

## Cacao Diseases: Important Threats to Chocolate Production Worldwide

## Cacao Diseases—The Trilogy Revisited

Harry C. Evans

CAB International, UK Centre, Silwood Park, Ascot, Berkshire, SL5 7TA, UK.

## ABSTRACT

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This paper reviews the significant advances by the diseases themselves, as well as by the scientists, in the intervening period since the disease trilogy was first delimited in 1989. The impact of these diseases, black pod, witches' broom, and frosty pod rot, has increased dramatically. In addition, there have been radical changes in the taxonomic profiles of these pathogens, which have been based on both traditional (morphological, cytological) and modern (molecular) approaches. Black pod is caused by a complex of *Phytophthora* species, in which *P. palmivora* still is the most important worldwide. However, recent invasion of the principal cacao-

growing countries of West Africa by the more virulent *P. megakarya* has been cause for concern. The latter evolved in the ancient forests straddling the Cameroon-Nigerian border as a primary coloniser of fallen fruit. Conversely, frosty pod rot, caused by *Moniliophthora roreri*, and witches' broom, caused by *M. (Crinipellis) perniciosa*, both neotropical diseases, are hemibiotrophic, coevolved pathogens. Respectively, *M. roreri* arose on *Theobroma gileri* in submontane forests on the north-western slopes of the Andes, whereas *M. perniciosa* developed as a complex of pathotypes with a considerably wider geographic and host range within South America; the cacao pathotype evolved on that host in the Amazon basin. The inter-relationships of these vicariant species and their recent spread are discussed, together with control strategies.

*Theobroma cacao* is a relatively common understory tree in the forests of the Upper Amazon basin (15). However, there is a clear geographic distinction between the center of origin or diversity of cacao and the area of its earliest domestication in Mesoamerica, where it may have been cultivated for millennia (53). In Mesoamerica, and free of its coevolved natural enemies, cacao thrived and formed the basis of the modern-day chocolate industry. Cacao is a highly prized commodity, and chocolate is probably the most easily accessible or affordable of all man's luxuries. Moreover, when grown in traditional form under thinned, forest shade, cacao affords sustainable benefits not only to the farmer but also to the environment (22). However, this sustainability is under increasing threat as both coevolved and new-encounter diseases, which now constitute the most serious constraint to cacao production (32), expand their geographic ranges.

Unlike many exotic crops and, indeed, neophytes in general, cacao has proved to be highly susceptible to major new-encounter diseases as well as pests. This is, in part, because related hosts occur in the tropical forests wherever cacao has been introduced, and their natural enemies adapted rapidly to this new host. This phenomenon has been established for *Cacao swollen shoot virus* and vascular-streak die-back, amongst others (50,55). Fulton (30) identified a "trilogy of crippling fungal diseases"—black pod, *Monilia* pod rot, and witches' broom—affecting cacao production in the Neotropics. He concluded with the statement that: "The future is exciting, and the means are at hand to manage the cacao disease trilogy". Certainly, the first part was prophetic, but probably not in the sense he intended. The latter part cannot be further from reality as the diseases threaten to get completely out of hand. The application of molecular tools has allowed for advances in our understanding of the phylogeny of the causal agents, particularly the finding that the two South American diseases are

caused by sister species within the Agaricales, and that both should be placed in the genus *Moniliophthora* (3,4). Other dramatic discoveries have been the common Protistan origins of the Fungal and Animal Kingdoms and the subsequent movement of *Phytophthora* (Oomycota) into a new kingdom, the *Stramenopila*, together with the algae (54). Obviously, this is having repercussions on what technically constitutes a fungus (44).

No less dramatic have been the advances of the diseases themselves, as witches' broom and frosty pod rot have swept into new areas in Latin America, and the more aggressive form of black pod has spread rapidly northwards in West Africa. Indeed, journalists have had a field day as predictions of doom and gloom resurface every time another cacao-producing country is invaded or threatened: "Meltdown in Chocolate Town" and "Chocololics under Threat", being some of the less sensational headlines.

Only an overview of the development post-Fulton (30) is presented here, together with personal thoughts on areas of research that may lead to their better management. More in-depth analyses are provided in the specialist papers that follow (3,35,49). The diseases are arranged in order of their global impacts, or, in socio-economic terms, according to the losses they cause; although this is not necessarily a reflection of their potential importance.

