



Review Article

Four Decades of Research on Phytoplasma Diseases of Palms: A Review

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Abstract

Phytoplasmas are important pathogens of hundreds of plant species all over the world. They have been reported to affect not only yield and product quality, but also plant's survival. Palms are cultivated in tropical and subtropical areas of the world. Phytoplasmas affecting palms (date palms, oil palms and coconut trees) have received great attention from researchers due to the importance of palms as a main food commodity in different parts of the world. Phytoplasmas result in different symptoms in various palm species, collectively known as lethal yellowing diseases. Several diseases outbreaks have been reported in palms due to phytoplasmas, including the “coconut bud rot” which resulted in extensive yield loss and stopped the commercial production of coconuts in the Caribbean. This review discusses the most common phytoplasma groups affecting palm species as well as their history, distribution and host range. In addition, information is provided about losses due to phytoplasma diseases in palms, potential methods of transmission, the interaction between palms, phytoplasmas and vectors and potential management strategies. © 2020 Friends Science Publishers

Keywords: Lethal yellowing; MLO; *Phoenix dactylifera*; Date palm; *Cocos nucifera*; Coconut; *Elaeis guineensis*; Oil palm

Introduction

Palms belong to the *Arecaceae* family, which comprises about 180 genera and 2600 species. They are ecologically and economically important as they provide humans with medicine, food, and fuel and are commonly used for ornamental purposes (Chao and Krueger 2007). Amongst these species, three are most important, including date palm (*Phoenix dactylifera* L.), coconut (*Cocos nucifera* L.), and the African oil palm (*Elaeis guineensis* L.). Date palm is the most important fruit crop in the Middle East, North Africa, and Arabian Peninsula. This crop was also introduced in India, southern Africa, South America, Australia, and the United States. Based on FAO statistics, date palm production significantly increased from 1.8 Million ton (Mt) in 1962 to 8.5 Mt in 2018, which Egypt been the first in date production (1.6 Mt), followed by Saudi Arabia (1.3 Mt), Iran (1.2 Mt) and Algeria (1.1 Mt) (FAO 2019). Coconut palm, with a total cultivated area of 12 million ha and 62 million tone of production, is grown in tropical areas (mainly in Asia) in 90 countries and it is the main income source and staple food for many developing countries (FAO 2019). Oil palm production reached 272 Million tons in 2018 from about 19 million ha of cultivated area (FAO 2019).

Phytoplasmas are wall-less prokaryotes associated

with more than 600 diseases (Maejima *et al.* 2014; Kumari *et al.* 2019; Solomon *et al.* 2019). They are transmitted by phloem-sucking insects in the families Cicadellidae, Cixiidae, Cercopidae, Derbidae, Delphacidae and Psyllidae (Weintraub and Beanland 2006; Linck and Reineke 2019; Quaglino *et al.* 2019; Jakovljević *et al.* 2020) and colonize the vector by entering the midgut lumen, adhering to midgut epithelium cells eventually invading the hemolymph and reaching the salivary glands for further dissemination (Marzachi 2004). There are several reports on the transovarial transmission of phytoplasmas to the progeny by infected females (Kawakita *et al.* 2000; Tedeschi *et al.* 2006; Mittelberger *et al.* 2017).

In this review, up-to-date information is provided about phytoplasma associated with palm diseases, vectors, management methods and phytoplasma biology and interaction with palms.

Lethal Yellowing Diseases

Lethal yellowing diseases (LYD) are defined as a syndrome with similar and specific symptoms (Gurr *et al.* 2016; Solomon *et al.* 2019). Lethal yellowing is also called lethal decline, lethal yellowing type syndrome, and coconut lethal yellowing (Narvaez *et al.* 2016; Bahder *et al.* 2017). It is caused by many groups and subgroups of phytoplasma in

the world. The incidence and appearance of the symptoms vary greatly depending on host species, variety, phytoplasma group, and geographical location (Harrison *et al.* 2014). General symptoms observed in all LYD are the drop of the immature and ripe fruits (Mazivele *et al.* 2018). The tips of the fronds become yellow in color, especially on the oldest fronds, followed by falling of fronds from the stem (Bila *et al.* 2019; Pilet *et al.* 2019; Solomon *et al.* 2019).

LYD was first observed and reported from the Caribbean in the 1800s, followed by Ghana, Tanzania, and Togo (Dollet *et al.* 2009). An outbreak of “coconut bud rot” resulted in extensive yield loss and stopped the commercial production in the Caribbean (Johnson 1912). Simultaneously, an epidemic was reported from Jamaica, Honduras, southern Mexico, Florida, Cuba, Haiti, Bahamas, and Belize (Harrison *et al.* 2002a; Baudouin *et al.* 2008; Lebrun *et al.* 2008; CABI 2012). Because of the similarity of the typical symptoms in hosts in different parts of the world, researchers suspected that they had the same causative agent. However, the differences in symptom progression raised a question that there may be different pathogens. The development in the identification techniques, especially molecular identification, helped characterize the different groups and subgroups of phytoplasma associated with this syndrome (Table 1) (Dollet *et al.* 2009; Eziashi and Omamor 2010; Bertaccini *et al.* 2014; Contaldo *et al.* 2019; Córdova *et al.* 2019; Zamharir and Eslahi 2019).

