History of lethal yellowing with emphasis on the susceptibility of royal palms (*Roystonea* spp.)

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ABSTRACT

Objective: To explore the available literature relating to lethal yellowing (LY) in order to assess the susceptibility of royal palms (*Roystonea* spp.) to this disease.

Design/methodology/approach: Bibliographic material in English and Spanish was consulted in physical and digital libraries in search of unequivocal and plausible LY reports in *Roystonea* palms. Information gathered was then reviewed and discussed.

Results: We found evidence of LY susceptibility of royal palms dating back to the beginning of the 20th century. In addition to Mexico, possible LY outbreaks in *Roystonea* palms might have occurred in Cuba, Haiti, the Dominican Republic, and Antigua and Barbuda.

Limitations on study/implications: Reports of LY predating molecular diagnostic tools, particularly in *Roystonea* palms, cannot be assumed as unequivocal evidence of susceptibility to this disease.

Findings/conclusions: Royal palms have shown evidence of susceptibility to the LY pathogen throughout the Caribbean Basin. In light of this, their potential role as long-term phytoplasma reservoirs should be examined in order to better comprehend this disease's pathosystem.

Keywords: Lethal yellowing, Texas Phoenix palm decline, lethal bronzing, royal palms, susceptibility.

Citation: Palma-Cancino, P. J., Ramos-Hernández, E., & Ortiz-García, C. F. (2023). History of lethal yellowing with emphasis on the susceptibility of royal palms (*Roystonea* spp.). *Agro Productividad*. https://doi.org/10.32854/agrop.v16i4.2488

Academic Editors: Jorge Cadena Iñiguez and Libia Iris Trejo Téllez

Received: January 26, 2023.
Accepted: March 14, 2023.
Published on-line: June 13, 2023.

Agro Productividad, 16(4). April. 2023. pp: 133-147.

INTRODUCTION

Royal palms —genus *Roystonea*— are native to the Caribbean Basin and appreciated worldwide for their ornamental beauty (Zona, 1996). In Mexico, two species —*Roystonea dunlapiana* P.H. Allen and *Roystonea regia* (Kunth) O.F. Cook— are naturally distributed in the Yucatan Peninsula and in Tabasco, Chiapas and Veracruz (Orellana *et al*., 2018). Both are economically important non-timber forest products for rural communities in the Yucatan Peninsula, used in


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construction and honey production (Noguera-Savelli and Cetzal-Ix, 2021). In addition, they are also frequently used as street trees in many cities in southeastern Mexico. However, they are also susceptible to diseases caused by several types of pathogens, including phytoplasmas (Bajwa *et al*., 2020).

Between 2018 and 2022, we noticed a few declining *Roystonea* sp. in the cities of Villahermosa, Tabasco, Coatzacoalcos, Veracruz, and Merida, Yucatan, Mexico, with leaf yellowing and inflorescence necrosis symptoms, indicative of phytoplasma infection (Figure 1) (Palma-Cancino and Ortiz-García, personal observations). This prompted us to explore bibliographic material with the intention of assessing the susceptibility of *Roystonea* palms to a phytoplasma disease currently endemic to the Caribbean Basin: lethal yellowing (LY). However, to provide the context necessary for this topic to be addressed, we will also present a summary of LY and its history and provide up-to-date information on its distribution, as well as an updated list of susceptible palm taxa.

MATERIALS AND METHODS

Bibliographic material in English and Spanish was consulted in physical and digital libraries in search of unequivocal and plausible LY reports in *Roystonea* palms. Digital libraries and databases were accessed and examined through the use of search engines, primarily Google Search, Google Scholar, and Scopus. Keywords used for searching materials in English included "lethal yellowing", "royal palms", "*Roystonea*" and "phytoplasma", among others. Likewise, "amarillamiento letal", "palma real" and "fitoplasma" were used for searching sources in Spanish. Information gathered was then reviewed and discussed and the notion of relative susceptibility to LY —as implemented by McCoy *et al*. (1983)— was applied to estimate how susceptible royal palms are to LY.

