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FIFTY YEARS OF FROSTY POD ROT IN CENTRAL AMERICA: CHRONOLOGY OF ITS SPREAD AND IMPACT FROM PANAMA TO MEXICO

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SUMMARY

Moniliophthora roreri causes frosty pod rot (FPR) or moniliasis, an extremely destructive disease of cacao that is currently confined to 11 countries in tropical America. The arrival of FPR has had dramatic social and economic consequences in afflicted countries, clearly demonstrating the scale of damage that could result if it becomes dispersed into the major cacao producing countries. The disease has been recorded in Latin America for nearly 200 years, starting in north-eastern Colombia, where the center of genetic diversity and probable center of origin of the pathogen were recently determined. We have compiled data on the dispersal and impact of M. roreri in Central America and Mexico, where cacao came into cultivation over two thousand years ago and where the crop is still an important component of the region's culture and commerce. This information was complemented with field visits to the affected countries to corroborate in situ the disease impact and collect fungal samples for preservation and molecular and morpho-physiological studies. In Central America, FPR was first recorded in Eastern Panama in 1956. Subsequently, the pathogen has increased its range over the past fifty years with successive reports in Costa Rica (1978), Nicaragua (1979), Honduras (1997), and Guatemala (2002). In these countries, FPR invariably became the main yield-limiting factor for cacao production in the affected areas, rapidly surpassing the importance of Phytophthora palmivora (black pod disease), the predominant cacao pathogen in Central America prior to FPR. During recent years, a more active dispersal pattern of M. roreri was observed in the region, possibly attributable to the increasing efficacy of human-mediated dispersal. Thus, FPR was detected in the Stann Creek and the Toledo Districts in Belize in 2004 and 2005, respectively. In Mexico, FPR was first observed in northern Chiapas in March 2005. One month later, local organizations estimated that around 1.000 ha in the municipalities of Pichucalco, Juárez, and Ostuacán in Chiapas and Huimanguillo in Tabasco (near the border with Chiapas) were affected. Sequence analyses of two regions of the nuclear ribosomal DNA repeat (internal transcribed spacer region (ITS) and 28S large subunit (LSU)) showed that isolates from Panama, Costa Rica, Nicaragua, Honduras, Belize, and Mexico are 100% similar, suggesting that only one or few very related strains of M. roreri dispersed in this region, being able to thrive under a wide range of environmental conditions.

CINQUANTE ANS DE MONILIOSE DES CABOSSES EN AMÉRIQUE CENTRALE : CHRONOLOGIE DE SA DIFFUSION ET SON IMPACT DU PANAMA AU MEXIQUE

RESUME

Moniliophthora roreri est à l'origine de la moniliose des cabosses (frosty pod rot – FPR), une maladie du cacaoyer extrêmement destructrice qui est actuellement confinée à 11 pays d'Amérique tropicale. L'arrivée de la moniliose des cabosses a eu des conséquences sociales et économiques très graves dans les pays touchés, qui illustrent l'ampleur des dommages qui pourraient advenir si elle se propageait dans les principaux pays producteurs. La maladie a été mentionnée en Amérique latine pendant presque 200 ans, d'abord dans le nord-est de la Colombie, où l'on a récemment situé le centre de diversité génétique et le foyer probable à l'origine du pathogène. Nous avons réuni des données sur la dispersion et l'impact de *M. roreri* en Amérique centrale et au Mexique, où le cacaoyer a été mis en culture il y a plus de deux mille ans et où cette plante constitue encore une composante importante la culture et du commerce de la région. Ces informations ont été complétées par des visites de terrain dans les pays touchés, pour confirmer *in situ* l'impact de la maladie et recueillir des échantillons fongiques pour une conservation et des études moléculaires et morpho-physiologiques. En Amérique centrale, la moniliose des cabosses a été mentionnée pour la première fois dans l'Est du Panama en 1956. Par la suite, l'agent pathogène s'est développé sur une zone plus vaste au cours des cinquante dernières années avec des signalements successivement au Costa Rica (1978), au Nicaragua (1980), au Honduras (1997) et au Guatemala (2002). Dans ces pays, la moniliose est invariablement devenue le principal facteur limitant le rendement pour la production cacaoyère dans les zones affectées, dépassant rapidement en importance *Phytophthora palmivora* (pourriture brune de la