## THE DISEASE TRILOGY

**Black pod.** World losses due to black pod have been estimated recently as 450,000 metric tons (12), probably accounting for 20 to 25% of the expected crop, and making it the biggest constraint to production. However, originally thought to be caused by a single species, *Phytophthora palmivora*, the situation has changed considerably over the past few decades, and it is now known that each continent has a complex of species which can induce black pod symptoms in cacao. Thus, the main pathogen in Cameroon and Nigeria is *P. megakarya* (13), which until the late 1970s was thought to be a variant form of *P. palmivora*. The equivalent of Brazil is *P. capsici*, although recent research suggests that even this interpretation is simplistic with the discovery of the new spe-

Corresponding author: H. C. Evans; E-mail address: h.evans@cabi.org

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cies, *P. tropicalis* (5)—a situation predicted earlier: “It is very likely that the story will continue to become even more complex as further studies are made and more Phytophthoras move in to sample this new and attractive host plant” (23).

Black pod has been marginalized, and reduced to the status of a minor disease, in the main cacao-growing region of Brazil following the arrival of witches’ broom disease because of the latter’s much greater impact on crop yields, as well as on tree vigour (22). However, black pod caused by *P. megakarya*, continues to be the major actual and potential threat to cacao in West Africa (46). The greater virulence of *P. megakarya* compared to *P. palmivora* lies in its much denser sporulation on the pod surface, which significantly increases inoculum loads (12,23).

Results of a molecular study indicated that the areas of greatest genetic diversity of *P. megakarya* correspond to Ice Age forest refugia, created during the Quaternary period when glacial cycles caused much of Africa to become arid (45). Holmes et al. (38) investigated the ancient forests of Western Cameroon, which are also centers of diversity of the genus *Cola* (14), a close relative of *Theobroma*. Contrary to expectations, there was no evidence of black pod disease on the cauliflorous fruit of the *Cola* spp. examined. However, lesions on newly-fallen pods of the elephant mango tree (*Irvingia* sp.) produced typical *Phytophthora* sporangia. Internal transcribed spacer (ITS) fingerprinting of this isolate matched that of the *P. megakarya* isolates from cacao in Central Cameroon (38). It had been proposed that *P. palmivora* was originally a soil inhabitant of forest ecosystems “competing for fallen fruit” (17,18), and this now appears to have been born out by this discovery. According to classical biocontrol concepts (25), it is possible that specialized natural enemies of *P. megakarya* will be found in these forest ecosystems, and, indeed, a mycovirus may have infected several isolates from elephant mango that established poorly in culture and eventually died (38).

Another control strategy that has yet to be fully tested is manipulation of potential arthropod vectors, notably tent-building ants (16,17,18), which have been associated with disease foci in the cacao canopy (33). Removal of black pods from the soil surface would be a simple strategy to reduce inoculum spread by ants, as well as by flying vectors (18).

**Witches’ broom.** Holliday (37) reviewed some tropical plant pathogenic fungi of limited distribution—those not coextensive with their crop hosts and which, therefore, pose a continual threat. He included the causal agent of witches’ broom disease of cacao, describing it as: “unique, since it is due to the only serious, obligate species in the Agaricaceae”. This was before the agaricaceous origin of frosty pod rot was posited (27), and its close relationship to witches’ broom was confirmed (26), leading to the placement of both pathogens in the genus *Moniliophthora* (4). Holliday (37) went on to describe the devastating impacts of the disease on cacao production in those countries that it had invaded, but added that: “If discovered early enough, I consider witches’ broom of cacao to be a disease which could be eradicated without too much difficulty”. This statement was made at a time when annual losses were probably less than 50,000 tons, as no major cacao-producing areas were affected. However, losses have now been put at 250,000 metric tons per year (12), most of this in the Bahian region of Brazil, which saw annual production fall from over 400,000 tons to around 150,000 tons, a decade after the arrival of the pathogen (48). Clearly, despite all the forewarnings and action plans (22), eradication failed (47).

As highlighted by Evans and Barreto (24), although the pathogen has been the focus of much research over the past century, there is still much to be discovered about its basic ecology and biology. This followed the discovery of the disease on an indigenous solanaceous host, not, as previously, in the Amazon basin (8), but in the Brazilian State of Minas Gerais, far removed from its purported center of origin. Other solanaceous host species, as well as new host genera and families (Bignoniaceae, Malpighiaceae),

have been added to the list ever since (6,9–11,39). Recent surveys in Brazil have extended both the host and geographic ranges of *M. pernicioso* even further (R.W. Barreto and H. C. Evans, unpublished data).

