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PHYTOPTHORA PALMIVORA: A FACULTATIVE PATHOGEN OF COCONUT AND COCOA CROPPING SYSTEM –ECOLOGICAL DYNAMICS IN TROPICS AND MANAGEMENT STRATEGIES-A COMPREHENSIVE REVIEW

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ABSTRACT

Phytophthora palmivora is a destructive oomycete pathogen impacting key tropical crops coconut (*Cocos nucifera*) and cocoa (*Theobroma cacao*) causing bud rot and black pod disease, respectively, resulting in significant yield losses. This review synthesizes current knowledge on the pathogen's biology, epidemiology, and ecological dynamics within tropical cropping systems. Emphasis is placed on host–pathogen molecular interactions and disease progression mechanisms. Advanced molecular diagnostics, including qPCR, LAMP, SSR markers, and effector gene profiling, are evaluated for early detection and pathogen monitoring. Conventional management strategies, such as chemical control and resistant cultivars are discussed alongside emerging nanotechnology-based interventions nanopesticides, green-synthesized metal nanoparticles, and RNA interference delivery platforms that offer enhanced efficacy and environmental safety. This integrative review highlights prospects for combining traditional and novel approaches to sustainably manage *Phytophthora* diseases in coconut and cocoa under evolving tropical climates.

Key words : *Phytophthora palmivora*, Coconut, Cocoa, Black pod disease, Bud rot, Oomycete, Nanotechnology, Nanopesticides, RNA interference, Tropical agriculture, Sustainable plant protection.

Introduction

Phytophthora palmivora is a hemibiotrophic oomycete of global phytopathological concern, severely affecting two economically vital tropical perennial crops coconut (*Cocos nucifera*) and cocoa (*Theobroma cacao*). It causes bud rot in coconut and black pod disease in cocoa, both leading to substantial yield losses and long-term reductions in plantation productivity (Guest, 2007; Rajendran *et al*., 2010). As a facultative pathogen, *P. palmivora* can survive both saprophytically in soil, plant debris, and water, and parasitically within host tissues, allowing it to persist between seasons and rapidly initiate new infections through wounds or natural openings (Judelson and Blanco, 2005; Drenth and Guest, 2004).

Tropical agroecosystems characterized by high humidity, warm temperatures, and seasonal rainfall create ideal conditions for pathogen sporulation, dispersal and infection. Yield losses can reach 30–80% in cocoa during peak rainy seasons (Opoku *et al*., 2000) and bud rot in coconut frequently leads to palm mortality if not addressed early (Rajendran *et al*., 2010). The persistence of *P. palmivora* in field environments is exacerbated by poor sanitation, monoculture practices and increasingly erratic climatic conditions (Drenth and Guest, 2004; Ploetz, 2007).

Economically, *P. palmivora* poses a major threat to millions of smallholder farmers across the tropics by reducing yields, increasing input costs, and necessitating intensive chemical use raising environmental and health concerns (Togbe *et al*., 2021). Effective management remains challenging, as no single strategy offers complete control. While cultural practices, chemical fungicides, biological control agents and the use of tolerant or resistant varieties contribute to disease reduction, their isolated application often yields limited success.

Recent advances in molecular diagnostics including quantitative PCR (qPCR), loop-mediated isothermal amplification (LAMP) and species-specific SSR markers have significantly improved early detection and population-level differentiation of *Phytophthora* species (Appiah *et al*., 2004; Rêgo, Mora-Ocampo and Corrêa, 2023). Studies on host–pathogen molecular interactions have revealed complex defense responses in cocoa, such as elevated clovamide levels and upregulation of pathogenesis-related (PR) genes in resistant genotypes (Knollenberg *et al*., 2020; Perrine-Walker, 2020).

Beyond conventional control, emerging technologies such as nanopesticides, green-synthesized metal nanoparticles, and RNA interference (RNAi)-based delivery platforms offer new avenues for sustainable and targeted disease management (Chowdappa and Hedge, 2019). Biological control agents particularly *Trichoderma asperellum*, *Pseudomonas fluorescens* and beneficial endophytes have demonstrated efficacy in suppressing *Phytophthora* in both nursery and field conditions (Latha *et al*., 2023; Prathibha *et al*., 2023).

This comprehensive review consolidates current knowledge on *P. palmivora*'s biology, ecology and infection strategies, with particular focus on its facultative hemibiotrophic behavior and adaptability to tropical environments. It examines ecological factors influencing disease dynamics, assesses impacts on crop health and farmer livelihoods, evaluates integrated disease management strategies. Finally, it identifies key research gaps and future priorities for strengthening crop resilience and sustainable disease control under changing climate conditions.

Biology, Life cycle and Infection strategies of *P. palmivora*

P. palmivora (Butler) is a highly destructive oomycete pathogen affecting key tropical crops such as coconut and cocoa, where it causes bud rot and black pod disease, respectively. Though often misclassified as a fungus, *P. palmivora* is phylogenetically related to diatoms and brown algae (Kamoun *et al*., 2015). Its facultative hemibiotrophic lifestyle initial biotrophic colonization followed by necrotrophy allows it to adapt to diverse environments and persist in plant debris, soil and water (Judelson and Blanco, 2005).

The pathogen reproduces both sexually and asexually. Asexual reproduction involves lemon-shaped sporangia that release motile, biflagellate zoospores under moist conditions, facilitating rapid spread via water films (Drenth and Guest, 2004). Sexual reproduction, typically heterothallic, results in oospore formation durable survival structures in soil (Gallegly and Hong, 2008).

In coconut, *P. palmivora* invades the apical meristem, leading to bud rot, tissue collapse and palm death, especially under high humidity and poor drainage (Rajendran *et al*., 2010). In cocoa, it causes black pod disease and stem cankers, marked by water-soaked lesions, rapid pod decay, and significant yield loss (Opoku *et al*., 2000).

Environmental conditions in tropical regions high rainfall, humidity and poor drainage—favour sporulation, zoospore movement and epiphytotics. Combined with continuous cropping and limited sanitation, these factors enhance the pathogen's persistence and spread (Ploetz, 2007).

