

Review Article

Host Range and Control Strategies of *Phytophthora palmivora* in Southeast Asia Perennial Crops

Nadhirah Misman¹, Nurul Hidayah Samsulrizal^{1,2}, Abdul Latif Noh^{1,2}, Mohd Aswad Wahab³, Khairulmazmi Ahmad³ and Nur Sabrina Ahmad Azmi^{1,2*}

¹Department of Plant Science, Kulliyah of Science, International Islamic University Malaysia, Pahang, Malaysia

²Plant Productivity and Sustainable Research Unit, Kulliyah of Science, International Islamic University Malaysia, Pahang, Malaysia

³Department of Plant Protection, Faculty of Agriculture, Universiti Putra Malaysia, Selangor, Malaysia

ABSTRACT

Phytophthora palmivora is a destructive plant pathogenic oomycete that has caused lethal diseases in a wide range of hosts. It is a pan-tropical distributed pathogen that can infect plants at all growth stages. Extensive studies have linked *P. palmivora* to severe diseases in several crops, such as black pepper, rubber, cocoa, and durian, causing global economic losses. This review covers the following topics in depth: (i) *P. palmivora* as phytopathogen; (ii) identification and infection mechanism in rubber, cocoa, and durian; and (iii) management and control applied for *P. palmivora* diseases. Effective management strategies were studied and practiced to prevent the spread of *P. palmivora* disease. Genetic resistance and biocontrol are the best methods to control the disease. A better understanding of *P. palmivora* infection mechanisms in our main crops and early disease detection can reduce the risk of catastrophic pandemics.

Keywords: Cocoa, disease control, durian, *Phytophthora palmivora*, rubber

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E-mail addresses:

nadhmisman@gmail.com (Nadhirah Misman)

hidayahsamsulrizal@iiium.edu.my (Nurul Hidayah Samsulrizal)

latifnoh@iiium.edu.my (Abdul Latif Noh)

mohdaswad@upm.edu.my (Mohd Aswad Wahab)

khairulmazmi@upm.edu.my (Khairulmazmi Ahmad)

sabrinaazmi@iiium.edu.my (Nur Sabrina Ahmad Azmi)

* Corresponding author

INTRODUCTION

Food security has become a global issue affecting the agricultural revenue of many countries. The rising costs of overcoming challenges have driven up the price of staple foods. Pests and diseases are important biotic factors that cause over 20% to 40% of agricultural productivity, affecting the

global economy (Oerke, 2006). Agriculture provides endless wealth and nutrition to tropical people. Crops (such as cocoa, coconut, and rubber), fruits (such as durian, jackfruit, papaya, and pineapple), and root crops (such as potato and taro) were initially planted for domestic consumption. These crops have recently gained popularity in tropical regions and are now one of the country’s primary sources of agricultural income. Lethal diseases caused by the *Phytophthora* genus have always posed a significant threat to crop yield and have a global impact on the agricultural industry.

Phytophthora is a genus of destructive plant-pathogenic oomycetes responsible for economic losses in agriculture and ecosystem damage worldwide. *Phytophthora*

means “plant destroyer” and was initially classified within the fungi kingdom until a phylogenetic study revealed the differences between oomycete and true fungi (Vanegtern et al., 2015). More than 150 *Phytophthora* species have been identified and could cause devastating diseases in annual and perennial crops in tropical and temperate regions (Yang et al., 2017). *Phytophthora* species vary greatly in host specificity as they could infect multiple plants from different families, while others are host-specific (Latifah et al., 2018). *Phytophthora palmivora* is highly virulent and can have a significant impact on the production of valuable crops, as well as the economies of the leading agricultural producing nations (Table 1).

Table 1
The total production of rubber, cocoa, durian, and oil palm in selected Southeast Asian countries and estimated average loss caused by *Phytophthora palmivora* diseases

Crop	Country	Production (Metric tons)	Disease loss (%)	References
Rubber	Malaysia	705,292 ^a	30-50	Sunpapao and Pornsuriya (2014)
	Indonesia	3,801,631 ^a	30-50	
	Thailand	5,335,134 ^a	30-50	
	Philippines	475,840 ^a	30-50	
	Vietnam	1,306,412 ^a	30-50	
Cocoa	Malaysia	1108 ^a	20-30	Hebbar (2007)
	Indonesia	734,796 ^a	20-30	
	Thailand	125 ^a	20-30	
	Philippines	9358 ^a	20-30	
	Vietnam	NA	NA	
Durian	Malaysia	390,635.44 ^c	20-30	Drenth and Sendall (2004)
	Indonesia	128,376 ^b	20-30	
	Thailand	1,017,097 ^c	20-30	Drenth and Sendall (2004)
	Philippines	79,280 ^d	20-30	
	Vietnam	434,179 ^f	10	Thao et al. (2020)

Note. ^aFood and Agriculture Organization of the United Nations (FAO) (2019); ^bMinistry of Agriculture of The Republic of Indonesia (MOA) (2016); ^cDepartment of Agriculture (DOA) (2019); ^dPhilippine Statistics Authority (PSA) (2019); ^eThongkaew et al. (2021); ^fThao et al. (2020)

**MODE OF ACTION OF
PHYTOPHTHORA PALMIVORA**

Phytophthora species use a hemibiotrophic lifestyle, infecting and feeding on living cells during the biotrophic phase, then on dead or dying cells during the necrotrophic phase to colonize and feed on living host cells. Extensive research suggests this lifestyle is a driving force underpinning the success of *Phytophthora* species. *Phytophthora* reproduces sexually via dispersal spores (sporangia and zoospores) and asexually via resting spores (oospores and chlamydozoospores) (Figure 1) (Erwin & Ribeiro, 1996; Judelson & Blanco, 2005; Perrine-walker, 2020). Sporangia and zoospores help *Phytophthora* species to spread and escape from the deteriorating environment, whereas chlamydozoospores are reserved and remain viable in the soil for a long time, waiting for favorable and conducive conditions for sporulation and dispersal (Butubu, 2016).

In favorable humid conditions, the flagellated zoospores swim chemotactically or electrostatically onto plant tissue and encyst in soil water or thin water film chemotactically or electrostatically (Butubu, 2016; Widmer, 2014). The germ tube then emerged from the mononucleate cyst. During cyst germination, the nucleus in the cyst undergoes closed mitosis and travels actively in the bilateral movement. The ability of the nucleus to form a hydrodynamic shape helps to maintain long distances and free flow movements within the elongated hyphae. (Evangelisti et al., 2019).