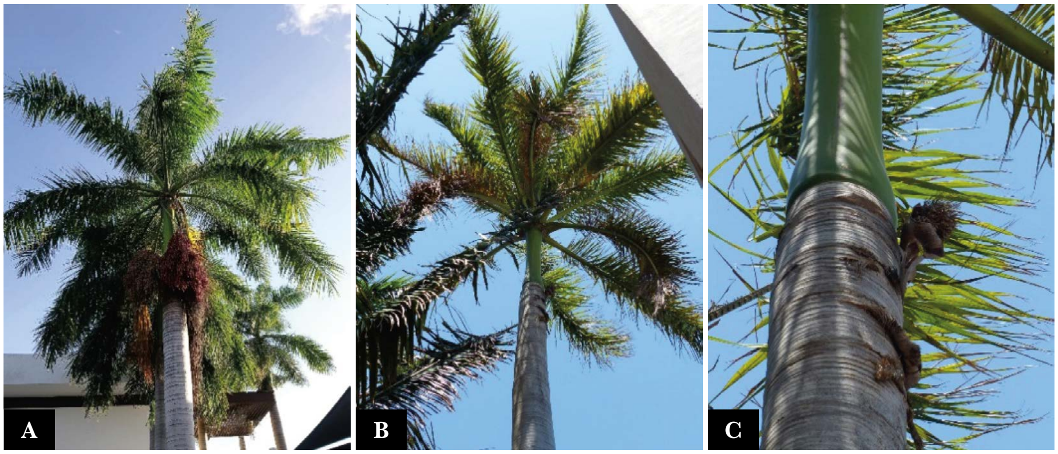

Figure 1. *Roystonea* palms in the city of Merida, Yucatan, Mexico. A. A flowering, visibly healthy *R. regia*. B. *Roystonea* sp. with leaf decay of mature leaves and foliar discoloration in the upper crown. C. Detail of the same palm showing necrosis and atrophy in an inflorescence, a symptom indicative of phytoplasma infection.

RESULTS AND DISCUSSION

LY: discovery and general characteristics

LY, a devastating disease of coconut (*Cocos nucifera* L.) and at least 44 other palm species (Table 1), has apparently been active in the Caribbean Basin for almost two centuries (Figure 2). Its first account may have been given by the 2nd Marquess of Sligo, who, in 1834, reported the destruction of all the coconuts in the leeward side of Grand Cayman, in the Cayman Islands, by a strange disease (Fawcett, 1889). By May 1888, the disease was still active at Grand Cayman according to the British botanist William Fawcett, who, upon inspecting its symptoms —which included premature fruit drop, blackening of new inflorescences, and leaf yellowing advancing upwards through the crown (Figure 3)— suspected that the disease was "due to the presence of a bacterium" (Fawcett, 1889). However, his statement had to wait until 1972 for confirmation, when phytoplasmas —which are considered a special type of parasitic bacteria— were finally determined to be the cause of LY (Beakbane *et al.*, 1972; Plavšić-Banjac *et al.*, 1972).

Despite some instances of success, the vast majority of phytoplasmas cannot as yet be cultured axenically (Contaldo and Bertaccini, 2021). For that reason, phytoplasma strains associated with LY are often referred to as members of group 16SrIV, subgroup A (Lee *et al.*, 1998), instead of having a conventional scientific name, although '*Candidatus* Phytoplasma palmae' has also been proposed as a name for the taxon (Bertaccini *et al.*, 2022). So far, the cixiid planthopper *Haplaxius crudus* Van Duzee is the only proven vector of this phytoplasma subgroup (Dzido *et al.*, 2020), nevertheless, additional putative vectors of group 16SrIV phytoplasmas have also been discovered (Brown *et al.*, 2006; Ramos-Hernández *et al.*, 2020; Fernández-Barrera *et al.*, 2022).

While LY diagnoses today consist of the specific detection of subgroup 16SrIV-A phytoplasma DNA in symptomatic palms, usually by nested PCR or real-time PCR

