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Diversity of Cacao Pathogens and Impact on Yield and Global Production

Dele Adeniyi

Abstract

Cacao, *Theobroma cacao* L., an important cash crop in foreign exchange earnings and also a major income source for many smallholder farmers in growing ecologies of West Africa. Global cocoa production has been rising fairly steadily over the years by increasing production in growing countries with most of the production taking place in areas of high pathogen biodiversity. Thus, the sustainability of the cocoa economy is under threat as diseases of various statuses now constitute the most serious constraint to production. Most important among these is the black pod disease caused by *Phytophthora* genus with annual losses of 30–90% of the crop. This economically important pathogen is very diverse in nature and varied across growing countries including species such as *palmivora*, *megakarya*, *capsici* and *citrophthora* distinguished based on chromosome number, sporangial characteristics and pedicel length. World losses of 20–25% in cacao production are due to black pod disease, an estimate of 700,000 metric tons on global scale reducing global cocoa production. High cacao loss to diseases is a prime factor limiting production; consequently, significant effort is required to deal with problems associated with disease control to ensure a sustainable cacao. The effective and sustainable management of black pod disease requires integrated approach encompassing different control measures.

Keywords: *Phytophthora*, pathogen, diversity, yield, production, management

1. Introduction

Cacao, *Theobroma cacao*, is a major cash crop in the tropics and the source of chocolate, one of the world's most popular foods. In addition, cacao-based agroforestry systems provide a promising means to address the challenges of deforestation and create a habitat for biodiversity while simultaneously providing a profitable crop for agricultural communities [1]. Cocoa is mainly grown by smallholder farmers in West Africa and around the world where favourable tropical environments occur. The farmers plant their cocoa traditionally at random under thinned forest and/or plantain as shade crop. Moreover, when grown in traditional form under thinned, forest shade, cacao affords sustainable benefits not only to the farmer but also to the environment [2]. This low-input cultivation system uses the forest soil fertility and the existing shade.

2. Cocoa production status

The West Africa region has some 6 million hectares of cocoa and provides around 70% of the total world production. In recent time, Côte d’Ivoire, Ghana, Nigeria and Cameroon have been rated as top cocoa-producing countries and the production from around 2,000,000 metric tons to around 3,000,000 metric tons in 10 years plus [3]. The world cocoa production is around 4.3 million tons, and almost 71% of it produced in a relatively small region of West Africa which comprised of Cote d’Ivoire, Ghana, Nigeria and Cameroon with 56, 29, 8 and 7% productions, respectively [3].

However, the average yields remain low, and this could be attributed to many factors ranging from pests and diseases to old and moribund farms and extensive cultivation methods, among others. Steady growths in cocoa production have been reported in Nigeria; production increase from 165,000 metric tons in 1999–2000 to 250,000 metric tons in 2013–2014 has been linked to high grower prices and government support to a limited extent through the 2011 Cocoa Transformation Action Plan [4]. The total harvested area in Nigeria was reported as 640,000 hectares with the average yield of about 400 kg per hectare.

The Cocoa Transformation Action Plan of the Federal Government of Nigeria envisaged improving cocoa situation and rising production to 500,000 metric tons by 2015; however, the yield improvement constrains were required to be better managed. The crop is seriously affected by the impact of diseases and the low-yielding potential of most plantations due to genetic and management reasons [5]. The sustainability in cocoa is currently under an increasing threat as both coevolved and new-encounter diseases of various statuses now constitute the most serious constraint to cacao production [6, 7] (Figure 1).

