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Review

Diversity of *Colletotrichum* Species Associated with Anthracnose Disease in Tropical Fruit Crops—A Review

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Abstract: In tropical fruit crops, anthracnose is mainly caused by species belonging to the fungal genus, *Colletotrichum*. These phytopathogens can infect several parts of the fruit crops; however, infection during postharvest or ripening stages is responsible for major economic losses. Due to the formation of black to dark brown sunken lesions on the fruit surface, anthracnose reduces fruit quality and marketability. Among the most common tropical fruit crops susceptible to anthracnose are mango, papaya, banana, avocado, guava, and dragon fruit; these are economically relevant products in many developing countries. It is important to document that the newly recorded *Colletotrichum* spp. associated with fruit anthracnose can infect multiple hosts, but some species may be host-specific. By using multiple markers, many phylogenetic species of *Colletotrichum* have been reported as anthracnose-causing pathogens. Taking into account that disease management strategies strongly rely on adequate knowledge of the causative agents, updated information on *Colletotrichum* species and the hazard posed by the most recently identified species in tropical fruit plantations and harvested fruits becomes vital. Besides, the newly recorded species may be important for biosecurity and should be listed as quarantine pathogens, considering that tropical fruits are traded worldwide.

Keywords: *Colletotrichum*; anthracnose; tropical fruit crops; diversity; pathogenic; phylogenetic species

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1. Introduction

Asia and countries of the Pacific region are major tropical fruit crop producers, followed by Latin America, the Caribbean, and Africa [1]. Minor producers include the United States and Oceania. The main tropical fruits are mango, pineapple, avocado, and papaya; with mango representing the most relevant production worldwide. The majority of tropical fruits are produced in India, the leading producer of mango and papaya, followed by Thailand, Mexico, China, Brazil, and Indonesia [2,3]. Minor tropical fruits include guava, longan, litchi, durian, passion fruit, rambutan, and mangosteen, with China and India being the largest producers [4].

Tropical fruit crops are susceptible to infection by *Colletotrichum* species, which typically cause anthracnose. Figure 1 summarizes the anthracnose disease cycle in tropical fruit crops. Anthracnose infection commonly occurs in the fields during the flowering and fruiting stages. Different factors may affect *Colletotrichum* infection, including humidity, temperature, fruit condition, and inoculum concentration [5,6].

Host infection generally begins with conidial germination and is followed by the formation of appressoria and penetration pegs, which are fungal structures that assist in the penetration into host tissues. In some cases, direct penetration occurs through wounds or natural openings [7,8].

After infection, many anthracnose pathogens adopt quiescence or latency, which is common in pathogens causing postharvest diseases, including *Colletotrichum*. During the latent period, anthracnose pathogens remain dormant within the host tissues until environmental conditions, and the host physiology are conducive for their reactivation and further development [9]. Reactivation occurs particularly when fruits ripen. Anthracnose symptoms often develop after harvest, during storage, transportation, and marketing [6,10].

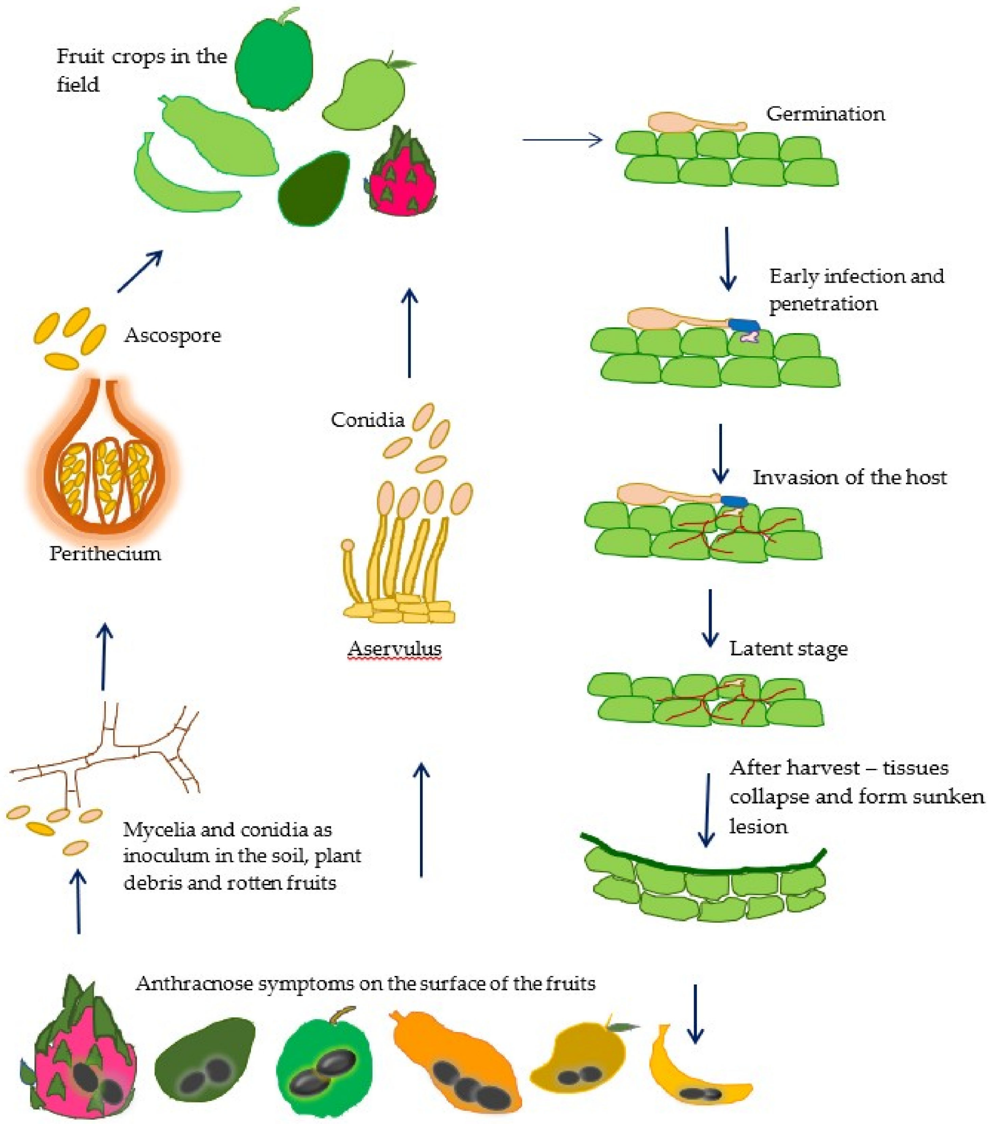

Figure 1. Anthracnose disease cycle of tropical fruit crops. (Drawn by Latiffah Zakaria).