Unlike fungi, oomycetes lack melanins and septins needed for appressorium formation. Instead, *Phytophthora* penetrates its hosts by utilizing hyphal slicing, also known as the naifu mechanism, which cuts through the host surface at an oblique angle with minimal energy. This strategy facilitates the oomycete invasion through actin-mediated polar force application that

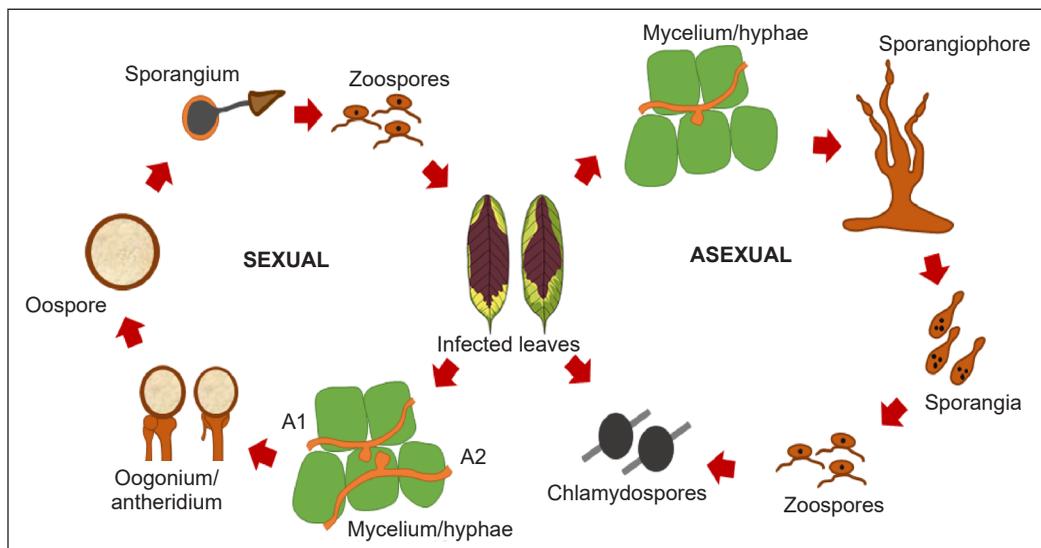


Figure 1. The life cycle of *Phytophthora palmivora*

helps disrupt the targeted host's cytoskeletal structure. The turgor pressure produced and the disruption of the cytoskeleton structure will allow the hyphae to invade through the crack along the direction of the oblique angle, initiating the host surface fracture (Bronkhorst et al., 2021). These discoveries of the *Phytophthora* infection mechanism can be a good initiative to develop durable resistance in the plant by interrupting the crucial steps during nuclear movement and hyphal slicing.

FACTORS CONTRIBUTING TO *PHYTOPHTHORA PALMIVORA* INFECTION

In the intervening years, extensive studies have explored the driving factors of *P. palmivora* in invading and colonizing their hosts. The hot-humid tropical climate in Malaysia and other Southeast Asian countries with high annual rainfall is ideal for developing and spreading *P. palmivora* diseases (Lee & Lum, 2004). A high humidity area or even a splash of water will make it easier for the flagellated zoospores to swim and infect the hosts. On top of that, the geographical area of the infected crops is also one contributing factor. For instance, flat open areas and lower areas of the fields where irrigation water may accumulate are favorable for *Phytophthora* species infection (Pscheidt & Ocamb, 2022).

The transmission of *P. palmivora* is most likely accelerated by numerous biotic and abiotic factors, such as extreme weather events that play a crucial multifaceted role in various ecological communities and interactions (Mohamed Azni et al., 2019).

Global warming poses significant impacts on plant and animal diseases, thus threatening food security (Mariette et al., 2016). The exceptional high temperature will cause heat stress on plants and significantly accelerate soil water evaporation, thus decreasing soil moisture content making the soil drier, and eventually causing soil erosion. Soil erosion causes excessive nutrient leaching, decreasing resistance to plant pathogen infection, and causing new strains and diseases to emerge (Paterson et al., 2013).

Drastic climate changes have high impacts on the modification and evolution of an individual, population, species, or even ecosystems (Bellard et al., 2012). In host-pathogen interaction, climate change exerts significant influence on the pathogen evolutionary adaptation pattern and host resistance by affecting important stages of the life cycles of either or both hosts and pathogens, as well as their reproductive mechanisms, dispersal ability, and their interactions with other biotic and abiotic factors in the environment (Addison et al., 2013; Dysthe et al., 2015; Eastburn et al., 2011; Mboup et al., 2012; Urban Mark et al., 2012). Some hosts might struggle to adapt well to the changing environment, thus allowing the pathogens that could evolve rapidly and adapt to the abrupt changes in thermal environments to invade easily (Paterson et al., 2013). *Phytophthora* species that are well known for their high adaptability skills are not exceptional. Temperature acclimation notably enhances *Phytophthora*'s fitness and genetic adaptation at both low and high

temperatures by increasing their colony size and aggressiveness (Wu et al., 2020). Additionally, Paterson (2020) predicted that *P. palmivora* can still infect all the oil palms that survived extreme global warming by 2050 and, even worse, cause the emergence of *P. palmivora* diseases in oil palm plantations in Malaysia and Indonesia if there are no extra protective measures taken.

On top of that, global migration is also known as one of the crucial key points that cause plant pathogen evolution. Wang et al. (2020) suggested that *P. palmivora* is a native pathogen of South American hosts that has spread and diversified in Southeast Asia. Single colonization of *P. palmivora* on cocoa was responsible for the global pandemic of black pod rot disease in cocoa and the migration of *P. palmivora* infection to other hosts (Wang et al., 2020). Global trade and migration have exposed plant pathogens to new hosts, facilitating host jumps (Zhan et al., 2015).

HOST RANGE OF *PHYTOPHTHORA PALMIVORA*

Phytophthora palmivora is a threatening tropical and subtropical oomycete that infects a wide range of hosts worldwide. Recent reports suggest that *P. palmivora* had attacked over 170 species of agricultural and horticultural plants, causing huge production losses (Drenth & Guest, 2013). In addition to attacking different hosts, *P. palmivora* can infect multiple plant tissues such as roots, stems, flowers, leaves, and fruits of individual plant species - all at once.

