Bud Rot Caused by *Phytophthora palmivora*: A Destructive Emerging Disease of Oil Palm

G. A. Torres, G. A. Sarria, G. Martinez, F. Varon, A. Drenth, and D. I. Guest

First, second, third, and fourth authors: Pests and Diseases Program, Colombian Oil Palm Research Centre, Cenipalma Bogota, Colombia; fifth author: Centre for Plant Science, The University of Queensland, Australia; and sixth author: Faculty of Agriculture and Environment, The University of Sydney, Australia.

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ABSTRACT

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Oomycetes from the genus *Phytophthora* are among the most important plant pathogens in agriculture. Epidemics caused by *P. infestans* precipitated the great Irish famine and had a major impact on society and human history. In the tropics, *P. palmivora* is a pathogen of many plant species including cacao (*Theobroma cacao*), citrus (*Citrus* sp.), durian (*Durio zibethines*), jackfruit (*Artrocarpus heterophyllus*), rubber (*Hevea brasiliensis*), and several palm species including coconut (*Cocos nucifera*), and the African oil palm (*Elaeis guineensis*) as determined recently. The first localized epidemics of bud rot in oil palm in Colombia were reported in 1964. However, recent epidemics of bud rot have destroyed more than 70,000 ha of oil palm in the Western and Central oil palm growing regions of Colombia. The agricultural, social, and economic implications of these outbreaks have been significant in Colombia. Identification of the pathogen after 100 years of investigating the disease in the world enabled further understanding of infection, expression of a range of symptoms, and epidemiology of the disease. This review examines the identification of *P. palmivora* as the cause of bud rot in Colombia, its epidemiology, and discusses the importance of *P. palmivora* as a major threat to oil palm plantings globally.

Horticulture provides tremendous wealth and nutritional value to the people of the tropics. Plantation crops such as cacao, coconut, rubber, and oil palm; fruits such as citrus, durian, jackfruit, papaya, pineapple, mango, and avocado; and root crops like potato and taro feed many people in the tropics and beyond and contribute billions of dollars to international trade (<http://faostat3.fao.org/home/E>).

In all of the above crops, pathogens within the oomycete genus *Phytophthora* have major global impacts. In the tropics and subtropics, *P. palmivora* can attack more than 170 different species of host plants, including monocots and dicots, ranging from small vegetables to trees, and causes significant losses to production (Drenth and Guest 2013; Erwin and Ribeiro 1996). In addition to attacking many different host plant species, *P. palmivora* is also capable of attacking a wide range of different plant tissues from roots, stems, flowers, leaves, and fruit of individual plant species making it an especially troublesome plant pathogen in the tropics

(Chee 1974; Erwin and Ribeiro 1996). The importance of *P. palmivora* on cacao, for example, has been well documented (Drenth and Guest 2013; Guest 2007), with an annual impact on the global cacao industry of at least one billion U.S. dollars.

While *P. palmivora* has a pan-tropical distribution, the damage it causes is increasing as agriculture in the tropics intensifies. In this paper, we will discuss the growing impact and threat of *P. palmivora*, the causal agent of bud rot in oil palm (*Elaeis guineensis*) in Colombia as an example. Two recent outbreaks of bud rot of oil palm in Colombia have been estimated to have caused losses of 250 million U.S. dollars (Mosquera Montoya et al. 2014) and the disease poses a serious threat to other oil palm producing regions in the world. Oil palm is an important crop in tropical parts of the world due to its high productivity and year round production. The area under cultivation has steadily grown to meet the world's increasing demand for edible oils. The total area planted with vegetable oil crops in the world exceeds 251 million hectares and the oil palm, with only 5.1% of the global area planted to oil crops, produces more than 36% of the world's vegetable oils (Mesa Dishington 2014). Colombia, the world's fourth largest producer of palm oil behind Indonesia, Malaysia, and Thailand, produces more than 30% of the palm oil in America.

Plant disease problems have been reported in all areas where oil palm has been planted (Turner 1981), with problems affecting the

Corresponding author: G. A. Torres; E-mail address: gtorres@cenipalma.org

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spear leaf and heart of the palm being the most important in the Latin American oil palm industry (Mariau 2001). Since bud rot has appeared in different countries in Latin America, on different oil palm cultivars, and at different stages of plantation development and in the absence of a clear causal agent, it has been given different names including bud rot (Torres et al. 2010b; Turner and Bull 1967), spear rot (Van de Lande and Zadoks 1999), heart rot (Richardson 1995), lethal yellowing (Van Slobbe and Rocha de Souza 1991), little leaf (Kovachich 1953), and crown disease (Suwandi et al. 2012; Turner and Bull 1967). However, careful observations and experimental infection studies have shown that all those described symptoms under different names reflect different stages of symptom expression of the same disease, caused by *P. palmivora* (Sarria et al. 2013).