Anthracnose pathogens infect not only fruits, but also other plant organs, including the leaves, flowers, twigs, and branches. The conidia and spores formed in these infected tissues are subsequently released and dispersed during rainy days through water splashes or during high humidity periods, thus becoming the primary inoculum for fruit infection at the preharvest stage [11]. The most visible anthracnose symptoms are black or dark brown sunken lesions containing conidial masses on the surface of infected fruits [7]. Small individual lesions may merge to produce larger lesions. These black or dark brown lesions on the surface appear unattractive to consumers and significantly reduce the market value of such fruits. Figure 2A–E show the anthracnose lesions form on the surface of several tropical fruit crops.

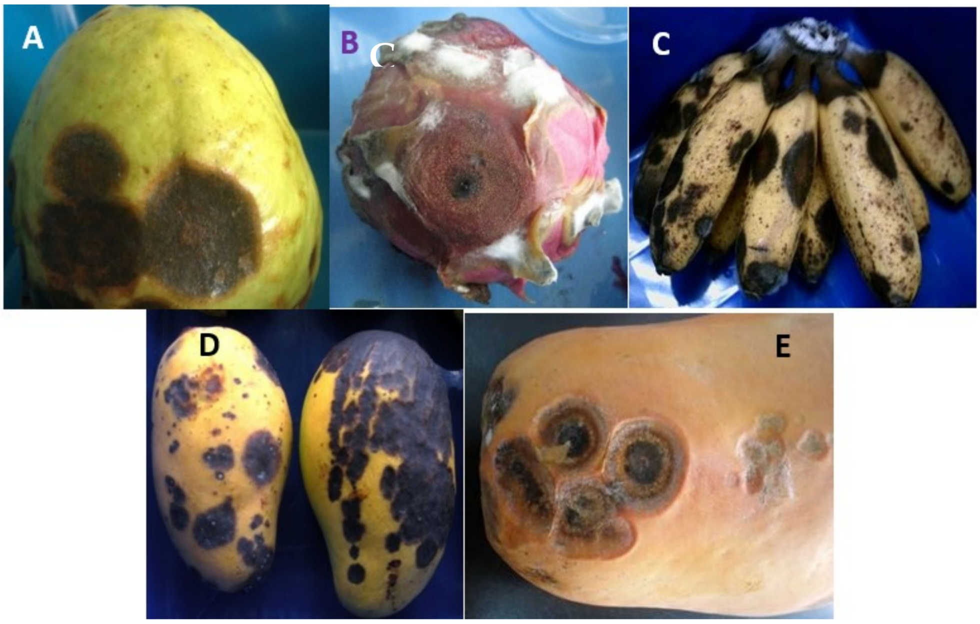

Figure 2. Anthracnose symptoms on several tropical fruit crops. (**A**) Guava, (**B**) dragon fruits, (**C**) banana, (**D**) mango, (**E**) papaya. (Photographs taken by Latiffah Zakaria and postgraduate students).

Before the application of molecular-based phylogenetic analysis using multiple markers for the taxonomic and systematic revision of *Colletotrichum* spp., only two species, *Colletotrichum acutatum* and *Colletotrichum gloeosporioides*, were reported to be associated with anthracnose symptoms in many tropical fruit crops. However, more recent phylogenetic analysis established that these two species belong to two complexes called "*acutatum*" and "*gloeosporioides*", with several other species included within them [12,13]. Table 1 summarized the *Colletotrichum* species reported to be associated with anthracnose of tropical fruit crops from several countries. Many of the species were identified based on phylogenetic analysis of multiple markers.

Many *Colletotrichum* species that are part of these complexes are reported to cause anthracnose [14–16]. Some species are known to infect specific hosts, while others infect multiple hosts. Anthracnose pathogens that infect multiple hosts may indicate the development of cross-infection ability. Based on a cross-pathogenicity study by Phoulivong et al. (2012) [16], several species within the *C. gloeosporioides* complex were found to have the capacity to infect multiple hosts. Some examples include *C. asianum*, detected in infected chili, mango, and rose apple, and *C. fructicola*, a fungus initially reported to infect coffee berries, but now recognized as a phytopathogen in other plant species, such as chili, citrus fruits, rose apple, avocado, grapes, and papaya [17].

Previous studies (published before systematic revisinions of *Colletotrichum* genus based on phylogenetic analysis of multiple markers) indicate cross-infection among different anthracnose pathogens. For instance, Freeman et al. (2001) [18] showed that *C. acutatum sensu lato* isolated from strawberry is able to infect various fruit crops. Moreover, cross-infection studies by Sanders and Korsten (2003) [19] show that isolates of *C. gloeosporioides sensu lato* from mango could infect and produce symptoms in guava, chili, and papaya. Therefore, cross-infection of tropical fruits by various *Colletotrichum* species can occur in the field. Likewise, anthracnose pathogens may infect the same fruit crop in various countries. Therefore, it is important to identify these pathogens correctly and assign appropriate scientific names. Furthermore, information on the lifestyle and mode of infection of each species is key point to implement suitable control measures [14]. Moreover, a deeper knowledge of species distribution and population size can provide valuable insights into breeding strategies directed to achieve durable resistance to anthracnose, as well as to improve control methods.

Table 1. Species of *Colletotrichum* associated with tropical fruit crops reported in several countries.

