



A REVIEW OF *PHYTOPHTHORA MEGARKAYA* IN COCOA PRODUCTION AND THE RESISTANCE OF COCOA AGAINST THE PATHOGEN

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ABSTRACT

Cocoa (*Theobroma cacao* L.) is an important tropical crop with production limited by black pod disease caused by *Phytophthora megakarya* in West and Central Africa. Here, we review the biology, infection process, environmental interactions, and pathogenic variability of *Phytophthora megakarya*, and the resistance mechanisms of cocoa to this pathogen. The life cycle of *Phytophthora megakarya* involves fast asexual reproduction, formation of motile zoospores, and survival in the form of chlamydospores, which allows the pathogen to persist and spread over long distances in humid conditions. Environmental factors such as high rainfall, temperature, and canopy density affect disease development, while genetic variability within populations of *Phytophthora megakarya* complicates disease management by increasing virulence and adaptability. The review also points out that host resistance is a possible sustainable control strategy and that it is quantitative and polygenic; cocoa resistance is a multilayered process that includes genetic, morphological, biochemical, and physiological mechanisms such as activation of defense-related enzymes, accumulation of phenolic compounds, and structural barriers such as thicker pod husks. Tolerant cocoa varieties have been bred using advances in molecular breeding and identification of resistance-associated traits, but pathogen diversity and environmental effects can limit the durability of resistance. The study emphasizes that host resistance must be combined with cultural and environmentally friendly management practices for effective and sustainable control of black pod disease in cocoa production systems.

Keywords: *Theobroma Cacao*, *Phytophthora Megakarya*, Black Pod Disease, Host Resistance, Disease Management

INTRODUCTION

Cocoa (*Theobroma cacao* L.) is one of the most economically significant perennial crops grown in the tropics and is the principal raw material for chocolate production (Olaomi, 2023). Cocoa is one of the most economically important crops, contributing to the livelihood of millions of smallholder farmers worldwide, and 70% of cocoa production originates from West Africa (Septiani *et al.*, 2024). Of all cocoa diseases, black pod disease caused by species of the genus *Phytophthora* is the most destructive worldwide (Neeraja *et al.*, 2025).

Phytophthora megakarya and *Phytophthora palmivora* cause Black pod disease, with *Phytophthora megakarya* being the most virulent species in West and Central Africa (Carlos *et al.*, 2025). *Phytophthora megakarya* infects cocoa pods, stems, and leaves, causing rapid tissue necrosis and severe yield losses. The disease thrives in humid tropical conditions where sporangia form and zoospores can disperse (Simamora *et al.*, 2021). Severe infections can result in significant decreases in pod production and may result in total crop failure in unmanaged plantations. *Phytophthora megakarya* produces motile zoospores that are disseminated by rain splash and soil water, colonizing cocoa pods and surrounding tissues rapidly (Membang *et al.*, 2024). The pathogen produces mycelia that invade host tissues and break down cellular components, causing blackened lesions and pod rot. The pathogen can survive in infected plant debris and soil, providing a reservoir of inoculum for future infection cycles (Carlos *et al.*, 2025). *Phytophthora megakarya* is morphologically similar to fungi but physiologically and genetically distinct; it has cellulose-based cell walls and diploid vegetative structures, like other

members of the phylum Oomycota, and is thus well-adapted to the humid tropical environments where cocoa is grown (Akrofi, 2015; Youassi-Youassi *et al.*, 2024).

Phytophthora megakarya is endemic to West and Central Africa, where climate conditions allow it to survive and become epidemic, and where it has been shown to be more aggressive and to cause more rapid lesion expansion, and higher sporulation than other cocoa-infecting *Phytophthora* species (*Phytophthora palmivora*), leading to severe yield losses in infected cocoa-growing regions (Maledy *et al.*, 2022). The pathogen can persist in soil and infected plant debris to facilitate reinfection cycles over multiple growing seasons (Kamga *et al.*, 2022).

