Frosty Pod of Cacao: A Disease with a Limited Geographic Range but Unlimited Potential for Damage

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ABSTRACT

Moniliophthora roreri, the cause of frosty pod rot (FP), is a specialized fungal pathogen (family Marasmiaceae) that invades only actively growing pods of cacao, Theobroma cacao, and related species of Theobroma and Herrera. FP damages pods and the commercially important seeds that some of these species produce. M. roreri was confined to northwestern South America until the 1950s. Its appearance in Panama in 1956 signaled a change in its geographic distribution. Now, it is found in 11 countries in tropical America. The fungus is currently in an active dispersal phase, possibly due to an increase in human-mediated spread. FP is more destructive than black pod (Phytophthora spp.) and more dangerous and difficult to control than witches’ broom, caused by Moniliophthora (Crinipellis) perniciosa. The aggressiveness of M. roreri, its capacity to survive different environmental conditions, its rapid natural dispersal, its propensity for man-mediated dispersal, and the susceptibility of most commercial cacao genotypes, all indicate that FP presents a substantial threat to cacao cultivation worldwide.

Moniliophthora roreri is a neotropical plant parasitic fungus (family Marasmiaceae) that is still confined to tropical America (2). It causes frosty pod rot (FP, also known as moniliasis), an economically important disease of cacao (Theobroma cacao) that is a permanent threat to all cacao-producing countries. In this paper, we describe some basic biological aspects of this successful pathogen, the history of the expansion of the disease, and the extent of yield losses. We also examine the capacity of M. roreri to spread to other regions of the world and review the main prospects for disease management.

M. roreri: A highly specialized fungus that destroys cacao fruits. M. roreri is able to thrive under a wide range of environmental conditions, from sea level to over 1,000 m above sea level and from very dry to very humid zones (15). Phillips-Mora (29) collected samples of the fungus from 0 to 1,520 m above sea level from places where annual precipitation is in the range of 780 to 5,500 mm and mean annual temperature falls between 18.6 and 28°C. This high level of adaptation to different environments, and the huge numbers of long-lived spores that are generated by each infection have made M. roreri a very effective pathogen and a formidable invader of new geographic regions (Fig. 1) (17,29).

Spores are the only infective propagules of M. roreri, and the fruits of Theobroma and Herrera species are the only susceptible organs (Fig. 2) (15). T. cacao fruits are infected when they are young (0- to 3-months old), and become less susceptible as they mature. Fruit maturity occurs 5 to 6 months after pollination. External fruit symptoms may include small water-soaked lesions, deformation, premature ripening, and chocolate-colored spots.

Fruits that are infected in very early stages usually die. In advanced infections, the internal pod tissues appear to form a compact mass surrounded by a watery substance as a result of tissue maceration, which causes the total loss of the seeds. The chocolate-colored spots develop a layer of white mycelium within 4 to 5 days, which becomes darker as the spores mature. After ca. 3 months, these fruits become dry and mummified on the trees and remain attached to the trunk. These fruits become the major source of inoculum for waves of infection that then occur over a long period of time. Spores are produced in great abundance on diseased fruits (over 7 billion per fruit) (Fig. 1), and become widely distributed after they are released. Wind is the main mode by which spores disperse; however, wind dispersal fails to explain the spread of FP over significant distances and geographical barriers. This spread is easier to explain by human activities. The long period of fruit colonization prior to the manifestation of visible symptoms allows apparently healthy, systematically infected fruits to be selected and transported for use as a source of planting material (16).

Historical spread of FP on cacao. The spread of M. roreri has been relatively well documented since the beginning of the 20th century, when the fungus caused an outbreak in Ecuador, the world’s major cacao producer at the time (36,37). This outbreak was widely considered to be the first record of FP in cacao and, therefore, Ecuador was regarded as the probable place of origin for the disease. Conversely, Phillips-Mora (29) indicated that FP may have first appeared in Colombia, specifically in the northeastern Department of Norte de Santander in 1817 (3,4,5), and then in the central Department of Antioquia in 1851 (1,10,28). Molecular evidence, including amplified fragment length polymorphism (AFLP), ISSR profiles, and ITS sequence data, indicate that the greatest genetic diversity in M. roreri is found in the Northeastern-Central region of Colombia (29,33). These studies also provide evidence that Colombia, rather than Ecuador, may be the center of origin of FP.

Currently, FP is present in all major cacao-producing areas of Colombia and Ecuador. In Venezuela, it was first reported in the...
area of the Catatumbo river, State of Zulia in 1941 (25), where it remained for an indeterminate time (14). At present, the fungus is restricted to the Western region of Venezuela, which is geographically separated from the main cacao-producing areas located in the Eastern and Barlovento regions. McLaughlin (24) recorded FP in the Peruvian Departments of Cajamarca, Huánuco and Cuzco in 1950. However, this report remained controversial until Hernández (19) reported the appearance of the fungus in the Department of Amazonas in 1988. This later report is regarded by Evans (18) as the first validated record of the disease in Peru. Within Peru, *M. roreri* has spread to approximately 1,100 km over the past 10 years, from the northern Amazonas Department to Cuzco Department in the south. By 1999, nearly all cacao plantings in Peru were affected.