Fruit Crop	Reported *Colletotrichum* spp.	Country	References
Banana (*Musa* spp.)	*C. paxtonii*	St Lucia	Damm et al. (2012a) [12]
	C. gloeosporioides sensu lato	Malaysia	Intan Sakinah et al. (2013) [20]
	C. scovillei	Hainan Province, China	Zhou et al. (2016) [21]
	C. siamense	India	Kumar et al. (2017) [22]
	C. siamense, *C. tropicale*, *C. chrysophilum*, *C. theobromicola*	Brazil	Vieira et al. (2017) [23]
	C. gloeosporioides	Ecuador	Riera et al. (2019) [24]
	C. siamense	Turkey	Uysal and Kurt (2020) [25]
	C. chrysophilum	Mexico	Fuentes-Aragón et al. (2020) [26]
Mango (*Mangifera indica* L.)	*C. asianum* and *C. gloeosporioides*	Panama	Rojas et al. (2010) [27]
	C. asianum, *C. fructicola*, *C. tropicale*, *C. karstii*, *C. dianesei*	northeastern Brazil	Lima et al. (2013) [28]
	C. fragariae sensu stricto, *C. fructicola*, *C. jasmine-sambac*, *C. melanocaulon*	India	Sharma et al. (2013) [29]
	C. asianum, *C. gloeosporioides*	Sri Lanka.	Krishnapillai and Wijeratnam (2014) [30]
	C. asianum	Malaysia	Latiffah et al. (2015) [31]
	C. asianum, *C. gloeosporioides*	Colombia	Pardo-De la Hoz et al. (2016) [32]
	C. asianum	Sanya City, China	Qin et al. (2017) [33]
	C. asianum, *C. fructicola*, *C. siamense*	Guangxi, South China	Mo et al. (2018) [34]
	C. scovillei (mango leaves)	Guangxi, China	Qin et al. (2017) [33]
	C. asianum, *C. cliviicola*, *C. cordylinicola*, *C. endophytica*, *C. fructicola*, *C. gigasporum*, *C. gloeosporioides*, *C. karstii*, *C. liaoningense*, *C. musae*, *C. scovillei*, *C. siamense*, *C. tropicale*	southern China	Li et al. (2019) [35]
	C. asianum, *C. fructicola*, *C. siamense*, *C. tropicale*, *C. scovillei*	Taiwan	Wu et al. (2020) [36]
	C. alienum, *C. asianum*, *C. fructicola*, *C. siamense*, *C. tropicale*	Mexico	Tovar-Pedraza et al. (2020) [37]
	C. asianum	Philippine	Alvarez et al. (2020) [38]
	C. alienum	Beijing, China	Ahmad et al. (2021) [39]
Papaya (*Carica papaya* L.)	*C. gloeosporioides*, *C. capsici*	Yucatan peninsula, Mexico	Tapia-Tussell et al. (2008) [40]
	C. gloeosporioides, *C. capsici*	Malaysia	Rahman et al. (2008) [41]
	C. gloeosporioides, *C. capsici*	Miyako Islands, Okinawa, Japan	Yaguchi et al. (2008) [42]
	C. gloeosporioides, *C. capsici*	South Florida	Tarnowski and Ploetz (2010) [43]
	C. magna, *C. gloeosporioides*	Brazil	Nascimento et al. (2010) [44]
	C. gloeosporioides, *C. capsici*, *C. dematium*	Yucatan, Mexico	Santamaría Basulto et al. (2017) [45]
	C. acutatum, *C. simmondsii*	Australia	Damm et al. (2012a) [12]
	C. karstii	Brazil	Damm et al. (2012b) [46]
	C. queenslandicum	Australia	Weir et al. (2012) [13]
	C. siamense	South Africa	Weir et al. (2012) [13]
	C. gloeosporioides, *C. capsici*	Trinidad Island	Rampersad (2011) [47], Maharaj and Rampersad (2013) [48]
	C. karstii	India	Sharma and Shenoy (2013) [49]
	C. brevisporum	Brazil	Vieira et al. (2013) [50]
	C. fructicola, *C. gloeosporioides*	India	Saini et al. (2016) [51]
	C. magnum	Mexico	Tapia-Tussell et al. (2016) [52]

Table 1. *Cont.*

Fruit Crop	**Reported *Colletotrichum* spp.**	**Country**	**References**
	C. salsolae	India	Saini et al. (2017) [53]
	C. truncatum, *C. gloeosporioides sensu lato*, *C. magnum*	Costa Rica	Molina-Chaves et al. (2017) [54]
	C. brevisporum	Taiwan	Duan et al. (2018) [55]
	C. truncatum	Korea	Aktaruzzaman et al. (2018) [56]
	C. plurivorum	Taiwan	Sun et al. (2019) [57]
	C. brevisporum	China	Liu et al. (2019) [58]
	C. truncatum	Brazil	Vieira et al. (2017) [23]
	C. okinawense	Brazil	Dias et al. (2020) [59]
	C. okinawense	Taiwan	Sun and Huang (2020) [60]
	C. siamense	China	Zhang et al. (2021) [61]
Dragon fruits (*Hylocereus* spp.)	*C. gloeosporioides sensu lato* (*H. undatus*)	Okinawa Prefecture, Japan	Taba et al. (2006) [62]
	C. gloeosporioides sensu lato (*H. undatus*)	Miami-Dade County, Florida, USA	Palmateer et al. (2007) [63]
	C. gloeosporioides sensu lato (*H. megalanthus*)	Brazil	Takahashi et al. (2008) [64]
	C. gloeosporioides sensu lato (*H. polyrhizus*, *H. undatus*, *Selenicereus megalanthus*)	Malaysia	Masyahit et al. (2009) [65]
	C. gloeosporioides (*H. undatus* young stems)	China	Ma et al. (2014) [66]
	C. truncatum (*H. undatus* fruits)	Yuanjiang County, Yunnan Province, China	Guo et al. (2014) [67]
	C. aenigma and *C. siamense* (*H. undatus* stem and fruit)	Thailand	Meetum et al. (2015) [68]
	C. truncatum (*H. polyrhizus* stem)	Malaysia	Suzianti et al. (2015) [69]
	C. gloeosporioides, *C. truncatum*, *C. boninense* (*H. polyrhizus*, *H. undatus*, *H. costaricensis*)	Taiwan	Lin et al. (2017) [70]
	C. siamense (*H. polyrhizus* stem)	China	Zhao et al. (2018) [71]
	C. siamense (*H. undatus*)	Andaman Islands, India	Abirami et al. (2019) [72]
	C. karstii (*H. undatus* stem)	Brazil	Nascimento et al. (2019) [73]
Guava (*Psidium guajava* L.)	*C. gloeosporioides sensu lato*	Egypt	Omar (2001) [74]
	C. gloeosporioides sensu lato	Ibadan, Nigeria	Amusa et al. (2005) [75]
	C. gloeosporioides	Hawaii	Keith and Zee (2010) [76]
	C. psidii	Italy	Weir et al. (2012) [13]
	C. guajavae	India	Damm et al. (2012a) [12]
	C. gloeosporioides sensu lato	Florida, USA	Merida and Palmateer (2013) [77]
	C. gloeosporioides sensu lato	Malaysia	Intan Sakinah et al. (2014) [78]
	C. simmondsii	Brazil	Cruz et al. (2015) [79]
	C. abscissum	USA	Crous et al. (2015) [80]
	C. siamense	India	Sharma et al. (2015b) [81]
	C. abscissum	Brazil	Bragança et al. (2016) [82]
	C. gloeosporioides sensu lato	China	Yao et al. (2018) [83]

Table 1. *Cont.*

Fruit Crop	Reported *Colletotrichum* spp.	Country	References
Avocado (*Persea americana* Mill.)	*C. gloeosporioides sensu lato*	USA	Nelson (2008) [84]
	C. gloeosporioides, *C. acutatum*, *C. boninense*	Mexico	Silva-Rojas and Avila-Quezada (2011) [85]
	C. gigasporum	Sri Lanka	Hunupolagama et al. (2015) [86]
	C. godetiae	Mexico	Hernandez-Lauzardo et al. (2015) [87]
	C. gloeosporioides	Mersin Province, Turkey	Akgul et al. (2016) [88]
	C. alienum, *C. fructicola*, *C. siamense*	Australia	Shivas et al. (2016) [89]
	C. gloeosporioides, *C. siamense*	Ghana	Honger et al. (2016) [90]
	C. aenigma, *C. alienum*, *C. fructicola*, *C. gloeosporioides sensu stricto*, *C. karstii*, *C. nupharicola*, *C. siamense*, *C. theobromicola*, *C. perseae*	Israel	Sharma et al. (2017) [91]
	C. fructicola	Hidalgo, Mexico	Fuentes-Aragón et al. (2018) [92]
	C. alienum, *C. asianum*, *C. fructicola*, *C. karstii*, *C. siamense*	eastern Australia	Giblin et al. (2018) [93]
	C. kahawae subsp. *cigarro*	Jinju, South Korea	Kwon et al. (2020) [94]
	C. karstii	Turkey	Uysal and, Kurt (2020) [25]
	C. jiangxiense	Mexico	Ayvar-Serna et al. (2020) [95]
	C. karstii, *C. godetiae*, *C. siamense*, *C. fioriniae*, *C. cigarro*, *C. chrysophilum*, *C. jiangxiense*, *C. tropicale*, *C. nymphaeae*,*Colletotrichum* sp. 1, *Colletotrichum* sp. 2	Mexico	Fuentes-Aragón et al. (2020) [96]
	C. siamense, C. kartsii	south eastern Brazil	Soares et al. (2021) [97]