The first published report of an oil palm plantation destroyed by bud rot in Latin America was from Suriname, where a 4-year-old plantation was completely destroyed in 1920 (Malaguti 1953). In 1927, Reinking reported the presence of bud rot of oil palm in Panama (Richardson 1995). As listed in Table 1, epidemics of bud rot have subsequently been reported from Venezuela in the 1950s (Malaguti 1953), Colombia in the 1960s (De Rojas and Ruíz 1972), Ecuador in the 1970s (de Franqueville 2003; Dollet 1991), Surinam in the 1980s (Van de Lande 1991), and Peru and Brazil in the 1990s (de Franqueville 2003).

The first report of bud rot in Colombia in 1964 documented the destruction of approximately 2,000 ha of oil palm in Turbo, near the border of Panama (De Rojas and Ruíz 1972). Epidemics in Colombia have since been reported from the East in the late 1980s (Gómez et al. 1995; Santacruz et al. 2000), and in the Western part of Colombia more than 30,000 ha were destroyed between 2004 and 2009 (Martínez 2009). More recently, in Central Colombia more than 35,000 ha of oil palm plantations have been destroyed due to the disease (Martínez et al. 2013). These epidemics were associated with unusually wet weather; long periods of continuous precipitation, accompanied by cloudy mornings and wet palm canopies (Martínez 2009).

The aim of the present review is to illustrate the process of identification of *P. palmivora* as the causal agent of the oil palm bud rot disease, its biology, epidemiology, and management, showing the complexity of the resulting disease in a perennial crop.

THE CAUSAL AGENT: *P. PALMIVORA*

Despite the fact that individuals of the genus *Phytophthora*, including *P. palmivora*, had been isolated previously from infected oil palm in different parts of the world (Alvarez et al. 1999; Bull and Robertson 1959; Faparusi 1973; Ghesquiere 1935; Joseph and Radha 1975; Richardson, 1995; Sharples 1924) and proven to be the causal agent of the spear rot disease in Congo (Kovachich 1957), it is interesting to note that it has taken until recently to demonstrate by Koch's postulates that the cause of bud rot in oil palm in Colombia is *P. palmivora* (Drenth et al. 2013; Torres et al. 2010b). Although many bacterial and fungal pathogens, such as *Fusarium* and *Thielaviopsis*, were often isolated, inoculation experiments with these pathogens could never recreate the bud rot symptoms in healthy oil palms (reviewed in de Franqueville 2003). Data on the spread and distribution of the pathogen, indicating that a vector may be involved (Van de Lande and Zadoks 1999), gave rise to the search for virus, virus-like pathogens, and phytoplasmas. However, previous experimental data had failed to find any evidence of their involvement (Dollet 1991).

Although overwhelming evidence demonstrated that bud rot had a biotic origin and it can occur in many different soil types under different environmental conditions, research was focused on finding evidence supporting an abiotic cause, delaying the identification of the causal agent. Poor drainage, compacted, heavy soils (Acosta et al. 1996; Munevar et al. 2001), soil acidity, boron deficiency (Broeshart et al. 1957; Turner and Bull 1967), and aluminum toxicity (Munevar et al. 2001) among others, have all been proposed as causes of bud

rot, but these factors also occur, either singly or in combination, in areas not affected by bud rot. It was also shown that N, P, K, Mg, and Ca deficiencies could not directly induce bud rot symptoms, but are involved in predisposing palms to bud rot (Cristancho et al. 2012). An analysis of micronutrients in Colombia failed to identify a clear correlation between micronutrients and bud rot (Munevar et al. 2001).