Currently, this disease is considered an important issue in the coconut production industry in Central America and the Caribbean (Ntushelo *et al.* 2013). This disease is presently occurring in Nigeria, Mozambique, Ghana, Benin, Lenya, Togo, Tanzania, India, Sri Lanka, Indonesia (Table 1) (Dollet *et al.* 2009; Eziashi and Omamor 2010; Perera *et al.* 2012; Ramjagathesh *et al.* 2012, 2019). Smallholder and subsistence farmers were more affected by the lethal yellowing disease due to their heavy reliance on coconut nutrition and economy (Myrie *et al.* 2011).

LYD is widely reported from coconut (Fig. 1), although it also occurs on date palm and oil palm (Kra *et al.* 2017; Zamharir and Eslahi 2019). Table 1 presents the other palm species host of LYD. The most devastating outbreak has been reported on coconut. For example, 86% of coconut trees died from 1961 to 1983 in Jamaica (Jones 2002). Other outbreaks referred to as “Akwa wilt”, “Cape St. Paul Wilt”, and “Kian-cope” diseases killed millions of coconuts in Nigeria, Ghana, and Togo, respectively (Eziashi and Omamor 2010). It is estimated that 38% of coconut trees were destroyed in Tanzania since the 1960s (Mugini 2002). This disease is not always “lethal”, and slight symptoms were observed in other species like date palm (Manimekalai *et al.* 2014a; Zamharir and Eslahi 2019).

The first report of an association between phytoplasma and date palm dates back to 1998 when Tymon *et al.* (1998) reported the association of 16SrIV-C with silver date palms. Two years later, slow decline, or El Arkish was reported

from Sudan in which 16SrXIV was found associated with this disease (Cronjé *et al.* 2000). In 2002, date palm yellows associated with 16SrIV-A was reported from Kuwait (Al-Awadhi *et al.* 2002), which was the first report of phytoplasma disease occurring in date palms in Asia. Al-Wijam disease, associated with 16SrI-B phytoplasma, was observed in Saudi Arabia in 2007 (Alhudaib *et al.* 2007). In addition, the 16SrII phytoplasma has been found associated with date palm in Saudi Arabia (Omar *et al.* 2018). In America, 16SrIV-F was first reported on date palm in 2013 (Ntushelo *et al.* 2013). Alkhazindar (2014) reported the association of 16SrI phytoplasma with date palm in Egypt. Recently, the 16SrVI-A and VII-A phytoplasmas were reported on date palms in Iran (Zamharir *et al.* 2016; Zamharir and Eslahi 2019). Although phytoplasma diseases on date palm are not lethal so far, significant economic losses were observed in this region (Fig. 2). For example, fruit failure at harvest has been reported due to Al-Wijam in Kuwait and Saudi Arabia (Alhudaib *et al.* 2007).

Origin and causes of LYD

According to the report of LYD outbreak in the Caribbean, it is speculated that the disease originated in this region (Johnson 1912). However, this hypothesis was rejected by Ogle and Harries (2005), who stated that coconut palms were healthy after introduction to this region for several hundred years in the 16th century. Importing grasses from India to the Caribbean is the recent hypothesis indicating that insects harboring phytoplasma could have transferred to the Caribbean on cattle fodder in the 19th century. This speculation is supported by the fact that West Africa was the destination of fodder transportation from India, where LYD occurred (Ogle and Harries 2005). Taking into account the above facts, it can be hypothesized that the origin of LYD was in Asia (Ogle and Harries 2005). However, by the identification and discovery of many associated phytoplasma groups with LYD, it has been suggested that there were diverse origins. For instance, according to the low mortality of *Sabal Mexicana* (Texas palmetto), Vázquez-Euán *et al.* (2011) suggested the phytoplasma 16SrIV-D could have originated in Mexico. Lethal yellowing disease occurred when a vector was introduced in new areas indicating the non-native origin of the disease in the Caribbean (Elliott 2009), while the potential vectors of the recent epidemic of Bogia coconut syndrome are all native species in Papua New Guinea (Pilotti *et al.* 2014). Additional information regarding the discovery and naming can be found in Lee *et al.* (2007).

Phytoplasmas are classified into groups and subgroups by comprising the gene targeting the 16S ribosomal gene sequences. Currently, 44 groups and more than 100 subgroups have been identified and are yearly increasing. In addition to this gene, other genes like *tuf*, *secA*, *rp*, *groEL*, *secY*, and the 16S-23S rRNA spacer region are used for further distinction (Seruga Musić *et al.* 2014; Al-Subhi *et al.* 2018; Balakishiyeva *et al.* 2018; El-Sisi *et al.* 2018;

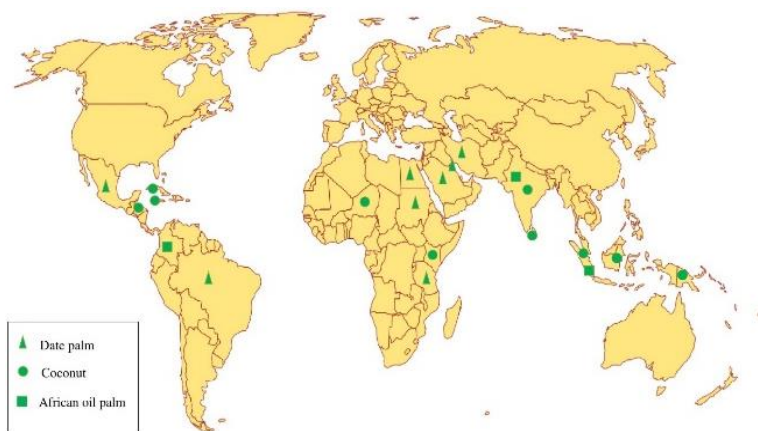


Fig. 1: A map indicating distribution of phytoplasma diseases in most important species of palms



Fig. 2: Symptoms of yellowing and leaf stunting in *Phoenix dactylifera* associated with 16SrII-D phytoplasma

Jamshidi *et al.* 2019; Oliveira *et al.* 2020). Also, specific antibodies, vector transmission, and host range can be used for additional discrimination (Fránová *et al.* 2013; Ntushelo *et al.* 2013).