Due to the economic importance of anthracnose in the context of tropical fruit production and commercialization, this review focuses on the current knowledge regarding *Colletotrichum* species associated with tropical fruit crops reported in several fruit-producing countries. Emphasis is laid on *Colletotrichum* species associated with mango, papaya, banana, avocado, guava, and dragon fruit because these fruit crops are cultivated in many tropical countries as an income source, contributing significantly to the economic well-being of their inhabitants.

2. Banana Anthracnose

Banana (*Musa* spp.) is one of the most important fruit crops and the most popular fruit consumed worldwide, with over 100 billion bananas eaten every year [98]. More than 150 countries have banana plantations; they are mainly distributed in Asia, Latin America, and Africa. The largest banana producer is India, followed by China, the Philippines, Ecuador, and Brazil [99].

International banana trade mainly involves the Cavendish type, which replaced the Gros Michel variety due to its resistance to Fusarium wilt. Currently, Cavendish is produced for export and local consumption worldwide in small farms, as well as in extensive plantations [100].

Anthracnose caused by *Colletotrichum* spp. is an important postharvest disease of bananas. *Colletotrichum* species infect banana in plantations and become latent pathogens. Bananas are often harvested before ripening; during storage, as the fruits ripen, anthracnose symptoms appear as brown or black lesions. Later, these lesions enlarge, become sunken, and produce spore masses. Wounds and scratches on banana peel caused by handling and transportation enhance the occurrence of anthracnose symptoms [101], which greatly impair the quality of bananas for export and local consumption.

Colletotrichum musae has long been associated with banana anthracnose worldwide [23,102–107]. In addition to anthracnose, *C. musae* can also cause stem-end, crown, and blossom-end rots in bananas [108]. Since *C. musae* is prevalent in bananas, Vieira et al. (2017) [23] suggested that this species might be host-specific to the plant. However, a detailed study on a global scale is required to confirm this hypothesis. Vieira et al.

(2017) [23] have also developed *C. musae* species-specific primers for the rapid identification of this fungal species; this strategy results in cost savings compared to the sequencing of multiple genes. A study carried out by Li et al. (2019) [35] on mango anthracnose identified *C. musae* as one of the species involved, indicating that *Colletotrichum* species may not be host-specific to banana, as previously considered.

Among the main banana-producing countries, detailed studies on anthracnose pathogens were only conducted in Brazil, where five species were found to be associated with the disease [23]. *Colletotrichum musae* is still the most prevalent species reported in Brazil. Information regarding *Colletotrichum* spp. causing banana anthracnose in India, China, the Philippines, and Ecuador is rather scarce. The available data mainly consist of disease reports or newly recorded species; only one or two species are commonly reported to be involved.

Colletotrichum species causing banana anthracnose in Brazil were found to be *C. siamense*, *C. tropicale*, *C. chrysophilum*, and *C. theobromicola* [23]. *Colletotrichum scovillei* was reported in China [21], *C. siamense* in India [22] and Turkey [25], *C. gloeosporioides* in Ecuador [24] and *C. chrysophilum* in Mexico [26]. Other reported species include *C. paxtonii* [12], *C. karstii* [46], *C. gloeosporioides sensu lato* [20], and an undescribed species assigned to *C. siamense sensu lato* clade [106].

One of possible reasons lack of comprehensive studies on banana anthracnose might be many studies focusing on other diseases affecting bananas that are known to cause significant yield losses, such as wilt caused by *Fusarium oxysporum* Tropical Race 4, and Moko disease caused by *Ralstonia solanacearum*.

3. Mango Anthracnose

Mango (*Mangifera indica* L.) is planted mostly in Asia, particularly in India, which contributes to about 50% of the world's mango production, followed by China, Thailand, Pakistan, and Indonesia. Brazil and Mexico are the largest mango producers in America, while Nigeria and Egypt are major producers in Africa [109]. For many of these countries, mango production is economically relevant.

Almost all mango cultivars grown in these countries are susceptible to anthracnose due to high temperature and humidity that characterize these tropical regions. The incidence of fruit anthracnose is almost 100% under wet conditions [110]. Not only fruits, but also the leaves, twigs, and flowers are affected by mango anthracnose. Leaf symptoms comprise black necrotic spots with irregular shapes on both sides of the leaves. Similar symptoms can appear on twigs and flowers. These black necrotic spots may coalesce to form larger infected areas. Infected tissues become dry; eventually, the infected parts of the plant die [5,110].

Colletotrichum gloeosporioides sensu lato is an important pathogen responsible for mango anthracnose worldwide [5,93,111]. In some cases, *C. acutatum sensu lato* has also been reported to be associated with mango anthracnose [5,112]. Phylogenetic analysis based only on internal transcribed spacer (ITS) sequences shows that *C. gloeosporioides* consists of diverse groups or species sub-populations, suggesting that other *Colletotrichum* spp. might be associated with mango anthracnose [111,113]. In contrast, several studies show that *Colletotrichum* isolates obtained from mango may consist of pathogenically and genetically distinct populations of *C. gloeosporioides* [114–116]. According to Ploetz (1999) [117], the *C. gloeosporioides* population on mango has restricted host range and is highly virulent only on mango.

After the reports published by Phoulivong et al. (2012) [16] and Weir et al. (2012) [13] describing phylogenetic analyses of the genus *Colletotrichum* using multiple markers, several species within *C. gloeosporioides* and *C. acutatum* complexes (including *C. gloeosporioides*) were reported to be associated with mango anthracnose. In addition, comprehensive studies on mango anthracnose pathogens using multilocus phylogenetic analysis were conducted in Brazil by Lima et al. (2013) [28] and Sharma et al. (2013) [29], in South China by Mo et al. (2018) [34] and in Mexico by Tovar-Pedraza et al. (2020) [37]. Other data on anthracnose-causing agents in mango have been communicated as first reports or disease notes.

In northeastern Brazil, five *Colletotrichum* species, namely *C. asianum*, *C. fructicola*, *C. tropicale*, *C. karstii*, and *C. dianesei* were found as anthracnose pathogens in mango; all species were reported for the first time in mango in Brazil [28]. Multiple genetic markers (glyceraldehyde-3-phosphatedehydrogenase (GAPDH), actin, β-tubulin, calmodulin, glutamine synthetase (GS), and the ITS region) were used to identify such species. Interestingly, only *C. karstii* could not infect two mango cultivars (Keith and Palmer) in a pathogenicity test carried out by Lima et al. (2015) [118], indicating that preference for certain mango cultivars may exist among *Colletotrichum* species. However, these authors found no host specificity in a cross-pathogenicity test, which included papaya, banana, guava, and bell pepper, indicating that these species have a broad host range [118].