Rubber (*Hevea brasiliensis*)

The rubber tree (*Hevea brasiliensis*) is a tropical crop native to South America cultivated for its latex, which is known as the primary source of rubber in the rubber industry. Until the late 1980s, Malaysia was the world's largest rubber producer before Indonesia and Thailand took over (Balsiger et al., 2000; Ratnasingam et al., 2011). Rubber plantations require well-distributed high annual rainfall, deep and well-drained soils, stable high temperatures, and continuous moisture throughout the year to produce high-quality latex. A young rubber tree can tolerate temperatures as low as 15 °C for extended periods. However, prolonged exposure to low temperatures and dry conditions for more than 2 to 3 months will reduce the quantity and quality of latex produced.

The environment where the rubber is planted makes them vulnerable to diseases caused by *P. palmivora*. In Thailand, leaf fall epidemics happen during high rainfall (June to December), when rain splashes spread pathogen zoospores from infected leaves onto a trapping panel (Johnston, 1989). *Phytophthora palmivora* causes black stripe and abnormal leaf fall, reducing latex production globally (Verheye, 2010). Both diseases were reported in almost all countries where *H. brasiliensis* were planted, such as Malaysia, Sri Lanka, Myanmar, Indonesia, Thailand, Vietnam, and the Philippines (Drenth & Guest, 2004).

Infection Mechanism in Rubber. The infection began with the germination of

resting chlamydo spores in infected dried pods or leaves left in the soil or on trees (Drenth & Guest, 2004). The green pods will develop; symptoms include water-soaked dull-grey-colored lesions, a cheesy coating on the pods, and latex oozing. Mycelia penetration and sporangia production developed a cheese coating on the pods. The disease then spreads to the leaves, which are more common on the petioles. The dark brown lesion on the petioles oozes a drop of coagulated latex. While defoliating, infected leaves remain. A water-soaked lesion on the leaf lamina causes the leaves to turn black (Jacob et al., 2006, as cited in Krishnan et al., 2019, p. 35). In favorable climatic conditions, the leaf falls become more severe, especially in susceptible varieties, causing heavy defoliation that will lead to the formation of a leaf carpet covering the entire ground and a significant latex reduction.

To prevent pathogen infection of healthy and unaffected tissues, *H. brasiliensis* synthesizes several anti-fungal compounds. In Thailand, resistant clones (RRIC 100 and BPM 24) had a higher concentration of phenolic compounds than susceptible clones (RRIC 121, RRIM 600, and PB 86), suggesting that the lignin produced from phenolic aldehydes surrounding diseased plant portions improves host resistance (Jayasuriya et al., 2003).

Cocoa (*Theobroma cacao*)

Phytophthora diseases threaten global cocoa production (Peter & Chandramohan, 2011). *Phytophthora palmivora* is the

primary pathogen responsible for black pod rot, stem canker, seedling blight, chupon wilt, and flower cushion infection in cacao trees (Akrofi et al., 2003; McMahon & Purwantara, 2004). However, black pod rot is the most significant factor limiting production spread in the cocoa-growing region, accounting for 10-30% of annual yield losses of cocoa beans worldwide and up to 40% losses in wet and humid conditions (Hebbar, 2007; Purwantara et al., 2004; Vanegtern et al., 2015). An outbreak in nearly every cocoa-producing country, primarily in South America and Southeast Asia, has resulted in annual losses of up to 450,000 metric tons (Wahyudi & Misnawi, 2008). It is also reported to have cost Malaysia over 30% of its annual cocoa production (Alsultan et al., 2019). *Phytophthora megakarya* and *P. palmivora* are black pod rot's most important causal agents worldwide. *Phytophthora palmivora* causes the disease in Asia, Central America, and South America, while both species may exist and can cause black pod rot in West Africa (Widmer, 2014). *Phytophthora palmivora* can infect all age ranges of cacao trees, both young and matured trees, causing multiple diseases, such as seedling blight, leaf blight, stem canker, and black pod rot (Purwantara et al., 2015). Infection of cocoa pods occurs in the two months before ripening, causing the most significant loss. After that, the pathogen can easily spread from the pod husk to the bean's seed coat, causing a total loss (Wahyudi & Misnawi, 2008).

Infection Mechanism in Cocoa. The infection of black pod rot began with an early penetration into the waxy cuticle. Then, it progressed to the epidermis, causing a small translucent spot to develop into a brownish lesion. The lesion will darken and expand rapidly, gaining 12 mm in 24 hours. The infection quickly spread throughout the entire pod, causing a severe black lesion in the infected area. In favorable conditions, clusters of white sporangia will gradually spread on the pod surface (Purwantara et al., 2015; Wahyudi & Misnawi, 2008). The authors have further explained that most cacao ripe pods can be recovered from a light infection, but advanced infection causes total loss (Purwantara et al., 2015).

Durian (*Durio zibethinus*)

Durian (*Durio zibethinus*) is one of Southeast Asia's most valuable tropical fruits. Initially from Peninsular Malaysia and Borneo, it has spread globally to Sri Lanka, Northern Australia, and Hawaii (Honsho et al., 2004). Thailand is the largest producer and export of durian, followed by Malaysia and Indonesia, while the Philippines and Vietnam focus on domestic consumption (O'Gara, Sangchote, et al., 2004; Somsri, 2014). For growth and cultivation, durian prefers a tropical climate with high temperatures and consistent rainfall of over 2,000 mm per year (Somsri, 2008).

A major threat to durian production, durian canker caused by *P. palmivora*, has caused devastating economic losses estimated at US\$2.3 billion in five Southeast Asian countries: Malaysia, Indonesia,

Thailand, the Philippines, and Vietnam (Drenth & Sendall, 2004). The death of durian trees due to durian stem canker was first reported in Penang, where *P. palmivora* was successfully isolated from the main trunk, and canker-like symptoms were observed on the affected trees (Thompson, 1934). In addition, *P. palmivora* causes patch canker, root rot, fruit rot, and leaf blight in durian at all stages of growth (Figure 2) (Lim & Luders, 1998).

Infection Mechanism in Durian.

Phytophthora palmivora thrives in the tropical hot-humid conditions where durian is grown. Furthermore, heavy clay soil and poor drainage will promote the proliferation of the devastating disease in durian, as durian roots are highly sensitive to standing water and susceptible to root rot caused by *P. palmivora* (Somsri, 2008). Besides, the durian leaf surface features help *P. palmivora* pre-penetrate into the host (O'Gara, Sangchote, et al., 2004). Trichomes are found on the abaxial leaf side, petiole, young stem, and fruit of *D. zibethinus*. Three distinct types of trichomes are found on durian leaves (i) glandular trichomes that are not lignified; (ii) stellate trichomes that are not lignified to varying degrees; and (iii) peltate trichomes that are heavily lignified and form the external layer, giving the abaxial surface a silver to golden hue (Husin et al., 2018).