LYD Phytoplasmas are commonly classified into the 16SrIV group, although some have now been reclassified into the groups 16SrXXII (Harrison *et al.* 2014), 16SrI, 16SrXI, and 16SrXIV (Bertaccini *et al.* 2014) (Fig. 3). Based on vectors, plant hosts, and variety, the 16SrIV group is divided into six subgroups A–F (Martinez *et al.* 2008; Vázquez-Euán *et al.* 2011). These subgroups might vary in

symptoms, host range, and vectors. For instance, 16SrIV-A affect palms 18 months and older; another subgroup of 16SrIV (not given) could infect bearing and non-bearing palms (Harrison *et al.* 2002b). Different phytoplasma groups have been reported in different regions. For example, it has been demonstrated that the prevalent groups in West and East Africa are XXII-B, IV-C, and a new unclassified coconut-associated phytoplasma (Bila *et al.* 2015). On the other hand, 16SrXIV and 16SrXXIII groups have been reported from Malaysia (Nejat *et al.* 2009b).

Numerous plant species and/or varieties of palm are

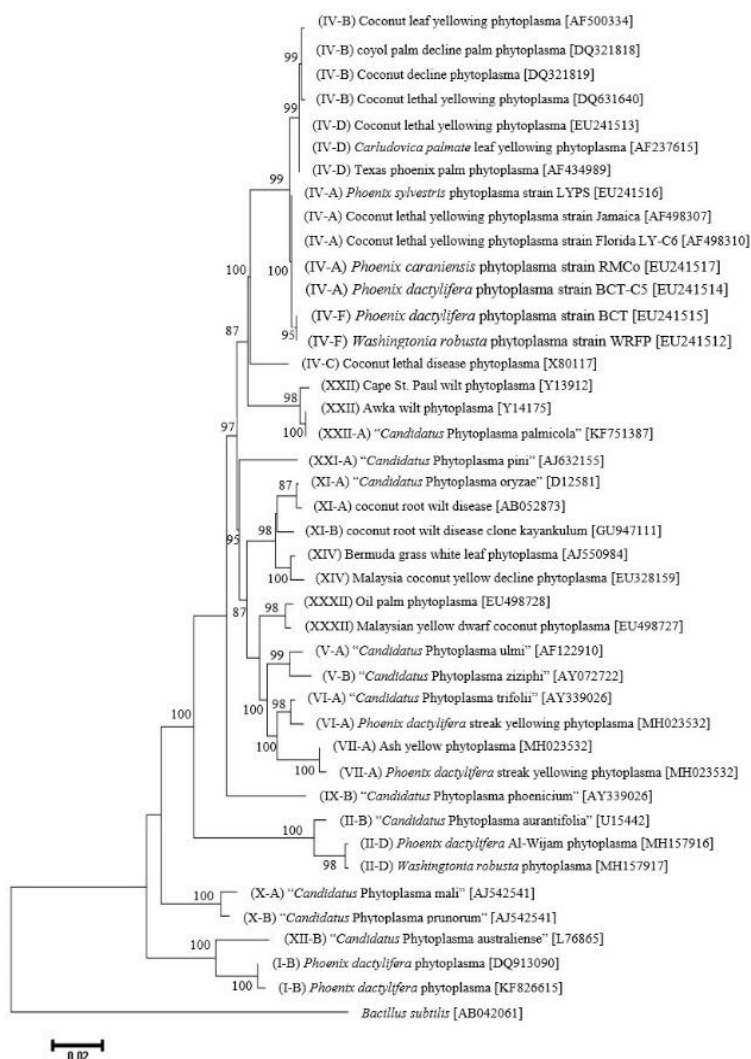


Fig. 3: A phylogenetic tree representing phytoplasma groups and subgroups associated with palms

infected with some phytoplasma subgroups (Table 1). In Mexico, 16SrIV-A is found in *T. radiata* and *C. nucifera* in the same area, while *Pseudophoenix sargentii* and *S. mexicana* are affected by 16SrIV-A. Also, it is likely that one subgroup only infects a palm species (Table 1). However, mixed infection with subgroups of a group in one palm species is not unexpected as *S. mexicanat* could be a host of 16SrIV-D and 16SrIV-A (Fránová *et al.* 2013).

Spread of phytoplasma-associated palm diseases

LYD phytoplasmas can be spread via different means. Oropeza *et al.* (2017) confirmed that seed transmission could occur in LYD from embryos to plantlets by *in vitro* germination of the zygotic embryo of infected seeds. Phytoplasmas can also spread via movement of infected plant materials (Cordova *et al.* 2003). Geographical barriers such as mountain ranges can significantly affect the rate of spread (CABI 2012). Human activity could play a

substantial role in the spread of plant diseases globally, including LYD. In Mexico, for example, studies found that the export of palms and grasses from Florida introduced LYD to Mexico before spreading to Central America. Other diseases have been introduced to a new area in as the same scenario (Bertin *et al.* 2007).