Subsequent microscopic analysis of infected tissue of the heart of the palm revealed the presence of chlamydospores. The cultures resulting from these isolations were all confirmed as *P. palmivora* using microscopy (Fig. 1) and ITS sequence analysis (Cooke et al. 2000; Drenth et al. 2006). Spore suspensions of the pure cultures were inoculated back into over a hundred young palms and 85% developed typical bud rot symptoms. *P. palmivora* was isolated from these symptomatic plants again to fulfill Koch's postulates (Torres et al. 2010b). Confusion and misinformation concerning the cause of bud rot in the past has seriously hindered the development and implementation of effective control strategies and allowed the epidemic to progress unabated, causing millions of dollars of preventable losses.

DISEASE CYCLE

Many of the symptoms caused by *P. palmivora* in oil palm are typical of *Phytophthora* diseases in general. The first visible symptom is the formation of small, water-soaked lesions in the tender tissue of the leaflets at the base of the spear leaf (Fig. 2A and B). This is typically followed by an increase in the number and size of these lesions (Fig. 2C and D). Lesions can be seen extending to developing leaflets in the heart tissue of diseased palms if they are carefully dissected. When these lesions dry out, the middle lamella falls out, leaving a shot-hole appearance on the middle of the leaflet (Fig. 2E), destruction of the interveinal tissue (Fig. 2E), or bite-like symptoms when the lesions form at the edge of the leaflet (Martínez 2009; Sarria et al. 2013). These symptoms visibly expressed at an early stage of bud rot are known by many growers as spear rot.

Under environmental conditions of high rainfall and high humidity, favorable for development of disease, sequential infections cause more and larger lesions affecting an increasing number of leaflets near the heart of the affected palm. In advanced stages of the disease, the emerged outer part of the spear leaf looks totally dry (Fig. 2F), while the white unemerged central tissues, and the tissues immediately above the meristem, are completely destroyed (Fig. 2G) (Martínez 2009; Martínez and Torres 2007; Sarria et al. 2013). Despite the wide variety of symptom expression associated with bud rot, the final symptom is the destruction of the young developing tissue and the meristem that gives the name to the disease (Fig. 2H to J). With the meristem destroyed by *P. palmivora*, no more young leaves develop and the bud putrefies due to subsequent invasion by saprophytic microorganisms and insects. It was the misidentification of these secondary invaders as the bud rot pathogen that confounded the development of effective management strategies for decades.

The lifecycle of *P. palmivora* in the tropics is complex due to a large host range and multiple tissues of the same host plant affected, such as roots, stems, leaves, flowers, and fruits (Chee 1974; Drenth and Guest 2013; Erwin and Ribeiro 1996; Waterhouse 1974; Zentmyer 1973). A number of different spores such as zoospores, sporangiospores, chlamydospores, and oospores can be produced, and airborne, soilborne, water-borne, and vector-borne spread of propagules is possible (Drenth and Guest 2013; Erwin and Ribeiro 1996; Konam and Guest 2004; Ribeiro 1978).

Infection of oil palm by *P. palmivora* starts under conditions of high humidity, which is a common factor among almost all oil palm growing areas in Colombia for certain periods of the year. The first external macroscopic symptom of bud rot in the field can be observed when small, necrotic and water-soaked lesions appear

TABLE 1
Summary of bud rot-related symptoms in oil palm (organisms isolated from diseased palms or attributed cause)