MATERIALS AND METHODS

Morphology and Life Cycle

Phytophthora megakarya has both asexual and sexual reproductive stages, which allow the pathogen to multiply rapidly and survive for long periods of time. The asexual stage is responsible for epidemic development in cocoa plantations; the pathogen produces sporangia on infected tissues that release motile zoospores that swim in free water films on plant surfaces. Upon contact with host tissue, zoospores encyst and then germinate, producing germ tubes that penetrate the epidermis of cocoa pods and other susceptible tissues. Environmental conditions, especially humidity and temperature, are significant factors in the production of sporangia, which form optimally at temperatures between 24°C and 28°C and relative humidity above 90% (typical of rainy seasons in cocoa-growing regions) (Maledy *et al.*, 2022).

Environmental conditions such as high humidity and moderate temperatures are required for sporangia production, with optimal sporangial formation occurring at temperatures between 24°C and 28°C and relative humidity above 90%, conditions frequently found in cocoa-growing regions during the rainy season (Mahob *et al.*, 2021). The rain splash and surface runoff dispersal of zoospores is a major factor in the rapid spread of the disease in plantations. Besides asexual reproduction, *Phytophthora megakarya* also forms thick-walled survival structures, chlamydospores that enable the pathogen to survive in unfavorable environmental conditions; chlamydospores can remain viable in soil and plant debris for several years, and are the main source of primary

inoculum for subsequent cropping cycles (Kamga *et al.*, 2022). *Phytophthora megakarya* is generally considered to be heterothallic and needs compatible mating types to undergo sexual reproduction, but sexual structures are rarely found under natural field conditions (Akrofi, 2015). The infection cycle usually starts when zoospores or germinating sporangia contact susceptible cocoa tissues, with lesions first appearing on pods in contact with the soil or exposed to rain splash. Lesions then rapidly spread over the pod surface, resulting in total pod rot, and infected pods become coated with white sporulating mycelia under humid conditions, which are sources of secondary inoculum for further spread of the disease (Maledy *et al.*, 2022).

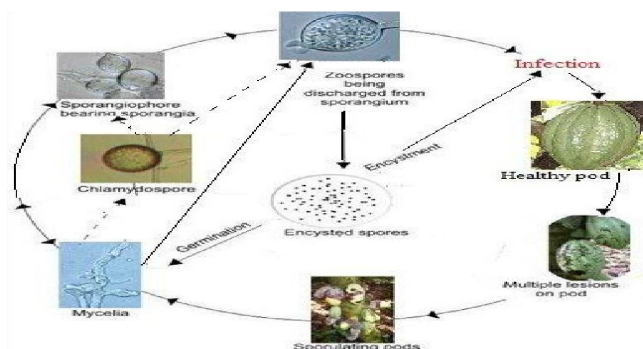


Figure 1: Life cycle of *Phytophthora megakarya* (Source: Nembot *et al.*, 2017)

RESULTS AND DISCUSSION

Infection Process and Host Colonization

Phytophthora megakarya infection occurs through a series of biochemical and structural interactions between the pathogen and host tissues. After encystment of zoospores, germ tubes penetrate host tissues either through natural openings such as stomata, or directly by enzymatic degradation of cell walls (Youassi-Youassi *et al.*, 2024). The pathogen secretes a variety of cell wall-degrading enzymes, including cellulases, pectinases, and hemicellulases, which promote tissue maceration and pathogen colonization. A number of pathogenicity-related genes involved in host colonization and virulence have been identified through recent molecular studies (Kamga *et al.*, 2022; Omotoso *et al.*, 2026).

The effector proteins secreted by *Phytophthora megakarya* are important in suppressing host defense responses to allow the infection to occur and the pathogen to grow intercellularly and intracellularly, extracting nutrients from host cells and causing progressive tissue necrosis. An important feature of *Phytophthora megakarya* infection is the rapid expansion of lesions, which begin as dark brown spots that expand quickly and eventually cover the entire pod surface and destroy the fruit (Mahob *et al.*, 2021).