Vectors play a crucial role in phytoplasma distribution and spread (Rashidi *et al.* 2014; Linck and Reineke 2019). Although many papers have been published on phytoplasma vectors, the vectors of many phytoplasmas still to be identified. Auchenorrhyncha and Sternorrhyncha comprise most vectors of phytoplasmas (Howard *et al.* 2001). Palms are hosts for many Auchenorrhyncha, although most of them do not cause a direct injury. Having the ability to vector pathogens makes them the most important threat to palms. Insects should be able to acquire and retransmit phytoplasma to the healthy plants in order to be considered a vector (Bosco and Tedeschi 2013). The only confirmed

Table 1: Current distribution, phytoplasma groups and host plants of phytoplasma diseases on palms

Location	Name	16Sr Group	Host	References
			Asia	
Iran	Streak yellow date palm	VI-A, VII-A	<i>Phoenix dactylifera</i>	(Zamharir and Eslahi 2019)
Kuwait	Yellows date palm	IV-A	<i>P. dactylifera</i>	(Al-Awadhi et al. 2002)
King Saudi Arabia	Al-wijam	I-B	<i>P. dactylifera</i>	(Alhudaib et al. 2007)
	lethal Yellowing palm disease		<i>P. dactylifera</i>	(Omar et al. 2018)
	Lethal yellowing Mexican fan palm	II-D	<i>Washingtonia robusta</i>	
India	Kerala wilt disease	IV-C	<i>Coconut nucifera</i>	(Edwin and Mohankumar 2007)
India	Root (wilt) disease	XI-A, XI-B	<i>C. nucifera</i>	(Manimekalai et al. 2014b; Yadav et al. 2015)
India	Oil palm stunting (OPS)	I-B	<i>Elaeis guineensis</i>	(Mehdi et al. 2012)
Sri Lanka	Weligama coconut leaf wilt disease	XI	<i>C. nucifera</i>	(Perera et al. 2012; Kumara et al. 2015)
Malaysia	Coconut yellow decline	XIV	<i>C. nucifera</i>	(Nejat et al. 2009a, c)
Malaysia	Ca. P. malaysianum	XXXII-B, XXXII-C	<i>C. nucifera, E. guineensis</i>	(Nejat et al. 2013)
Malaysia	Coconut lethal yellowing (CLY)	XIV-A, I-B, XXXVI-A	<i>Wodyetia bifurcata</i>	(Naderali et al. 2013, 2017)
Malaysia	Royal pam yellow decline	I	<i>Roystonea regia</i>	(Naderali et al. 2015)
Malaysia	Coconut yellow decline	I-B	<i>Cyrtostachys renda</i>	(Naderali et al. 2014)
Indonesia	Kalimantan wilt and natura wilt	XI, XIII	<i>C. nucifera</i>	(Ogle and Harries 2005; Warokka et al. 2006)
Africa				
Nigeria	Awka disease	XXII-A	<i>C. nucifera</i>	(Ekpo and Ojomo 1990; Tymon et al. 1998; Wei et al. 2007; Osagie et al. 2015)
Tanzania	Coconut lethal disease	IV-C	<i>P. dactylifera</i>	(Tymon et al. 1998)
Kenya	Coconut lethal disease	IV-C	<i>C. nucifera</i>	(Córdova et al. 2014)
Mozambique	Coconut lethal disease	IV-B, IV-C, XXII-A	<i>C. nucifera</i>	(Córdova et al. 2014; Harrison et al. 2014; Bila et al. 2015)
Ghana, Cote d'Ivoire, Nigeria, Togo, Cameroon, Benin	Cape St. Paul wilt, CSPW keta disease, Kinacope, Kribi disease or Cote d'Ivoire lethal yellowing disease	XXII-B, XXII-C	<i>C. nucifera, Elaeis guineensis, Borasus aethiopicum, Raphium vinifera</i>	(Harrison et al. 2014; Arocha-Rosete et al. 2015; Osagie et al. 2015; Kra et al. 2017)
Egypt	Date palm yellows	I-B	<i>P. dactylifera</i>	(Alkhazindar 2014)
Sudan	Slow decline or El Arkish, or White Tip die-back	XIV	<i>P. dactylifera</i>	(Cronjé et al. 2000)
America				
Florida	Coconut lethal yellowing (CLY)	IV-F	<i>W. robusta, P. dactylifera</i>	(Harrison et al. 2008; Ntushelo et al. 2013)
Dominican Republic	CLY	IV-E	<i>C. nucifera</i>	(Martinez et al. 2008; Ntushelo et al. 2013; Córdova et al. 2014)
Mexico, Honduras	Yucatan coconut lethal decline, lethal yellowing disease	IV-B	<i>C. nucifera, Acrocomia aualeata</i>	(Roca et al. 2006; Ntushelo et al. 2013)
Florida, Caribbean Basin	CLY	IV-A	<i>C. nucifera and 38 other palm species</i>	(Gurr et al. 2016)
Mexico, Texas and Florida, Puerto Rico	Texas Phoenix palm decline (TPPD) <i>C. palmate</i> yellows (CPY) phytoplasma or Sabal Mexicana lethal decline, Lethal yellowing-like syndrom	IV-D IV-A IV-A	<i>P. canariensis, P. dactylifera, P. reclinata, P. roebelienii, P. sylvestria, Sabal palmetto, Syagrus romanzoffiana, Carlodovicia palmate, Sabal Mexicana, Pseudophoenix sargentii, Pritchardia pacifica, Thrinzaradiata, Carpentaria acuminata, Caryota mitis, Roystonea spp., Adonidia merrillae, Tharinax radiata, Coccothrinax readii, Roystonea regia, Acrocomia mexicana</i>	(Harrison et al. 2002c; Narvaez et al. 2006; Vázquez-Euán et al. 2011; Córdova et al. 2014; Narvaez et al. 2016; Lara et al. 2017)
Colombia	Oil palm lethal wilt	I-B	<i>Elaeis guineensis</i>	(Alvarez et al. 2014)
Florida (Hossonborg county)	Lethal bronzing disease of palm	IV-D	<i>Syagrus romanzoffiana, Sabal palmetto</i>	(Bahder et al. 2018)
Florida	Texas phoenix palm decline (TPPD)	IV-D	<i>Bismarckia nubilis</i>	(Dey et al. 2018)
Louisiana	Lethal yellowing	IV-A, IV_D	<i>P. sylvestris; Trachycarpus fortunei</i>	(Singh and Ferguson 2017; Ferguson and Singh 2018)
Cuba	Lethal yellowing	IV-A	<i>C. nucifera</i>	(Llauger et al. 2002)
Guatemala	Lethal yellowing	IV-A	<i>C. nucifera</i>	(Mejia et al. 2004)
Jamaica	Lethal yellowing	IV-A	<i>C. nucifera</i>	(Myrie et al. 2007)
Oceania				
Papua new Guinea, Solomon Islands	Banana wilt associated phytoplasma (BWAP)	XXII-A	<i>C. nucifera</i>	(Davis et al. 2015)