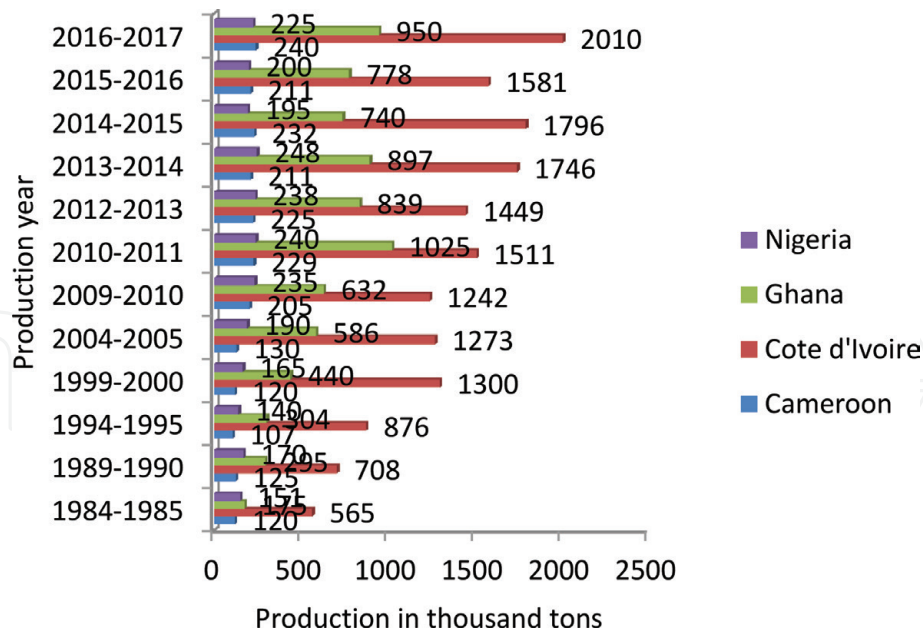


Figure 1. Shows the status of cocoa production in growing countries of West Africa. (Sources: [8–10]).

3. Pathogen and disease distribution

The cacao trees in the absence of disease infestation and good farm management provide improved productivity to the maximum of the potential of the crop, under ideal field condition (Figure 2).



Figure 2.
 Healthy cocoa trees at varied stages (A, B and C) of maturity.

However, many factors including poor farm management can introduce diseases or reawaken the inoculum from their resting stage for infection. *Phytophthora* pod rot, commonly called “black pod”, is the most economically important disease of cocoa. Four species of *Phytophthora* are mainly responsible for this disease, *P. palmivora*, *P. megakarya*, *P. capsici* and *P. citrophthora*, while four additional species of *Phytophthora* have also been isolated from cacao, *P. katsurae*, *P. arecae*, *P. nicotianae* and *P. megasperma* [11], but no economic impact of these has been reported. *Phytophthora palmivora* is the most common, being present in most of the cacao-growing countries around the world, causing yield losses of 20–30% and tree deaths of 10% annually. *Phytophthora megakarya* occurs only in West and Central Africa countries but considered to be the most virulent among other species on cacao. *Phytophthora capsici* is widespread in Central and South America and prevalent in Brazil.

The estimate of genetic diversity and structure of *Phytophthora* isolates from Ghana, Togo, Nigeria, Cameroon, Gabon and Sao Tome using the isozyme and RAPD markers [12] separated the isolates into two different genetic groups, with one located in Central Africa and the other in West Africa. The two centres of major diversity are located in Cameroon and on the Cameroon/Nigeria border region. This distribution however coincides with two major biogeographical domains reflecting an ancient evolution of *P. megakarya*. A lower genotypic diversity was also found in isolates from Ghana, Togo and Nigeria when compared with isolates from Gabon and Sao Tome. Again, four intermediate marker patterns were observed which correspond to isolates near the border between Nigeria and Cameroon and assumed it is a genetic exchange between the Central and West African groups. Black pod disease incidence in the field is influenced by environmental conditions. Numerous studies have established the role of climatic factors on incidence of black pod disease, caused by *Phytophthora* spp. [13, 14]. Rainfall, high relative humidity and low temperature are known to create favourable humid conditions for the development of the disease. [13] showed that in Ghana, black pod disease developed when the relative humidity, particularly within the day, remained above 80% under the cocoa canopy and that the rate of disease development was influenced by the frequency and amount of rainfall. [14] also reported a significant positive correlation between rainfall when assessed after 1-week lag, and *P. megakarya* pod rot incidence in Cameroon, and emphasised the role of rainfall in the disease epidemics [14]. Further, the time and/or period for black pod peak infection in Ghana varied annually and also with location depending on the rainfall [15].

In Ghana, it is known that primary infections usually occur around June, but the peak of *P. megakarya* black pod disease generally occurs between August and October [16, 17]. Such information on periods for attaining disease infection peaks is useful in forecasting the pattern of disease development, and it is an important tool for disease management since conditions immediately preceding the infection peaks must be favourable for disease development. The black pod disease situation in Nigeria is similar to that of Ghana and depends on growing ecologies, pattern of rainfall, high humidity and farmers' management practices. The disease inoculum can remain in the soil for a long time, the spores are brought back to viability at onset of rain and other conditions are suitable. Thus, rain splashes, infected tools and equipment and poor farm management, among others, contribute to the spread of the pathogen in the field.

3.1 Expression of black pod and *Phytophthora* on cacao

Phytophthora pathogens are ubiquitous and so cause economic loss to a greater or lesser extent in all cocoa-producing countries but most especially in those with prolonged periods of high relative humidity at, or near to, saturation levels. It infects every part of cacao plants at different developmental stages [18] and under wet and humid atmospheric conditions. *Phytophthora palmivora* is present in most of the cacao-growing countries around the globe and has a broad host range [19]. *Phytophthora megakarya* occurs only in the countries of West and Central Africa and is considered a significant pathogen only on cacao. Black pod was originally thought to be caused by a single species, *P. palmivora*, but increased knowledge have shown otherwise over the past few decades and that each continent has a complex of species of *Phytophthora* which can induce black pod symptoms in cacao. Thus, the main pathogen especially in Nigeria is *P. megakarya*, which was thought to be a variant form of *P. palmivora* but was first identified taxonomically as a species [20].