Environmental Factors Influencing Pathogenicity

Black pod disease caused by *Phytophthora megakarya* is strongly influenced by environmental conditions: high rainfall and long periods of leaf wetness favor sporangia formation, zoospore release, and pathogen dispersal, and disease outbreaks are most severe during rainy seasons when moisture levels are high (Maledy *et al.* 2022). Temperature also affects pathogen growth and infection efficiency: mycelial growth rates of *Phytophthora megakarya* increase dramatically within the temperature range characteristic of tropical climates, allowing for rapid colonization of host tissues (Tchameni *et al.* 2023). Yet, high temperatures can

decrease pathogen viability and sporulation. Pathogen survival can be influenced by soil properties, including moisture content, organic matter levels, and drainage, with poorly drained soils promoting pathogen survival as they provide a longer period of water availability for zoospore motility (Akrofi, 2015). Disease incidence is often higher in plantations with a dense canopy structure, because less air circulates and humidity is higher (Youassi-Youassi *et al.*, 2024).

Variability in Virulence and Strain Diversity

There is a large amount of variation between isolates of *Phytophthora megakarya* in growth rate, sporulation capacity, and virulence, and genetic diversity within pathogen populations contributes to variation in disease severity in different cocoa-growing regions (Maledy *et al.*, 2022). Certain isolates have higher pathogenicity and can infect cocoa varieties that were thought to be tolerant. *Phytophthora megakarya* populations have substantial genetic variation, and molecular characterization techniques like polymerase chain reaction and DNA sequencing have shown that resistant cocoa varieties could become susceptible to new pathogen strains, making continuous monitoring of pathogen populations necessary to support breeding programs to develop resistant cocoa varieties (Kamga *et al.*, 2022). Pathogen variability must be considered for long-term effectiveness of resistance-based disease management strategies (Mahob *et al.*, 2021).

Implications for Disease Management

The biology of *Phytophthora megakarya* poses a challenge to its control due to its rapid reproductive cycle, high sporulation capacity, and soil and plant debris survival (Akrofi, 2015); therefore, integrated disease management approaches involving host resistance, cultural practices, and environmentally safe control measures are required. Understanding the biology and pathogenicity of the

pathogen is essential for evaluating cocoa varietal tolerance and for the development of botanical fungicides.

Host Resistance and Tolerance Mechanisms in Cocoa Varieties

Host plant resistance is one of the most effective and sustainable approaches to manage black pod disease of cocoa (*Theobroma cacao* L.) caused by *Phytophthora megakarya* (Ebaiarrey *et al.* 2024). While chemical control methods are needed to manage the disease, they can be expensive, have to be reapplied, and can have environmental impacts. As a result, the development and evaluation of cocoa varieties with increased tolerance to *Phytophthora megakarya* have been the focal point of cocoa improvement programs in West and Central Africa, where the disease is still highly endemic (Ebaiarrey *et al.* 2024). Tolerance to *Phytophthora megakarya* is typically described as slower lesion development, delayed pathogen colonization, and increased yield stability under disease pressure.

Genetic Basis of Resistance in Cocoa

In cocoa, resistance to *Phytophthora megakarya* is mostly regulated by quantitative genetic mechanisms, which are often polygenic in nature and provide partial resistance (Ebaiarrey *et al.*, 2024). Several breeding populations of cocoa have been found to have quantitative trait loci associated with black pod resistance, suggesting that resistance traits can be successfully bred into improved varieties; recent genomic studies have identified candidate resistance genes related to pathogen recognition and defense signaling in cocoa. These genes code for proteins involved in pathogen-associated molecular pattern recognition and plant immune response activation, leading to localized cell death, reinforcement of cell walls, and production of antimicrobial compounds that inhibit pathogen growth (Kumar and Singh, 2024). Breeding programs have accelerated the development of tolerant cocoa genotypes by using molecular markers linked to resistance traits. Some of the improved hybrids bred in West Africa have shown moderate to high tolerance to *Phytophthora megakarya*, and hybrids derived from Upper Amazonian germplasm have shown particularly high resistance levels due to the genetic diversity and adaptive traits of these genotypes (Ebaiarrey *et al.*, 2024). These hybrids often combine disease tolerance with desirable agronomic characteristics such as high yield potential and early fruiting.