cabosse), l'agent pathogène prédominant pour le cacaoyer en Amérique centrale avant la moniliose. Au cours des dernières années, une tendance à la dispersion plus active de *M. roreri* a été observée dans la région, qui est peut-être imputable à l'efficacité accrue de la dispersion par une intervention humaine. Ainsi, la moniliose des cabosses a été détectée dans les Districts de Stann Creek et de Toledo au Belize en 2004 et 2005 respectivement. Au Mexique, la moniliose a été observée pour la première fois dans le nord du Chiapas en mars 2005. Un mois plus tard, des organisations locales estimaient qu'environ 1000 ha avaient été touchés dans les municipalités de Pichucalco, Juárez et Ostuacán au Chiapas et de Huimanguillo au Tabasco (près de la frontière avec le Chiapas). Des analyses de séquences de deux régions de séquences répétées de l'ADN ribosomal nucléaire (région de l'espaceur transcrit interne (ITS) et 28S grandes sous-unités (LSU)) ont montré que des isolats de Panama, du Costa Rica, du Nicaragua, du Honduras, du Belize et du Mexique sont similaires à 100 %, ce qui laisse à penser qu'une seule ou un tout petit nombre de souches de *M. roreri* s'est dispersée dans cette région, avec la capacité de prospérer dans des conditions d'environnement très diverses.

CINQUENTA ANOS DE PODRIDÃO PARDA NA AMÉRICA CENTRAL: CRONOLOGIA DO SEU AVANÇO E IMPACTO DO PANAMÁ AO MÉXICO

SUMARIO

Moniliophthora roreri causa a doença da podridão parda (FPR) ou monolíase, uma doença extremamente destrutiva do cacau que actualmente está confinada a 11 países da América tropical. A chegada de FPR tem tido consequências sociais e económicas dramáticas nos países afectados, demonstrando claramente a escala de danos que pode originar se se dispersar pelos maiores países produtores de cacau. A doença tem sido registada na América Latina já há cerca de 200 anos, iniciando-se no Nordeste da Colômbia, onde o centro de diversidade genética e provável centro da origem do patógeno foram recentemente determinados. Compilámos dados sobre a dispersão e o impacto de M. roreri na América Central e México, onde o cacau começou a ser cultivado há mais de duzentos anos e onde o cultivo é ainda um importante componente da cultura e do comércio da região. Esta informação foi complementada com visitas de campo aos países afectados para corroborar in situ o impacto da doença e recolher amostras de fungos para preservação e com estudos moleculares e morfo-fisiológicos. Na América Central, FPR foi registada pela primeira vez no Leste do Panamá em 1956. Subsequentemente, o patógeno tem aumentado a sua dispersão nos últimos cinquenta anos com registos sucessivos na Costa Rica (1978), Nicarágua (1980), Honduras (1997), e Guatemala (2002). Nestes países, FPR tornou-se invariavelmente o principal factor de limitação de lucro para a produção de cacau nas áreas afectadas, ultrapassando rapidamente a importância da Phytophthora palmivora (doença da podridão negra), o patógeno predominante no cacau na América Central antes de FPR. Nos últimos anos, um padrão de dispersão mais activo de M. roreri tem sido observado nesta região, possivelmente devido ao aumento da eficácia da dispersão pelos humanos. Portanto, FPR foi detectada nos Distritos de Stann Creek e de Toledo em Belize em 2004 e 2005, respectivamente. No México, FPR foi observada pela primeira vez no Norte de Chiapas em Março de 2005. Um mês depois, as organizações locais calcularam que cerca de 1.000 ha estavam afectados nas municipalidades de Pichucalco, Juárez, e Ostuacán em Chiapas e em Huimanguillo no Tabasco (perto da fronteira com Chiapas). As análises de sequência de duas regiões de repetições de ADN ribossómico nuclear (regiões do Internal Transcribed Spacer (ITS) e 28S grandes subunidades (LSU)) demonstraram que os isolados do Panamá, Costa Rica, Nicarágua, Honduras, Belize, e México são 100% similares, sugerindo que apenas uma ou poucas variedades relacionadas de M. roreri se dispersaram nesta região, conseguindo desenvolver-se sob as mais variadas condições ambientais.

CINCUENTA AÑOS DE PRESENCIA DE MONILIASIS DEL CACAO EN CENTRO AMERICA: CRONOLOGIA DE SU DISPERSION E IMPACTO DESDE PANAMA HASTA MEXICO