Under nursery operation, seedling infection leads to blight and root rot, while infections of stem, chupons and branches cause cankers [21, 22]. Infection of the pod leads to black pod which can occur at any stages of pod development, and all parts of the pod are also susceptible to infection [22]. However, immature pods of 10 and 20 weeks have the highest disease incidence when the dynamics of pod production and black pod disease were evaluated in relation to environmental factor impact, chemical fungicide and biological control [14]. Infected immature pods are rendered useless, while infection of ripe pods reduces the bean quality [4].

The black pod caused by all *Phytophthora* species is developed by an initial symptom showing appearance of a small translucent spot on cocoa pods [22], appearing around 2–3 days after infection, then turns brown, eventually darkens and the spot covers the entire pod between 7 and 14 days under humid conditions. Whitish spores are produced 3–5 days after the appearance of the first symptom. These species attack pods of all sizes and are harboured in the roots of cocoa during the dry season making it very hard to control [23].

Black pod symptoms due to *P. megakarya* are, however, characterised by multiple lesions which spread fast and coalesce (**Figure 3**) showing abundant bloom of white zoospores on the lesion except for about a centimetre from the advancing margin of the lesions (arrowed). Pods at every stage of development may be infected, and infection may start from the proximal, distal or lateral (**Figure 4A–C**) portion of the pod, and extreme cases of black pod could also affect pods at different stages of development.

Cacao fruits can become infected at all stages from setting to maturity. Observations in Nigeria suggest that the relative frequencies of different infection sites may be affected by fruit length. It was found that the mean length of distally



Figure 3.
Coalescing lesions.

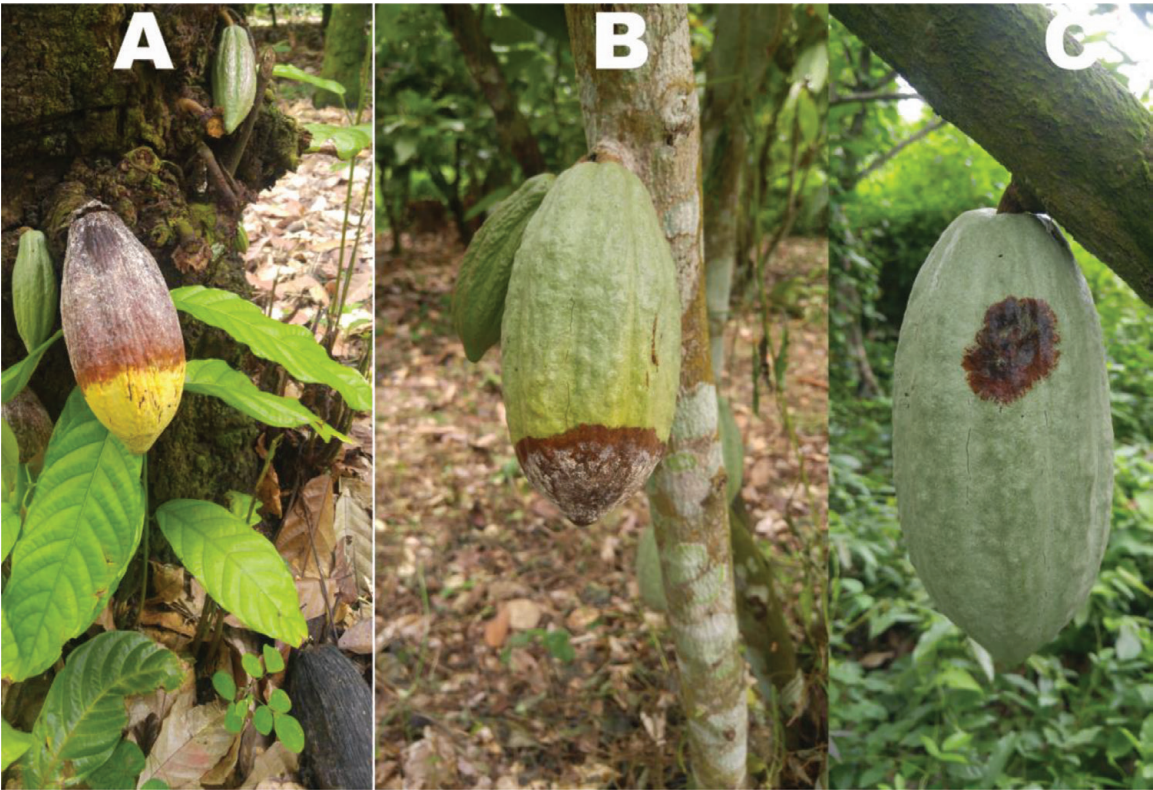


Figure 4.
Sites of pod infection in black pod disease. A, proximal; B, distal; and C, lateral.