The appearance of frosty pod rot in Panama in 1956 (27) marked a significant expansion of the range of the fungus, and it has since spread throughout the Mesoamerica. In fact, during the last 50 yrs, *M. roreri* spread to over 2,500 km to seven countries; including the main cacao-producing areas in this region: Costa Rica in 1978 (12), Nicaragua in 1980 (22), Honduras in 1997 (34), Guatemala in 2002 (J. Sánchez, FHIA, Honduras, personal communication), Belize in 2004 (31), and Mexico in 2005 (32). With the last report, *M. roreri* has reached the northern limit of cacao cultivation in continental America.

**Yield losses caused by FP.** The devastating effects of FP on cacao have been dramatic and are well documented across different countries, including Colombia in 1817 (4), Ecuador in 1918 (36), Costa Rica in 1978 (13), and Mexico in 2005 (32). Current losses are highly variable, ranging from 10 to 100% (6,20), and depend on factors such as length of time disease is present in a site; age of plantation; crop and disease management; presence of neighboring affected plantations; and weather conditions. Most reports mention average pod losses over 30%, but losses can exceed 90% under favorable conditions. Severe disease outbreaks have led to the total abandonment of cacao cultivation in extensive areas as has occurred in most affected countries. For example, in Perú 16,500 ha of cacao (over 50% of the cultivated area) (21), and in Costa Rica around 7,000 ha (13) were abandoned, mostly as a result of FP. In some areas of Colombia, such as San Vicente del Caguán (Department of Caquetá), and in different municipalities of the Department of Chocó, the disease has caused pod losses of over 80%, leading to the abandonment of many plantations (9,23).

In a global context, the current annual loss from FP is small, but the potential danger presented by the disease is enormous. *M. roreri* ranks with any of the other major cacao pod pathogens in terms of its economic impact during an epidemic (16). FP has been reported to be twice as destructive as black pod (*Phytophthora* spp.) (11), and more dangerous (26) and difficult to control (7) than witches’ broom (*M. perniciosa*). In Colombia, where FP and witches’ broom are widely distributed, Aranzazu (7) noted that FP continues to be the most limiting disease for cacao production. When the disease appeared in Peru in 1987, it rapidly became the most important disease problem, displacing witches’ broom disease (18). The impact of FP from Panama to Mexico has been substantial, and it has invariably become the main yield-limiting factor for cacao production in the affected countries, with frequent reports of pod losses higher than 80%.

**Potential for spread to other regions of the world.** Considered collectively, the apparent susceptibility of most commercial cacao genotypes, the aggressiveness of this airborne fungus, its outstanding capacity to survive different environmental conditions, and its rapid natural and man-mediated dispersal all result in FP presenting a substantial threat for cacao cultivation worldwide. It can be reasonably anticipated that FP will continue to spread unless dramatic steps are taken to arrest its progress. If there are no extensive geographic barriers to inhibit spore dispersal, there is little that can be done to prevent the entry of this pathogen into new territories (16). Thus, few geographical barriers

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**Fig. 1.** A cacao pod thoroughly colonized by *Moniliophthora roreri*, cause of frosty pod. The explosiveness of frosty pod epidemics is due, in large part, to the high numbers of resilient, easily dispersed spores that the pathogen produces on fruit.

**Fig. 2.** Frosty pod on relatives of cacao: clockwise and from the lower left, *Theobroma mammosum*, *T. gileri*, *T. bicolor*, *Herrania* sp., and *T. grandiflorum*. 
exist to prevent its dispersal from the affected plantations in Peru into Brazil. The natural dispersal of *M. roreri* in the Brazilian Amazon may be slowed because wild and planted cacao has a scattered distribution along the headquarters of the Amazon (16). However, spread of the disease could certainly be fostered by the increase of human activities in this area.

**Propects for control.** Avoidance is the best strategy to be followed in countries or areas that are still free of the disease. Because human-mediated dispersal of this fungus into new areas and countries represents the most serious threat, major efforts should be made to strengthen quarantine measures and educate producers about the risks of moving pods from affected areas.

Various cultural, chemical, and biological strategies have been tested for the control of FP. Whereas some of these measures have been very effective on an experimental scale (8,21,35), only those based on cultural practices (periodical removal of diseased pods, pruning of the cacao and shade trees, maintenance of the drainage system, etc.) are being adopted by smallholders who grow cacao. These farmers are now stimulated by current high cacao prices and in certain cases, by the technical or economical support received from local or foreign organizations. However, it is important to note that cultural management of FP is difficult and labor intensive. In fact, the frequency and cost of these practices (in particular, the weekly removal of diseased pods), have played a major role in discouraging their use, especially when cacao prices are low.

Distribution of improved resistant genotypes as part of an integrated approach to manage the disease represents an environmentally friendly long-term strategy for smallholder farmers (30). Resistant genotypes could provide a more durable and less costly means of control that could be used to complement other controls; however, with a tree crop such as cacao this is a very long-term approach. A regional breeding program at Tropical Agricultural Research and Higher Education Center (CATIE), Costa Rica has focused on the identification of resistant material during the last 10 years. The program has made significant progress toward developing cacao material with a suitable combination of desirable properties, in particular resistance to FP and high yields. The first selected clones will be released for farmers use in 2007. Besides that, multi-location trials will be established in Central America in 2008 to test the performance of 20 new promising CATIE’s selections under different environmental conditions.

Success in the development and dissemination of effective strategies for disease control depends on sound knowledge of specific aspects of fungal biology, such as the level and distribution of genetic diversity. In this sense, genetic distance analysis specific aspects of fungal biology, such as the level and distribution of genetic diversity. In this sense, genetic distance analysis

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