RESUMEN

Moniliophthora roreri es el agente causal de la moniliasis, una enfermedad extremadamente destructiva del cacao confinada en 11 países de América tropical. Los graves efectos socioeconómicos causados por la moniliasis en diferentes países, muestran claramente la magnitud de los daños que una eventual diseminación del hongo provocaría en los principales países productores de cacao. La enfermedad ha sido reportada en Latinoamérica por casi 200 años, empezando en el noreste de Colombia en donde recientemente se determinó que existe la mayor diversidad genética y el posible centro de origen de la especie. Se recopiló información sobre la dispersión e impacto de M. roreri en Centroamérica y México, región en donde el cacao fue domesticado hace más de dos mil años y en donde el cultivo todavía es un importante componente de la cultura y comercio regional. Esta información fue complementada con visitas de campo a los países afectados para corroborar in situ el impacto de la enfermedad y colectar muestras del hongo para su preservación y para

realizar estudios moleculares y morfofisiológicos. En Centroamérica, la moniliasis fue reportada por primera vez en el oriente de Panamá en 1956. Subsecuentemente, el patógeno ha incrementado su rango de dispersión durante los últimos cincuenta años con reportes sucesivos en Costa Rica (1978), Nicaragua (1980), Honduras (1997) y Guatemala (2002). En estos países, la moniliasis se convirtió invariablemente en el principal factor limitante de la producción de cacao en las áreas afectadas, superando rápidamente la importancia de Phytophthora palmivora (mazorca negra), el patógeno predominante en el área antes de la moniliasis. Durante los últimos años se ha observado un patrón más activo de diseminación de M. roreri en la región, debido posiblemente a la participación cada vez más activa de los seres humanos como agentes de dispersión. En Belice, la moniliasis fue detectada en los distritos de Stann Creek y Toledo en 2004 y 2005, respectivamente, y en México fue observada por primera vez en el norte de Chiapas en marzo 2005. Organizaciones locales estimaron un mes después, que alrededor de 1.000 ha en los municipios de Pichucalco, Juárez y Ostuacán en Chiapas y Huimanguillo en Tabasco (cerca de la frontera con Chiapas) estaban infectadas. La secuenciación de dos regiones del ADN nuclear (ITS y 28S) mostró que los aislamientos de Panamá, Costa Rica, Nicaragua, Honduras, Belice y México son 100% similares, sugiriendo que solo uno o muy pocos aislamientos relacionados de M. roreri se han dispersado en esta región, donde se han adaptado exitosamente a un amplio rango de condiciones ambientales.

INTRODUCTION

Cacao (Theobroma cacao L.) has been an important component of Mesoamerican culture and commerce since pre-Columbian times. Early Mesoamerican portrayal and accounts of the species are a mixture of mystical or religious symbolism and economic usage (Young, 1994). The species was introduced into this region from South America in prehistoric times (Cheesman, 1944; Motamayor et al., 2002), early cacao cultivation apparently taking place in northern Central America and the lowlands of Mexico 2,000 years ago (Cheesman, 1944; Cope, 1976). The principal areas of pre-Columbian cultivation on the Pacific and Atlantic coasts extended, respectively, from the State of Chiapas to south of Lake Nicaragua, and from the State of Veracruz to a region around Lake Izabal in Guatemala (Bartley, 2005). By the middle 20th century, the entire cacao crop of Central America was virtually produced on the Caribbean coast of Costa Rica, Panama and to a lesser extent in Nicaragua (Bergmann, 1957). Criollo were the only varieties existing in the region until 19th century, when introductions of Forastero types initiated the mix and near total disappearance of the original genotypes. Foreign introductions included Nacional genotypes from Ecuador into Guatemala and other areas in 1861, Calabacillo from Trinidad into Nicaragua in 1893, and Matina/Ceylán (Martinique Créole) into Costa Rica, Mexico and other countries in 1900's (Bartley, 2005).

Mesoamerican cultivation of the crop currently includes approximately 80,000 smallholders and 100,000 hectares of plantings mostly concentrated in the states of Tabasco and Chiapas in Mexico (80.2%), with the remaining in Panama (6%), Nicaragua (6%), Honduras (3%), Guatemala (2.7%), Costa Rica (1%), Belize (0.8%), and El Salvador (0.3%). Different factors have contributed to the decline of cacao production in the region, the most relevant being the impact of pod diseases, low yield-potential of the plantations (100-500 kg ha^{-1} $year^{-1}$), and historical fluctuations of the cacao prices. This decline has occurred despite the historical importance of the crop and the significant potential of the region as a relevant cacao-producing area, which has an available labor force, high local consumption, close proximity to major markets, and extensive suitable areas for cacao cultivation, which for Nicaragua alone have been estimated from 350,000 ha (Thienhaus, 1992) to 1 million of hectares (López-Guadamuz, 2004).

Three major diseases are present in this region. The destructive witches' broom disease, caused by Moniliophthora (=Crinipellis) perniciosa (Stahel) Aime & Phillips-Mora, is still confined south of the Panama Canal, and thus inflicting very limited damages. Conversely, black pod disease (Phytophthora palmivora (Butler) Butler and/or P. capcisi Leonian) is endemic to this region and was the most important disease prior to the appearance of FPR. Moniliophthora roreri (Cif.) Evans et al. is the causal agent of FPR, an extremely destructive disease. Most reports of FPR count pod losses at greater than 30%, but losses can exceed 90% under favorable conditions, leading to the total abandonment of cacao cultivation in certain areas as has occurred to some extent in all affected countries. M. roreri is still restricted to tropical America where it has been successively reported in eleven countries over a period of nearly 200 years, starting in Colombia in 1817, Ecuador in 1917, and Venezuela in 1941 (Phillips-Mora, 2003).