infected fruits tended to be less than the mean length of either laterally or proximally infected fruits. These observations can be interpreted as indicating that distal infections tend to occur on relatively shorter and younger fruits, as compared with laterally and proximally infected fruits [24]. It was suggested that proximal infection might be favoured through moisture being retained in the annular depression where the stalk is inserted and at the distal ends of young fruits [25]. However, in Nigeria, the annular depression at the base may not necessarily be favourable for infection as compared with the distal end of the pod.



Figure 5.
Densely sporulating cacao pods indicating the presence of *Phytophthora megakarya*.

The predominance of *P. megakarya* on cacao in Nigeria started in the 1980s, alongside Cameroon, Equatorial Guinea, Gabon and Togo [22]. Recent studies showed that *P. palmivora* is no longer routinely isolated from cacao in Nigeria and Cameroon [12, 26, 27]; however, the displacement of *P. palmivora* by *P. megakarya* from cacao in these countries remains unclear [28]. However *P. megakarya* continues to be the major actual and potential threat to cacao in West Africa [16]. The much denser sporulation exhibited by *P. megakarya* on the surface of cacao pod (**Figure 5A–C**) indicates greater virulence of this species than *P. palmivora* and such significantly increases inoculum loads of *P. megakarya* [7, 29].

4. Characteristic and genomic diversity of *Phytophthora* species

Five major diseases of cacao (*Theobroma cacao* L.), *Phytophthora* pod rot (black pod), witches broom, swollen shoot virus, vascular streak dieback and monilia pod rot, account for over 40% annual loss of cocoa [30]. Correct identification of plant pathogens is critical and fundamental to population genetics, epidemiological studies and the development of disease control strategies. Due to the similarity in growth patterns of *Oomycetes* including *Phytophthora* species and fungi, *Oomycetes* were previously considered as a class within the fungi. Fundamental differences between *Oomycetes* and fungi have been established [31–33], and the two are now known to be taxonomically distinct in spite of their common infection strategy [34]. As a result of the initial consideration of *Oomycetes* as a class within the fungi, [35] reported that researchers have for several decades pursued a wrong track in addressing the menace caused by *Phytophthora infestans*. For example, chitin was earlier reported as a minor component of oomycete cell walls and, therefore, insensitive to chitin synthase inhibitors, but it is now known to be an important component of hyphal tips in *Oomycetes* [36]. Isolations of *P. palmivora* from diseased cacao pods in Nigeria have been found to be “typical” in culture [37] with respect to

general characters including early production of sporangia. *Phytophthora palmivora* tends to have a more rapid growth rate than *P. megakarya* in culture, possibly contributing to its ability to cause accelerated necrosis in mechanically wounded cacao tissues compared to *P. megakarya* [38]. There have been no indications of important local variations with respect to the characters of this pathogen nor as regards the nature of the black pod rot infection. Variations in dimensions of sporangia were in respect to age and nature of substratum.

Phytophthora palmivora was first considered the only causal agent of black pod disease. However, a reclassification of some of the isolates previously described as *P. palmivora* into distinct species was suggested [39, 40]. Classification of species within the genus *Phytophthora* has progressed through the use of several criteria, including morphological dataset of colony, sporangium and oogonium characteristics; the presence or absence of chlamydospores and hyphal swellings, physiology [20, 41], isozyme patterns [42]; and lately the combined use of molecular markers and morphological characteristics [43]. Consequently, based on the size and number of chromosomes, they introduced the S- and L-type designations, which represented isolates having comparatively smaller chromosomes with $n = 9-12$ and isolates having large chromosomes with $n = 5$, respectively. However, the earlier work of [20] and recently [28] has established the variation in genetic characteristics of *Phytophthora* species commonly associated with cacao in Nigeria, and *P. megakarya* was found as the most virulent of the species.