Date	Disease	Location	Symptoms	Diagnosis	References
1917	Bud rot	Nigeria	Fruit rot and rot at youngest leaf that conduct to bud rot.	Unknown.	Wakefield (1920)
1921	Bud rot	Suriname	Bud rot.	Unknown physiological cause.	Malaguti (1953)
1922	Bud rot	Malaysia	Base of the youngest leaves is affected, leading to their collapse. Water-soaked lesions are observed and meristem is not directly affected.	Only <i>Phytophthora</i> -related species are able to cause this damage. Isolation was not performed.	Sharples (1922)
1928	Bud rot	Almirante on Panama	Bud rot. The disease starts at the tips and sides of the young central group of folded leaves of the heart of the plants and gradually works downward until the bud is killed.	Bacteria, <i>Fusarium</i> sp., and <i>Phytophthora</i> . Inoculation was not performed.	Richardson (1995)
1929	Bud rot	Africa	Not described in the review for the specific symptomatology.	Nitrogen uptake might be related to bud rot.	Bull and Robertson (1959)
1933	Yellow leaf	Nigeria	Yellow leaf.	Physiological.	West (1938)
1934	Bud rot	Malaysia	Collapse of the unopened leaves (spear).	Bacterial infection associated with the damage of the beetle <i>Oryctes rhinocerus</i> or light striking.	Bunting et al. (1934)
1935	Bud rot	Coquilhatville Province in the Belgian Congo	Bud rot.	<i>P. palmivora</i> , <i>Bacillus coli</i> . Only isolation was used as diagnosis.	Ghesquiere (1935)
1944	Bud rot	Dahomey (present Benin)	Bud rot.	Bacteria and a <i>Phytophthora</i> -like microorganism.	Bull and Robertson (1959)
1948	Bud rot	Congo	The disease is similar to bud rot in coconut (caused by <i>P. palmivora</i>).	Association of insect damage with bacteria and fungi.	Wardlaw (1948)
1950	Bud rot	Venezuela	Reduced development of new tissue, with lysis of the internal tissue above the meristem with or without dead of the palm.	Physiological.	Malaguti (1953)
1951	Little leaf	Congo	Short and erect leaves. Dark brown rotting of the unopened pinnae, followed by the collapse of the central spear. In high severity the trunk apical meristem may be destroyed.	Deficiency or unbalance of nutrients.	Kovachich (1952, 1953)
1954	Bud rot	Sibiti, in the Congo-Brazzaville	Bud rot.	Bacteria and <i>F. oxysporum</i> , <i>F. solani</i> , and <i>F. roseum</i> .	Bachy (1954)
1957	Spear rot	Yaligimba, Congo	Presence of localized rotten areas on the median leaflets of the spear leaf. Lesions are colorless initially and then present a water-soaked appearance. Old lesion turns pale brown with a thin marginal orange-brown border.	<i>P. arecae</i> was suggested as the tentative isolated species. Its role as spear leaf causal agent was proven with Koch's postulates.	Kovachich (1957)
1960	Bud rot	Congo	Small lesion in the spear leaves then increase in size and number in new tissue. Spear leaf collapse with the increment of incidence.	Three steps are required: (i) initial damage <i>Thermophilochaeta quadripustulata</i> (ii) infection of bacteria (iii) damage of <i>Platygenia barbata</i> and <i>Rhynchophorus palmarum</i>	MacGarvie (1960)

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TABLE 1
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Date	Disease	Location	Symptoms	Diagnosis	References
1963	Bud rot/little leaf	Congo	Bud rot and little leaf. Wet brown rot on the arrow. In serious cases the rachis is involved and the spear collapses, followed by bud rot. Then, little leaf is observed.	<i>Erwinia lathyri</i> .	Duff (1963)
1965	Bud rot	The Arenosa, Coldesa, Turbo, Antioquia, Colombia	The spear rot–bud rot complex.	Unknown.	De Rojas and Ruíz (1972) Turner (1981)
1973	Oil palm wilt	Nigeria	Not described.	Tapping palms for palm wine production serve as entry for <i>P. palmivora</i> in oil palm.	Faparusi (1973)
1975	Bud rot	India	Not described.	<i>P. palmivora</i> . The microorganism was isolated, but not reinoculated.	Joseph and Radha (1975)
1976	Bud rot	The Arenosa, Coldesa, Turbo, Antioquia, Colombia	The spear rot–bud rot complex.	<i>F. oxysporum</i> , <i>F. solani</i> , and bacteria.	Renard (1976)
1983	Bud rot	Shushufindi, Ecuador	Spear rot and bud rot.	The author proposed <i>Phytophthora</i> and <i>Pythium</i> as one of the possible causes of bud rot, but only <i>Pythium</i> was isolated.	de Franqueville (2003) Renard and Quillec (1985)
1991	Bud rot	Suriname	Yellowing leaves 1, 2, 3, spear rot, and bud rot.	Unknown.	Van de Lande (1993)
1991	Lethal yellowing–bud rot	Denpasa, Brazil	Yellowing and bud rot.	Unknown.	Van Slobbe and Rocha de Souza (1991)
1991	Bud rot	Ecuador Eastern	Yellowing and bud rot.	Unknown, virus was the hypothesis.	Perthuis (1991)
1991	Bud rot	Sushufindi, Ecuador	Yellowing, vein banding and bud rot.	Unknown.	Renard (1991)
1991	Bud rot	Atlantic Coast and Eastern zone, Colombia	Yellowing of young leaves, drying of lower leaflets, necrotic spots, and spear bud rot.	<i>Fusarium</i> sp.	Acosta (1991)
1996	Bud rot	Western Zone in Colombia	Spear rot and bud rot.	<i>Fusarium</i> spp., <i>Pythium</i> spp., and <i>Thielaviopsis paradoxa</i> .	Nieto Páez et al. (1996)
1999	Bud rot	Western Zone in Colombia	Bud rot.	<i>Phytophthora</i> sp. Koch's postulates were not performed.	Alvarez et al. (1999)
2008	Bud rot	Central and South Western Zone in Colombia	External symptoms on youngest spear leaf as necrotic small lesions, and in some cases there is an increase in the number and size of the lesions, which in more severe cases include the whole spear leaf.	<i>P. palmivora</i> . Koch's postulates were fulfilled.	Sarria et al. (2008) Torres et al. (2010b)
2012	Common spear rot	Indonesia	Crown diseases. Necrotic lesions on spear leaf leaflets, followed by extensive rotting of leaflets as the leaf expands.	<i>Thielaviopsis paradoxa</i> .	Suwandi et al. (2012)