Until the 1950's M. roreri was geographically isolated, being confined to northwest South America, and therefore of interest only to a handful of countries. However, its appearance in Panama fifty years ago increased the geographic confines of the pathogen and changed the perception of the disease (Evans, 1986). FPR spread to the countries north of Panama invariably becoming the main yield-limiting factor for cacao production in this emblematic region. This paper aims to compile the available information on the appearance, dispersal and impact of FPR from Panama to Mexico, most of which is fragmented and restricted to local and/or informal sources. Since this disease presents a substantial threat for cacao cultivation on a worldwide scale, the information provided here is intended to call attention to the scale of damage that could result if the pathogen becomes dispersed into new countries and to the necessity of taking urgent steps

to arrest its progress and reduce the eventual impact of the disease.

MATERIALS AND METHODS

We carried out a bibliographical search on the appearance, dispersal and impact of FPR in Central America and Mexico by collecting formal and informal references, which were summarized and organized in Endnote v. 7.0 (Thomson ISI ResearchSoft, Carlsbad, CA). This information was complemented with field visits to most countries to corroborate the presence and impact of the disease in situ, and to collect fungal samples for preservation and for conducting molecular and morpho-physiological studies not described here. DNA samples of M. roreri from all countries except Guatemala were compared and their levels of homology determined by analyzing two regions of the nuclear ribosomal DNA repeat—internal transcribed spacer region (ITS) and 28S large subunit (LSU). These segments were amplified and sequenced with fungal specific primers ITS1-F/ITS4 (ITS) and LSU4-B/LR6 (LSU) as described in Aime & Phillips-Mora (2005).

RESULTS

The presence of M. roreri was recorded for the first time in Panama in 1956, and thereafter was successively detected in Costa Rica in 1978, Nicaragua in 1980, Honduras in 1997, and Guatemala in 2002. The fungus continued with its invasive behavior and was recently reported in Belize in 2004 (Phillips-Mora et al., 2005a), and Mexico in 2005 (Phillips-Mora et al., 2005b). El Salvador, a very important cacao producer and trader during pre-Columbian and colonial times is the only country in this region where FPR has not yet been reported. The impact of the disease in Central America has been substantial, fostered by the predominating environmental conditions in most cacao areas: altitudes lower than 500 m.a.s.l., precipitation regimes between 2,000 and 4,000 mm year^{-1}, and average temperatures higher than 24°C. Other factors favoring the dispersal and impact of FPR in the region are the apparent general susceptibility of the planted varieties, and the existence of wild hosts (Theobroma spp. and Herrania spp.). The low genetic diversity of M. roreri within this region is consistent with a rapid, recent spread of the fungus from a common founder population (Phillips-Mora, 2003; Aime & Phillips-Mora, unpublished). Apparently, there have been just one or very few introductions of M. roreri into Central America and most of the spread of the disease can be attributed to the rapid expansion of a single clonal isolate. A detailed description of the appearance, dispersal and impact of the disease is given by country as follows.

PANAMA

Cacao is mainly produced in Panama in Bocas del Toro Province, where around 6,000 hectares of plantings and 2,000 smallholders are involved in cacao cultivation. Orellana (1956) recorded FPR for the first time in this country in April 1956. The disease was found in Ailigandi, Comarca of San Blas in the eastern extreme of the Atlantic coast and in Paya, Province of Darién 15 km from the Colombian border. Wellman (1956) expanded this list by adding the following places as invaded by the fungus: Achutuppu and Puerto Obaldía in San Blas and Tuira in Darién. He also confirmed the diagnosis made by Orellana (1956) by analyzing specimens from the Province of Colón, on the Atlantic side of Panama. Consequently, by 1956 FPR had been described in this country in the Departments of Darién and Colón, and in the Comarca of San Blas.

Orellana (1956) suggested a recent introduction of M. roreri into Panama and, based on the analogies of the cacao Amelonado observed in both areas he also suggested that a possible spread of the disease into this country occurred from infected pods brought from the region of San Jerónimo-San Vicente area, Department of Antioquia, Colombia. AFLP and ISSR analyses carried out by Phillips-Mora (2003) support this hypothesis, since an isolate from San Jerónimo and all Central American isolates showed nearly identical molecular profiles, as do DNA sequence data from several hypervariable loci (Aime & Phillips-Mora, unpublished). Evans (2002) believes that dissemination into eastern Panama in the 1950s from Colombia may have been by airborne spores although he recognizes that man, as previously postulated by Orellana, probably introduced the pathogen accidentally. It is important to take into account that the mountain range of Darién constitutes a considerable barrier for fungal spores from Colombia into Panama.