LYD vectors are *Haplaxius crudus* (van Duzee) in Florida (Howard et al. 1983) and *Proutista moesta* in India (Rajan 2013). Putative vectors of LYD phytoplasmas are listed in Table 2.

Alternate Hosts of LYD

Different palm species and few non-palm related species are considered as alternative host plants of LYD in Florida (Gurr et al. 2016; Rosete et al. 2016). Mixed infection of 16rXXII-A with a new group of LYD was detected in coconut farms near pine trees. The new group (closely

related to *Ca. P. pini*, 16SrXXI) is suggested to infect coconut palms as well as the pine (Bila et al. 2015). Attempts to find alternative host plants in Jamaica revealed that some weeds being the host of 16SrIV-A, including *Synderella nodiflora* and *Emilia fosbergii*. The number of alternative host plants increased, in which *Cleome rutidosperma*, *Stachytrapheta jamaicensis* and *Macroptilium lathyroides* were known to be infected by 16SrIV-E (Brown and McLaughlin 2011). Danyo (2011) reported *Desmodium adscendeus* were positive in PCR when screening for alternative hosts for Cap St. Paul Wilt disease.

Table 2: A list of the vectors of lethal yellowing disease

Location	Disease name/ Phytoplasma group	Vector	Testing technique	status	references
Florida	Lethal yellowing/16SrIV-A	<i>Haplaxius crudus</i>	Cage transmission test	confirmed	(Harrison <i>et al.</i> 2008)
Mexico	Lethal yellowing/16SrIV-A, IV-D, IV-E	<i>H. crudus</i>	Observation/PCR	Suggested/Putative	(Córdova <i>et al.</i> 2014; Narváez <i>et al.</i> 2018)
Ghana	Cape St. Paul Wilt/16SrXXII	<i>Myndus apiopodoumensis</i>	Cage trials were unsuccessful but detected positive in PCR	Putative	(Pilet <i>et al.</i> 2009)
Mozambique	Coconut lethal yellow syndrome/16SrXXII	<i>Platacantha lutea</i> , <i>Diostrombus mkurangai</i>	PCR	Putative	(Dollet <i>et al.</i> 2011; Bila <i>et al.</i> 2017)
Tanzania	Coconut lethal disease/16SrIV-C	<i>Diostrombus mkurangai</i>	PCR	Putative	(Mpunami <i>et al.</i> 2000)
India	Kerala wilt disease	<i>Stephanitis typical</i> , <i>Proutista moesta</i> , <i>Sophonia greeni</i>	Cage transmission	Positive	(Mathen <i>et al.</i> 1990)
Sri Lanka	Weligama coconut leaf wilt disease/16SrXI	<i>Zophiuma pupillata</i>	Survey/ PCR PCR	Putative/negative Putative	(Rajan 2013) (Pilotti <i>et al.</i> 2014)
Cote D'Ivoire	Cote D'Ivoire lethal yellowing/16SrXXII-B	<i>Nedutepa curta</i>	PCR	Putative	(Kwadjo <i>et al.</i> 2018)

In addition to the alternative hosts of phytoplasmas, plants including acid limes grown under certain environmental conditions, are subject to phytoplasma infection without developing disease symptoms (Marcone 2014; Al-Ghaithi *et al.* 2017). Detection phytoplasma in such plants by PCR cannot specify if phytoplasma presence is for a short time feeding of the visiting insects or if the plant is an actual alternative host of the phytoplasma (Bertaccini *et al.* 2014). These plants may be considered more important than the alternative hosts developing symptoms, as they may act as a source of phytoplasma without been noticed.