The motile zoospores of *P. palmivora* bind randomly and individually onto the adaxial side of durian leaves, which have a continuous cuticle with no stomata or

trichomes. The abundant and overlapping peltate trichomes on the abaxial side of the leaf trapped a greater proportion of *P. palmivora* spores. Under favorable environmental conditions, *P. palmivora* can bind, produce extensive hyphae, and re-sporulate, thus completing the life cycle on infected durian tissue within eight hours post inoculation (Vawdrey et al., 2005).

In early penetration, *P. palmivora* can directly penetrate the cuticle and epidermis of the adaxial side of durian leaves, as well as the trichome-free area between the fruit spines. To date, there is no recorded successful penetration of *P. palmivora* through the heavily lignified peltate trichomes. However, an attempted penetration was marked by appressoria-like

swellings and dissolution of the trichome surface at the attachment area. Unsuccessful penetration attempts usually result in hyphal branch formation on another infection site. A single zoospore will repeat this process until the infection is successfully established. If not, the well-developed hyphae will grow over the edge of the trichome across the leaf surface and spread infection into the host tissue via open stomata (O’Gara, Sangchote, et al., 2004). Once the penetration and infection are established, *P. palmivora* will rapidly colonize the entire leaf lamina, and lesions will appear within two days post-inoculation, ranging from dark brown with a distinct margin to the water-soaked light grey lesion. *Phytophthora palmivora* will proliferate within the host, releasing new sporangia into the environment via stomata or epidermis eruption. As a result, severely infected durian fruits have a whitish bloom (O’Gara, Sangchote, et al., 2004). In fruit, the stylar is the most infected part because rainwater dries slowly and concentrates the spores. When spores land on the fruit surface in favorable conditions, they can infect 50% of the fruit in seven hours and 100% in 17 hours (Siriphanich, 2011).

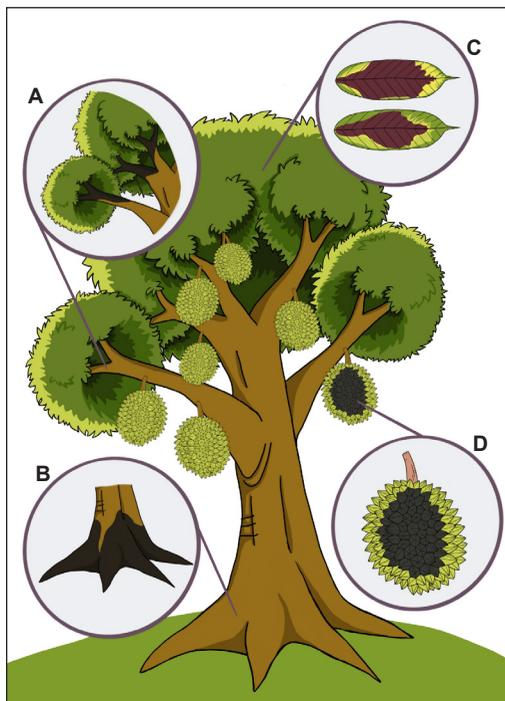


Figure 2. Symptoms caused by *Phytophthora palmivora* in durian: A) patch canker; B) root rot; C) leaf blight; and D) fruit rot

Oil Palm (*Elaeis guineensis*)

Oil palm (*Elaeis guineensis*) is an economically important crop originating in Africa, with Malaysia and Indonesia being the largest producers worldwide (85%). Malaysia is currently earning RM 46.12 billion (US\$11.33 billion) in palm oil export revenue to India and European Union markets (Kushairi et al., 2018). Malaysian

palm oil production began commercially as early as 1917 (Ommelna et al., 2012). The crop is also largely planted in Latin American countries such as Colombia, Ecuador, Suriname, Brazil, Costa Rica, and Panama (Rocha et al., 2005). Following Indonesia, Malaysia, Thailand, and Nigeria, Colombia is the fifth largest oil palm producer with an estimated planting area of 450,000 ha and produces more than 30% of America's palm oil (Sundram & Mohamed Azni, 2017; Torres et al., 2016). However, several global diseases hamper the rapid expansion of oil palm cultivation. The oil palm industry in South Africa and Central America is currently threatened by the bud rot disease caused by *P. palmivora*. The disease has been reported in various Latin American countries on various oil palm cultivars and plantation stages (Martínez et al., 2010). Numerous bacterial and fungal pathogens, including various *Phytophthora* species, were previously isolated from multiple infected oil palm parts globally and suggested as causal agents of bud rot disease (Alvarez et al., 1999, as cited in Torres et al., 2016, p. 321; Faparusi, 1973; Richardson, 1995). Until recently, *P. palmivora* has been proven to be the causal agent of bud rot disease in oil palm trees in Colombia through Koch's postulates method, where 80% of inoculated young oil palms developed the exact typical bud rot symptoms (Drenth et al., 2013).

Despite being the world's largest oil palm producer, Southeast Asia has yet to report any bud rot cases related to *P. palmivora* infection reported in the region (Lee & Lum, 2004; Mohamed Azni et al.,

2019). Sharples and Lambourne (1922) described the bud rot disease of oil palms in Malaysia with symptoms at the base of the youngest leaves, causing the collapse of the oil palm. Nevertheless, no affected tissue samples were collected. Later, in Malaysia, oil palm bud rot disease was linked to *Oryctes rhinoceros*, or lightning strikes (Bunting et al., 1934). Another study found that 5% of bud rot incidents in Malaysia were fatal cases (Turner & Bull, 1967). This situation is made more concerning by previous research indicating that Malaysian oil palm planting materials are susceptible to *P. palmivora* bud rot infection based on trials conducted in an oil-palm growing area in eastern Colombia (Navia et al., 2014). Another study found that Malaysian *P. palmivora* isolates (PP3 and PP7) are highly pathogenic to cocoa, durian, and rubber but not healthy Malaysian oil palm planting (*Dura* × *Pisifera*) materials. Even in flooded environments, a localized brown lesion on wounded and inoculated oil palm seedlings did not develop between 28 and 126 dpi (Mohamed Azni et al., 2019).