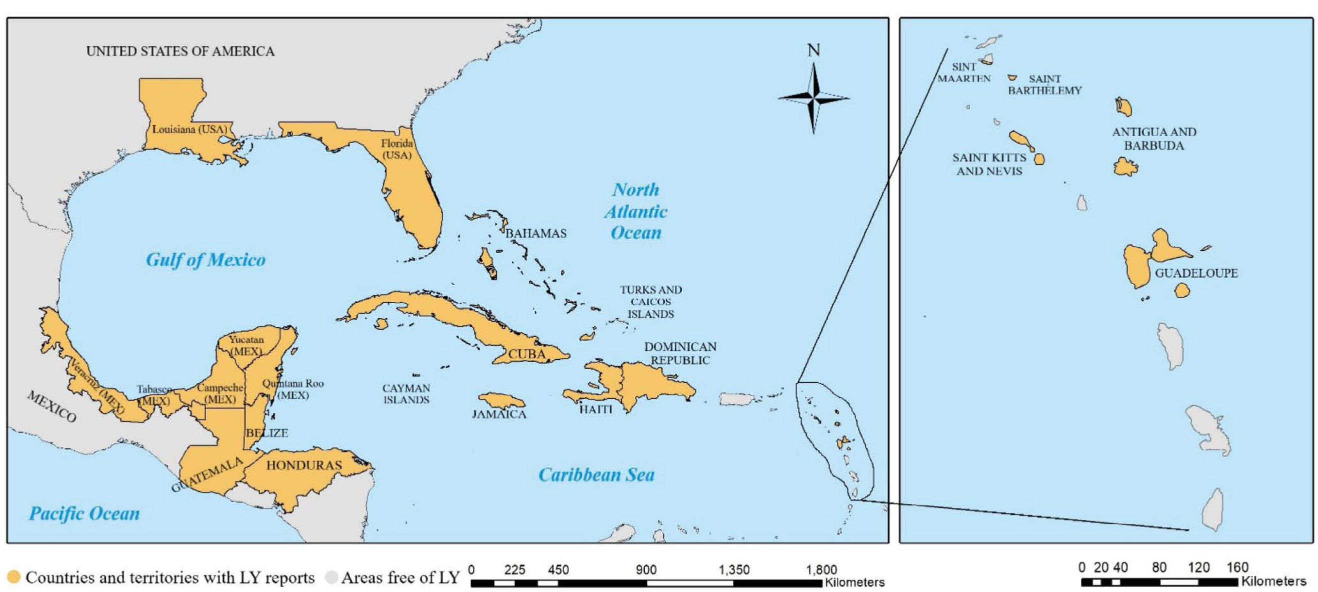

Figure 2. Current distribution of LY (associated with subgroup 16SrIV-A phytoplasmas) in the Caribbean Basin.

Table 1. Host range of subgroup 16SrIV-A phytoplasmas, associated with LY.

Taxa[1]	Known to be susceptible in	Phytoplasma ID[2]		Reference
		Confirmed	Unconfirmed	
Acrocomia aculeata (Jacq.) Lodd ex. Mart.	Mexico (Yucatan)	✓		Narvaez *et al.* (2016)
Adonidia merrillii (Becc.) Becc.	Mexico (Tabasco, Yucatan), USA (Florida)	✓		Lara *et al.* (2017)
Aiphanes lindeniana (H. Wendl.) H. Wendl.	USA (Florida)		✓	Harrison *et al.* (1999)
Allagoptera arenaria (Gomes) Kuntze	USA (Florida)		✓	Harrison *et al.* (1999)
Arenga engleri Becc.	USA (Florida)		✓	Harrison *et al.* (1999)
Bismarckia nobilis Hildebrandt & H. Wendl.	Antigua and Barbuda		✓	Myrie *et al.* (2014)
Borassus flabellifer L.	USA (Florida)		✓	Harrison *et al.* (1999)
Caryota mitis Lour.	USA (Florida		✓	Harrison *et al.* (1999)
Caryota rumphiana Mart.	USA (Florida)		✓	Harrison *et al.* (1999)
Chelyocarpus chuco (Mart.) H.E. Moore	USA (Florida)		✓	Harrison *et al.* (1999)
Cocos nucifera L.	Caribbean Basin (widespread)	✓		Ntushelo *et al.* (2013)
Coccothrinax readii H.J. Quero	Mexico (Yucatan)	✓		Narvaez *et al.* (2006)
Corypha utan Lam.	USA (Florida)		✓	Harrison *et al.* (1999)
Cryosophila warscewiczii (H. Wendl.) Bartlett	USA (Florida)		✓	Harrison *et al.* (1999)
Cyphophoenix nucele H.E. Moore	USA (Florida)		✓	Harrison *et al.* (1999)
Dictyosperma album (Bory) H.L. Wendl. & Drude ex Scheff.	USA (Florida)		✓	Harrison *et al.* (1999)
Dypsis cabadae (H.E. Moore) Beentje & J. Dransf.	USA (Florida)		✓	Harrison *et al.* (1999)
Dypsis decaryi (Jum.) Beentje & J. Dransf.	USA (Florida)		✓	Harrison *et al.* (1999)
Gaussia attenuata (O.F. Cook) Becc.	USA (Florida)		✓	Harrison *et al.* (1999)
Gaussia maya (O.F. Cook) H.J. Quero	Mexico (Yucatan)	✓		Narváez *et al.* (2018)
Howea belmoreana Becc.	USA (Florida)		✓	Harrison *et al.* (1999)
Howea forsteriana (F. Muell. & H. Wendl.) Becc.	USA (Florida)		✓	Harrison *et al.* (1999)
Hyophorbe verschaffeltii H. Wendl.	USA (Florida)		✓	Harrison *et al.* (1999)
Latania lontaroides (Gaertn.) H.E. Moore	USA (Florida)		✓	Harrison *et al.* (1999)