Consequently, the species were reclassified into three types: chromosome number, sporangial characteristics and pedicel length [20]. The S-type was regarded as *P. palmivora* sensu Butler (MF1) with 9–12 small chromosomes, papillate sporangia varying from near spherical to ovate-elongate shape and a short pedicel (2–5 μm) and being worldwide in distribution. The L-type was reclassified as *P. megakarya* (MF3), with five to six large chromosomes, papillate near spherical sporangia shape and pedicel of medium length (10–30 μm) and found only in West and Central Africa. Thus, the name “megakarya” is derived from the relatively large (mega) chromosomes. The third group was classified as *P. capsici* (MF4), with characteristics similar to *P. capsici* from black pepper [44, 45], and had longer pedicel (20–150 μm). The MF2, however, remains a variant of *P. palmivora*. The occurrence of hybridization is an important phenomenon in *Phytophthora*, given that hybridization may result in genetic variation that will adapt to new hosts or environments. Further confusion in the *P. palmivora* complex can occur due to heterothallic mating behaviour of the species. Sexual reproduction in *P. megakarya* and *P. palmivora* results in the production of oospores, and this requires the two opposite mating types, A1 and A2. Mating types in *P. megakarya* and *P. palmivora* show a curious imbalance, with A1 predominating in *P. megakarya* and A2 in *P. palmivora* [20]. This imbalance in mating types might favour hybridization between species, but not sexual reproduction within species. In spite of the two species coexisting on cocoa fields, no hybrids have been observed. The differences in chromosome numbers between *P. megakarya* and *P. palmivora* may also hinder hybridization and, hence, the rare occurrence of oospores in nature. *Phytophthora megakarya* was first described as a new *Phytophthora* species on cacao in West Africa based on chromosome number, sporangial characteristics and pedicel length. *Phytophthora megakarya* is indigenous to West and Central Africa, and it has become the main yield-limiting factor for cocoa production in affected areas [17] and rapidly surpassing *P. palmivora*.

In a susceptible cacao genotype, mechanical wounding may not be required for infection establishment in *P. megakarya* [38]. The genome size of *Phytophthora*

megakarya and *P. palmivora* was estimated at 126.88 and 151.23 Mb, respectively and number of genes 42,036 and 44,327, respectively [46]. *Phytophthora palmivora* appeared to have gone through whole genome duplication and subsequent gene diversification which expanded its genetic capacity for nutrient acquisition and breakdown of complex structures like the cell walls. This capacity may have influenced *P. palmivora* vigorous growth and broad host range, even without extended co-evolution with cacao. *Phytophthora megakarya* on the other hand has undergone amplification of specific gene families, some of which are clearly virulence-related like RxLRs, CRNs, elicitors and NPPs [46]. During *Phytophthora* infection, appressoria release effectors even before penetrations that enter host cells in an attempt to suppress pathogen-associated molecular pattern (PAMP)-triggered immunity [47]. Under the conditions of high and frequent rainfall in Cameroon, *P. megakarya* can cause yield losses of up to 100% when no control measures are taken [48]. In Ghana, losses ranging between 60 and 100% have been reported [15].

Some other species of *Phytophthora* have been reported on cacao and such include *P. botryosa*, causing cacao pod rot in Malaysia, and *P. citrophthora* in Bahia, Brazil [49, 50]. *P. capsici*, *P. citrophthora* and *P. heveae* were reported in Mexico [51], *P. katsurae* in Côte d'Ivoire [52] and *P. megasperma* in Venezuela [45]. Apart from the cosmopolitan *P. palmivora*, the other species have only been recorded in certain countries or geographical location/regions. However, factors responsible for the geographical separation of the *Phytophthora* species are yet to be elucidated, but it is possible that lack of intensive surveys, coupled with isolation of isolates from the same location, from a few plant species and on a narrow range of media could be responsible for this observation. Another possibility is that these species occur rarely on cacao; nonetheless, more investigations are required to ascertain these claims.

5. Impact of *Phytophthora* on cacao yield and bean quality

Major economic losses in cocoa production are caused by pests and diseases, particularly in the many small and isolated farms that lack adequate control measure across West Africa region. These species cause mean annual pod losses of about 40% and even higher in parts of Ghana and Côte d'Ivoire [17, 53]. The highest incidence of black pod disease is found in the shaded cocoa in Cameroon. World losses in cacao production due to black pod disease caused by various species of *Phytophthora* have been estimated to cause about 450,000 metric tons [7]. This disease probably accounts for 20–25% of the expected crop and making it the biggest constraint to production. **Figure 6** shows the usual harvesting exercise/activities in cocoa farms where both mature healthy cocoa pods and the disease black pods (arrowed) are usually lumped together on farmer's field and processed.

Losses due to black pod can be especially severe in West and Central Africa, an area that contributes 60–70% to the worldwide cacao production [7]. In Africa, it can cause 30–90% annual crop loss for farmers, and, thus, it poses a severe threat to the cacao industry and to producers. Part of the contributory factors which is major in limiting productivity in cacao is related to the practices of farmers. Apart from the practice indicated in **Figure 6**, the observation of piles of cocoa pod husks on different locations on farmers' fields serves as the sources of inoculum of the pathogen of black pod disease. The spores of *Phytophthora* species on infected cocoa pods are usually left on the field after extraction of the beans (**Figure 7**) and are reactivated under suitable conditions to infect fresh cocoa pods.