However, the epidemic that devastated the Colombian oil palm industry and the susceptibility of Malaysian oil palm planting materials has raised awareness in other oil-producing countries, especially in Southeast Asia. This endemic pathogen, *P. palmivora*, has caused various diseases in other crops, such as durian and rubber, in Malaysia and Indonesia. Without good management practices, this highly virulent pathogen may have the potential and easily attack oil palm plantations and spread the bud rot disease in Southeast Asia.

Infection Mechanism in Oil Palm.

Phytophthora palmivora is the initiator that causes initial lesions and leads to tissue colonization by other fungi and bacteria that further decompose palm bud, leading to bud rot (Torres et al., 2016; Velez et al., 2008). The bud rot disease causes small brown lesions with a water-soaked edge at the base of the spear leaves, which quickly spread to the developing leaflets. When the lesion starts to develop on the edge of the leaflet, the symptoms worsen with the detachment of the middle lamella exhibiting a shot-hole appearance on the middle leaflet, the bite-like symptoms development, and the destruction of the interveinal tissue (Torres et al., 2016; Villa et al., 2013). Under high rainfall and high humidity conditions, sequential infection will aggressively affect the leaflets near the infected palm, causing more severe lesions. The infected palm's meristem and developing spears are destroyed in advanced stages. With these severe symptoms, no more young leaves will develop, and the bud will further deteriorate due to the invasion of pathogens and insects (Torres et al., 2016).

Black Pepper (*Piper nigrum* L.)

Popularly known as the "King of Spices" or "Black Gold", black pepper (*Piper nigrum* L.) is one of the most essential spices used across the globe. Black pepper is primarily grown in Kerala, India, and has since been spread to other nations, predominantly in Southeast Asia (Hao et al., 2012). As of 2016, Vietnam is known as the world's greatest producer of black

pepper, with a total production of 140,000 metric tonnes, followed by Indonesia (70,000 metric tonnes), India (48,500 metric tonnes), and Brazil (45,000 metric tonnes) (Hao et al., 2012; Ten, 2017, as cited in Takooree et al., 2019, p. S211). Apart from its immense importance in international trade and as a gourmet spice, black pepper is also beneficial for its diverse therapeutic purposes (Takooree et al., 2019).

Phytophthora foot rot is known as one of the most significant threats to the production of black pepper across the growing region worldwide. The disease was first reported in Indonesia in 1885 (Erwin & Ribeiro, 1996). The disease symptoms observed on infected black pepper in Sarawak are yellowing, defoliation, and collar rot. Due to limited knowledge of the morphological and molecular characterization of the *Phytophthora* sp. in the early stage of its discovery, it was difficult to identify the main causal agent of *Phytophthora* disease in black pepper. After examining several isolates from various hosts and geographical areas, Turner (1960) concluded that all the *Phytophthora* isolates from *Piper* in Southeast Asia belong to the same species and should be described as an atypical strain of *P. palmivora*. It is supported by a review that also recognized black pepper isolates as an atypical strain due to their unique morphological features not found in the MF1 strains (Waterhouse, 1974). However, a later study revealed that the pathogens isolated from black pepper in Thailand did not match the description of the atypical strain of *P. palmivora* or any of the *Phytophthora* sp. reported pathogenic to the black pepper.

The isolates have long pedicels on the caducous (deciduous) sporangia (Tsao & Tummakate, 1977). These findings further generate interest among researchers who have made extensive efforts and tried to compare the cocoa isolates of *P. palmivora* worldwide. Originally, there were two morphological forms of *P. palmivora* found in cocoa in West Africa based on their chromosome, which are ‘S type’ (small chromosomes [$n = 9-12$] at metaphase) and ‘L type’ (large chromosomes [$n = 5-6$] at metaphase). Later, the ‘S’ and ‘L’ types were redesignated and further classified into MF1, MF2, MF3, and MF4 based on the morphology characterization (Brasier & Griffin, 1979; Griffin, 1977). Most sporangia of MF1 had a rounded base, papillated and shed with a short, occluded stalk (pedicel) that was typically < 5 μm in length. The culture of MF1 on CA is stellate or radiate and has a smooth-combed appearance. The characteristic of MF2 isolates was similar to MF1, while MF3 was reclassified as *P. megakarya* (Brasier & Griffin, 1979; Griffin, 1977). In contrast, the MF4 Brazilian isolates have a papillated sporangia with long, non-occluded stalks (pedicel) and a sporangial base tapered to its connection with the pedicel giving a “sloping shoulders” appearance (Griffin, 1977). The black pepper isolates from Malaysia and Thailand showed similar characteristics to the Brazilian MF4 cocoa isolates, in which both have different characteristics from the typical *P. palmivora* strains. Therefore, Tsao and Tummakate (1977) believed that the *P. palmivora* isolates from black pepper should

be classified as different species. Later, through taxonomic and genetic studies of the isolates, *P. palmivora* MF4 was reclassified as *Phytophthora capsici* (Alizadeh & Tsao, 1985). These species’ reclassification was further confirmed through evolutionary analysis (Cooke et al., 2000). In a recent study, a pathogen isolated from infected black pepper in Sarawak displayed classic morphological characteristics of *P. capsici* by producing globose oogonia and paragynous antheridia, chlamydospore, and lemon-shaped sporangia with long pedicels (Farhana et al., 2013).

Coffee (*Coffea arabica*)

Coffee (*Coffea arabica*) is one of the most important commercial crops globally, cultivated in more than 80 countries, and contributes significantly to the livelihoods of smallholder farmers (Pham et al., 2019). Global coffee consumption was steadily growing and projected to grow by 3.3%, reaching 170.3 million 60-kg bags in 2021/2022 compared to 164.9 million 60-kg bags produced in the previous year (International Coffee Organization [ICO], 2022a). *Coffea arabica* and *Coffea canephora* (robusta) are the two most widely cultivated coffee species worldwide, which account for 60% and 40% of worldwide production, respectively (Leitão, 2019; Vega et al., 2020). Vietnam is known as the major coffee exporting country after Brazil, with 29,000 60-kg bags of coffee produced in 2020, followed by Indonesia (12,100 60-kg bags) and Thailand (500 60-kg bags) (ICO, 2022b).