Table 1. Continues...

Taxa[1]	**Known to be susceptible in**	**Phytoplasma ID**[2]		**Reference**
		Confirmed	**Unconfirmed**	
Livistona chinensis (Jacq.) R. Br. ex Mart.	Antigua and Barbuda, USA (Florida)		✓	Myrie *et al.* (2014)
Livistona rotundifolia (Lam.) Mart.	USA (Florida)		✓	Harrison *et al.* (1999)
Nannorrhops ritchiana (Griff.) Aitch.	USA (Florida)		✓	Harrison *et al.* (1999)
Phoenix canariensis hort. ex Chabaud	USA (Florida)	✓		Harrison *et al.* (2008)
Phoenix dactylifera L.	Antigua and Barbuda, USA (Florida)	✓		Harrison *et al.* (2008)
Phoenix reclinata Jacq.	USA (Florida)		✓	Harrison *et al.* (1999)
Phoenix rupicola T. Anderson	USA (Florida)		✓	Harrison *et al.* (1999)
Phoenix sylvestris (L.) Roxb.	USA (Florida, Louisiana)	✓		Ferguson and Singh (2018)
Pritchardia maideniana Becc.	USA (Florida)		✓	Harrison *et al.* (1999)
Pritchardia pacifica Seem. & H. Wendl.	Antigua and Barbuda, Mexico (Yucatan), USA (Florida)	✓		Dzido *et al.* (2020)
Pritchardia remota Becc.	USA (Florida)		✓	Harrison *et al.* (1999)
Pritchardia thurstonii F. Muell. & Drude	USA (Florida)		✓	Harrison *et al.* (1999)
Ravenea hildebrandtii C.D. Bouché	USA (Florida)		✓	Harrison *et al.* (1999)
Roystonea regia (Kunth) O.F. Cook	Antigua and Barbuda, Mexico (Yucatan)	✓		Narvaez *et al.* (2016)
Sabal mexicana Mart.	Mexico (Yucatan)	✓		Vázquez-Euán *et al.* (2011)
Sabal palmetto (Walter) Lodd. ex Schult. & Schult. f.	USA (Florida)	✓		Mou *et al.* (2022)
Syagrus romanzoffiana (Cham.) Glassman	Antigua and Barbuda	✓		Myrie *et al.* (2014)
Syagrus schizophylla (Mart.) Glassman	USA (Florida)		✓	Harrison *et al.* (1999)
Thrinax radiata Lodd. ex Schult. & Schult. f.	Mexico (Yucatan)	✓		Vázquez-Euán *et al.* (2011)
Trachycarpus fortunei (Hook.) H. Wendl.	USA (Florida, Louisiana)	✓		Ferguson and Singh (2018)
Veitchia arecina Becc.	USA (Florida)		✓	Harrison *et al.* (1999)

[1]Botanical names included in this list are in accordance with their current usage in systematic botany and thus may differ from their original citing source.
[2]Phytoplasma ID was considered confirmed if the presence of subgroup 16SrIV-A phytoplasmas in that palm species was verified by DNA sequencing.