Occurrence and Distribution of *P. palmivora* in Coconut and Cocoa Cropping systems

P. palmivora is a globally distributed oomycete pathogen, widely recognized for its ability to infect over 200 plant species, including economically important tropical crops such as coconut and cocoa (Drenth & Guest, 2004; Kamoun *et al*., 2015). Its occurrence is primarily concentrated in humid tropical and subtropical regions, where high rainfall, elevated humidity, and poor drainage favor pathogen proliferation and dispersal.

Distribution and Incidence of *P. palmivora*

P. palmivora is globally distributed and significantly impacts cocoa and coconut production in tropical regions. It is widely reported from all major cocoa-growing regions including West Africa, Central and South America, and Southeast Asia (Ploetz, 2007). As a major cause of black pod disease in cocoa, *P. palmivora* contributes to annual losses ranging from 20% to 30%, with unmanaged plantations experiencing up to 80% yield loss, especially during extended rainy periods (Opoku *et al*., 2000; Guest, 2007). In Indonesia, incidence levels as high as 44% have been recorded under high humidity and continuous cropping (Ploetz, 2007).

In coconut, the pathogen is associated with bud rot disease, causing severe damage to the apical meristem. Countries like India, Sri Lanka, the Philippines, Thailand, Brazil, and Pacific islands report significant yield limitations due to this disease (Rajendran *et al*., 2010; Foale and Ashburner, 2006). Bud rot is prevalent during heavy rainfall and water stagnation, particularly affecting palms aged 3–10 years. In severely affected regions, outbreaks can lead to losses of 25–35% of palms (Peiris *et al*., 2004).

In India, *P. palmivora* is prevalent across major coconut and cocoa-growing states Kerala, Tamil Nadu, Karnataka, and Andhra Pradesh where warm, humid conditions and intensive cultivation practices favor disease development (Nambiar *et al.,* 2003; Rajendran *et al*., 2010). In coconut, bud rot occurs most frequently during the southwest monsoon, especially in poorly drained soils. Surveys in Kerala indicate incidence levels from 8% to 32%, with palm mortality exceeding 20% in unmanaged cases (CPCRI, 2018). In coastal Tamil Nadu, the disease severity index has reached over 50% during peak monsoons (Rajendran *et al*., 2010).

In cocoa plantations in Kerala and Karnataka, pod infection due to black pod disease ranges between 15% and 45%, with severity linked to cultivar, orchard sanitation, and rainfall (Nambiar *et al*., 2003). The monsoon season (June–October) corresponds with peak disease incidence, and stem cankers caused by the pathogen further contribute to chronic yield decline.

Environmental and agronomic factors such as >85% relative humidity, prolonged leaf wetness, dense canopies, and waterlogged soils promote sporulation, zoospore dispersal, and infection. Poor sanitation and climate change-induced extremes in rainfall are also contributing to the expanding distribution and severity of *P. palmivora* outbreaks globally (Bebber *et al*., 2013).

Symptomatology of *Phytopthora* induced Pod Rot in cocoa

Pod rot, or black pod disease, is a major constraint to global cocoa production, predominantly caused by *P* species such as *P. palmivora*, *P. megakarya* and *P. capsici*. Of these, *P. palmivora* has the broadest distribution, while *P. megakarya* dominates in West and Central Africa (Guest, 2007; Opoku *et al*., 2007).

Early symptoms begin as small, water-soaked, light-brown lesions on the pod surface, typically at the base or tip where moisture accumulates. These lesions expand rapidly under humid conditions, turning dark brown to black and potentially girdling the pod within days (Perrine-Walker, 2020; Nyassé *et al*., 1995). As infection progresses, the pod tissue becomes necrotic and flaccid. A hallmark of active infection is the appearance of white, cottony sporulation (sporangiophores and sporangia) within 2–4 days under moist conditions (Iwaro *et al.*, 2005).

Disease severity increases with pod maturity, as older pods are more susceptible due to changes in cuticle and defense compound profiles (Nyassé *et al*., 1995). Infection often originates from pod surfaces contacting the trunk or from rain splash, affecting lower canopy pods more frequently. In severe cases, infection extends to the peduncle and adjacent stem tissue, forming cankers that can girdle and kill young plants.

Though foliar symptoms are rare in natural settings, artificial inoculation can induce necrotic leaf lesions and chlorosis useful for screening resistant genotypes (Pokou *et al*., 2019). Environmental conditions such as high humidity (>90%), frequent rainfall and warm temperatures (25–30°C), especially during the rainy season, favor disease development (Opoku *et al*., 2007).

Symptom variability is influenced by host genotype. Resistance may be expressed as reduced lesion expansion, slower disease progression, or limited sporulation. This resistance is categorized into penetration resistance (blocking initial infection) and post-penetration resistance (limiting spread) (Pokou *et al*., 2019; Iwaro *et al*., 2005).

Symptomatology of Phytophthora induced Stem Canker in Cocoa

In addition to black pod, *Phytophthora* species such as *P. palmivora*, *P. megakarya* and *P. capsici* are also responsible for stem canker, a serious yet often overlooked disease of cocoa. Unlike pod rot, stem canker progresses more insidiously, leading to branch dieback, chronic decline, and tree mortality if unmanaged (Nyassé *et al*., 1997; Guest, 2007).

Infections typically begin through wounds or natural openings at the base of pods, branch junctions, or trunk surfaces. Early symptoms include sunken, water-soaked lesions that darken and enlarge longitudinally and circumferentially. As the disease progresses, bark tissues may crack and slough off, exposing necrotic internal tissues with reddish to purplish discoloration (Iwaro *et al*., 2003; Thevenin *et al*., 2009).

A distinct reddish-brown exudate may ooze from active lesions in humid conditions, and in susceptible clones, cankers can girdle stems, block vascular tissues, and cause dieback or death (Perrine-Walker, 2020). In young plants, stem collapse may occur rapidly. Histologically, *Phytophthora* invades cortical and vascular tissues, damaging cambial layers and xylem integrity. While resistant clones may limit infection via callus formation, susceptible genotypes show delayed or ineffective defense (Diniz *et al*., 2017).