In effect, this ongoing research is demonstrating that there is a continuum of plant families, genera and species as hosts of *M. pernicioso* in Brazil, from Rondonia, Amazonas, and Pará States in the north to Minas Gerais in the southeast. Undoubtedly, there are degrees of specificity between these populations but this still requires critical testing. What appears to be certain is that more hosts remain to be found. Why do new hosts continue to be discovered, especially in view of the spectacular symptoms? In part, of course, these are noneconomic hosts and not generally investigated by plant pathologists. Only further collections and subsequent molecular comparison of the isolates will provide the answers as to the origins of the pathogen. For example, which is the oldest lineage and did the various pathotypes evolve and radiate out from a common progenitor? Whatever the final results may be, it is obvious that this remarkable fungus has an enormous natural host and geographic range within South America.

**Frosty pod rot.** Holliday (36) was one of the first to appreciate the international threat posed by frosty pod rot to cacao production. He later included it along with witches’ broom in his description of tropical plant diseases of limited distribution but potential importance, commenting that “were it not for some familiarity with it [*Moniliophthora roreri*] in the field I might find insufficient justification for labelling it a major pathogen” (37). Thurston (56) expanded upon this theme of threatening plant diseases and, once again, frosty pod rot made the list. Both these authors stressed the paucity of information on the pathogen, particularly its biology, and, erroneously (21), they also included Peru in its limited geographic range (37,56). The eventual arrival of the disease in Peru was confirmed in 1989 (29), followed by Honduras and Guatemala (22); with the rider that, surely it must be only a matter of time before it invades plantations in southeast Mexico. Unfortunately, this has been sooner rather than later, with the final Mesoamerican cacao outpost (Belize) also being invaded (4).

Moniliasis, the previous common name of this highly destructive disease, and which is still widely used in the cacao literature, has caused considerable confusion amongst even the most illustrious of plant pathologists not familiar with the pathogen and who naturally assume that it is caused by an Ascomycete. This is despite the proposal made more than two decades ago that frosty pod should be used as the common English name (21) and the raft of publications since which confirms the placement of *M. roreri* in the Basidiomycota (3,4,26,27,28,34). Agrios (1) in the fourth edition of his plant pathology treatise, placed “*Monilia roreri*” amongst the *Monilinia* brown rots of stone fruits (Sclerotiniaceae; Ascomycota). In the latest 2005 edition (2), it is still included in the Ascomycota, close to the brown rot pathogens, with the following description, “*Moniliophthora* pod rot... caused by the fungus *Moniliophthora roreri*, anamorph *Monilia roreri*...” To add chaos to confusion, the chosen illustration with the legend—“clump of cacao pods infected severely with the pod rot disease”—shows, in fact, papaya fruits with a whitish spore bloom of what is probably *P. palmivora*.

The disease is still mainly limited to Spanish-speaking countries, where the farmers know it from either the characteristic external symptoms (helada, hielo, mal paludico, pasmo), or the internal watery symptoms (podredumbre acuosa). Arguments have been put forward to retain the *Monilia* epithet for the disease, or even worse, Moniliasis = Candidiasis, a disease of humans caused by *Candida* spp. (41). However, these names are used mainly in scientific and extension publications, a world far removed from the peasant farmers who employ descriptive rather than technical terms for diseases.

No less controversial has been the status of the pathogen within the Basidiomycota. Molecular evidence has shown that *M. roreri*

sits alongside species with pink to red basidiocarps, such as the witches' broom pathogen, in the section *Iopodinae* of the genus *Crinipellis* (34). However, a more complete molecular characterization has revealed that these two cacao pathogens form a distinct lineage or monophyletic clade within the Marasmiaceae (3,4,49), leading to the proposal to transfer *C. pernicioso* to the previously monotypic genus *Moniliophthora* (4). The phylogenetic implications are discussed further (3).

The proposed life cycle of *M. roreri* makes it unique within the Agaricales (26,28), although there may be analogies in the rust fungi with uredinioid or aeciooid teliospores. The supposed conidia have been shown, using cytological evidence, to function as meiospores. It is suggested that these spores represent a much-modified basidium, with the thick, fleshy pseudostroma on which they are produced being the vestigial pileus. The spores are multifunctional, serving not only for genetic exchange, but also for dispersal and infection, as well as for survival. Older spores develop thick walls and become darker, which may mark the onset of a dormancy phase (21).