Figure 3. Symptoms induced by subgroup 16SrIV-A phytoplasmas (associated with LY) in *Cocos nucifera* and two other palms. A. Premature fruit drop in *C. nucifera*. B. Blackening of new inflorescences in the same species. C. Progressive (uppwards) leaf yellowing in *C. nucifera*. D. Leaf yellowing in *Thrinax radiata*. E. First stage of foliar decay in *Adonidia merrillii*.

protocols, it is important to keep in mind that, prior to the late 1980s, phytoplasmas were differentiated only by some of their biological properties such as host range, geographic distribution, and the symptoms induced in affected plants, thus, LY reports before that period, including those cited in this article, should be regarded as plausible, but not unequivocal evidence of subgroup 16SrIV-A's involvement. Also, it should be noted that LY was not always referred to as such. Previous names applied to this disease in the first half of the 20th century included "fever", "bud rot", and "West End bud rot" (Smith, 1905; Johnston, 1912; Ashby, 1915). Other authors used the terms "bronze leaf wilt" (Martyn, 1945) and "unknown disease" (Leach, 1946), to avoid confusion with the "common" bud rot caused by *Phytophtora palmivora* (Butler) Butler.

Early LY outbreaks in the Caribbean Basin: "unknown disease" period

Following the apparent emergence of LY in the Cayman Islands, the disease was next spotted in Cuba. Translating from Cuban naturalist Carlos de la Torre y Huerta: "The coconut plague, according to the people who studied it for the first time in Cuba, dates back to a time very close to the famous hurricane of 1870" (de la Torre, 1906). By the 1900s, LY became widespread in Cuba (Smith, 1905; Horne, 1908), and the devastation caused by it was such that banana groves had to replace many coconut plantations, especially around Baracoa (de la Torre, 1906).

About the same time as in Cuba, LY started to be noticed in Jamaica as well. In 1891, large-scale coconut deaths caused by an unknown disease —now considered to have been LY— were reported at Montego Bay, on the northwest shore of the island (Fawcett, 1891), however, prior to 1872, a disease of similar characteristics had already wiped out the coconut population along forty miles of the southwest shore, in Saint Elizabeth Parish (Martyn, 1945). By the beginning of the 20th century, LY was restricted to the western end of Jamaica, along the shoreline between Savanna-la-Mar and Montego Bay, and, though it was not greatly feared by local farmers at that time, it was nonetheless considered a potentially dangerous condition (Johnston, 1912).

Curiously, LY's first account in Haiti may have been given by the famous poet Oswald Durand, in a footnote to his poem *La mort de nos cocotiers*, included in the first edition of *Rires et pleurs* (Durand, 1896). According to him, around 1880, all the coconuts in and in the vicinities of Cap-Haïtien were affected by a disease that destroyed them in a short time, leaving only bare trunks. No further spread of LY was reported in Haiti until 1943, when the disease was observed in Gonaïves, killing nearly 8,000 coconuts (Leach, 1946).

Other countries within the Caribbean Basin that were affected by LY during the first half of the 20th century were The Bahamas, in the 1920s (Leach, 1946), and the Dominican Republic, probably as early as 1925 (Ciferri and Ciccarone, 1949). Eventually, the disease reached United States territory in 1937 via Key West, Florida (Martinez and Roberts, 1967), however, it wasn't until 1955 that a new outbreak in Key West led to the constant monitoring of LY in that country (Corbett, 1959).

LY outbreaks in North America's mainland: "expanded host range" period

LY was documented for the first time on the Florida mainland in 1971, in Miami and Coral Gables (Seymour *et al.*, 1972). Until then, it was considered to be primarily a disease of *C. nucifera*, however, shortly after the emergence of said outbreak, multiple diseased individuals from three additional species, *Adonidia merrillii* (Becc.) Becc., *Pritchardia pacifica* Seem. & H. Wendl., and *Pritchardia thurstonii* F. Muell. & Drude, were detected in the southwest area of Miami (Parthasarathy and Fisher, 1973). By 1974, a total of 12 palm species were known to be susceptible to LY in Florida (Thomas, 1974). This number grew to 25 by 1978 (Thomas, 1979). Finally, three decades after arriving in Miami-Dade County, LY was known to affect 36 palm species in the whole of Florida (Howard and Wilson, 2001). This aggressive expansion in host range by the LY phytoplasma was viewed as a consequence of the higher diversity and abundance of palms, both native and exotic, present in the urban landscapes of South Florida (as well as in the living collections of botanical gardens located within the area) compared to that of other locations in the Caribbean that were also affected by LY at that time (the 1970s and early 1980s) (McCoy *et al.*, 1983). Naturally, this meant that new palm hosts of subgroup 16SrIV-A phytoplasmas had to be found in other regions with a different species composition than that of Florida.