Stem cankers may persist as chronic lesions, acting as sources of secondary inoculum, releasing sporangia during rains and spreading the disease via splash dispersal (Opoku *et al*., 2000). Environmental conditions such as high humidity (>90%), prolonged wetness, and temperatures of 25–30°C are highly conducive to canker development and spread. Shaded, poorly ventilated plantations often experience greater disease severity (Thevenin *et al*., 2009).

Clonal resistance varies significantly. Resistant genotypes typically exhibit smaller, self-limiting cankers with defined margins, while susceptible clones show rapidly expanding, diffuse lesions. These differences are important for resistance breeding and cultivar selection (Iwaro *et al*., 2003; Pokou *et al.*, 2019).

Symptomatology of *Phytophthora*-Induced Diseases in coconut

Among the major diseases affecting coconut bud rot caused by *P palmivora* is one of the most lethal, especially in humid tropical regions. The disease poses a significant threat to coconut cultivation, as it targets the apical meristem the only growing point of the palm and typically results in plant death if not diagnosed and managed early (Manoharachary *et al.*, 2005; Iyer and Rasmi, 2005).

Initial symptoms

The disease commonly begins with infection of the youngest unopened leaf, also known as the spindle or spear leaf. The first visible symptom is yellowing and wilting of the spindle leaf, which soon becomes necrotic and brown. At this stage, one of the diagnostic signs is that the spindle leaf can often be pulled out easily, as the pathogen degrades tissues at its base (Rao *et al.*, 2014). Upon removal, the base of the leaf is typically water-soaked, discolored, and emits a foul odor due to bacterial and fungal secondary colonization of decaying tissues.

Progression of symptoms

As the infection progresses, the apical bud undergoes necrosis, leading to the collapse of new leaf emergence. This is a critical stage because the apical meristem is the only growing point in monocotyledonous palms. Once it is destroyed, no new leaves can form, and the palm eventually dies. Following bud death, the older leaves begin to lose turgor, show yellowing or browning, and progressively dry out from the crown downward. In some cases, rotting may extend downward into the central stem tissues, producing a soft, mushy core with a characteristic odor (Broschat and Elliott, 2005).

In younger palms and seedlings, disease progression is faster, often leading to complete death within a few weeks of symptom onset. In mature palms, however, the process may be more prolonged, with a noticeable period of crown decline before death occurs. Depending on environmental conditions, particularly high humidity and rainfall, visible symptoms can develop and intensify rapidly (Iyer and Rasmi, 2005).

Morphological Features and Field Diagnosis

The affected crown often exhibits a sunken or depressed appearance, especially after the top leaves have wilted or fallen off. Cross-sectioning of infected crowns reveals dark brown to black necrosis of internal tissues. Sporulation of *Phytophthora* may be observed under moist conditions as a whitish mycelial mat, although sporulation is not always prominent in the field.

Because early external symptoms are subtle and resemble abiotic stress or insect damage, field diagnosis can be challenging. Laboratory isolation and identification of *P palmivora* are often needed for confirmation (Maheswarappa, 2023).

Disease Favorability and Spread

Environmental conditions play a crucial role in symptom expression and disease progression. Bud rot is most prevalent during monsoon and post-monsoon seasons, when high rainfall, warm temperatures (25–30°C), and poor drainage create an ideal environment for pathogen activity. The disease is favored by waterlogged conditions, which stress the palm and facilitate zoospore mobility and infection (Manoharachary *et al*., 2005).

Disease transmission occurs through rain splash, infected tools and possibly through soil or planting material. The pathogen may survive in infected plant debris or in alternate hosts, posing challenges to eradication and containment.

Resistance and Symptom Variation

Some coconut cultivars and hybrids exhibit partial resistance, where infection may be delayed or confined to non-lethal symptoms such as spindle yellowing without full bud necrosis. These resistant palms may recover if managed promptly. However, most traditional tall cultivars, such as the West Coast Tall are highly susceptible, showing rapid symptom development and high mortality (Maheswarappa, 2023; Iyer and Rasmi, 2005).

Epidemiology of *Phytophthora* diseases in Cocoa

Phytophthora species represent some of the most destructive pathogens affecting cocoa, causing a range of diseases including black pod rot, stem cankers and seedling blight. Over the decades, epidemiological studies have significantly advanced our understanding of pathogen spread, environmental influences, and effective control strategies.

Distribution, Spread and Host range

In West Africa, *P megakarya* has emerged as a dominant and highly aggressive species. A longitudinal study by Akrofi *et al*. (2015) tracking the spread of *P. megakarya* in Ghana from 1985 to 2012 revealed a dramatic expansion from localized outbreaks in Akomadan and Bechem to more than 50 administrative districts. Interestingly, the pathogen was also isolated from asymptomatic non-cacao "economic plants" such as shade and intercrop species, suggesting these may serve as alternative hosts or inoculum reservoirs, thus complicating control efforts (Akrofi *et al*., 2015).

In southwestern Côte d'Ivoire (Méagui department), the incidence of black pod disease was found to be significantly influenced by plantation management and canopy density. Foliar coverage and poor hygiene were positively correlated with disease prevalence, with *P. megakarya* responsible for approximately 79% of infections and *P. palmivora* for the remaining 21% (Oro *et al*., 2020). These findings reinforce the notion that cultural practices play a pivotal role in disease dynamics.

Mapping the regional movement of *P. megakarya*, Akrofi (2014) reported its westward spread from Cameroon through Nigeria and Togo into Ghana and Côte d'Ivoire, as well as southward into Gabon and Equatorial Guinea. Its rapid dissemination is attributed to both natural dispersal mechanisms and anthropogenic factors such as trade and movement of planting material.

Temporal and Spatial Patterns of epidemics

A multi-year study conducted between 2009 and 2016 in Ghana examined the spatial and temporal development of *P. megakarya* epidemics in newly planted cocoa plots. Early infections appeared randomly, indicating exogenous sources of inoculum. However, as time progressed, infection patterns became aggregated, with significant spatial autocorrelation observed at distances of 3 to 9 meters, suggesting short-distance spread through rain splash and canopy drip (Ofori *et al*., 2020).