What were the evolutionary pressures that led to this fundamental change in morphology? *M. roreri* has been found on the supposed original host, *T. gileri*, in its holotype locality in north-west Ecuador (25). It was considered that this rare wild host was the source of the disease outbreak in coastal Ecuador in the early 1900s (22). However, the subsequent morphological and pathogenicity studies show that not only was this isolate distinct from the cacao strains at the varietal level, but it was also nonpathogenic to cacao (26). It is hypothesized that the uplift of the Andes, which created the Chocó refuge of western Colombia and north-west Ecuador (31), separated not only *Theobroma* species, but also populations of *M. pernicioso*. The limited number of host species on the western side of the Andean Cordillera (15), probably scattered through the coastal and submontane forests, placed dispersal and survival pressures on the pathogen. This was not only to increase spore production, but also to develop a more resistant form than the short-lived, short-range basidiospores. Indeed, these are the very reasons why frosty pod rot has so quickly displaced both black pod and witches' broom in importance in those countries that have been invaded (22). It is further postulated that the cacao form of *M. roreri* is of recent origin and that this evolved in north-west Colombia: a region where domesticated cacao has probably intermingled with related indigenous species over the past few thousand years (7). Indeed, there is reason to believe that the local *Theobroma* species in north-west Colombia, originally considered to be *T. gileri*, is a morphologically distinct taxon (B. D. G. Bartley, *personal communication*).

Therefore, there is the possibility that there may be two separate *Theobroma* species as wild hosts of *M. roreri* at the extremes of its natural range. What is beyond doubt is that the populations of the Ecuadorian *T. gileri* in humid, submontane forests have been isolated from cacao and, hence, *M. roreri* var. *gileri* retains a narrow host range, as well as the more primitive, basidium-like, thinner-walled spores. Nevertheless, given the vast amount of meiospores produced, adaptation to related host species and to drier habits would be rapid. Thus, the cacao isolate has extremely wide ecological as well as host ranges, within *Theobroma* and the related genus *Herrania* (21).

## DISCUSSION

The potential importance of these three diseases on cacao production is inversely related to their actual world ranking. Thus, black pod in Bahia was relegated to a minor problem shortly after the arrival of witches' broom disease (22). Conversely, the invasive frosty pod rot quickly overtook witches' broom as the principal constraint to production in Peru (29). There is no doubt, that frosty pod rot represents one of the greatest global threats to cacao cultivation, perhaps reflecting the analogous situation of rub-

ber and its coevolved pathogen, *Microcyclus ulei* (22). The major region of production of these vital crops is in the Palaetropics which remain free of their most serious South American diseases. Without question, therefore, quarantine is the key to helping maintain the status quo; ideally movement of germplasm would be restricted as budwood through a tightly-controlled, third-country quarantine facility (22,23). Nevertheless, there is always the threat from bioterrorism which, until the recent revelations of the deliberate introduction of witches' broom disease into Bahia for political motives (40), seemed more like bad fiction rather than reality.

In theory, the trilogy should be amenable to control through good crop sanitation, and sweeping statements have been made to this effect: "To an experienced epidemiologist, the field management of Monilia pod rot would appear to be a piece of cake" (30). Schematic models have been presented for each disease to highlight weaknesses in the life cycle, particularly where low-cost, cultural control can be employed most effectively (18,20,21). A model of the field dynamics of *M. roreri* was developed later, which also stresses the need for frequent harvesting to reduce inoculum levels (42). However, with added "real world" variables, the control equation becomes much more complex and, ultimately, is dependent on the socio-economic status of the farmer.

Efforts to manage the disease, therefore, must be in improving the quality of the planting material supplied. Breeding programs have been, and are still trying to address this issue, but given the potential for genetic variability of the pathogens, especially *M. pernicioso* and *M. roreri*, such strategies are fraught with danger. Can other factors be built into these systems to strengthen long-term or sustainable resistance? Now that the close relationship of the South American pathogens has been established, the prospects of such a solution have improved considerably because of the likelihood of common pathogenicity pathways. The possible mechanisms whereby the parasitic phase of *M. pernicioso* is controlled have been discussed elsewhere (19) and a recent study has now identified glycerol as a key component in the process, and how, in its absence, the infective stage can be switched off (43). This would seem to offer a potential method of manipulation of the pathogen in cacao tissues; at least, we are moving towards identifying the signaling mechanisms involved in pathogenicity which, ultimately, should benefit breeding programs.

A further strategy, that of biological control, is giving promising results, especially with species of *Trichoderma*, at both the experimental level (39,52), as well as in practice (51). However, it is the considered opinion here that, in order to maximize the chances of success, a more long-term, user-friendly approach should be adopted, specifically, targeting coevolved endophytic fungi, and a wide range of species has been found to be associated with wild *Theobroma* hosts (25,52). These highly specialized fungi live asymptotically within the tissues of the host plant and may increase host defenses through various mechanisms: direct antagonism, competitive displacement, and induced resistance. The future may lie, therefore, in harnessing this potential so that genetically-improved cacao material is distributed routinely to the farmer complete with selected, beneficial endophytes and thus offer a wider spectrum of resistance to the disease trilogy.

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