Figure 6.
Harvested cocoa pods on farmer's field with black pod (arrowed).



Figure 7.
Cocoa pod husk pile on farmer's field.

In the year 2012, Ghana lost more than 200,000 tonnes of cacao beans (25% of the annual output) due to black pod, costing the nation \$230 million (Ghana Cocoa Board report). Until the mid-1980s, only *P. palmivora* was present in all the cacao-growing regions of Ghana, causing limited crop losses of 4.9–19% [54]. After 1985, black pod became a major disease in Ghana and was attributed to the emergence of *P. megakarya* as a pathogen of cacao [55]; various reports from Ghana indicated a rapid spread of *P. megakarya* to various cacao districts by the late 1990s causing 60–100% crop losses [17].

5.1 Impact of *Phytophthora* on cocoa beans

The *Phytophthora* species affects different parts of the cacao, but infection of the pod is the major economic loss as pods or cherelles may be infected at any parts on the surface. Observation of the disease indicates a firm, spreading, chocolate-brown lesion which eventually covers the whole pod. The beans inside the pod may remain undamaged for several days after initial infection of the husk, but in advanced infections, *Phytophthora* invades the internal pod tissues and causes discoloration and shrivelling of the cocoa beans (**Figure 8A–C**), thus tampering with the mucilage colouration (**Figure 9**) and affecting quality of the cocoa bean.

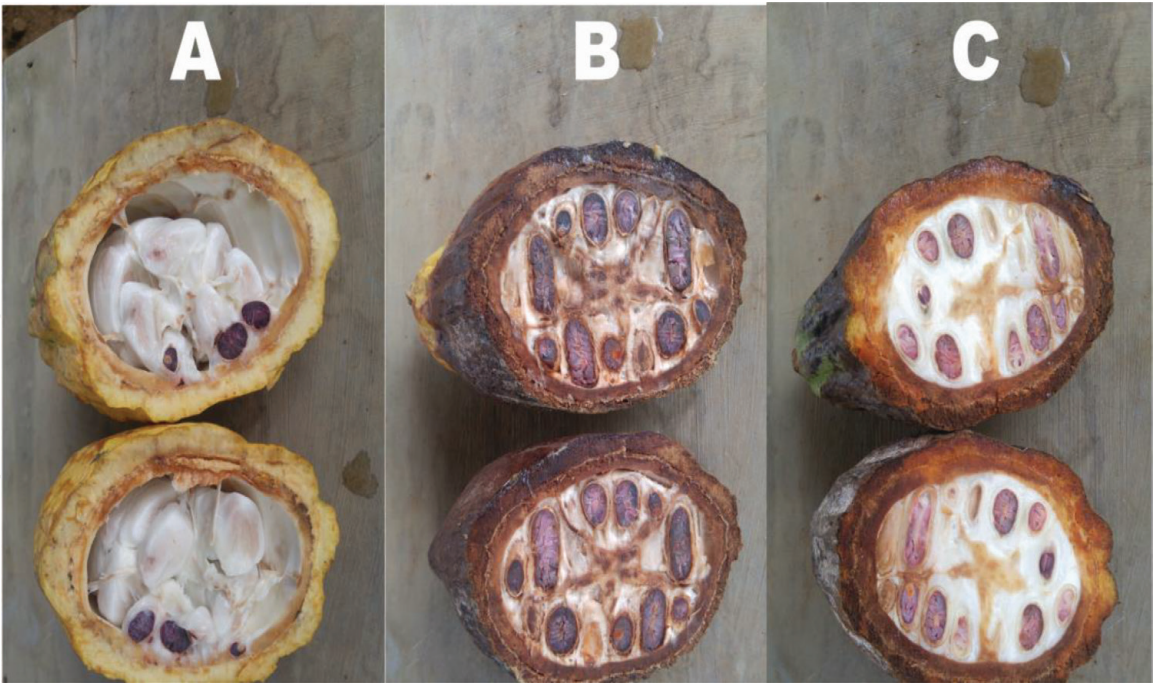


Figure 8.
Status of black pod disease on cocoa bean. A: Ripe and healthy cocoa pod with quality mucilage and beans. B: Ripe but diseased cocoa pod with infected beans. C: Unripe but diseased cocoa pod with infected beans.



Figure 9.
Effect of black pod disease on cocoa mucilage and beans in ripe cocoa pod.

