusarium wilt (Panama disease), replaced Gros Michel in all countries except Panama in 1960s. In the 1980s, Valery was replaced with a dwarf cultivar, Grande Naine (48,49; C. Stephens, *personal communication*), which is one of the most widely grown cultivars today (Fig. 9).

Conclusion

Gowen and Queneherve (20) stated that the widespread distribution of the burrowing nematode often is associated with areas where banana corms of the Cavendish subgroup were imported. The evidence provided in the present review does not refute that assumption. However, there are reasons to believe that the spread of *R. similis* commenced in Central America and the Caribbean islands in the early 1820s when Gros Michel arrived in Martinique (55). It is very likely that Cavendish culti-

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vars did not have any contact with burrowing nematodes until their arrival in the Americas. Because the Canary Islands and Mauritius apparently do not have *Radopholus* spp. infecting banana (20), and because this nematode has not been reported from China (70) or Vietnam (5), places from which Dwarf Cavendish and Valery were initially collected, *R. similis* must have contacted these cultivars elsewhere. *Radopholus similis* was not known in the Philippines, from which Lacatan was collected, before its introduction with infected Cavendish planting material in the 1960s (A. Salas, *personal communication*). The fact that the Cavendish cultivars, which are more susceptible than Gros Michel and Cocos to *R. similis* (64,65), became important replacements of the latter cultivars (59) definitely contributed to widespread dispersal of the nematode in the banana-growing countries.

The circumstantial evidence for a common origin of nematode populations in Central America and the Caribbean is strong. The highly conserved genome of this nematode (14,21,27,28,35) can be explained from this perspective. With more precise knowledge of the distribution of the nematode in this area, it is possible to narrow even more the genetic relationship among populations. The reported variation in aggressiveness among populations of this parasite (15,35,42,50), in spite of a high degree of genetic similarity among populations, is probably due to evolution of the populations under specific environmental conditions. This variation also could be influenced by the rapid changes in cultivars during the twentieth century.

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