on the edge of infected spear leaves. When the spear leaf opens, the necrotic tissue might release sporangia and zoospores that are carried toward the base of the spear leaf package by drops of water (Drenth et al. 2013).

When young oil palms are inoculated with *P. palmivora* under optimal controlled conditions for development of disease (relative humidity >80%, 24 to 26°C), all typical initial early symptoms of

bud rot on the emerging spear leaves are expressed within 7 days after inoculation (Sarria et al. 2013; Vélez et al. 2014). Secondary infections, typically below the initial point of infection, develop several weeks later under regular misting conditions that promote sporangia production which are caducous and wash down to the base of newly forming leaflets (Sarria et al. 2013). Here they germinate or differentiate into zoospores and under conditions of

high humidity cause new infections of the youngest leaf tissue emerging from the heart. The emerging leaf then elevates the lesion further away from the heart of the palm. Secondary infections are repeated over and over when environmental conditions are appropriate for the development of the disease, resulting in small clusters of lesions along the length of the emerging spear leaf (Sarria et al. 2013).

In addition to infected tissues, *P. palmivora* zoospores have been collected from runoff water and flooding zones on oil palm affected fields (Sarria et al. 2013). As demonstrated with other species of *Phytophthora* including *P. capsici* (Gevens et al. 2007), irrigation of new fields using infested water is a very effective way of dissemination that can result in a rapid colonization of unaffected areas.

FIGURE 1

Asexual structures of *Phytophthora palmivora*. **A and D**, Sporangia on oil palm tissue. **B**, Sporangia on growing media. **C**, Chlamydospores on oil palm tissue.

FIGURE 2

Symptoms observed in palms affected by the bud rot disease. **A and B**, Lesions present in young or unopened tissues of the palm leaves known as spear leaf. **C**, Secondary infections manifested as an increased number of larger lesions on new leaves. **D**, If conditions favor the development of disease, these small lesions may affect other tissues on nearby leaflets leading to new infections. **E**, When the spear leaf opens, the necrotic tissue may fall down. **F**, In advanced stages of the disease, the complete spear leaf is affected with a dry appearance of the external leaflets. **G**, Extirpated bud with advanced lesions on the unexposed spear leaves. **H**, Close up of the affected spear leaves; notice the wet decay appearance. **I and J**, Internal lesion on the youngest tissue; from this affected area it is possible to isolate *P. palmivora*. Scale bar represents 3 cm in length.

In our studies of the infection process, we have observed zoospore encystment and germination greater than 90% within the first hour after they were placed onto oil palm leaflets (Sarria et al. 2013, 2015; Vélez et al. 2014). As in durian, zoospores were first attracted to leaf trichomes, where they germinated and formed an appressorium-like structure that subsequently penetrated the tissue (O'Gara et al. 2004; Sarria et al. 2015). Germinated zoospores were also observed penetrating the stomata or intercellular spaces. After penetration, hyphae colonized the intercellular leaf spaces, followed by intracellular invasion, penetration of the vascular bundles and spread throughout the host tissue. No symptoms were observed in the inoculated leaflets until 48 h postinoculation, when 90% of the leaflets showed symptoms of water-soaked yellow lesions and tissue degradation (Sarria et al. 2015). By 72 h after inoculation the lesions became brown with irregular growth and water-soaked edges while further behind the front of the lesion sporangia were formed just behind the edge of the lesion, and intercalary and terminal chlamydospores in older colonized tissues (Fig. 1C; Vélez et al. 2014). While sporangia are not commonly observed on decayed tissue from within the heart of the palm, chlamydospores were found to be present in over 80% in those tissues. Sporangia, chlamydospore, and zoospore release was observed within 36 to 48 h after inoculation, starting a cycle of secondary infections (Sarria et al. 2013).