Pardo-De la Hoz et al. (2016) [32] reported some level of host preference among *Colletotrichum* spp. associated with mango anthracnose in Colombia, which included *C. asianum* and *C. gloeosporioides*. Both species have also been reported as common mango anthracnose pathogens by Rojas et al. (2010) [27] in Panama and Krishnapillai and Wijeratnam (2014) [30] in Sri Lanka.

Many reports published in India, the largest mango producer in the world, point out *C. gloeosporioides* as the main causative agent of mango anthracnose, which, in some cases, might not be accurate. Based on restriction analysis and sequencing of the ITS region, Chowdappa and Kumar (2012) [111] reported that *C. gloeosporioides* associated with mango anthracnose in India comprise diverse subgroups. Pathogenicity tests demonstrate variation in the degree of virulence among *C. gloeosporioides* isolates, suggesting the existence of more than one species causing the disease. By using multigene phylogenetic analysis, Sharma et al. (2013) [29] later identified four phylogenetic species, namely, *C. fragariae sensu stricto*, *C. fructicola*, *C. jasmine-sambac*, and *C. melanocaulon*. Besides, five *Colletotrichum* lineages without species names were associated with mango anthracnose in India. Sharma et al. (2013) [29] also reported that none of the *Colletotrichum* isolates obtained from mango samples group with *C. gloeosporioides sensu stricto*, and are in line with the findings previously documented by Phoulivong et al. (2012) [16].

A multigene phylogenetic analysis carried out by Mo et al. (2018) [34] in different parts of Guangxi, south China, shows that three species of the *C. gloeosporioides* complex are pathogenic to mango fruits and its leaves. These species were identified as *C. asianum*, *C. fructicola*, and *C. siamense*. Later, Qin et al. (2017) [33] reported *C. scovillei*, a species within the *C. acutatum* complex, as another anthracnose-causal pathogen in mango leaves in Guangxi, China.

Among species in the *C. gloeosporioides* complex, *C. asianum* is the most common anthracnose pathogen in mango worldwide. This species has been reported in Brazil [28], Sri Lanka [30], Sanya City [33], and other areas of China [58], South Africa [119], Malaysia [31], Taiwan [36], Mexico [37], the Philippines [38] and Indonesia [120].

More *Colletotrichum* spp. were identified in association with mango anthracnose; this might be related to larger sampling areas, which may have allowed the access to more diseased-mango individuals and the detection of more isolates. In southern China, study on *Colletotrichum* spp. associated with mango anthracnose was reported by Li et al. (2019) [35], who analyzed infected mangoes from six provinces, Fujian, Guangdong, Guizhou, Hainan, Sichuan, and Yunan. In the study, 13 species are associated with mango anthracnose: linebreak *C. asianum*, *C. cliviicola*, *C. cordylinicola*, *C. endophytica*, *C. fructicola*, *C. gigasporum*, *C. gloeosporioides*, *C. karstii*, *C. liaoningense*, *C. musae*, *C. scovillei*, *C. siamense*, and *C. tropicale*. Two species, *C. asianum* and *C. siamense*, are the most common species identified, each accounting for 30% of the total species. *Colletotrichum cordylinicola*, *C. endophytica*, *C. gigasporum*, *C. liaoningense*, and *C. musae* were the first reported *Colletotrichum* spp. associated with mango anthracnose [35].

Wu et al. (2020) [36] reported on *Colletotrichum* spp. associated with mango anthracnose in Taiwan. These authors identified *C. asianum*, *C. fructicola*, *C. siamense*, *C. tropicale*, and *C. scovillei*, which were some of the species previously recognized by Li et al. (2019) [35] in China. Another comprehensive study of mango anthracnose was reported by Tovar-Pedraza et al. (2020) [37] in Mexico. Five species were identified using mating type Mat1-20 (ApMat) marker, namely *C. alienum*, *C. asianum*, *C. fructicola*, *C. siamense*, and *C. tropicale*. In terms of virulence, *C. alienum* and *C. fructicola* were the least virulent whereas *C. siamense* and *C. asianum* were the most virulent. Some of the species except *C. aleinum* have been reported as causal pathogens of mango anthracnose. *Colletotrichum alienum* was the first reported species associated with mango anthracnose worldwide at the time the report was published [37]. Later, Ahmad et al. (2021) [39] reported that *C. alienum* was associated with mango fruits cv. Jin-Hwang anthracnose in Beijing, China.

To date, 17 species of *Colletotrichum* are associated with mango anthracnose worldwide. By using, multiple markers phylogenetic analysis, it is likely more new species will be reported from other mango producing countries.

4. Papaya Anthracnose

It is widely accepted that papaya (*Carica papaya* L.) originated in Central America and southern Mexico. Currently, this fruit crop is planted commercially in many tropical countries, with India as the leading producer, followed by Brazil, Mexico, Indonesia, and the Dominican Republic [121]. Other papaya-producing countries are Thailand, the Philippines, China, Peru, and Nigeria.

Papaya is a climacteric fleshy fruit commonly harvested at the pre-climacteric stage. Therefore, the ripening stage starts after harvest, and the shelf life is relatively short. Several fruit rot pathogens may cause fruit damage during this period, including *Colletotrichum* spp. Though papaya anthracnose symptoms may occur both in fruits and leaves, *Colletotrichum* infection is usually more severe in fruits. Refrigerated papayas are particularly susceptible to disease; thus, fruits intended for export may develop anthracnose symptoms as they ripen [122].

In earlier studies, particularly in those conducted before application of multiple markers became usual tools for identification, *C. gloeosporioides* and *C. capsici* were indicated as common anthracnose pathogens in papaya in several regions and countries, including the Yucatan peninsula, Mexico [40]; Malaysia [41]; the Miyako Islands, Okinawa, Japan [42]; South Florida [43]; and Trinidad Island [47,48]. In addition to *C. gloeosporioides* and *C. capsici*, *C. dematium* has been found to be the causative *agent of papaya anthracnose in Yucatan, Mexico* [45].

To date, several species belonging to *C. gloeosporioides*, *C. truncatum*, *C. magnum*, and *C. orchidearum* complexes have been reported to be associated with papaya anthracnose, indicating that more than two *Colletotrichum* species are involved. Given that *C. capsici* is now a synonym of *C. truncatum*, the former name is no longer used in many publications.

In Australia, *C. acutatum*, *C. simmondsii* and *C. queenslandicum* have been described on papaya [12] while *C. siamense* in South Africa [13] and in China [61]. In India, using multi-gene phylogenetic analysis, several species have been identified as papaya anthracnose pathogens. The species reported include *C. karstii* [49], *C. fructicola*, *C. gloeosporioides* [51], and *C. salsolae* [53]. Most of the species reported are not host-specific and occur in many locations in papaya-producing countries.