Canopy height also influences infection dynamics. Classic studies by Weststeijn (1969) demonstrated that pods situated closer to the ground were more susceptible, likely due to higher humidity, prolonged wetness, and pathogen propagule splash from soil surfaces.

Climatic variables particularly rainfall, humidity, and temperature exert significant influence on epidemic severity. In Côte d'Ivoire, black pod incidence was found to correlate positively with rainfall and humidity across multiple localities, with variations attributed to microclimatic conditions (Fofana *et al*., 2025).

Pathogen Diversity, Inoculum Sources and Genetic structure

Molecular epidemiological studies have shed light on the genetic diversity and structure of *Phytophthora* species infecting cocoa. In Malaysia, Alsultan et al. (2021) analyzed *P. palmivora* isolates using ITS rDNA, COX1 and EF-1á markers, along with RAPD and ISSR profiling. The results revealed significant intraspecific diversity and regional clustering, suggesting multiple introductions or long-standing population subdivision.

In Ghana, Akrofi *et al*. (2015) observed diverse morphological characteristics among *Phytophthora* isolates from both symptomatic cocoa tissues and non-cacao economic plants. However, molecular and microscopic analyses confirmed that most isolates were either *P. megakarya* or *P. palmivora*, with the former being predominant. The ability of *P. megakarya* to survive and multiply in alternative hosts increases the complexity of its epidemiology.

Environmental Drivers and Cultural factors

Environmental conditions such as high relative humidity, frequent rainfall, warm temperatures, and poor drainage are crucial for disease initiation and spread. Studies have shown that lower canopy levels, leaf litter, and pod debris act as focal points for inoculum build-up, facilitating rapid infection under humid conditions (CABI, 2020).

Cultural practices also exert considerable influence on epidemic outcomes. Oro *et al.* (2020) showed that good agronomic practices such as regular pruning, shade regulation, and sanitation reduced disease prevalence significantly. In contrast, poorly maintained plantations with dense canopy and abundant plant debris experienced higher disease incidence.

Implications for Disease Onset, Epidemic Growth, and control

The onset of *Phytophthora*-induced epidemics in cocoa plantations typically results from exogenous inoculum sources, such as infected pods, rain splash from infected debris, or contaminated tools. Once established, localized spread through rain splash, sporangial dispersal, and potentially insect vectors contribute to rapid spatial expansion. The pathogen's capacity to produce various spore types, survive in plant debris and colonize alternative hosts makes it particularly resilient and challenging to control (Akrofi *et al*., 2015; Alsultan *et al*., 2021).

Management strategies must therefore focus on integrated approaches, including early detection, removal of infected materials, proper shade and moisture management, and deployment of resistant or tolerant varieties. However, the genetic variability observed in pathogen populations suggests that resistance breeding efforts must consider regional pathogen diversity to ensure long-term effectiveness.

Epidemiology of *Phytophthora* diseases in coconut

P. palmivora is a major pathogen causing bud rot and premature nut fall in coconut, particularly under humid tropical conditions. Extensive epidemiological studies across regions such as India, Indonesia, and the Philippines have contributed valuable insights into inoculum sources, cultivar susceptibility, environmental influences and disease spread dynamics.

In Kerala, India, Iyer and Rasmi (2005) reported higher bud rot incidence in hilly tracts (e.g., Kasaragod, Kannur, Calicut) compared to plains, correlating with higher humidity and cooler night temperatures. *P. palmivora* propagules were found in the soil, root zones, and crown debris of both healthy and diseased palms. Rain splash was confirmed as a major dispersal mechanism, as rainwater from infected gardens carried viable propagules (Iyer and Rasmi, 2005).

Cultivar-based differences were noted by Bachiller (n.d.) at the Davao Research Center (Philippines), where hybrid cultivars like CAMT × Malayan Red Dwarf had higher *P. palmivora* inoculum densities in soil and crown debris than dwarf types. This suggests that hybrids may act as stronger pathogen reservoirs due to susceptibility or microbe-environment interactions.

Microclimatic studies by Giyanto (2002) in Indonesia indicated that moderate canopy shading (75%) reduced disease intensity, with optimal temperatures (25–30°C) and 75% relative humidity suppressing lesion development. In contrast, open fields (0–50% shade) experienced greater disease pressure, likely due to faster drying and micro-injury to the crown.

A novel vector pathway was reported in southern India by Sharadraj and ChandraMohanan (2015), who identified slugs (*Deroceras* sp.) as vectors of *P. palmivora*. Slug feces collected from endemic areas contained viable propagules, showing their role in disease dissemination, especially during rainy seasons.

In terms of temporal dynamics, peak incidence in Kerala aligns with the monsoon and post-monsoon periods, with infections persisting into January due to sustained favourable humidity and temperatures. Propagules also survive during drier months in crown debris, creating a latent inoculum reservoir (Iyer and Rasmi, 2005).

In plantation settings, Brahmana and Kelana (1987) reported a block-wise spread of bud rot in hybrid coconut (PB121) estates in North Sumatra, with uniform infestation in mature (>4-year-old) palms. Incidence reached 9% in monoculture blocks, indicating that homogeneous plantings and age structure facilitate rapid horizontal spread.

Importantly, epidemiological forecasting models developed in Kerala used temperature, humidity, and rainfall data to predict disease outbreaks in endemic zones, offering potential tools for early intervention and precision disease management (Iyer and Rasmi, 2005).

Disease Physiology and Host–pathogen Biochemical Interactions in *Phytophthora* diseases of Cocoa

Pathogen Infection Strategy and Initial interaction

P. palmivora and *P. megakarya*, hemibiotrophic oomycetes, initiate infection through sporangia or motile zoospores that land on cocoa tissues and germinate to form appressoria or haustoria for host penetration and nutrient uptake (Perrine-Walker, 2020). The pathogen initially maintains host cell viability (biotrophy) before switching to a necrotrophic phase marked by the release of cell wall-degrading enzymes and toxins causing tissue necrosis.Host anatomical features such as stomatal density, wax thickness, and exocarp toughness influence early lesion formation. However, post-penetration lesion development is governed more by biochemical defenses than by structural traits (Iwaro *et al*., 1997).