Regarding *Phytophthora* root and stem rot disease, there is only one incident reported in 2001 that attacked a coffee orchard in Thailand, and it was said to be insignificant as the disease only causes 0.4% infestation (Sangchote et al., 2004). However, this incidence shows that coffee can be susceptible to *Phytophthora* infection. It can be concerning considering the widespread practice of intercropping among smallholder farmers. Intercropping practice helps to increase the diversity of an agricultural ecosystem and provide additional income in the years prior to the main crop production (Mousavi & Eskandari, 2011; O’Gara, Guest, et al., 2004). Together with langsat, longan, and papaya, coffee is among the crops planted for intercropping practice by Vietnamese farmers in durian orchards to provide shade and additional income (O’Gara, Guest, et al., 2004). A survey on a cocoa plantation in Nigeria also revealed that all farmers intercropped their cocoa plantation with various food crops, including coffee (Oladokun, 1990). As coffee is widely used for intercropping durian and cocoa, *P. palmivora* inoculum has a high probability of evolving and initiating a host jump from their primary hosts to coffee. Thus, extensive control measures must be taken to prevent the disease outbreak caused by *P. palmivora* in coffee.

MANAGEMENT OF *PHYTOPHTHORA PALMIVORA*

Phytophthora palmivora has become a danger to important crops and has wreaked havoc

on the global economy, so effective disease management techniques are required. The Malaysian industry is currently concerned about *P. palmivora*’s attacks on cacao and durian (Mohamed Azni et al., 2019). Most of the commercial cultivars of oil palm, cocoa, and durian are highly susceptible to diseases caused by *P. palmivora*. Therefore, disease management, such as cultural practices, disease-resistant germplasm, chemical control, and biocontrol, are studied and applied. Although many methods exist, effective disease control often combines several strategies (Drenth & Sendall, 2004).

Cultural Control

Phytophthora palmivora thrives in a tropical and subtropical climate that favors the spread and multiplication of the pathogen (Martínez et al., 2010). Therefore, regulating water systems and irrigation is crucial to controlling *Phytophthora* diseases. The amount, frequency, and duration of plants exposed to water and water drainage must be seriously considered. Several suggested methods can be considered to control water drainage and prevent *Phytophthora* diseases. Farmers are urged to avoid growing plantations in forest regions, flood-prone places, and areas with poor drainage because of the possibility of water-assisted dispersal. The selection of fields with low *P. palmivora* concentration and a good drainage system is the first line of defense against this disease. Farmers may also grow their plants in a highly porous potting soil mix or plant their crops on raised beds (Pscheidt & Ocamb, 2022).

Fruit postharvest handling and storage are crucial to avoid contamination from phytopathogens, especially from an easily spread pathogen like *P. palmivora*. For instance, rinsing jackfruits with chlorinated water after sorting and grading them is a common phyto-sanitation measure practiced in India to remove foreign matter, latex, and field contamination to avoid fruit rot disease. Before fungicide application, phyto-sanitation was performed, which included removing decaying plant material, weeding, pruning, thinning, and shade reduction. A study in India proved that implementing such cultural practices as nutrient management, pruning, and field hygiene reduced cocoa black pod rot disease by 50% (Peter & Chandramohan, 2014).

Chemical Control

Agrochemicals are widely used to increase yields and protect crops from pests and pathogens to protect crops from pests and pathogens. Chemical controls are intended to reduce pest and pathogen populations without harming crops (Brunner, 2014). Fungicide application is a conventional strategy for controlling phytopathogen diseases. Common fungicides to combat *P. palmivora* diseases include metalaxyl, mefenoxam, and phosphonates (Drenth & Guest, 2004; Torres-londono, 2016).

Metalaxyl (methyl-*N*-(2,6-dimethylphenyl)-*N*-(2-methoxyacetyl)-DL-alaninate) is a well-known fungicide for controlling *P. palmivora* diseases. Metalaxyl inhibits fungal RNA synthesis (Drenth & Guest, 2004; Torres-londono,

2016). Metalaxyl can slowly penetrate through the leaf cuticle and into the xylem of a low lipophilic host (Phetkhajone et al., 2021). After penetration, metalaxyl accumulates and is transported upward by the transpiration stream. The study also concluded that metalaxyl foliar application at 4g/L is sufficient to control *P. palmivora* in two months. However, a lower concentration is suggested for soil drenching to treat the root and stem rot disease in durian trees (Phetkhajone et al., 2021). Protectant fungicide, mefenoxam, is a purified active isomer of metalaxyl that can affect mycelium growth and sporulation (Schwinn & Staub, 1995; Ware & Withacre, 2004). Furthermore, 30 g a.i./ha is the recommended rate for mefenoxam (Torres-londono, 2016). Durian farmers depend more on metalaxyl than other fungicides to control *Phytophthora* diseases. In Southern Thailand, the metalaxyl fungicide is used excessively, approximately 2-3 times per month, especially during the rainy season from May-October. Consequently, long-termed and excessive use of metalaxyl fungicide has resulted in the development of metalaxyl-resistant isolates with a 50% effective concentration (EC₅₀) higher than 100 mg/L (Kongtragoul et al., 2021). This issue will have a serious economic impact on the farmers as they are still applying the same metalaxyl-based fungicides but with higher dosage and greater frequency. The excessive fungicide application will further become hazardous to humans and the environment.

On the other hand, due to the high cost of metalaxyl-based fungicides and plant pathogens' resistance to metalaxyl, phosphorous acid has become another inexpensive alternative for oomycetes di management (Gómez-merino & Treio-Téllez, 2015). Phosphonates are proven to be highly effective against *Phytophthora* diseases in various crops. This inorganic compound acts synergistically with plant physiology to control the infection (Montiel et al., 2013). Both downward and upward phosphonate translocation are known as xylem-and phloem-translocated in the host (Ouimette & Coffey, 1990). They cause fungistasis and activate the host defense response by disrupting the pathogen's phosphorus metabolism (Drenth & Guest, 2004; Guest et al., 1995). Due to their phloem-translocated nature, phosphonates can be applied to any plant part and transported to other parts based on the source-sink relationship. Phosphonate fungicides in fosetyl-aluminum are widely used in the Philippines to overcome durian patch canker. Unlike metalaxyl, no phosphonate-resistant isolates of *Phytophthora* spp. have been reported after 20 years of use (Drenth & Guest, 2004).