Phytoplasma Interaction with Vectors and Host Plants

Pacifico *et al.* (2015) suggested that phytoplasmas change their metabolism to adapt to new hosts. Phytoplasma infection can alter the expression and signaling level of host plant genes, which can affect plant development (Himeno *et al.* 2011; Bel and Musetti 2019; Wei *et al.* 2019; Parakkunnel *et al.* 2020). Makarova *et al.* (2015) studied the genomic response of the host plants and vectors. They revealed that 34 genes in the vector and 74 genes in the host plants were up regulated after infection, indicating the role of genes in host adaptation. Nejat *et al.* (2015) revealed that coconut, ecotype Malayan Red Dwarf, has downregulated more genes (21860 unigene) than the upregulated ones (18013 unigene) in response to 16SIV-related strain infection. Most genes were responsible for innate immunity, chlorosis, and biosynthesis of secondary metabolites. The changes of endogenous cytokinin content in response to LYD phytoplasma revealed that cytokinin levels drastically decreased in the infected plants compared to the healthy ones (Aguilar *et al.* 2009). They stated that the symptom appearance in the host plants is due to the changes in cytokinin level.

Phytoplasmas live in the phloem and can be found in the sieve elements of infected plants (Santi 2019; Zimmermann *et al.* 2019). It has been demonstrated that the disruption of the carbohydrate transport system and the

photosystem II reaction center efficiency by phytoplasmas result in LYD symptoms (Maust *et al.* 2003). Coconut infected by RWB increased hydrogen peroxide and super oxide anion (Sunukumar *et al.* 2014).

The relationship between the plant host and the vector can play a crucial role in the disease management (Gonella *et al.* 2019; Tedeschi and Bertaccini 2019; Weintraub *et al.* 2019). In epidemiology, the chance of outbreak will increase if there are two factors, the completion of one generation of the vector, and reacquiring phytoplasma from that plant host (Oppedisano *et al.* 2020). Some phytoplasma can complete their generation on one non-crop species, and therefore, the plant may die and acquiring phytoplasma by the vector will not occur. Bios Noir (lethal disease of grapevines in Europe) is one example of this issue. Insect vectors feeding on palms do not complete their life cycle. In addition, it has been demonstrated that mature palms are susceptible to LYD. Some vector species feed on only mature palm species and infrequently found on immature ones (Howard *et al.* 2001). On the other hand, BCS in PNG is susceptible at all growth stages to LYD (Kelly *et al.* 2011).

Transovarial transmission of phytoplasma in the vectors has been recently reported (Alma *et al.* 2019; Tedeschi and Bertaccini 2019). Vectors harboring phytoplasma were reared, and offspring were hatched and reared on healthy plants. The new nymphs were positive in PCR and were able to transmit the phytoplasma to the new host plants (Hanboonsong *et al.* 2002; Weintraub and Beanland 2006).

Mixed infection has been observed in polyphagous insect vectors with closely related phytoplasmas (Brown *et al.* 2006; Rashidi *et al.* 2014). For example, *Euscelidius variegatus* can acquire CYP (chrysanthemum yellows phytoplasma) and FDP (Flavescence dorée phytoplasma). It has been reported that FDP can be affected by CYP, and CYP was dominant in its body regardless of the order of infection. Due to the facts that CYP had a shorter latent period and FDP cannot multiply in the salivary gland, CYP is dominant than FDP in the vector body (Rashidi *et al.* 2014).

Some phytoplasmas have a positive relationship with their vectors, which can be designated as mutualistic (Queiroz *et al.* 2016; Galetto *et al.* 2018). For example, AYPs (Aster yellows phytoplasma) increased their host range preference as well as the fecundity of the vector. Such a relationship shows that there is a long-time association between them (Beanland *et al.* 2000; Ebbert and Nault 2001). Conversely, some phytoplasmas decreased the fitness of the vector such as the decrease in longevity, body size and fecundity (Malagnini *et al.* 2010; Mayer *et al.* 2011).

Infected host plants are more preferred by the vectors as indicated in some pathosystems (MacLean *et al.* 2014; Krüger *et al.* 2015). Nevertheless, phytoplasma infected *Cacopsylla picta*, the vector of “*Ca. P. mali*”, do not prefer to oviposit on infected than un-infected trees (Mayer *et al.* 2011).

Management

Presently there is no curative treatment for LYD, though some success in controlling the outbreaks has been reported. An integrated pest and disease management suggested by Black, a pioneer of palm growers, has been the most successful approach in reducing the incidence of LYD (Gurr *et al.* 2016). This approach focuses on on-farm quarantine, severe weekly surveillance, and cutting down and burning of symptomatic palms. It is also recommended to plant resistant and high yielding varieties, controlling weeds in the whole farm and using a good fertilization schedule (Myrie *et al.* 2012). A significant reduction in the number of LYD infected palms was observed in four farms using Black’s method, while three farms continued to be destroyed by the disease without any management. The farms with daily surveillance lost only 0.0001% (10 out of 62000) of palms, while other farms lost thousands of palms annually (Serju 2012).