A second introduction of the pathogen occurred apparently from Costa Rica into the western Province of Bocas del Toro in 1979 (Enríquez et al., 1982). The disease is now widely dispersed there, as well as in Colón, Darién and San Blas. FPR is also present in the Province of Chiriquí but is apparently restricted to the sector of Paso Canoas on both sides of the Costa Rican-Panamanian border. Pod losses due to FPR in Panama are as high as 80% especially in Bocas del Toro Province.

COSTA RICA

Cacao was traditionally an export crop in Costa Rica from colonial days until the end of the 1970's. The crop was mostly cultivated in the Province Limón (Atlantic Region), but also in the Northern, Southern and Central Pacific regions. Currently only scattered plantations (approximately 1,000 hectares) exists in these regions, mainly concentrated in places such as Talamanca and Upala.

FPR was reported for the first time in Cahuita, Baja Talamanca, Province Limón in 1978 (Enríquez & Suárez, 1978), although farmers in the area had noticed its presence in previous harvest seasons but had attributed the damage at that time to Phytophthora palmivora (Enríquez et al., 1979). According to Evans (1986), the arrival in Costa Rica may have been by airborne inoculum

from Panama. However, the huge distance that separates the cacao plantations in Costa Rica from the infected plantations in the Province of Colón in Panama over 300 km away make it more likely to have been introduced accidentally by contaminated pods.

The spread of the pathogen within Costa Rica was very rapid. Within two years, the fungus had moved from the Atlantic coast to the Pacific (approximately 130 km from east to westwards) and from the Panamanian to the Nicaraguan border (approximately 300 km south to north). The Central Pacific region remained free of the disease during this phase. The discontinuity and distance that separate the main cacao growing regions in Costa Rica and the presence of important geographical barriers to natural distribution, the most important being the mountainous system (Cordillera Central) that cross the country north to south, suggest that the intervention of human beings was decisive in spreading the fungus within Costa Rica. Conversely, Evans (1986) has suggested that this spread was due to the ability of the spores of M. roreri to be airborne transported, which could explain some of the dispersal events but not all.

Inspections made in 1979 to detect the geographic distribution of FPR on the Atlantic coast of Costa Rica showed that the disease was present in some 900 ha of cacao located in a triangle formed by the drainage of La Estrella River and the communities of Cahuita and Pandora (Enríquez et al., 1982). One year later, the disease had spread to the whole southern part of the Limón Province and to numerous scattered plantations along the highway, totaling some 7,150 ha of affected cacao. In June 1979, the disease was discovered attacking trees of different species (T. mammosum, T. grandiflora, T. angustifolia and Herrania purpurea) in La Lola farm in Matina (Enríquez, 1981).

FPR was recorded in Golfito on the Pacific coast in 1980 (Brenes, 1980a) and in Santa Clara and San José, Canton de Upala close to the Nicaraguan border in October 1980 (Brenes, 1980b). It seems plausible that the incidence of the disease in the region of Upala may have originated from cacao plantations in Nicaragua (where it was first reported in 1979) rather than from more distant plantations within Costa Rica, leading to the suggestion that the disease appeared first in Nicaragua and then was dispersed into the northern area of Costa Rica (Enríquez et al., 1982).

Damage to the cacao industry of Costa Rica has been substantial. Nine hundred hectares were initially affected in the Atlantic Zone in 1978, but by one year later, the disease had spread throughout the country, affecting eight times as many hectares (Enríquez et al., 1982). Between 1978 and 1983 cacao production in Costa Rica declined by 72% and dry cacao bean exports decreased by 96%. Many farms abandoned cacao or turned to other crops, especially bananas. Since then, Costa Rican cacao production has not recovered. The disease impact has been such that, present, this country is not able to fulfill its own domestic cocoa market, and so has moved from a cocoa exporter to a net cocoa importer in only a few years.

NICARAGUA

Although Nicaragua never became a major international supplier of cacao (Bergmann, 1957), the Nicaraguan Criollo cacao was highly appreciated during the colonial period due to its fine quality and large seed size. Now cacao is grown by smallholders in different localities of Nicaragua mostly located in the Department of Matagalpa in the Municipalities of Waslala, Río Blanco, La Dalia, Rancho Grande and Matiguás. Other important areas in order of importance are the Región Autónoma Atlántico Sur, the Región Autónoma Atlántico Norte and the areas of Río San Juan and Rivas/Granada. In the North Atlantic coast there are various ethnic groups such as Sumus and Misquitos for whom cacao is an important crop for local consumption.