6. Management strategies for *Phytophthora* species

Phytophthora can persist in soil and debris for several years making the control of black pod difficult [56]. Also, since susceptible pods may be present on the trees most of the year, the pathogen may always be present in the canopy, ready to cause major epidemics when environmental conditions become favourable for sporulation and dispersal [29]. Although much research has been published over the past few decades on black pod disease, sustainable management strategies that are applicable to smallholder farms are still lacking in most producing countries. Crop losses and cost of controlling *Phytophthora* (black pod) diseases constitute a significant financial burden on agricultural enterprises and have serious socioeconomic and environmental consequences wherever these pathogens are found. Neglect of cocoa

farms infected with *P. megakarya*, cultivation of crops other than *T. cacao* in infected areas [16] and establishment of *T. cacao* in *P. megakarya*-free forest areas have significant impacts on the economies of the cocoa-producing countries in West Africa. It also has effects on biodiversity and functioning of the natural ecosystems.

Phytophthora megakarya has spread within the West and Central African subregions, and it is still in its invasive phase. The spread of this pathogen from one location to another in Ghana has been linked with the movement of planting materials [16, 57, 58]. The faster communication, travel and trade links and the relatively free movement of people and commodities all over the world pose a serious risk of introducing *P. megakarya* to other cacao-growing regions. On the other hand, there is a risk of introduction of other major cocoa diseases from other cocoa-producing areas into West and Central Africa [59]. This will have negative impact on world cocoa production. A devastating impact on the world's cocoa supply is eminent and extremely serious in social, economic and environmental problems. Such pathogen introduction can also be experienced within a growing country from the region of high incidence to low one. To minimise such risks, preventive measures and effective testing procedures and exchange of materials through intermediate quarantine facilities must be enforced. Consequently, there is an urgent need for effective and sustainable control of *P. megakarya*/black pod disease. The effective and sustainable management of this disease requires integrated approach of several methods, including quarantine, cultural, chemical and biological control and use of resistant cocoa varieties.

6.1 Cultural practices to combat black pod disease

Activities to combat the menace of yield losses and decline in cocoa production resulting from black pod disease incidence in cocoa-growing communities are enormous. Cultural control practices that promote crop growth, inhibit and obstruct pathogen establishment, growth and development is one of the first approaches in plant disease control. Cultural practices are not only essential for increasing yield but also for providing the right environment for efficient performance of fungicides [60]. For the small holdings, low-input and low-income cocoa farmer use of cultural practices remains the least expensive disease control option for managing black pod disease. However, frequent harvesting saves partly infected mature pods, removal of infected pods, and reduces sources of sporangial inoculum. The regular and timely removal of infected pods and reduction in the shade to increase the humidity which in turn reduce pod losses however, additional chemical control by regular spraying of fungicides is required.

In Nigeria, frequent removal of diseased pods complemented sprayed programmes in controlling *P. megakarya*, but, often, excessive tree heights hampered the effectiveness of the technique [61]. Similarly, in Togo, *P. megakarya* diseased pod removal was recommended as part of a package to reduce disease incidence [62]. In Cameroon, inoculum levels were successfully reduced by the pruning and weekly removal of pods but only in concert with spraying [63]. Another cultural method occasionally recommended is the removal or spraying of pod husk piles where they occur on farms (**Figure 7**). It is known that these pod husk piles serve as disease foci on *P. megakarya* farms. In Nigeria and Sao Tome, burying of husks was recommended, but its limited effectiveness and expense caused this option to be dropped [64]. However, in Ghana the husks are burnt into potash and used in the production of soap. Cultural practices on cacao farms are labour intensive and inadequate when applied alone for *P. megakarya* control. They need to be supplemented with other control methods, such as spraying of fungicides to reduce losses on farms [58, 65–67]. Most farmers, however, are unable to adopt this technology because of

the high costs of the fungicides and application problems. In practice little fungicide is used [17, 68]. However, 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 [69]. Reduction in canopy humidity and consequent sporulation can be achieved by pruning and appropriate tree spacing to increase aeration. Maintenance of leaf litter or mulches to prevent soil inoculum of *P. megakarya* reaching pods has been suggested [70], while leaf litter was found to reduce pod infection from soil inoculum [71]. The spread of the disease from infected pods can be reduced by frequent harvesting to lessen the danger of spread of disease from infected pods. Black pod disease is also managed by regular pruning to remove infected chupons and increase air circulation. Other measures, such as the removal of infected pods and husk piles, may have some effect on inoculum levels.