Thus, Mexico would end up becoming a testing ground of sorts for this assumption to be proven, as the arrival of LY to Mexican shores during the same period was considered imminent.

History took its course and LY eventually reached Mexico via the Yucatan Peninsula: the disease was first hinted on the island of Cozumel, state of Quintana Roo, in 1977 (Romney and Harries, 1978), and was later confirmed during an outbreak in Cancun that started in 1981 (McCoy *et al.*, 1982). Subsequently, in 1985, LY was reported at El Cuyo, in the neighboring state of Yucatan (Villanueva *et al.*, 1987). Then, in 1990, the disease finally reached the state of Campeche, thus affecting the entire Mexican portion of the Yucatan Peninsula (Robert *et al.*, 1991).

Regarding the existence of additional hosts of subgroup 16SrIV-A phytoplasmas, they were studied in Yucatan since the 1990s. After PCR-based techniques became the standard for phytoplasma detection and identification, several studies demonstrated the existence of a total of six new palm hosts of subgroup 16SrIV-A phytoplasmas, all of them native to the Yucatan Peninsula (see Table 1). Surprisingly, one of such hosts was *R. regia* (Narvaez *et al.*, 2016), a species that, according to observations made in Florida, was not considered to be susceptible to LY (McCoy *et al.*, 1983). This apparent contradiction will be discussed in the following segments, meanwhile, let us to conclude this summary of LY in Mexico by mentioning its advance to the states of Tabasco, in 1993 (Escamilla *et al.*, 1995), and Veracruz, in 1999 (Sánchez Anguiano, 2002).

From the 1990s to today, LY continued spreading to the following countries and territories: Belize (Escamilla *et al.*, 1994), Honduras (Ashburner *et al.*, 1996), Guatemala (Mejía *et al.*, 2004), Saint Kitts and Nevis (Myrie *et al.*, 2006), Turks and Caicos Islands (Brown *et al.*, 2007), Antigua and Barbuda (Myrie *et al.*, 2014), Saint Barthélemy (Jeger *et al.*, 2017), Sint Maarten (Myrie *et al.*, 2019), and Guadeloupe (Pilet *et al.*, 2023). The disease is apparently spreading more rapidly in the Lesser Antilles than in Central America, threatening to eventually reach South America (Yankey *et al.*, 2018).

Evidence of susceptibility of royal palms to LY and other LY-like diseases

As previously mentioned, unequivocal evidence of susceptibility of royal palms to subgroup 16SrIV-A phytoplasmas was first presented in Yucatan, Mexico, during the last decade (Narvaez *et al.*, 2016). However, accounts from early literature concerning LY provide interesting glimpses that suggest an even longer history of interaction between *Roystonea* palms and this particular phytoplasma subgroup.

Cuba, home to five *Roystonea* species, although one of them now extinct (Moya López, 2020), previously had two instances of mortality of royal palms that were possibly associated with LY. Horne (1908), who studied LY in the 1900s, encountered several bare trunks of royal palms which might have died from the disease in a badly affected coconut grove near Naguaraje. He also observed a young royal palm around the same location, which "showed as nearly a typical case of bud rot [syn. LY] as one could imagine possible". A few years later, Johnston (1912) noted about 15 to 20 dead or diseased royal palms near Baracoa, over the course of three years. Though not without hesitations, he suspected the cause could be LY. Moreover, the symptoms he observed in the affected palms were very similar to the ones later described by Narvaez *et al.* (2016) in the Yucatan Peninsula.