Three species, namely, *C. magna*, *C. gloeosporioides* [44], and *C. brevisporum* [50], were reported as causative agents of papaya fruit rot and papaya anthracnose in Brazil. Although Nascimento et al. (2010) [44] referred to the disease as papaya fruit rot, *Colletotrichum* spp. were isolated from the lesions that constitute typical anthracnose symptoms, sometimes described as chocolate spots. *Colletotrichum karstii* has also been reported from papaya [46]. Papaya anthracnose caused by *C. truncatum* and *C. okinawense* was reported by Vieria et al. (2020) [123] and Dias et al. (2020) [59], respectively. Both species are the latest report on papaya anthracnose in Brazil.

Colletotrichum brevisporum and *C. plurivorum* have also been reported as a pathogens of papaya anthracnose in Taiwan. These pathogens were recovered from anthracnose lesions found on papaya fruits [55,57]. In addition to Taiwan and Brazil, *C. brevisporum* was also a causal pathogen of papaya anthracnose in China [58]. Another species, *C. okinawense*, which was first reported in Brazil, was found to be associated with papaya anthracnose in Taiwan [60].

Colletotrichum magnum was identified as causative agents of papaya anthracnose in Mexico [40] and Costa Rica [54]. Using the ITS region and specific primers, Molina-Chaves et al. (2017) [54] depicted *C. truncatum*, *C. gloeosporioides sensu lato*, and *C. magnum* as pathogens of papaya anthracnose in Guácimo, Costa Rica. *Colletotichum trucatum* has also been reported as papaya anthracnose in Korea [56].

Comprehensive studies focusing on the causative pathogens of papaya anthracnose are still lacking. Most available studies are either first disease reports or disease notes. A study on genetic variation in *C. magnum* was conducted by Pérez-Brito et al. (2018) [124] as an attempt to understand pathogenicity patterns and response to different fungicides. One of the reasons that may account for the lack of comprehensive studies focused on papaya anthracnose may be the occurrence of viral and bacterial diseases in papaya under field conditions, which frequently results in plant decay and decreased yields. Among viral diseases, papaya ringspot caused by the *Papaya ringspot virus* (PRSV) is the most serious and has been detected in many papaya producing countries in the tropics, as well as in subtropical areas. As for bacterial diseases, papaya dieback is a very destructive disease; and 100% yield losses have been recorded in Malaysia due to this pathogen [125].

In studies on control methods of papaya anthracnose, "*C. gloeosporioides*" is widely used as the causal pathogen. This should be treated with cautious as there are several other *Colletotrichum* species within *C. gloeosporioides* complex associated with papaya anthracnose (Table 1).

5. Dragon Fruit Anthracnose

Dragon fruit (*Hylocereus* sp.) is believed to have originated in Central and South America, and now this fruit crop is widely cultivated in many countries, including Vietnam, China, Mexico, Colombia, Nicaragua, Ecuador, Thailand, Malaysia, Indonesia, Australia, and United States [126]. China has also started a large-scale planting of dragon fruit, with 20,000 ha distributed in Guangdong and Guangxi provinces. Currently, the main dragon fruit producer is Vietnam, followed by Thailand, Taiwan, the Philippines, Malaysia, Sri Lanka, Australia, and Israel. In South America, dragon fruit is cultivated in Mexico, Ecuador, Colombia, Nicaragua, and Guatemala [127]. Two common species of cultivated dragon fruits are *Hylocereus polyrhizus* (red-fleshed) and *Hylocereus undatus* (white-fleshed).

The name "dragon fruit" probably derives from the fruit's appearance, characterized by the presence of bracts or scales in the outer part [128]. This fruit is also known by other local names including strawberry pear or night-blooming cereus (English-speaking regions), pitahaya (Latin America), buah naga or buah mata naga (Malaysia), thanh long (Vietnam), kaeo mangkon or luk mangkon (Thailand), päniniokapunahou or päpipi pua (Hawaii), and paw wong fa kor (China).

Dragon fruit is often eaten fresh; its white, purple, or red flesh has a sweet taste (particularly the last one). Apart from being served as fruit salad, dragon fruit is used to flavor juices, sorbets, jams, yogurts, ice creams, jellies, candy, and dried fruit. Flower buds are used to make soups, or can be mixed in salads and tea preparations [129]. Besides, nutritional benefits have been assigned to this fruit as it contains vitamin C and other antioxidant metabolites, including betalains, flavonoids, and hydroxycinnamates, as well as fiber, iron, and magnesium.

Dragon fruit anthracnose caused by *Colletotrichum* affects the stems and fruits of *Hylocereus* spp. In earlier studies, *C. gloeosporioides sensu lato* is reported as the most common anthracnose pathogen in *Hylocereus megalanthus* in Brazil [64]; *H. undatus* is reported to be common in Okinawa Prefecture, Japan [62] and in Miami-Dade County, Florida, USA [63]. *Colletotrichum gloeosporioides sensu lato* has also been reported as an anthracnose-causing pathogen affecting the stems and fruits of *H. polyrhizus*, *H. undatus*, and *Selenicereus megalanthus* in Malaysia [65]. Using only ITS sequences, Lin et al. (2017) [70] identified three species, *C. gloeosporioides*, *C. truncatum*, and *C. boninense*, as anthracnose agents in *H. polyrhizus*, *H. undatus*, and *H. costaricensis* plants growing in several counties in Taiwan.

After the application of multiple markers for the identification of *Colletotrichum* species, several members within the *C. gloeosporioides* complex have been reported as anthracnose pathogens in *Hylocereus* spp. Ma et al. (2014) [66] reported *C. gloeosporioides* as an anthracnose pathogen in the young stems of *H. undatus* in China. In a later study, Zhao et al. (2018) [71] found *C. siamense* to be the causative agent of stem anthracnose in *H. polyrhizus* in China. Besides, *C. aenigma* and *C. siamense* are reported to be associated with stem and fruit anthracnose in *H. undatus* grown in Pathum Thani, Nakhon Pathom, and Samut Sakhon, Thailand [68]. *Colletotrichum siamense* is also responsible for fruit anthracnose in *H. undatus* growing in the Andaman Islands, India [72]. In Brazil, *C. karstii* was reported to be the causal pathogen of *H. undatus* stem anthracnose [73].

In addition to species within the *C. gloeosporioides* complex, *C. truncatum* is also reported as an anthracnose pathogen in *Hylocereus* spp. *Colletotrichum truncatum* is the causative agent of *H. polyrhizus* stem anthracnose in Malaysia [69], and *H. undatus* was also reported in fruits sold in a market in Yuanjiang County, Yunnan Province, China [67].

Seven *Colletotrichum* species were identified as causal anthracnose pathogens of different types of dragon fruits (Table 1). However, information on anthracnose pathogens associated with fruits and stems in several main producing countries including Vietnam, Indonesia and Si Lanka is still lacking.