Preformed and Induced Host Biochemical Defenses

Cocoa exhibits preformed chemical defenses, notably clovamide, a hydroxycinnamic acid amide (HCAA), which has shown significant antifungal activity. Resistant genotypes like *Scavina 6* contained up to 58 times more clovamide than susceptible ones like *ICS1* and this compound inhibited pectinase and protease activity *in vitro* (Knollenberg *et al*., 2020). Other induced phenolics, including flavonoids, proanthocyanidins and HCAAs, also accumulate in resistant clones. Genes in the phenylpropanoid pathway are notably upregulated during infection, affirming the pathway's central role in defense (Rêgo, Mora-Ocampo and Corrêa, 2023).

Immune Recognition, ROS Generation and Defense Signaling

Upon detection of pathogen-associated molecular patterns (PAMPs), cocoa activates pattern-triggered immunity (PTI). Resistant genotypes exhibit faster and stronger PTI responses, including ROS bursts and PR gene expression (Perrine-Walker, 2020).

Reactive oxygen species (ROS), such as hydrogen peroxide, act as both antimicrobial agents and signaling molecules. However, excessive ROS is controlled by peroxidases and superoxide dismutases to avoid host damage. Enhanced ROS regulation is a hallmark of resistant genotypes (Rêgo *et al*., 2023). Enzymes like â-1,3-glucanases, chitinases, and protease inhibitors further bolster resistance by degrading pathogen cell walls and neutralizing virulence factors. Clovamide's role in enzyme inhibition also supports its multifunctional defense role (Knollenberg *et al*., 2020).

Genetic and Molecular Basis of Resistance

Comprehensive genetic profiling has revealed that resistant genotypes show higher basal expression of defense-related genes and faster inducible responses post-infection. These include genes linked to ROS detoxification, amino acid metabolism (e.g., proline accumulation), and cell wall stabilization (Rêgo *et al*., 2023). QTL mapping and transcriptomics have identified candidate genes such as receptor-like kinases, peroxidases, and stress-responsive transcription factors that regulate defense pathways and hormonal responses.

Pathogen–Host Dynamics and Disease outcomes

During the necrotrophic phase, Phytophthora secretes cellulases, pectinases, and proteases to degrade host tissues. In turn, cocoa reinforces its cell walls with lignin and phenolics, and produces enzyme inhibitors to suppress pathogen advancement (Knollenberg *et al.*, 2020; Perrine-Walker, 2020). Resistant clones show delayed lesion development, reduced lesion size, and lower sporulation, indicating that both biochemical and anatomical defenses collectively modulate disease severity and progression.

Disease Physiology and Host–pathogen Biochemical interactions in *Phytophthora* Diseases of Coconut

Bud rot in coconut primarily caused by *P palmivora* Butl., is a severe disease that destroys the apical meristem (bud), leading to death of the palm if not detected in time (Iyer and Rasmi, 2005; Gangaraj and Rajesh, 2022). In recent years, molecular and biochemical studies have begun to clarify the interactions between host and pathogen that determine the speed, severity and potential for resistance or tolerance in various coconut genotypes.

Early Infection, Recognition and Host response

Infection begins when sporangia or zoospores of *P. palmivora* land on young tissues at the crown (spindle or spear leaf, bud region), especially under high humidity or wet conditions. Gangaraj *et al*. (2021) developed an *in vitro* leaf inoculation assay using surface sterilized spindle leaves and found that visible lesions appear within 12–24 hours post inoculation. Electrolyte leakage in these early hours indicated membrane perturbation, while histological sections showed epidermal and subepidermal cell loss and disruption, confirming that the pathogen damages host cell integrity very early in the infection process (Gangaraj *et al*., 2021).

A recent dual RNA seq study (Gangaraj, Rajesh, Jangam *et al*., 2024) tracked changes in both host and pathogen transcriptomes at 12, 24 and 36 hours post infection. In coconut, genes associated with stress response, plant–pathogen interaction and hormone signaling (notably in the ethylene and jasmonic acid pathways) were upregulated within these early time points. Meanwhile, *P. palmivora* differentially expressed effector genes and carbohydrate active enzyme (CAZy) genes, consistent with active penetration of host tissues and suppression of host defenses (Gangaraj *et al*., 2024).

Pathogen Virulence Factors and effectors

One detailed study by Gangaraj and Rajesh (2022) characterized an RXLR motif containing effector (RXLR6744) from *P. palmivora* isolated from bud rot disease in coconut. The open reading frame (ORF) is 411 bp, encoding a 136 amino acid protein (approx. 15.52/ kDa), predicted to possess six α helices. Phylogenetic analyses show that the effector is closely related to RXLR effectors in *P. palmivora* (cocoa black pod) and *P. megakarya*. Structural modelling, including Ramachandran plot analysis, indicated excellent stereochemical quality (96.3% residues in preferred regions) (Gangaraj and Rajesh, 2022). Such effectors are likely involved in suppressing or evading host immune responses during early infection.

Host Biochemical and Physiological responses

Biochemical defenses in coconut remain less comprehensively characterized than those in other tropical crops such as cocoa. However, emerging evidence from recent molecular and physiological studies highlights several key defense mechanisms that are activated during *P palmivora* infection.

Membrane Integrity and Electrolyte leakage

A rapid and early physiological response observed during infection is the loss of membrane integrity, which can be quantified through electrolyte leakage assays. Gangaraj *et al*. (2021) reported significant electrolyte leakage from coconut spindle leaves within 24 hours post-inoculation, indicating early-stage cellular disruption caused by pathogen ingress.

Histological damage

Microscopic observations revealed that *P. palmivora* causes physical and biochemical damage to the epidermal and subepidermal tissues during penetration and colonization. Histological changes include cell wall degradation and tissue maceration, consistent with enzymatic action from the invading pathogen (Gangaraj *et al.*, 2021).