6.2 Chemical strategies to combat black pod disease

Fungicides have been used to control *Phytophthora* pod rot of cocoa for over a century, and several experiments on different chemical control measures have been conducted in all cocoa-growing countries. The history of the development of fungicides on cocoa has been extensively reviewed [72–74]. Recommendations adopted in the different countries are based on local factors, such as species of pathogen, climatic conditions, cocoa variety, planting density and social and economic considerations [64]. Traditionally, expensive copper-based fungicides (or systemic) have been applied frequently (sometimes every 10 days) in areas of high infection. Without prophylaxis, the losses could reach 100% in areas of continuous high humidity and high disease incidence, although the disease has a normal range of 5–90%. In order to limit yield loss to black pod disease in Ghana, three preventive rounds of copper fungicide were applied during the rainy season under a national spray programme in *P. megakarya* prevalent areas. This however puts immense pressure on resource-poor farmers in the form of reduced farm-gate prices, leading to ecological, socioeconomic and possibly political instability. In Nigeria, many fungicides of varied active ingredients are used by farmers across growing ecologies. The Cocoa Research Institute of Nigeria has the national mandate to screen *in vitro* and *in vivo* such fungicides among other pesticides prior to being used on cacao in Nigeria. Many of the active ingredients (product of different agrochemical companies) that have undergone a 3-consecutive-year field trials include but not limited to copper hydroxide, cuprous oxide + metalaxyl-M, cuprous oxide and metalaxyl-M + copper-1-oxide and recently are copper-1-oxide + metalaxyl, mandipropamid + mefenoxam, initium + dimethomorph and pyraclostrobin + dimethomorph + ametoctradin. The relative effectiveness of certain treatments and inconsistencies in results between countries and locations depends on the different combinations of these factors. For example, while fungicides are applied at two weekly intervals in Cameroon to control black pod disease, due to the relatively high and frequent rainfall, fungicides are applied at three to four weekly intervals in Ghana [16], and spray interval of 3 weeks is also advised in Nigeria. The reason for the difference among countries has to do with the amount and frequency of rainfall.

In West Africa, protectant fungicides that are mainly “fixed” copper compounds, e.g., copper hydroxides and copper oxides, or systemic fungicides containing copper and metalaxyl as mixtures are routinely sprayed onto pods with lever-operated knapsack sprayers for *Phytophthora* pod rot control. These fixed copper compounds are finely divided molecules that are readily mixed and easy to apply at low volumes. This is in contrast to earlier products such as the Bordeaux mixture, which had to be applied in relatively large volumes. These copper fungicides form a

chemical barrier on the surface of the pod and guard against infection [58, 75]. The spraying of copper and metalaxyl mixtures is to take advantage of multisite action of the different active ingredients and to reduce the possible build-up of metalaxyl resistance in *Phytophthora* species on cocoa. Furthermore, it must be emphasised that correct dosage of fungicides, timing of initial application in relation to the epidemic, frequency and target of application are all critical factors to ensure successful and economic chemical control.

6.3 Alternative practices to combat black pod disease

Many natural substances, including plant extracts and bioactive compounds produced by microorganisms, have been tried to control *Phytophthora* on cacao [76, 77]. Rosemary (*Rosmarinus officinalis*) and lavender (*Lavandula officinalis*) leaf extracts when supplemented to agar plates at different dilutions were found to inhibit germination of *P. capsici*, *P. megakarya* and *P. palmivora* zoospores. Rosemary extracts, containing caffeic acid, rosmarinic acid or derivatives, thereof, reduced necrosis of cacao leaf discs caused by *P. megakarya* zoospores [77]. Another promising class of natural microbial compounds with activity against *Phytophthora* species is the cyclic lipopeptides (CLPs) [78–81]. Studies showed that massetolide A (massA) produced by *P. fluorescens* strain SS101 caused zoospore lysis through induction of pores, reduced sporangium formation and increased branching and swelling of hyphae of *P. infestans* [78, 82]. MassA also induced systemic resistance in tomato plants and reduced the number and expansion of late blight lesions on tomato caused by *P. infestans* [83, 84]. Given that hyphae, sporangia and zoospores are important sources of inoculum and play major role in cacao black pod epidemic, there is the need to investigate if CLPs or CLP-producing microorganisms can be exploited for the management of black pod disease caused by *P. megakarya*.

7. Conclusion

Phytophthora megakarya infestation of cacao is a threat to the economies of growing countries in West Africa. This diverse pathogen is spreading fast in the subregion, displacing the original populations of the less severe *P. palmivora*. The mechanisms for this shift in population composition of the black pod disease complex remain unknown, although the possibility of further spread to other cacao-producing regions is a great concern. The available and fast-emerging genomic and genetic information on oomycete pathogens and their hosts, including *Theobroma cacao*, should be utilised and explored for the development of new sustainable management practices for *Phytophthora* species. Current methods of control through routine spraying of inorganic fungicides are expensive, hazardous and environmentally unfriendly. Programmes of integrated pest management with precise fungicide application which give less residue in the cocoa beans, combined with field sanitation and proper farm management, should be encouraged in all areas where *Phytophthora* species cause significant losses on cocoa.

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Author details

Dele Adeniyi

Cocoa Research Institute of Nigeria (CRIN), Ibadan, Nigeria

*Address all correspondence to: modeleadeniyi@gmail.com

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