Morphological and Anatomical Factors Contributing To Tolerance

Susceptibility to *Phytophthora megakarya* is also determined by morphological characteristics of cocoa pods and plant tissues such as pod thickness, cuticle structure, and stomatal density act as physical barriers to pathogen penetration, and varieties with thicker pod husks have lower infection rates because the pathogen takes longer to penetrate host tissues (Ebaiarrey *et al.*, 2024). Surface characteristics of pods also affect infection risk; smooth pod surfaces hold less moisture than rough surfaces, thereby decreasing conditions favorable for zoospore germination.

In addition, varieties with upright pod orientation may also have lower infection rates due to less contact with soil-borne inoculum (Ebaiarrey *et al.*, 2024). Disease tolerance is also affected by root architecture and canopy structure: cocoa varieties with extensive root systems may be better able to take up nutrients and be physiologically able to withstand pathogen stress, while open canopy structures allow for

better air circulation and lower humidity levels around pods, which indirectly limits disease development (Enoch, 2021).

Biochemical Defense Mechanisms

Biochemical defense responses are the main mechanism of cocoa resistance to *Phytophthora megakarya*, and cocoa plants respond to pathogen attack with a variety of biochemical processes that inhibit pathogen growth and colonization, such as the production of phenolic compounds, phytoalexins, and antifungal pathogenesis-related proteins (Ebaiarrey *et al.*, 2024). Phenolic compounds are particularly significant to cocoa defense, with high concentrations of phenolics observed in tolerant cocoa varieties following infection with *Phytophthora megakarya* (Enoch, 2021). Resistance mechanisms also involve enzymatic defenses, and induction of enzymes such as peroxidase, polyphenol oxidase, and chitinase in cocoa tissues infected by pathogens contribute to the degradation of pathogen cell walls and detoxification of pathogen-derived metabolites (Kumar and Singh, 2024). Research has demonstrated that tolerant cocoa genotypes have quicker and more intense activation of defense enzymes than susceptible varieties, limiting pathogen colonization and reducing disease severity (Ebaiarrey *et al.*, 2024).

Physiological Mechanisms of Tolerance

Tolerant cocoa plants may be able to maintain higher levels of photosynthetic activity and nutrient uptake even in the presence of a pathogen, which could help them sustain growth and productivity despite infection (Enoch, 2021). Water relations within plant tissues are also important; cocoa varieties that are able to maintain relatively stable water relations when humidity is high or when it is raining may be less susceptible to pathogen invasion. Excess moisture in the tissue promotes the germination and infection of zoospores; however, maintaining proper water regulation can lower infection risk (Ebaiarrey *et al.*, 2024). Antioxidant production and other stress tolerance mechanisms confer even more resistance to infection; antioxidant compounds neutralize reactive oxygen species produced during pathogen attack (Kumar and Singh, 2024). Balanced water regulation can decrease infection risk by preventing excessive tissue moisture, which promotes zoospore germination and infection (Ebaiarrey *et al.*, 2024).

CONCLUSION

This review has shown that *Phytophthora megakarya* is the most virulent causal agent of black pod disease of cocoa production systems in West and Central Africa, and its biology, with rapid asexual reproduction, efficient zoospore dispersal, and long-term survival by chlamydospores, makes the pathogen capable of surviving and spreading widely in humid tropical conditions, and its infection process, characterized by enzymatic degradation of host tissues and suppression of plant defense responses by effector proteins, leads to rapid lesion expansion, severe pod rot, and high yield losses. Effective disease reduction in cocoa will require integrated approaches combining resistant varieties, cultural practices (including sanitation, removal of infected pods, and improved drainage), and environmentally safe control measures. Further investment in breeding programs is required to develop and release cocoa varieties with durable, polygenic resistance to *Phytophthora megakarya*, especially those adapted to local environmental conditions, and to monitor *Phytophthora megakarya* genetic diversity and virulence patterns to identify strains that can overcome existing resistance.

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