FPR was first observed in Nicaragua in Los Guatuzos, Río San Juan Department in 1979 (López-Guadamuz, 2004), and its presence was confirmed in 1980 by López & Enríquez (1980), who indicated that the pathogen moved into this area from Costa Rica. Some areas in the department, such as La Esperanza and Palo de Arco, remained free of the disease in 1992. In March 1991 the pathogen was detected in the center of the country in the locality of La Patriota, Department Matagalpa, where most of the cacao plantations were concentrated (Ministerio de Agricultura y Ganadería de Nicaragua, 1992). By 1992, the pathogen had dispersed from this focus into other localities such as Rancho Grande and Waslala, although the Municipalities of Río Blanco and Nueva Guinea still remained free of FPR (Ministerio de Agricultura y Ganadería de Nicaragua, 1992). From La Patriota, the pathogen continued spreading in a northeasterly direction along the path of cacao cultivation (Porras & Enríquez, 1998). In March 1997, an expedition found the fungus in northern Nicaragua in the rivers Atapalito, Bocay and Wina, which are all tributaries of the Coco River (Porras & Díaz, 1997). In April 1997 M. roreri was identified along the Coco River itself (Porras & Enríquez, 1998). This river serves as border between Nicaragua and Honduras. An expedition in the same area between the communities of Raiti in the upper reaches of the Coco River and Waspam near the Caribbean coast of Nicaragua was carried out in March-April 1997. It was found that the disease was present in all cacao plantations inspected (Porras & Enríquez, 1998). Apparently, the fungus had spread to Waspam over a year earlier and, according to farmers, the spread had been hastened by the swelling of the rivers due to hurricane Cesar in September 1996 (Porras & Enríquez, 1998).

FPR is currently affecting most cacao plantations in the Departments of Matagalpa and Río San Juan and in the Región Autónoma Atlántico Norte. Dispersal of M. roreri in Nicaragua has been related to the fact that a high percentage of farmers use local seeds for new plantings, so that, the frequent movement of pods from one locality

to another is commonplace (Ministerio de Agricultura y Ganadería de Nicaragua, 1992). Also, the presence of wild trees of T. angustifolium and T. bicolor particularly in the Departments of Rio San Juan and Matagalpa, has possibly contributed to human-mediated dispersal by providing natural alternative hosts for the pathogen.

HONDURAS

Cacao production in Honduras is concentrated in three main yielding nuclei: Cuyamel (Cortés Department), Guaymás (Yoro Department) and La Masica (Atlántida Department). An incipient nucleus located in La Mosquitia (Gracias a Dios Department) nearly dissapeared due to the incidence of FPR and the effect of Hurricane Mitch in October 1998 (Jesús Sánchez, FHIA, personal communication).

Several expeditions carried out between 1993 and 1996 along the rivers Patuca and Coco (or Segovia) failed to find M. roreri in Honduras (Porras & Cruz, 1993; 1996). The fungus was first detected in the community of Wampusirpi, halfway up the Patuca River in the Honduran Mosquitia, Department Gracias a Dios innMarch 1997 (Porras & Enríquez, 1998). The pathogen was apparently restricted to this locality, since inspections carried out along the Patuca River, up and down stream from Wampusirpi, failed to detect it in communities such as Bilalmuk, Ahuas, Kurpa and Tukrun. However, the pathogen was also found in Rio Segovia (same department) and both margins of the River Patuca a few months later (Fundación Hondureña de Investigación Agrícola, 2001). Some local farmers believed that travelers spread the fungus into Wampusirpi from the Coco River in Nicaragua, as there is a direct route over the mountains that connect both sectors. Conversely, Porras & Enríquez (1998) concluded that M. roreri had reached Honduras as a result of hurricanes and floods, and less likely through exchanges of agricultural products or dried cacao.

Until 1999, M. roreri was restricted to a few localities in the Mosquitia including Wampusirpi and Wawina. Other places in this area such as Ahuas remained free of the disease. In March 2000, the fungus was detected in Guaymás, Yoró Department, some 310 km from this area, and five months later in Cuyamel, Cortés Department, near the Guatemalan border, nearly 80 km from Guaymás (Jesús Sánchez, FHIA, personal communication). The spread of the fungus from the Mosquitia to other areas was possibly fostered by the regular movement of dry cacao from there to other cacao areas in Honduras.