In addition to disease symptoms on the spear leaves and heart tissue of the oil palm, chlamydospores were also observed on 70% of the roots of affected oil palms, but no significant damage was observed on the root system (Clavijo et al. 2013). Infested roots could serve as source of inoculum of the disease (Clavijo et al. 2013). The link between *P. palmivora* residing in the roots of oil palm plants and high up in the spear leaf in the canopy is an interesting one. Insects have been shown as vectors capable of transmitting *P. palmivora* from the soil into the canopy of cacao (Konam and Guest 2004). Initial studies in Colombia, Ecuador,

and Peru also indicate that insects from the family Tettigoniidae may be involved in the dispersal of propagules of *P. palmivora* from the soil into the top of the palms, where the pathogen can infect the young spear leaf tissue (Torres et al. 2008). Our observations show a positive correlation between the sites at the base of the spear leaf used by adults of this family to oviposit, and initial symptoms of the disease, especially in areas with low pressure of bud rot (Torres et al. 2008). Once in the canopy, inoculum rapidly spreads between neighboring palms as documented by Van de Lande and Zadoks (1999) and as experienced during epidemics of bud rot in Colombia in the last decade (Martínez 2013).

EPIDEMIOLOGY

Evolution of epidemics in Colombian plantations. Before the 1970s, the incidence of bud rot in Colombia on average remained below 0.5% in all growing areas, and for about 2 decades after the 1970s the disease was only reported in small patches in the Central, Eastern, and Western regions (Gómez et al. 1995) (Fig. 3). The first local epidemic destroyed 2,400 ha of palms in a single plantation near the Colombia-Panama border in 1964 (De Rojas and Ruiz 1972). A second epidemic took place in the Llanos Orientales between 1986 to 1990, where the incidence of bud rot reached more than 85% in some plantations (Nieto Pérez 1993) (Fig. 3). Between 2006 and 2012, bud rot destroyed numerous plantations with a total area of 75,000 ha between Tumaco-Nariño and Puerto Wilches-Santander (Avendaño and Garzon 2013) (Figs. 3 and 4). From Puerto Wilches, the disease expanded radially to new unaffected areas in neighboring oil palm growing regions.

Epidemics developed differently in different parts of the country and developed more quickly in areas with high rainfall and high relative humidity for extended periods of time. For example,

FIGURE 3

Epidemic distribution of bud rot caused by *Phytophthora palmivora* in Colombia. Low, medium, and high incidence are represented by the letters L, M, and H, respectively. Font size represents the affected area size. The smallest are lower than 1,000 ha affected, the largest represent more than 10,000 ha affected, and medium (underlined) range is somewhere between these values.

“Plantation A” (cultivar Compacta × Ekona), located in the wet Western coastal area of Colombia, where average relative humidity is 86% and the number of rainy days exceeds 320, reported the initial increase of bud rot cases from the epidemic by the end of 2004 (Fig. 5). Despite attempts to control the epidemic once the impact of the disease became clear, 100% of the area was severely affected by May 2008 (Fig. 5) and the plantation closed its oil palm processing mill in 2009 (Avendaño and Garzon 2013). In contrast, “Plantation B” (cultivar Delhi × Ghana), located in the seasonally wet/dry mid-Magdalena valley in Colombia, with a longer dry season, presented the first cases of bud rot by August 2004, and by 2009, when the incidence in the western zone had already reached 100%, bud rot had affected only 41% of the total area of the plantation (Fig. 5).

Human decisions have exacerbated the occurrence of these epidemics. Despite the fact that the disease was well known prior to these epidemics, the disease was properly managed with timely eradication of affected palms as soon as symptom expression became visible in both regions; however, the eradication practice was stopped by 2004 in an effort to reduce costs associated with the practice of monitoring and removing affected palms, and trying to emulate some plantations from the Eastern area (los Llanos orientales), where natural recovery of some palms had been observed from 8 to 36 months after first symptoms were diagnosed. This natural recovery, where the disease progression slows down during the prolonged dry season, was never observed in the more humid Western and Central regions of Colombia. Subsequent investigations have shown that under drier conditions the disease develops more slowly due to unfavorable conditions for sporangia production and zoospore release and reinfection of the immature growing tissue.