6. Guava Anthracnose

Guava (*Psidium guajava* L.) is grown for its edible fruits that are rich in vitamin C and dietary fiber. Guava fruits are consumed fresh or as industrialized products, including purées, jams or marmalades, jellies, fruit pastes, juice, syrup, candy, and chutneys [130]. In addition, guava leaves are used in folk medicine owing to their medicinal properties that are useful in treating many ailments such as diarrhea, dysentery, gastroenteritis, hypertension, and diabetes, and to improve locomotor coordination [131].

This tropical fruit crop is native to Mexico, Central America, and South America, and receives different local names depending on the zones. For instance, it is known as jambu batu in Malay, amrood in Hindi, perakka in Malayalam, and farang in Thai. In French-speaking regions, guava is known as goyave or goyavier; Hawaiians call it kuawa, and in Portuguese-speaking areas, the fruit receives the name of goiaba or goiabeira [132].

India is the leading guava producer, with an estimated production of 17,650,000 metric tons annually, followed by Thailand and China. Other guava-producing countries are Pakistan, Mexico, Indonesia, Brazil, the Philippines, and Nigeria [133].

All guava-growing areas around the world are subjected to guava anthracnose. Fungi responsible for this disease infect guava fruits during pre- and post-harvest stages, particularly during high rainfall and high humidity periods. Young guava developing-flowers and fruits may also be infected. Anthracnose symptoms are obvious in mature fruits in the field, as well as in harvested fruits. Similar to that observed in other fruit crops, guava anthracnose symptoms consist mainly of sunken, dark necrotic lesions on the fruit surface. Spore masses are formed in these lesions under humid conditions [77].

Colletotrichum gloeosporioides sensu lato has been reported as a common anthracnose pathogen in several guava-growing countries [74,75,77,83]. In Hawaii, *C. gloeosporioides sensu lato* has also been reported to infect guava leaves [76]. Intan Sakinah et al. (2014) [78] reported *C. gloeosporioides sensu lato* as the most common species causing anthracnose disease in guava fruit, but suggest that other species of the *C. gloeosporioides* complex may also be associated with guava anthracnose. *Colletotrichum acutatum* has also been reported to cause anthracnose disease in guava [134–136].

More recently, multiple gene phylogeny studies for the identification of *Colletotrichum* spp. indicate that several species belonging to *C. gloeosporioides* and *C. acutatum* complexes are associated with guava anthracnose. The species of the *C. acutatum* complex reported include *C. simmondsii* in Brazil [79], *C. abscissum* in Brazil and the USA [80,82], and *C. guajavae* in India [12]. Among the species of the *C. gloeosporioides* complex associated with guava, *C. psidii* was detected in Italy [13] and *C. siamense* in India [81]. In a pathogenicity study performed by Bragança et al. (2016) [82], *C. nymphaeae* isolated from apple fruits in Brazil could cause lesions on guava fruits, demonstrating the cross-pathogenicity of this species.

To summarize, several *Colletotrichum* species are found to be associated with guava anthracnose. The information here provided may be useful for the development of integrated disease management to control guava anthracnose, as some of the species involved have a wide host range.

7. Avocado Anthracnose

Avocado (*Persea americana* Mill.) is a common tropical fruit. This plant species originated in Central America, more specifically, in Mexico and Guatemala. Mexico is the main producer and exporter of avocado, followed by Netherlands, Peru, Spain, Chile, and Colombia [137]. Among other producing avocado countries are India, Indonesia, Israel, China, Kenya, Vietnam, the Philippine, Australia and New Zealand.

Avocado is considered a rich source of nutrients, particularly fatty acids such as oleic acid and palmitic acid, minerals, and vitamins. The plant also contains phytochemicals like tannins, alkaloids, phenols, saponins, and flavonoids, as well as lutein, which is the predominant carotenoid in avocado fruits [138]. Due to the presence of those compounds and many other phytochemicals, avocado has shown numerous medicinal properties, including antimicrobial, anti-inflammatory, analgesic, antihypoglycemic, antihypertensive, antihepatotoxic, anticonvulsant, and vasorelaxant effects [138].

Anthracnose may occur in avocado wherever this fruit crop is grown, particularly during the wet season and in high rainfall areas. Major infections occur on the fruit; however leaves and stems can also become infected. The dark lesions of variable size produced by anthracnose pathogens tend to expand rapidly on the fruit skin and also infect the pulp, causing rot [84].

Before the use of multiple gene phylogeny for the identification of *Colletotrichum* spp., *C. gloeosporioides sensu lato* was the most common species found in association with avocado anthracnose, followed by *C. acutatum sensu lato* [84]. However, based on molecular analysis, *C. gloeosporioides* was also reported as the causative agent of avocado fruit anthracnose in Mexico [85], Mersin Province, Turkey [88], and Ghana [90]. Hunupolagama et al. (2015) [86] identified *C. gigasporum* as a causative agent of avocado anthracnose in Sri Lanka based on four markers, ITS, actin (ACT), GAPDH, and β-tubulin. In Mexico, two species *C. godetiae* [87] and *C. karstii* [139] were identified as anthracnose pathogens on avocado. Both species were identified using ITS and GAPDH sequences.

A comprehensive study on *Colletotrichum* spp. associated with avocado anthracnose was conducted in Israel [91]. Using multiple genes/markers (ITS, ACT, ApMat, calmodulin [CAL], chitin synthase [CHS1], GAPDH, GS, HIS3, and β-tubulin), Sharma et al. (2017) [91] identified nine *Colletotrichum* species. Eight of these species, *C. aenigma*, *C. alienum*, *C. fructicola*, *C. gloeosporioides sensu stricto*, *C. karstii*, *C. nupharicola*, *C. siamense*, and *C. theobromicola*, had been reported before as avocado anthracnose pathogens in other avocado-producing countries. A new species, *C. perseae*, is reported in association with avocado anthracnose for the first time. While *C. aenigma* is the most virulent species in Israel, *C. perseae* sp. nov. is considered most dominant.

Some other studies conducted in different avocado-producing countries reported either the same species or different *Colletotrichum* species identified by Sharma et al. (2017) [91], to be responsible for avocado anthracnose. Fuentes-Aragón et al. (2018) [92] reported *C. fructicola* as the causal pathogen of avocado anthracnose in Hidalgo, Mexico and Giblin et al. (2018) [93] isolated and identified five species previously considered as *C. gloeosporioides sensu lato* from avocado fruit in eastern Australia: *C. alienum*, *C. asianum*, *C. fructicola*, *C. karstii*, and *C. siamense*. Shivas et al. (2016) [89] also reported the presence of *C. alienum*, *C. fructicola*, and *C. siamense* in avocado in Australia. Kwon et al. (2020) [94] identified *C. kahawae* subsp. *cigarro* as the isolate obtained from an imported avocado variety in a market in Jinju, South Korea. Uysal and Kurt (2020) [25] reported *C. karstii* as causal pathogen of avocado fruit and leaf anthracnose in Turkey. In south eastern Brazil, *C. siamense* and *C. karstii* were found to be associated avocado anthracnose [97].