FPR has had a dramatic impact on the cacao industry in Honduras. Before the appearance of the disease there were 7,600 hectares in this country. As the direct effect of the arriving of FPR, 2,000 ha were abandoned and 2,600 turned to other crops such as maize or pastures within a few years. Cacao production progressively declined from 4,500 MT in 1997 to 1,200 MT in 2005 (a 73% reduction). For instance in Guaymás, 500 smallholders were seriously affected since the appearance of the disease in year 2000 due to the significant and progressive reduction of cacao yield that in some cases was as high as 93% of the pods (Anon, 2001). The fungus is currently present in all major cacao areas in Honduras, where it causes average pod losses estimated at 80% (Jesús Sánchez, FHIA, personal communication). Despite this situation, it is possible to find farms in Honduras where the disease incidence is lower than 20% permitting a profitable exploitation of the crop.

GUATEMALA

At the time of the conquest, the Pacific coastal plain of western Guatemala and adjacent Mexico (northern Chiapas) was one of the main source areas of cacao for the courts of Aztec emperors in the Valley of Mexico (Bergmann, 1957). The 2,713 hectares of cacao plantings currently existing in Guatemala are concentrated in two main regions: Department of Alta Verapaz (41% of the total area), and the Pacific coast from San Antonio Suchitepéquez to the Mexican border (50%), comprising the Departments of Suchitepéquez (24%), San Marcos (18%), Quetzaltenango (6%), Escuintla (1%), and Retalhuleu (1%) (Instituto Nacional de Estadística de Guatemala, 2003; Erich Eger, Control Integrado S.A., Guatemala, personal communication).

M. roreri was detected for the first time in one cacao plantation in the Department of Izabal (3% of the total area) near the border with Honduras in 2002 (J. Sánchez, FHIA, Honduras, personal communication). The fungus dispersed from Izabal into the neighboring Department of Alta Verapaz apparently in 2004. Average pod losses are currently estimated there at 80% (Erich Eger, Control Integrado S.A., personal communication). The disease has not been reported in other departments yet; however, systematic inspections have not been carried out in Guatemala, where the presence of the disease is not officially registered and available information on the dispersal and impact of FPR is very limited.

BELIZE

Cacao is a traditional crop in Belize currently grown in the District of Toledo (southern region), and to a much lesser extent in the District of Stann Creek (central region) by both Maya Mopán and Maya Kekchi Amerindians. Most cacaos are traded as organic under a fair trade agreement between Green & Black's Co. and the Toledo Cacao Grower's Association. By 2005, there were around 750 hectares of cacao plantations and 900 farmers in Belize involved in the activity, which is a significant increase of both since 2003.

In Belize, FPR was first detected in a small farm in the village of Maya Mopán, Stann Creek District in September 2004 (Phillips-Mora et al., 2006a). The presence of mummies (dehydrated/sporulated pods), the high disease incidence estimated to affect 60% of pods, and the extent of the disease within this plantation all suggested that FPR had been present there for at least six months. Following the initial discovery, the disease was detected in one additional farm in Maya Mopán in October 2004, and in three farms in the village of San Felipe (Toledo District)

in April 2005. Although the disease was initially concentrated in specific farms and was not widespread in the cacao-producing region, which offered great potential for it successful eradication, this scenario has changed as more farms have become infected in the villages of San Antonio, Crique Jute, and San Jose in 2006 (Jorge Cawich, CATIE, Personal communication)

Apparently, FPR was introduced into Belize from Guatemala or more likely from Honduras by infected pods. There is some evidence indicating that clandestine pods meant for use as planting material were introduced into Maya Mopán over the sea some months prior the appearance of FPR in this area. This could explain why the disease appeared in Maya Mopán and not in the Toledo District where cacao plantings are more abundant and closer to the infected plantations from Honduras and Guatemala.

MEXICO

In Mexico, cacao production involves approximately 37,000 farmers and 81,000 hectares located in two major producing zones: Tabasco State and Northern Chiapas State (85% of the total area), and The Soconusco, on the Pacific coast of Southern Chiapas (15%). Seventy-five percent of the cacao total area is in Tabasco. Additionally, there are some plantations in Guerrero and Oaxaca States representing 0.5% of the cultivated area. Ninety-two percent of the 44,000 MT produced in Mexico are consumed locally (Secretaría de Agricultura, Ganadería, Desarrollo Rural, Pesca y Alimentación de México, 2002).

FPR was first detected in several farms in the ranchería (village) of Ignacio Zaragoza, Pichucalco Municipality, Northern Chiapas in March 2005 (Ortiz-García, 2005, Phillips-Mora et al., 2006b). The high levels of incidence (>80%), extensive spread of the disease in the area, and the frequent presence of mummies, all indicate that FPR arrived there at least one year before detection. The presence of important geographical barriers and the wide separation between this area and the affected plantations in Guatemala, Honduras and Belize support the hypothesis that this event was human mediated. Since molecular profiles of the Mexican isolates resulted 100% similar to those from Panama, Costa Rica, Nicaragua, Honduras and Belize, it is probable that this spread occurred from a not identified source in Central America (Phillips-Mora et al., 2006b).