MANAGEMENT AND CONTROL

High-yielding cultivars of the African oil palm (*Elaeis guineensis* Jacq.) are commonly planted in America (Corley and Tinker 2003; Renard and Quillec 1985; Richardson 1995), and most of these commercial cultivars are highly susceptible to bud rot and *P. palmivora* is endemic in all areas. The Colombian National Federation of Oil Palm Growers (Fedepalma) has guided farmers to avoid establishing plantations on forest areas, where *P. palmivora* occurs naturally affecting a large variety of host species including palms, and areas prone to flooding and areas with bad drainage. These recommendations were based on the fact that these conditions favored the spread and multiplication of the pathogen (Martínez et al. 2009; Torres et al. 2010a). Farmers are advised to establish, correct,

and improve their drainage systems before initiating a new plantation to reduce conducive conditions for *P. palmivora* establishment and multiplication. The selection of a field with low *P. palmivora* inoculum pressure and good drainage systems constitutes the first defense line when establishing a new plantation.

The most effective management of bud rot, especially in areas with environmental conditions suitable for disease development, involves the use of resistant planting material (Avendaño and Garzon 2013; Bastidas et al. 2007; Meunier 1991). The genetic base of older cultivars (dura or thick-shelled fruit) and modern commercial oil palm cultivars (tenera or thin-shelled fruit) is extremely narrow, and a great majority of them are highly susceptible to bud rot. Genetic narrowness in commercial lines was confirmed when wild population of palms were compared with commercial ones using amplified fragment length polymorphic markers (Kularatne et al. 2001), which supported the hypothesis that most of the modern cultivars are descendants of only four oil palms brought to the Bogor Botanic Garden by the Dutch (Corley and Tinker 2003). Efforts to increase the *E. guineensis* gene pool have taken place in the last 2 decades, not only to identify resistance to different diseases, including bud rot, and limiting abiotic factors, but also to increase yield and to obtain better oil quality (I. Ayala, *personal communication*).

Although several cultivars of the American oil palm (*Elaeis oleifera*) have been shown to be tolerant to bud rot (Rey et al. 2004), they have a procumbent (branches trailing along the ground) growth habit and low oil extraction rate, which is undesirable for farming and processing, respectively (Corley and Tinker 2003). Interspecific hybrid crosses of *E. guineensis* × *E. oleifera* have been shown to possess desirable agronomic traits and reduced susceptibility, providing potential options for disease control (Alvarado et al. 2013; Corley and Tinker 2003; Meunier 1991; Navia et al. 2014; Preciado et al. 2011; Rey et al. 2004).

The cultivation of *E. guineensis* palms susceptible to bud rot can only be successful with intense monitoring for disease expression coupled with rapid agronomic interventions involving destruction of infected palms in the nursery and in plantations (Torres et al. 2010a). Because of the potential for water-assisted dispersal, it is important to improve drainage and avoid the use of overhead irrigation and to control the quality of the irrigation water. Nurseries must be established away from sources of inoculum and plantations, and a 200 m border zone free of diseased palms will reduce the movement of the pathogen (Martínez et al. 2009). This practice has been useful in the renewal of plantations after the epidemic in Tumaco (Martínez 2013).

FIGURE 4

General aspect of healthy and affected plantations. **A**, Healthy plantation. **B**, Destroyed plantation in Tumaco. **C**, Detailed aspect of diseased palm. **D**, Aerial photograph of an affected field. **E**, Affected palms. **F**, Detailed aspect of a healthy palm.

If the disease is detected in the early stages remedial action can be taken to save the affected palm. This intervention, also called surgery, involves removal of all the affected tissue to just above the meristem, quick flaming of the exposed area to control any surviving spores that may start an infection, and the application of a mixture of bactericides, fungicides, and insecticides to the exposed area. The aim of this program is not only to remove the tissue affected by *P. palmivora*, but to avoid the damage caused by the palm weevil (*Rynchophorus palmarum*), which is attracted to the exposed tissues, and to avoid the infection by secondary invaders such as *Erwinia* sp., *Fusarium oxysporum*, *F. solani*, and *Thielaviopsis paradoxa* that can colonize the untreated damaged tissue (Torres et al. 2009). In addition, neighboring palms are sprayed with the fungicides. When implemented early and rigorously, the “surgery” can prevent destruction of the single meristem and save the palm (Torres et al. 2009). Early detection is a key point in bud rot management (Martínez 2009; Martínez et al. 2013; Torres et al. 2010a). However, it is especially critical to treating young palms, since the healthy tissue above the meristem that can be removed is limited in comparison with the older ones. Surrounding palms should also be inspected and treated at the first signs of disease symptoms (Ariza et al. 2008).