Transcriptomic shifts

A dual RNA-seq study revealed significant transcriptional reprogramming in coconut during early infection (12–36 hpi). Upregulated genes were enriched for plant–pathogen interaction pathways, hormone signal transduction (ethylene and jasmonic acid) and stress response genes. These pathways likely include pathogenesis-related (PR) proteins, genes involved in reactive oxygen species (ROS) management and those associated with secondary metabolite biosynthesis (Gangaraj *et al.*, 2024).

Pathogen Enzyme activity and Host countermeasures

The same study revealed upregulation of *P. palmivora* carbohydrate-active enzyme (CAZy) genes, including those encoding pectinases and cellulases key effectors involved in host tissue degradation. These enzymatic attacks must be countered by the host through structural reinforcement of cell walls, PR protein production, or biochemical inhibitors, although the specific compounds involved in coconut remain largely uncharacterized (Gangaraj *et al.*, 2024).

Disease Progression and Physiological damage

Following initial pathogen entry and early host recognition, *P. palmivora* progresses to a destructive phase marked by extensive tissue necrosis. The disease leads to systemic deterioration of the apical region, especially the spindle leaf and bud tissues, culminating in the collapse of the shoot apex. Iyer and Rasmi (2005) noted that this cessation of new leaf development ultimately results in irreversible palm mortality. Observable symptoms include water-soaked lesions, browning, a characteristic foul odor, wilting of new leaves, and internal tissue disintegration (Gangaraj and Rajesh, 2022). These symptoms reflect both the necrotic activity of the pathogen and the systemic stress imposed on the palm through impaired vascular function and disrupted nutrient transport.

Molecular methods in Disease Indexing of *Phytophthora*

Molecular disease indexing involves identifying, mapping, or measuring genes, markers, or transcript profiles that correlate with resistance (or susceptibility) to *Phytophthora* in cacao. These methods include QTL mapping, association mapping, transcriptomics, marker development, gene expression profiling, and gene editing techniques. They allow more precise and early selection in breeding programs, and can uncover mechanisms of resistance.

QTL mapping and marker trait association

Quantitative Trait Loci (QTL) mapping has been widely used to locate genomic regions associated with resistance to *Phytophthora* spp. For example, *Risterucci et al.* (2003) identified QTLs related to cocoa resistance to three *Phytophthora* species (*P. palmivora*, *P. megakarya*, and *P. capsici*) using hybrid progenies in Côte d'Ivoire. They used leaf test inoculation, and mapped 151 hybrids with 213 molecular markers (190 AFLPs + 23 SSRs). They found QTLs in six genomic regions explaining between ~8 12% of phenotypic variance for individual QTLs, and between ~11.5 27.5% variance explained per strain overall. (Risterucci *et al* 2003;).

Association mapping / validation with SSR markers

The recent study "Structural and Functional Genomics of the Resistance of Cacao to *P palmivora*" (Mucherino *et al.*, 2021) validated 29 SSR markers flanking QTLs associated with resistance to *P. palmivora* in local ancient varieties from Bahia (Comum, Pará, Maranhão). They found four SSR loci significantly associated with resistance: two loci on chromosome 8 (explaining ~7.43% and ~3.72% of phenotypic variance), one on chromosome 2 (~2.71%) and one on chromosome 3 (~1.93%) variance. Additionally, they annotated candidate genes in the QTL regions (from *Criollo* and *Matina* reference genomes), finding genes with domains known for pathogen recognition (NBS LRR, RLK, etc.) (Mucherino *et al.*, 2021).

Transcriptomics / Differential Gene expression

Resistant vs susceptible genotype profiling: Resistant and susceptible cacao genotypes exhibit defense gene polymorphism and unique early responses to *P megakarya* inoculation was studied by comparing clone SCA6 (resistant) and NA32 (susceptible). Using RNA seq over a time course, the strongest transcriptomic response was seen ~24 h after inoculation in the resistant genotype. Key differentially expressed genes included pathogenesis related (PR) proteins, pattern recognition receptors (PRRs) and resistance (R) genes; also, polymorphisms in defense genes between genotypes. (Akrofi *et al*., 2019)

Pod transcriptome profiling: The work "Cacao pod transcriptome profiling of seven genotypes identifies features associated with post penetration resistance to *P palmivora*" compared seven cacao genotypes, some resistant (CCN51, Sca6, Pound7) and some susceptible (ICS1, WFT, Gu133, Spa9). Transcriptome (RNA seq) analysis after *P. palmivora* infection in pods revealed between ~1,600 and ~7,000 differentially expressed genes (DEGs) depending on genotype. They also identified correlation groups of genes, novel promoter motifs and candidates for post penetration resistance. (Fister *et al*., 2023).

Molecular Identification of Pathogen species

ITS PCR and RFLP: To differentiate species of *Phytophthora* infecting cacao, molecular methods of internal transcribed spacer (ITS) PCR followed by restriction fragment length polymorphism (RFLP) have been used. Appiah *et al*. (2004) amplified the ITS region (~900 bp) from isolates and digested with restriction enzymes (HaeIII, HinfI, PvuII and AluI) to distinguish *P. megakarya, P. palmivora* and *P. capsici*. This is useful in disease indexing insofar as correctly identifying which species are causing disease in a given population, since aggressiveness and resistance responses vary by species.

Preformed / Basal Expression of Defense genes

Some studies find differences in *basal* (pre infection) expression levels of defense associated genes in resistant vs susceptible genotypes, suggesting that higher constitutive expression may contribute to faster or stronger defense responses once challenged. For example, in the SCA6 vs NA32 study, there was differential basal expression of PRRs and defense genes before infection (Akrofi *et al*., 2019).

Phytophthora Disease Management in Cocoa and Coconut

Cultural methods

Cultural practices are fundamental in managing *Phytophthora* diseases in both cocoa and coconut by reducing inoculum levels and altering environmental conditions that favor disease development.

In cocoa, cultural strategies include regular removal of diseased pods, husks and plant debris, which reduces the primary inoculum (Rêgo, Mora Ocampo and Corrêa, 2023). Use of disease-free planting material and shade/ canopy management are crucial to limit humidity and improve pod drying (Rêgo *et al*., 2023). Ground mulching helps reduce soil splash dispersal of sporangia, and frequent harvest of ripe pods minimizes exposure time to infection (Rêgo *et al*., 2023).