As soon as FPR was detected in Ignacio Zaragoza, local organizations estimated that the disease was affecting around 300 hectares in this area. However, one month later, a more detailed inspection determined that at least 1,000 ha in the municipalities of Pichucalco, Juárez, and Ostuacán in Chiapas, and Huimanguillo in Tabasco (near the border with Chiapas) were infected. Inspections carried out by the first author in southern Chiapas (Soconusco) in April 2005, did not detected FPR in this region, which at present remains free of the disease.

To contain the dispersal and impact of FPR in Tabasco, a security belt 5 km wide extending from the border with the State of Chiapas was established in 2005. This area has been permanently monitored by CESVETAB (Comité de Sanidad Vegetal de Tabasco) to early detect new affected plantations and to apply a set of cultural practices for controlling the disease and avoid further spread. In spite of this effort, FPR continued its invasive behavior in Tabasco affecting 1,033 new hectares from May 2005 to April 2006 (CESVETAB-SAGARPA, 2006). The infected plantations are concentrated within eight major infection foci (Table 1). Although five of these foci are located within the Security Belt (1, 2, 3, 4, 7), there are three foci outside it (5, 6, 8) indicating that the fungus has already surpassed this barrier invading the two most important cacao producing municipalities in Mexico: Comalcalco (16,800 ha) and Cárdenas (15,500 ha). By July 2006, the only municipalities remaining free of the disease in Tabasco were Paraiso, Nacajuca and Tacaotalpa.

Table 1: Infection foci of frosty pod rot in Tabasco: location, affected area and date of detection. Source: CESVETAB-SAGARPA (2006)

Foci	Location	*Area*(Ha)	Detection date
1	On the straight margin of the Mezcalapa River, Ranchería Paredón, 2ª Sección, Huimanguillo Municipality. From here the fungus dispersed into the communities of San Manuel and Paredón 3ª and 1ª Secciones.	160	March 2005
2	On the left margin of the Mezcalapa River, Ranchería Caobanal 2ª Sección, Huimanguillo Municipality. Later dispersed into the rancherías of Caobanal 1ª Sección and Ostitán	253	May 2005
3	On the left margin of the Mezcalapa River, Rancherías Plátano y Cacao 4ª sección and Plátano 2ª Sección, Centro Municipality, Cunduacán.	16.2	May 2005
4	Rancherías Concepción, Puente Grande, Vicente Guerrero and San Lorenzo, Municipality of Teapa.	13.5	September 2005
5	Ejido La Champa, Cupilco, Comalcalco Municipality. Located at 60 km from Ignacio Zaragoza.	55.5	November 2005
6	Poblado C-15 del Plan Chontalpa, Municipality of Cárdenas.	7	December 2005
7	La Villa Juan Aldama, Municipality of Teapa.	28	January 2006
8	Ranchería Arroyo Hondo, Municipality of Comalcalco.	30.5	September 2005

According to the previous information, FPR is currently affecting the most important cacao producing areas in México, which comprises plantations in northern Chiapas and in central/southern Tabasco. By July 2005, the affected area in this country was estimated at around 2,000 ha, showing a variable level of infection ranging from 100% pod loss where the disease was first detected (Ignacio Zaragoza) to less than 10% in localities where the pathogen recently appeared. So far, the fungus has not been detected in southern Chiapas or in the States of Guerrero and Oaxaca.

CONCLUSIONS

Within the past fifty years, M. roreri has spread from Panama to Mexico, the northern limit of cacao cultivation in continental America. The fungus has dispersed across seven countries and approximately 3,000 km and is able to thrive under a wide range of environmental conditions in this region. The impact of the disease in the region has been substantial, invariably becoming the main yield-limiting factor for cacao production in the affected countries with frequent reports of pod losses higher than 80% in certain areas. Evidence suggests that most disease dispersal in this region have been human mediated. Evidence also indicates that the lack of information/ experience of farmers and technical personnel on the recognition of symptoms has been one of the most important factors fostering the rapid spread of FPR in new areas. Thus far it has been impossible to completely eradicate FPR once it becomes established in a region. In order to avoid any new introductions of FPR into those areas and countries that are still free of the disease, we strongly recommend the strengthening of phytosanitary controls along with enhanced education of the population about identification of FPR symptoms and the risk of transporting pods or other cacao materials from infected into FPR-free areas.

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