There are multiple sites of action for these compounds (systemic, semi-systemic, or in contact with various compounds), and their efficiency varies depending on the application method, dosage, and time of year (Akrofi et al., 2003; Deberdt et al., 2008). Fungicides can be applied by drenching, foliar spray, stem canker paint, or trunk injection. However, each application has its

downsides. For example, the foliar sprayed fungicide may not reach higher branches, allowing infected plant parts to remain on top and eventually infect the rest of the trees. Also, continuous rainfall may wash the fungicide off, which requires its frequent re-application. Due to soil degradation and leaching, soil drenching might also be ineffective (Drenth & Guest, 2004). Trunk injection application has proven to be a cost-effective alternative to overcome these problems, as it minimizes chemical waste while maximizing persistence (Darvas et al., 1984). For example, trunk injection of phosphite was proven to control severe root rot in avocado trees (*Phytophthora cinnamomi*) and trunk root rot in peach trees (*Phytophthora cactorum*) (De Boer et al., 1990). In a recent study, phosphonate application through trunk injection was proven effective against *P. palmivora* patch canker of durian in the Philippines, with a significant rise in yield at \$US3.00 per tree/year (Montiel et al., 2013).

Biocontrol

In the intervening years, chemical fungicides have been widely used to control diseases. It has the most effective method to combat *Phytophthora* diseases (Sunpapao & Pornsuriya, 2014). However, the dramatic effect on pests and pathogens resulted in their overuse, which favored the development of fungicide-resistance pathogens. Consequently, higher chemical doses are introduced to protect crops and plants, raising public concerns regarding fungicide residue in food products, the

expensive chemical fungicides, and their impact on soil (Syed Ab Rahman et al., 2018). In addition, villamizar-Gallardo et al. (2017) expressed their concern about the deleterious effects of fungicides on the fly *Forcipomyia* sp., which pollinates cocoa flowers, affecting the ecological system.

Over the past 25 years, researchers and farmers have gained the popularity of biological control as a cost-effective and environmentally friendly alternative to reduce agrochemical use and plant diseases effectively. There is increasing evidence that beneficial microorganisms can promote plant growth and provide new strategies to combat pathogen diseases. These microorganisms act as biocontrol by inhibiting pathogen infection within the host directly (via mycoparasitism, antibiosis, and nutrient competition) or indirectly (via triggering resistance responses intrinsic to the host) (Mejía et al., 2008).

Numerous studies have shown that antagonistic microbial agents can develop and promote host resistance against *Phytophthora* spp. (Table 2) (Bailey et al., 2008; Hanada et al., 2008, 2009; Samuels et al., 2000). *Trichoderma* spp., *Pseudomonas* spp., and *Chaetomium* spp. are among well-studied genera that have attracted the attention of researchers and have proven to combat *P. palmivora* diseases.

Trichoderma spp. has been extensively used as an antagonistic fungal agent against several pathogens. These fungi's antagonism is based on faster metabolic rates, antimicrobial metabolites, and physiological conformation (Verma et al., 2007). In the

interaction between *Trichoderma* spp. and *P. palmivora*, the most likely mode of action of *Trichoderma* spp. is parasitism and stimulation of the host's resistance reaction towards *P. palmivora* (Bailey et al., 2006; Harman et al., 2004). Recent research has examined the efficiency of *Trichoderma* spp. in controlling *P. palmivora* disease in durian, cocoa, and rubber (Table 2). *Trichoderma virens* (Tv) significantly reduces *P. palmivora* growth and disease development by producing antibiotic substances that inhibit the pathogen growth and act as mycoparasite, thus suggesting that it has multiple modes of action that contribute to its ability to suppress black pod rot and seedling blight of cocoa (Sriwati et al., 2015).

Instead of using a single crop management strategy, researchers have to combine *Trichoderma* spp. with potassium fertilizer to control cocoa black pod rot in Indonesia (Harni et al., 2020) (Table 2). Generally, potassium deficiency weakens plant resistance, allowing pathogens to penetrate (Damiri et al., 2011). Table 2 shows that *Trichoderma amazonicum* + 3g of potassium fertilizer (75.37%) suppresses leaf spots better than chemical fungicide (mancozeb) (70.86%). This ability of *T. amazonicum* to produce secondary metabolites that increase salicylic acid production may be the cause (Harni et al., 2019).

In recent years, more research has focused on antagonistic bacteria as a new environmentally friendly disease management strategy. *Pseudomonas* spp.

is popularly known to demonstrate high potential characteristics: the ability to produce antibiotics, plant growth promoters, hydrolytic enzymes, and hormones (Singh et al., 2013). Previously, various rhizosphere *Pseudomonas* spp. have been shown to control a range of plant pathogenic fungi and oomycetes (Acebo-Guerrero et al., 2015; Gravel et al., 2005; Miguélez-Sierra et al., 2019; Noori & Saud, 2012; Xu & Du, 2012). However, environmental conditions and competition for colonization in ecological niches can affect their potential and performance (Abraham et al., 2013). Due to these limitations, endophytic bacteria have recently gained popularity as a potential biocontrol agent against plant pathogens.

Several studies have been published on the antagonistic activity of endophytic *Pseudomonas aeruginosa* against *P. palmivora* infection on multiple hosts, especially in tropical countries (Kumar et al., 2005; Prakob et al., 2007; Siddiqui & Akhtar, 2007). It is supported by a study examining the effectiveness of 103 endophytic bacterial isolates isolated from healthy cocoa plants in seven Malaysian states against black pod rot disease caused by *P. palmivora* (Alsultan et al., 2019). Among all of the isolates, *P. aeruginosa* strain (AS1) that was isolated from the branch of a healthy cocoa plant in Perak, Malaysia, has been proven to have the highest inhibition rate against *P. palmivora* (Table 2) (Alsultan et al., 2019). The anti-fungal activity of *P. aeruginosa* is further supported by research demonstrating that *P. aeruginosa* produces several proteins

capable of inhibiting the growth of *P. palmivora* with high inhibition activity (Table 2) (Sowanpreecha & Rerngsamran, 2018).

Chaetomium is one of the largest genera in the Chaetomiaceae family, and it lives primarily in soil and as endophytes in several plants via a symbiotic relationship (Fatima et al., 2016). *Chaetomium* species are effective biocontrol agents against multiple phytopathogens such as *Fusarium* spp., *Alternaria* spp., *Pythium* spp., and *Phytophthora* spp. Chaetomin mycotoxin was first isolated from *Chaetomium* spp. in 1944, leading to the discovery of a wide variety of bioactive compounds later on (Chen et al., 2015; Geiger et al., 1944). These compounds have been found to have significant biological activities such as anti-fungal, anti-inflammatory, cytotoxic, and enzyme inhibition (Li et al., 2016).