In coconut, sanitation includes removal of infected buds, spindles, or crown tissues, pruning dead parts, and avoiding mechanical wounding that can facilitate pathogen entry (Prathibha *et al*., 2023; ICAR CCARI Goa). Good drainage is essential to prevent waterlogging, which promotes zoospore movement and infection (ICAR CCARI Goa; Iyer and Rasmi, 2005). Site selection, favoring hilly areas with better airflow and reduced humidity, may also reduce disease pressure (Iyer and Rasmi, 2005).

Chemical control

Chemical fungicides play a significant role in managing *Phytophthora* infections, especially during periods of high disease risk such as rainy seasons.

In cocoa, copper-based fungicides (e.g., Bordeaux mixture, copper oxychloride) are widely used to protect pod surfaces, while systemic fungicides like metalaxyl are employed to control internal infections (Rêgo *et al*., 2023). Fungicides are most effective when applied preventively or at early infection stages, with timing, rotation of fungicide modes of action, and dose optimization being critical to prevent resistance development (Rêgo *et al.,* 2023).

In coconut, Bordeaux mixture is frequently used as a preventive spray or paste applied to crown or wound sites (ICAR CCARI Goa). Field trials in Bangladesh showed chlorothalonil WP and other fungicides to be effective in reducing bud rot incidence (Prathibha *et al.*, 2023). Timing of application prior to or at early monsoon onset is crucial for successful disease management (Guest, 2002).

Biological control

Biocontrol agents offer eco-friendly alternatives or complements to chemical control, showing effectiveness against *Phytophthora* pathogens in both crops.

In cocoa, *Trichoderma* spp. and Pseudomonas spp. have demonstrated antagonistic effects against *Phytophthora* in vitro and in pod assays (Rêgo *et al.*, 2023). Additionally, endophytes derived from cocoa may enhance systemic resistance or compete with the pathogen for ecological niches (Rêgo et al., 2023). Integration with fungicides and cultural methods is encouraged and compatibility studies are necessary to prevent antagonistic interactions (Rêgo *et al.*, 2023).

In coconut, promising results have been observed with *Trichoderma asperellum*, *Bacillus subtilis* and AM fungi in nursery and field trials in Tamil Nadu, achieving over 70% disease suppression (Latha *et al*., 2023). Trichoderma coir pith cake was also effective in reducing bud rot in Bangladesh (Prathibha *et al*., 2023). These organisms may act through antagonism, competition or induced systemic resistance.

Screening and Host Plant Resistance

Host resistance remains the most sustainable, long-term strategy for managing *Phytophthora* diseases.In cocoa, resistance screening uses leaf disc, detached pod, and seedling assays to assess genotype responses. Standardization of inoculation methods (e.g., inoculum load, pod maturity, depth of inoculation) is vital for reproducibility (Iwaro, Sreenivasan and Umaharan, 1997; Rêgo *et al*., 2023). Genetic mapping tools such as QTL analysis and SSR markers have been used to associate molecular markers with *P. palmivora* resistance (Mucherino *et al*., 2021).

In coconut, resistance screening is less advanced, though variation in cultivar susceptibility has been observed. For example, hybrid cultivars in the Philippines (e.g., CAMT × Malayan Red Dwarf) exhibited higher propagule loads of *P. palmivora* in soil and leaf axils (Bachiller, 2005). Field epidemiological studies in Kerala also showed differing disease incidence based on cultivar and microclimate, supporting the possibility of selecting for resistant lines (Iyer and Rasmi, 2005). However, molecular breeding tools are still in early development stages for coconut.

Integrated Disease Management (IDM)

Integrated approaches combining cultural, chemical, biological, and host resistance methods are essential for sustainable and effective *Phytophthora* control.

In cocoa, IDM includes synchronized application of fungicides, biocontrol agents, resistant varieties, and field sanitation to minimize pathogen load and delay fungicide resistance (Rêgo *et al.*, 2023). Resistance must be evaluated across different infection stages (penetration vs. post-penetration resistance) and under field conditions, as performance can vary across environments (Iwaro *et al*., 1997; Rêgo *et al*., 2023).

In coconut, IDM involves combining nursery hygiene, disease-free planting material, mulching, organic amendments and timed fungicide applications (Chowdappa and Hegde, 2019; Guest, 2002). Multiyear integration of Trichoderma, chemical fungicides and sanitation has shown effective control of bud rot (Prathibha *et al*., 2023). Overall, IDM ensures long-term disease suppression with reduced environmental and economic costs.

Nanotechnology in management of *Phytophthora* Diseases in Cocoa and coconut

Phytophthora spp. are destructive oomycete pathogens that significantly affect tropical crops, notably causing black pod disease in cocoa and bud rot in coconut. The conventional approach of fungicide reliance is increasingly unsustainable due to pathogen resistance, environmental hazards, and rising costs (Manisha *et al*., 2025). Nanotechnology defined by the application of materials and systems within the 1–100 nm scale has emerged as a frontier for innovative disease management strategies (Zul Arham *et al*., 2024).

Types of Nanotechnologies explored against *Phytophthora*

Metal and Metal Oxide nanoparticles

Silver-doped titanium dioxide (TiO_2 –Ag) nanoparticles have demonstrated potent antifungal activity against *P palmivora*, particularly under visible light conditions. A nanosuspension with Ag-incorporated TiO_2 microspheres (~92.4 nm) was found to significantly inhibit fungal growth at a 0.5% concentration (Zul Arham *et al*., 2024).

Similarly, nano-carbon self-doped TiO_2 (C/TiO_2) composites, synthesized via sol-gel methods, showed broad-spectrum disinfection capability against *P. palmivora* (Muhammad Nurdin *et al*., 2023). These nanocomposites harness visible-light-activated photocatalysis to generate reactive oxygen species (ROS).