In the island of Hispaniola, where *Roystonea borinquena* O.F. Cook is extremely abundant (Zona, 1996), two other accounts of LY possibly affecting royal palms were also provided. Upon a visit to Gonaïves, Haiti, in late 1945, Leach (1946) informed the following: "associated with the outbreak of the disease on coconuts [LY]… there has been an equally sudden and serious mortality of date palms... and even a few royal palms... have been killed in the same area". In addition, he noticed a "small amount of dieback" on the inflorescences of diseased royal palms after cutting open some immature spathes, a symptom that, given the circumstances described by the author, strongly suggests LY. Likewise, in Santo Domingo, Dominican Republic, a similar event was witnessed a year later. Translating from Ciferri and Ciccarone (1949): "A disease with similar symptoms to those of bronze leaf wilt [syn. LY] attacks royal palms in the same area".

No further evidence of susceptibility of royal palms to LY was provided until the disease reached Antigua and Barbuda and group 16SrIV phytoplasmas were detected in a *R. regia* palm by means of real-time PCR (Myrie *et al.*, 2014). Similarly, in Tabasco, Mexico, group 16SrIV phytoplasmas were detected in a *R. regia* in 2015 (Ramos-Hernández *et al.*, unpublished data). Eventually, the work of Narvaez *et al.* (2016) confirmed that *R. regia* was a host of subgroup 16SrIV-A phytoplasmas. However, group 16SrIV encloses at least five other closely related phytoplasma subgroups (Palma-Cancino, 2020), including subgroup 16SrIV-D, which is associated with Texas Phoenix palm decline (TPPD, syn. lethal bronzing), another serious LY-like disease which also affects palm species of both economic and ornamental importance (Bahder *et al.*, 2019; Ferguson *et al.*, 2020; Palma-Cancino *et al.*, 2020). In fact, subgroup 16SrIV-D phytoplasmas are considered by some to represent an entirely different species from '*Ca*. P. palmae', namely '*Candidatus* Phytoplasma aculeata' (Soto *et al.*, 2021). In view of the above and considering the widespread occurrence of TPPD in the Caribbean Basin (Ntushelo *et al.*, 2013), this article will also review evidence of susceptibility of royal palms to subgroup 16SrIV-D phytoplasmas.

Earlier in the past decade, an outbreak of a LY-like disease affecting several palms —including one *Roystonea* sp. —in Guaynabo, Puerto Rico, was confirmed to be associated with subgroup 16SrIV-D phytoplasmas (Rodrigues *et al.*, 2010; Ntushelo *et al.*, 2013). Additionally, group 16SrIV phytoplasmas were detected in a *R. borinquena* during a subsequent survey conducted in Puerto Rico in the mid-2010s (Simbaña Carrera, 2019). While this last example cannot be precisely ascribed to any particular phytoplasma subgroup within group 16SrIV, it is worth mentioning that, so far, only subgroup 16SrIV-D is known to occur in Puerto Rico (Ntushelo *et al.*, 2013; Agosto, 2021).

To conclude this section, additional diseases of royal palms associated with phytoplasmas not enclosed in group 16SrIV will be mentioned briefly as LY-like diseases —as a whole— negatively impact palms not only in the Caribbean Basin but all over the world (Hemmati *et al.*, 2020). So far, the only known examples are the association of group 16SrII phytoplasmas with *R. borinquena* in Puerto Rico (Simbaña Carrera, 2019) and of subgroup 16SrII-D phytoplasmas with *R. regia* in Oman (Hemmati *et al.*, 2021). Lastly, in Malaysia, a new 16SrI phytoplasma subgroup was reported as infecting *R. regia* (Naderali *et al.*, 2015) but the figures included in that report actually depict diseased palms of a different genus.

On the relative susceptibility of royal palms to LY and TPPD

Based on what was mentioned in the previous section, is it possible to estimate how susceptible royal palms are to both the LY and TPPD pathogens? The short answer is: only subjectively.

Field resistance to LY —typically expressed as disease incidence or mortality rate— has only been sufficiently tested for the economically important coconut palm. The concept of relative susceptibility is applied to several other species instead, with varying degrees of success (McCoy *et al.*, 1983; Howard and Wilson, 2001). Likewise, relative susceptibility to the TPPD pathogen has been preliminary estimated for a few species (Palma-Cancino, 2021). However, *Roystonea* species have not been included in any of these ratings, mainly due to a lack of data. Therefore, a final discussion of all the evidence previously mentioned will follow in an attempt to assess the relative susceptibility of royal palms to LY and TPPD.