An integrated crop management system for bud rot at present includes cultivar selection, proper drainage, good fertilization, regular monitoring, infected tissue removal, and destruction of

affected tissue and/or whole plants in order to control bud rot disease in oil palm. Such an approach implemented on one of Cenipalma's research stations found a reduction from 20% incidence to 4% in a period of 4 months, with a final incidence of 0.5% 23 months after the treatments were initiated (Aya-Castañeda and Martínez 2011).

FUTURE DIRECTIONS

Current research is focused on providing farmers with short-, mid-, and long-term solutions for managing bud rot. In the short term it is necessary to understand how different active ingredients, including new and developmental compounds to control oomycetes, are moving inside the palms in order to identify which of them are reaching the zone used by the pathogen to colonize the palm and propagate. It is also important to understand *P. palmivora* populations in Colombia and elsewhere to determine if there are populations of the pathogen specific to oil palm or the presence of a single large population able to cause disease on multiple host plant species, as this has implications for breeding and selection programs. The effect of environmental conditions present in different regions in Colombia on the aggressiveness of *P. palmivora* requires further investigation. Regarding the early diagnosis, Cenipalma has explored the use of Agdia immunostrip (Agdia Inc, Elkhart, IN) and PCR and RT-PCR, for detection; however, more research is required to establish a reliable, economic, and fast testing system for the disease. In the

FIGURE 5

Diseases progress of bud rot in a plantation in Central (dry) and Western (wet) region in Colombia.

medium-term, oil palm breeding programs need to be equipped with rapid methodologies to evaluate resistance in new cultivars and develop forecast methods for growers that enable them to optimize agronomic practices in the field to reduce disease impact in their plantations. More long-term resistant and productive cultivars need to be developed with economically and dietary desirable oil characteristics and with good oil extraction properties.

CONCLUSIONS

In this review we have demonstrated that bud rot of oil palm caused by *P. palmivora* is a serious threat to oil palm production in the America's and elsewhere. The extent of the bud rot epidemics is a stark reminder of the destructive potential of *Phytophthora* pathogens in different crops. Species of the genus *Phytophthora* and *P. palmivora* in particular are a major impediment for crop production in the tropics as they have an ability to survive in the environment; it is a generalist pathogen with an extremely wide host range. The diversity and abundance of susceptible host plant species contributes to the survival and perpetuation of sources of inoculum. *P. palmivora* is a giant that has woken up and meets most criteria as outlined by Fisher et al. (2012) as a major emerging pathogen to seriously threaten not only oil palm production but many other susceptible food crops throughout the tropics.

While bud rot has been especially destructive in the Americas, previous reports of severely affected plantations in Africa (Bull and Robertson 1959; MacGarvie 1960; Robertson et al. 1968) and Asia (Turner and Bull 1967) have confirmed the presence of the disease in all oil palm growing areas in the world. At present, there have been no major outbreaks of bud rot reported from South Asia; however, "spear rot" is frequently reported from Asia (Pornsuriya et al. 2013; Suwandi et al. 2012), especially under conditions when fields get flooded (G. Y. Keng and N. Rajanidu, *personal communication*). Further work will be necessary to identify if *P. palmivora* is also related to "spear rot" in South Asia and establish if there is differentiation among pathogen populations in different oil palm growing regions of the world. Our research has demonstrated that the first steps to mitigate the destructive damage of *P. palmivora* in oil palm include not only the early diagnosis of the disease, but taking regional and global action to manage the disease. Individual actions are insufficient to control the disease; many cases have been reported where the disease affected farmers who invested significant time and resources to the manage the disease, but their neighbors did not take any action against the disease. In this sense, a global research network called "bud rot task force" has been created, providing farmers in other countries with a low bud rot incidence, such as Malaysia and Indonesia, access to information to help recognize the disease in the field and learn how to effectively manage it, thereby reducing the chances of catastrophic pandemics.

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