Zinc oxide nanoparticles (ZnO-NPs), though not widely studied in cocoa or coconut, have shown promising antifungal properties in related crops like durian (*Durio zibethinus*), with inhibition of *P. palmivora* growth at particle sizes of 25–50 nm (Acta Horticulturae, cited in Manisha *et al*., 2025).

Green-Synthesized and Botanical nanoparticles

AgNPs synthesized using *Artemisia absinthium* extract displayed effective inhibition of several *Phytophthora* spp., including *P. palmivora*, with low IC_{50} values (Ali *et al*., 2022). These biogenic nanoparticles disrupt mycelial development and zoospore germination.

Citronella oil nanoemulsions have been evaluated for black pod disease management in cocoa. The nanoemulsion significantly improved the stability and reduced volatility of the oil, enhancing in vitro and in vivo efficacy against *P. palmivora* (Harni *et al.*, 2020).

In coconut, AgNPs synthesized from coconut coir and medicinal plant extracts have shown general antimicrobial activity, though direct evidence against *Phytophthora* in planta remains limited (Asrul *et al.*, 2024).

Mechanisms of Antifungal / Anti-oomycete action

Nanoparticles exhibit antifungal action through several mechanisms. Physical disruption of the pathogen's cell wall and membrane is commonly observed, especially with metallic nanoparticles like Ag and TiO_2 (Raquel Villamizar-Gallardo *et al*., 2016).

Another primary mechanism is the generation of ROS, particularly under light activation, as seen in TiO_2-based nanomaterials (Muhammad Nurdin *et al.,* 2023; Mesoporous Silica Study, 2023). These ROS induce oxidative stress, damaging cellular components and inhibiting pathogen growth.

Additionally, the release of toxic metal ions such as Ag^{+} or Zn^{2+} from nanoparticles enhances antimicrobial action. Nano-carriers and emulsions further contribute by improving the stability and slow release of active ingredients, leading to prolonged efficacy.

Specific Studies in Cocoa and Coconut

TiO_2 is Ag formulations have shown significant in vitro and ex vivo efficacy against *P. palmivora* in cocoa pods under visible light (Zul Arham *et al*., 2024). Likewise, nano-carbon doped TiO, composites offer promise for development into nano-spray formulations (Muhammad Nurdin *et al*., 2023).

Citronella oil nanoemulsions demonstrated effective inhibition of *P. palmivora* both in vitro and on cocoa pods, suggesting their potential as eco-friendly alternatives to synthetic fungicides (Harni *et al.,* 2020).

Although, less direct work has been done in coconut, liquid smoke derived from coconut fiber has shown biofungicidal activity against *P. palmivora in vitro* (Asrul *et al*., 2024). Most coconut-related research currently emphasizes biocontrol agents like *Trichoderma* spp. rather than nanoparticle technologies (Manisha *et al*., 2025).

Advanced Formulations and Novel Delivery systems

In parallel with molecular diagnostics and resistance breeding, advancements in formulation technologies particularly nano- and bio-formulations have opened promising new avenues for managing *Phytophthora* spp. in tropical crops like cocoa and coconut. These advanced delivery systems aim to enhance the efficacy, specificity, and environmental safety of disease control interventions.

Nano-carriers for enhanced Fungicide delivery

One of the most promising strategies involves the use of nanocarriers to improve the delivery of conventional fungicides. For instance, a study by Salinas *et al.* (2025) developed nanocapsules loaded with fluazinam, a broad-spectrum fungicide, and tested them against *P cinnamomi* in walnut. The nanoformulated fluazinam exhibited significantly higher inhibitory activity than the conventional formulation, with better adhesion to the plant surface and reduced fungicide leaching. Although this work focused on walnut, the nanocarrier approach is highly transferable to cocoa and coconut systems, where systemic movement and canopy penetration are critical for controlling diseases such as black pod and bud rot (Salinas *et al.,* 2025).

RNA Interference (RNAi)-based Nanoformulations

Recent advances in RNA interference (RNAi) offer pathogen-specific strategies that can be delivered through nanocarriers. RNAi involves silencing of essential or virulence-associated genes in the pathogen via double-stranded RNA (dsRNA) or small interfering RNA (siRNA). However, RNA molecules are unstable in the field environment, limiting practical application. Nanoformulations using lipid nanoparticles, chitosan, or polymeric nanocarriers have emerged as a solution to protect RNA molecules and facilitate their uptake by the pathogen. A recent review by Mathur *et al.* (2025) highlights the potential of these RNAi-based nanoformulations in targeting *Phytophthora* effectors and regulatory genes, representing a frontier in biocompatible, precise disease control that may be particularly beneficial in high-value crops such as cocoa and coconut .

Diagnostics for Timely Disease management

Timely detection is a critical aspect of disease management. Molecular diagnostic tools such as quantitative PCR (qPCR), loop-mediated isothermal amplification (LAMP) and multi-locus sequence typing (MLST) are increasingly being adopted for early and accurate detection of *Phytophthora* pathogens in both soil and plant tissues. For example, the use of SSR markers and QTL mapping in cocoa has facilitated the identification of resistance loci associated with black pod resistance, enabling marker-assisted selection (MAS) in breeding programs (Batista *et al*., 2021). These diagnostic tools can inform targeted fungicide applications and reduce unnecessary treatments, aligning with integrated disease management goals.

High-throughput Proteomics for Effector and Biomarker Discovery

Proteomic profiling of *P. palmivora* has also provided insights into host-pathogen interactions. A recent study successfully identified over 8,000 proteins from the mycelial proteome of *P. palmivora*, including a number of candidate effectors expressed during early infection stages (Gangaraj and Rajesh, 2022). These proteins offer potential as biomarkers for diagnostics or as targets for novel inhibitors. High-throughput proteomics not only aids in functional annotation of pathogen genomes but also supports the development of precision fungicides or RNAi constructs aimed at essential proteins.

In summary, advanced delivery systems such as nanocapsule-based fungicides, RNAi-enabled pathogen gene silencing, molecular diagnostics and omics-driven target discovery represent a multifaceted strategy to combat *Phytophthora* in cocoa and coconut. These innovations, although still emerging in field applications, promise to complement existing integrated disease management (IDM) practices with greater precision and sustainability.

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