To slow the spread of LYD, the eradication of the infected palms is highly recommended in other parts of the world. This method was used in the Dominican Republic, as they implemented an eradication program combined with natural barriers stopping vector movement and profusion of resistant palms (Martinez *et al.* 2008, 2010). Along with ground inspection in Ghana, aerial surveillance was employed to detect infected palms showing green against the yellow canopy of infected palms. Recently, the drone (crewless aerial vehicles) equipped with cameras has come to help humans in large-scale surveys. The instant eradication of infected trees and cultivation of a resistant variety has slowed the spread of the disease (Nkansah-Poku *et al.* 2009). In addition, it has been reported that farmers burn the felled trees in Jamaica (Serju 2012). This method has not effectively slowed the spread, because the felled palms are not attractive to the vectors. A research conducted by Nkansah-Poku *et al.* (2005) in Ghana revealed that using insecticides followed by felling had no significant effect than felling alone in stopping the spread.

Quarantine

LYD can spread amongst close palm farms and also to hundreds of kilometers. Vector movement can be prohibited by natural landscape barriers. However, human activity can spread the disease even in the presence of barriers (Bertin *et al.* 2007). In Mexico, grasses are imported for landscaping, and the vectors may come through this importation (Dollet *et al.* 2009), unless quarantine measures are applied strictly.

Vector management

Alternate vector hosts

For the univoltine vector, the control of alternative hosts of a vector can be the most crucial approach of controlling phytoplasma diseases (Belien *et al.* 2013). For instance, *Haplaxius crudus* nymphs, a known vector of LYD, feed and develop on herbaceous plants root, while the adults live on trees and palms (Howard 1995). Four species of Cyperaceae and 37 species of Poaceae were identified to be the host of *H. crudus* nymphs. Grasses which are not potential host and shade-tolerant can be selected to be replaced with alternative hosts. Howard (1995) introduced some species that can be planted under palms as non-hosts, including *Hemarthria altissima* (Pior), *Brachiaria brizantha* (A. Rich) and *Chloris gayana* Kunth.

Mulches could be considered as a control approach. For instance, mulches of subtle pine, coconut frond, and eucalyptus are more attractive for female oviposition. Also, they provide better conditions for developing nymphs, resulting in higher adult emergence. On the other hand, using bark nuggets can result in less adult emergence (Howard and Oropeza 1998). It can be noted that mulch application is too expensive and practical.

Insecticides

Palms are evergreen and long living, so the vectors are able to transmit phytoplasmas anytime, contrary to temperate, and annual crops needing protection only for short times of susceptibility (Gitau *et al.* 2009). Palms are the host of many insect species, so the use of broad-spectrum insecticides can destroy the food chain of parasitoids and predators. In addition, the wider environment and human health are threatened by persistent pesticides (Stehle and Schulz 2015; Gangireddygar *et al.* 2017). Trunk injection and spraying insecticides are used for controlling the vector, although it has not been economically successful in coconut farms (Been 1995). Similarly, the control of Kerala Wilt Disease (KWD) in India was not successful using insecticides (Rajan 2013). In addition, a similar result was reported in Florida where the population of the vector and spread of the disease was reduced, but without stopping infection (Been 1995).

Host plant resistance

Jarausch *et al.* (2013) defined resistant and tolerant cultivars as the absence of symptoms associated with a low pathogen titer in the infected plants and mild symptoms under a light pathogen titer, respectively. It should be noted that complete resistance to LYD phytoplasma has not been reported (Baudouin *et al.* 2009).

As palms have to pass more time to be reproducible as well as produce few seeds per plant, genetic modifications and improvements are so difficult (Cardena *et al.* 2003). Also, because the latent period in palms is long, resistance screening of current genotypes is also difficult. However, detection of phytoplasma can be more accessible, reliable, and faster by PCR technology (Valiunas *et al.* 2019; Gholami *et al.* 2020; Wang *et al.* 2020). It has been documented that the level of resistance can be affected by environmental conditions (Baudouin *et al.* 2009). In some cases, it has been observed that resistance depends on environmental factors than genetic as the speculated resistant cultivars were infected in some regions, while on the other hand they were resistant in some other regions (Mpunami *et al.* 1999; Mpunami *et al.* 2002). In addition, a palm resistant to some strains will be likely threatened by a different group and subgroup of phytoplasma even by a new vector when planted in a new region (Odehale *et al.* 2012).

Information about the rate of mutations in phytoplasma is scarce due to the difficulty to culture these pathogens. In addition, no evidence is available on the effects of transmission or vectors on mutations in phytoplasmas. On the other hand, a study has shown that an induced mutation in the onion yellowing phytoplasma resulted in the loss of transmission ability of its insect vector compared to the wild type (Oshima *et al.* 2004).

There are several virulence factors in phytoplasmas including SAP11, SAP54, PHYL1 and TENGU, which can induce specific symptoms in the diseased plants. It has been shown that a mutation in the virulence factor TENGU resulted in plant resistance to insect vectors. The mutant phytoplasma could not change the color of the leaves and with such symptoms, the vectors were not attracted to the plants (Sugio *et al.* 2014). However, there is no documented literature on the effects of mutations in virulence factors on the breakdown of resistance.