The effectiveness of *Chaetomium* application has been proven against *P. palmivora*, causing stem and root rot of durian in an epidemic area of infested field soil planted with durian in Thailand (Table 2). Furthermore, the 2-year field experiments proved that the application of *Chaetomium* spp. every four months, alongside good cultural practices, can effectively inhibit *Phytophthora* rot in durian and significantly reduce pathogen inoculum and disease incidence compared to metalaxyl treatment (Soytong, 2010). This finding is also supported by another research that has firstly reported the usage of nanoparticles (nanoparticles constructed from hexane crude extracts [nano-CCH]

Table 2
Biocontrol application to control Phytophthora palmivora diseases

Biocontrol agent	Mechanism	Species	Host	Origin	Biocontrol effect	References
<i>Trichoderma</i> spp.	Antibiosis, mycoparasitism	<i>Trichoderma harzianum</i>	Rubber	Thailand	Controlled rubber leaf falls disease (66.22%)	Promwee et al. (2017)
	Antibiosis, mycoparasitism	<i>Trichoderma virens</i>	Cocoa	Indonesia	Produced antibiotic that inhibit pathogen growth and act as mycoparasite suppressing black pod rot and seedling blight of cocoa	Sriwati et al. (2015)
	Triggering host resistance response	<i>Trichoderma amazonicum</i>	Cocoa	Indonesia	Application with 3g potassium fertilizer have suppressed the number of leave spot, prolonged the incubation period, increased the growth of cocoa seedlings, and increased the lignin content in leaves (75.37%)	Harni et al. (2020)
<i>Pseudomonas</i> spp.	Antibiosis, competition	<i>Pseudomonas aeruginosa</i> (AS1)	Cocoa	Malaysia	Produce volatile metabolite and siderophores, causing the highest inhibition rate against <i>P. palmivora</i> growth (82.41%)	Alsultan et al. (2019)
<i>Chaetomium</i> spp.	Mycoparasitism, antibiosis, competition	<i>Chaetomium cupreum</i> (CC6) <i>Chaetomium globosum</i> (CG7)	Durian	Thailand	Inhibit <i>P. palmivora</i> growth through bi-culture antagonistic with high antagonistic activity and greenhouse test (85.56%)	Soytong (2010)
	Antibiosis	<i>Chaetomium cupreum</i> : Nanoparticles; Nano-CCH and Nano-CCE particles	Durian	Thailand	Nano-CCH and nano-CCE (15 ppm) inhibit colony growth of <i>Phytophthora</i> spp. (86%) and inhibit sporangia formation by 96.42% and 97.32%, respectively	Thongkham et al. (2017)
	Antibiosis	<i>Chaetomium brasiliense</i> : Nano-CBH, Nano-CBE, and Nano-CBM particles	Durian	Thailand	Crude ethyl acetate from <i>C. brasiliense</i> significantly against <i>P. palmivora</i> (ED ₅₀ value: 17.46 µg/ml) Nanoparticles significantly inhibit colony growth (90%) and spore production (100%)	Tongon et al. (2018)

and nanoparticles constructed from ethyl acetate crude extracts [nano-CCE]) from *Chaetomium cupreum* to inhibit *Phytophthora* spp. — causing durian root rot in Thailand (Table 2) (Thongkham et al., 2017).

Transgenesis and Breeding

Since the beginning of farming, plant pathogens have posed a significant challenge to food security despite all the control measures that have been introduced, such as agricultural practices, agrochemical use, and biological control. Over the past century, the development of disease control strategies has rekindled interest in transgenesis and host resistance breeding. Even though the earlier conventional breeding studies were primarily focused on major economic traits such as vigor and yield, the development of plants with disease resistance has drawn the attention of researchers over the years. Generally, there are three main components of resistance towards *Phytophthora* spp.: resistance to penetration, restriction of pathogen growth in the plant host, and the minimization of pathogen sporulation on the host.

The development of genetic resistance in cocoa trees has been proposed as the best alternative method for combating black pod rot disease (Susilo & Sari, 2014). Chang et al. (2020) screened a total of 50 potential cocoa genotypes available in Malaysia in which they tested their tolerance level against black pod rot. The *k*-means clustering method was used to

assess disease severity based on the rate of lesion area development from 1 to 7 days post-inoculation and the proportion of pod area infected with black pod rot. All tested genotypes are categorized based on four tolerant levels: tolerant, moderately tolerant, moderately susceptible, and susceptible. Out of all the tested genotypes, 10 genotypes were classified in group I (tolerant) with six genotypes, namely MCBC 13, PBC 221, BAL 209, KKM 19, QH 1176, and KKM 22, which were found to have lower disease severity values as than the control tolerant genotype, PBC 123. Therefore, these genotypes can be recommended to farmers for use as planting material (Chang et al., 2020).

As for durian cultivation in Malaysia, the D24 clone was previously found to be more resistant to stem canker than D2 and D10. The interspecific hybrid crosses of D24 × D10 and D10 × D24 done by the Malaysian Agricultural Research and Development Institute (MARDI) have successfully produced MDUR 78 and MDUR 88 clones that were found to be more resistant than D24 (Sani et al., 2015). Both clones are proven to be resistant to *P. palmivora* stem canker and have the potential to produce high-quality fruits with higher yields. The fruits can also be stored for a long term and thus exported worldwide. Another durian breeding program in Thailand has found the F₁ hybrid of durian, IICN-5-4-3-6, to be the most resistant against *P. palmivora* on stem and leaves (Somsri, 2014).

CONCLUSION

In this review, the infection mechanism of *P. palmivora* in multiple crops, i.e., rubber, cocoa, durian, and oil palm, has been identified and described. The ability of *P. palmivora* to infect various plant parts in a wide range of hosts is a major threat to the future global spread and epidemic. Tropical and subtropical climates support the survival and propagation of *P. palmivora* inoculum due to the conducive environment, and the spores can easily be spread by wind and water. The pathogen infects rubber, cocoa, and durian trees in tropical regions. Among the reported cases are bud rot, pod rot, and stem canker severely affect oil palm, cocoa, and durian trees. Cultural control, chemical pesticide use, and biocontrol strategies have all been proven to control and minimize the spread of *P. palmivora* diseases. Recent studies have shown that *Trichoderma* spp. is the most effective antagonistic species against *P. palmivora*. Further research is necessary to identify hybrids resistant to *P. palmivora* diseases, as resistant hybrids are needed for disease prevention in plantations. Therefore, a better understanding of the *P. palmivora* infection mechanism in the main crops and early disease detection can reduce the risk of catastrophic pandemics.

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