According to Narvaez *et al.* (2016), in Yucatan, subgroup 16SrIV-A phytoplasmas were encountered very rarely in *R. regia* palms. To put that in perspective, *R. regia* is one of the palms most frequently used as street trees in the city of Merida, Yucatan, where both LY and TPPD are currently active. In some areas of the city, this palm represents nearly 12% of all observable Arecaceae, only *C. nucifera* and *A. merrillii* are more common (Palma-Cancino, personal observations in 2020 and 2021). Thus, it appears that, despite being fairly abundant in urban landscapes of the region, *R. regia* is one of the least susceptible species to subgroup 16SrIV-A phytoplasmas in Yucatan, Mexico. Interestingly, the comparatively lower abundance of *R. regia* in the LY-affected urban areas of Florida (Fitzpatrick, 2005) could explain why the disease was never observed in *R. regia* palms in that region, given a relative susceptibility rating of low to minimal.

Similarly, if we consider the evidence presented in the previous segment for both Cuba and Hispaniola as genuine LY outbreaks in *Roystonea* palms, it would appear that the relative susceptibility rating of the *Roystonea* spp. from both islands sits somewhere between low to minimal, given the comparatively low numbers of diseased individuals —as opposed to those of *C. nucifera*— encountered by the authors (Horne, 1908; Johnston, 1912; Leach, 1946). Nevertheless, it is also possible that these mortality events were not actually associated with LY. In that case, the *Roystonea* spp. from Cuba and Hispaniola could be considered immune to LY. This assumption was previously put forth by Harries *et al.* (2001) as part of a means to explain why LY —even to this day— has not become epidemic in the Dominican Republic. Supposedly, the abundant *Roystonea* spp. populations from that country contribute to a kind of "buffer effect" that protects the more susceptible—but somewhat isolated— *C. nucifera* populations from LY. We are of the opinion that the first scenario —that is, that the royal palms in Cuba and Hispaniola have a low to minimal relative susceptibility to LY— is the most likely.

In comparison, royal palms have only shown evidence of susceptibility to subgroup 16SrIV-D phytoplasmas in Puerto Rico. At the moment, it is difficult to say whether this is because TPPD is not as widely distributed in the Greater Antilles —where most *Roystonea* spp. are native and therefore more abundant (Zona, 1996)— as LY, or to some other factor. However, considering that royal palms have not been found to be susceptible to subgroup 16SrIV-D phytoplasmas in regions like Florida and Yucatan, where TPPD has been active for several years (Harrison *et al.*, 2008; Vázquez-Euán *et al.*, 2011), we are of the opinion that royal palms, in general, are some of the least susceptible palms that are known to be affected by this phytoplasma subgroup.

As a final point, we wish to draw attention to a quotation on this issue by Horne (1908): "If royal palms are attacked [by LY] it is so rarely that probably there is no practical importance to be attached to the matter". However, as our knowledge of the pathosystems of group 16SrIV phytoplasmas continues to increase, we can now say that this is not the case. Even if royal palms have a low to minimal susceptibility to the LY and TPPD pathogens, they are still key elements of the pathosystems of both diseases for a number of reasons: 1) royal palms are amply distributed throughout the Caribbean Basin (Zona, 1996), thus, as inoculum sources, their relevance in terms of disease spread should not be underestimated; 2) due to their popularity as ornamental palms and their known association with *H. crudus* (Howard and Mead, 1980), *Roystonea* spp. have the potential of introducing group 16SrIV phytoplasmas to new areas by means of unrestricted movement of plant material within and between countries, whether directly (through diseased palms) or indirectly (through healthy palms carrying infective vectors); 3) as evidenced by Narvaez *et al.* (2006), some palm species in the Yucatan Peninsula can harbor subgroup 16SrIV-A phytoplasmas without showing symptoms of infection, therefore, the occurrence of this phenomenon should also be examined for *Roystonea* palms.

CONCLUSION

Royal palms have shown evidence of susceptibility to the LY pathogen throughout the Caribbean Basin. In light of this, their potential role as long-term phytoplasma reservoirs should be examined in order to better comprehend this disease's pathosystem.

ACKNOWLEDGMENTS

The authors would like to thank the Biodiversity Heritage Library (BHL) consortium for providing access to much of the literature that was consulted. Also, to Davira Y. Palma Cancino for the elaboration of Figure 2. The first author thanks the CONAHCYT for the scholarship no. 2008511.

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