Transmission trials with insect vectors are more reliable and real for resistance screening, though a distinction between resistance to the vector or the phytoplasma is so difficult (Jarausch *et al.* 2013). In this way, the population dynamics of the vector needs to be monitored. To test resistance in coconut, researchers test different varieties in which LYD is endemic (Baudouin *et al.* 2009; Odehale and Okoye 2013).

To search for resistant varieties, the researchers plant a range of resistant varieties in any growing area. Such a method is used to make plant adaptation to the phytoplasma

or vector population. However, after a period, the resistance may breakdown, and symptoms of the disease appear (Quaicoe *et al.* 2009). Variety evaluation and improvements should be carried out in the area as resistance has a degree of site-specificity, which may be affected by environmental factors, especially drought and poor soil conditions, and genetic variation between phytoplasma populations (Odehale *et al.* 2012). Adaption in phytoplasma may occur fast due to repetitive genomes and short time generation. Gene stacking has been newly suggested in order to stop resistance breaking down; however, no published work is available on the use of gene stacking to manage phytoplasmas in palms. CRISPR (Cluster Regulatory Interspaced Short Palindromic Repeats) is the newest tool for gene editing (Abdelrahman *et al.* 2018; Ipoutcha *et al.* 2019). By this method, phytoplasma resistance traits can be easily known and exploited for by gene silencing or insertion (Belhaj *et al.* 2013).

The most important challenge in host plant resistance in LYD management might be that such resistance to phytoplasma pathogen may change the susceptibility to other pathogens or pests. For instance, the resistance cultivars in PNG became more susceptible to two pests, including black palm weevil *Rhynocophorus bilineatus* (Montr.) and *Oryctes rhinoceros* (Ovasuru 1994).

Despite the challenges mentioned, such an approach was used in LYD management. For example, CSPWD (Cape Saint Paul Wilt Disease) was controlled using a hybrid of Vanuata Tall, and Sri Lanka Green Dwarf in Ghana (Quaicoe *et al.* 2009). Also, Jamaican farmers replaced the Maypan and Malayan dwarf varieties by a tall variety, which resulted in retrieval of the coconut industry (Harrison *et al.* 2002a).

Although replanting the cultivars may be costly and practical, this method can help the coconut industry as the average age of many plants in many parts is old. However, the long period, in which coconut last for sufficient production should be considered (Danyo 2011; Snaddon *et al.* 2013).

Antibiotic treatment

Using antibiotics can prevent or control phytoplasma infection in individual host plants (Tanno *et al.* 2018; Bogoutdinov *et al.* 2019). To get better results, antibiotics must be used bi-weekly for four months by systemic treatment. This method is costly and cannot be used in commercial production; however, it can be applied for beneficial and decorative palms in hotels or tourist sites (Eziashi and Omamor 2010). However, the use of antibiotics is forbidden in developed countries (Musetti *et al.* 2013). Because of the perceived health risks and cost of this approach, antibiotics can be used to protect cherished ornamental trees but have never been considered as a continuous way of management (Been 1995).

Effect of Abiotic factors and climate change on LYD

Little relative information is available on how LYD may be affected by abiotic factor. It was well known that moisture and temperature can affect the severity of associated phytoplasma (Krishnareddy 2013). As demonstrated in some studies, disruption in stomata can contribute to excessive water loss and leaflet flaccidity in palm root wilt (Rajagopal *et al.* 1986). Mulches and the density of host plants and the distance between coconut plantations could affect vector biology and ecology. The spread of LYD can be affected by landscape and climate (Mora-Aguillera 2002). Researches on “flavescence doreé” and chrysanthemum yellows revealed that multiplication in insects was faster under cooler with a low CO₂ concentration condition (18–22°C; CO₂ 400); contrary to plants (22–26°C; 800 ppm) (Galletto *et al.* 2011).

The establishment and spread of the phytoplasma vectors and associated phytoplasma might change due to climate change (Krishnareddy 2013). One centigrade increase in temperature resulted in shifting ecological zone by up to 160 km, as stated by Thuiller (2007). It has been known that an increase in temperature may result in insect species spread into new areas and even new countries (Parmesan and Yohe 2003).

Transmission success may be increased by higher feeding frequency or faster multiplication in the host due to an increase in temperature, which may increase the rate of spread of the phytoplasma (Maggi *et al.* 2014). In the case of LYD, it is so difficult to predict the consequences of climate change accurately due to lacking the information of the temperature range of LYDs. Halbert *et al.* (2014) demonstrated that LYD phytoplasma could overwinter consistently further north (N29°), therefore the LYD spread depends on insect physiology rather than ecology.

Conclusion

Phytoplasma diseases of palms are economically destructive diseases, which have resulted in significant effects on humans' economy and nutrition. There are many gaps in understanding the phytoplasma diseases of palms, including epidemiology, biology of the phytoplasmas, ecology and the biology of the vector, and the relationship between the hosts, vector and pathogen. This question opens a window for further investigation. Vectors play a crucial role in epidemiology. However, vertical transmission of phytoplasma in plant hosts has been confirmed. Proper quarantine and seed movement policies are needed to prevent disease spread. Although many attempts have been ongoing for the identification of the vectors species, little information is still available. It should be noted that a transmission trial to confirm a vector is logistically challenging. In disease management, early detection of the disease and vector can help implement the best approaches and prevent disease spread. This issue has been solved by

recent quick techniques in detection such as Polymerase Chain Reaction (PCR), Loop-mediated isothermal amplification (LAMP), and digital PCR (dPCR).

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