Another comprehensive study on pathogen of avocado anthracnose was performed by Fuentes-Aragón et al. (2020) [96]. Using six markers (GAPDH, ITS, ACT, CHS-1, ApMat and β-tubulin), the study indicated 11 species were the causal pathogens of avocado anthracnose in Mexico, namely *C. karstii*, *C. godetiae*, *C. siamense*, *C. fioriniae*, *C. cigarro*, *C. chrysophilum*, *C. jiangxiense*, *C. tropicale*, *C. nymphaeae*), and two new lineages designated as *Colletotrichum* sp. 1 and *Colletotrichum* sp. 2. The most prevalent species was *C. siamense* and the most widespread was *C. karstii*.

According to existing reports, *Colletotrichum* species associated with avocado anthracnose are similar to those reported in other tropical fruit crops. They include *C. asianum*, *C. fructicola*, and *C. siamense*, species known to infect a wide range of hosts.

So far, there are a lack of reports on the *Colletotrichum* species associated with avocado anthracnose from other major avocado producing countries, including Indonesia, Dominican Republic, Peru, and Venezuela. Many studies on control methods in these countries referred to *C. gloeosporioides sensu lato* as the causal pathogen of avocado anthracnose, which might not be accurate.

8. Present and Future Management of Anthracnose

Fungicides, chemicals (e.g., benzimidazoles such as thiabendazole, benomyl, and carbendazim), and sterol inhibitors (e.g., imazalil, prochloraz, and propiconazole) have long been used to effectively control anthracnose disease in banana, mango, papaya, and avocado plants [140]. Benzimidazoles are often applied as dips or sprays to inhibit the anthracnose-causing fungus, *Colletotrichum* spp. [141], but large-scale and continuous fungicide use has led to fungal-resistance. For example, benzimidazole-resistant *Colletotrichum* has been detected in mangos and bananas [140]. The excessive use of fungicides also negatively affects human health and the environment, as chemical residues often contaminate the soil and water [142]. Biocontrol is an alternative, non-toxic method for controlling fruit crop anthracnose. Biocontrol agents (i.e., antagonistic microbes) such as yeast, bacteria, and filamentous fungi (particularly *Trichoderma* spp.) have shown promising results and are gaining popularity because of their direct post-harvest application to fruit surfaces [143].

Yeasts (unicellular fungi) have several characteristics that make them a desirable biocontrol agent. They grow rapidly on a wide range of substrates and have a high reproductive rate and simple nutritional requirements. Moreover, yeasts are not mycotoxigenic and can grow in high-sugar environments [144–147]. There is also an increasing demand for chemical-free or reduced chemical treatments to control anthracnose, which has led to the development of alternative methods that are safer for consumers (e.g., edible coatings from chitosan and essential oils). Generally recognized as safe (GRAS) salt treatments, nanomaterials, and cold plasma technology have also been explored. Often, these alternative approaches are used in combination for more effective anthracnose pathogen growth inhibition and disease severity reduction.

Chitosan emerged as a target for edible coating formulations because of its antifungal properties, and it is often combined with other compounds (i.e., essential oils). The antifungal efficacy of chitosan in solution (conventional chitosan) and chitosan in submicron dispersion were tested against *C. gloeosporioides sensu lato,* a dragon fruit anthracnose pathogen, by Asgar et al. (2013) [147]. When applied to the fruit, the chitosan treatments reduced the anthracnose symptoms and disease development. Combining chitosan and *Cymbopogon citratus* essential oil also has inhibitory effects against five anthracnose pathogens (*C. asianum, C. siamense, C. fructicola*, *C. tropicale*, and *C. karstii*) when inoculated on guava, mango, and papaya [148]. Braga et al. (2019) [149] combined chitosan and peppermint essential oils (*Mentha piperita* L and *Mentha* x *villosa* Huds) and documented anthracnose pathogen growth inhibition (*C. gloeosporioides* and *C. brevisporum*) on papaya in vitro and reduced anthracnose lesions after 10 days of storage.

GRAS inorganic and organic salts used to preserve food have been evaluated as an edible coating for anthracnose pathogen control and to reduce the amount of rotting fruit. Carbonates, sorbates, benzoates, and silicates have low toxicological effects and antifungal properties, and satisfactory results have been reported for anthracnose pathogen inhibition [150]. These results suggest that GRAS salts may be an alternative to post-harvest pathogen management.

De Costa and Gunawardhana (2012) [151] found that sodium bicarbonate reduced appressorium formation, spore production, germination, and pathogen mycelial growth of the banana anthracnose pathogen, *C. musae*, in vitro. Anthracnose lesions were also reduced by dipping the fruit into a 300 mM salt solution for 10 min. Jitareerat et al. (2018) [152] showed that sodium carbonate and potassium sorbate inhibited *C. gloeosporioides* and *C. capsici* spore germination. Moreover, when the fruit was placed in a potassium sorbate and hot water solution (55 °C for 5 min) and cooled in water, the disease severity was reduced without affecting the fruit quality. Kalupahana et al. (2020) [153] tested the effectiveness of sodium bicarbonate and sodium metabisulfite against the mango anthracnose pathogen, *C. siamense*, and found that both salts inhibited mycelial growth.

Nanomaterials, such as copper, silver, nickel, and magnesium, have antifungal properties and may be effective at managing anthracnose pathogens and post-harvest disease [154]. The efficacy of zinc oxide, magnesium oxide, and their composites (52–219 nm) were tested against papaya and avocado *C. gloeosporioides*. Conidial germination was inhibited and the fungal cells were damaged, indicating that the nanomaterials had an antifungal effect [154]. This was supported by Jagana et al. (2017) [155], who reported that copper, silver, nickel, and magnesium (68 nm) extracted from the leaves of the medicinal plants ajwain (*Trachyspermum ammi*) and neem (*Azadirachta indica*) inhibited the spore germination of *C. musae* isolated from banana. The severity of banana anthracnose was also reduced with 0.2% silver-neem.

Nanomaterials composite with other materials can also control mango anthracnose. Antifungal properties were reported when chitosan-silver composite (495–616 nm diameter) was used, which suppressed *C. gloeosporioides* conidial germination. An in-vivo study reported that 0.5% and 1% nanomaterial composite reduced anthracnose disease by 45.7% and 71.3%, respectively [156]. Neem extract was used to synthesize copper oxychloride-conjugated silver (21–25 nm) and treat *C. gloeosporioides*, resulting in pathogen growth suppression [157].

Cold plasma technology is another approach to inhibit anthracnose pathogens in tropical fruit. Cold plasma is a partially ionized gas, where a small subset of atoms and molecules are ionized by electrical discharges at atmospheric or sub-atmospheric pressure [158,159]. Studies using cold plasma technology have been performed on spoilage and mycotoxigenic fungi-contaminated food and feed with promising outcomes [159]. Siddique et al. (2018) [160] isolated *C. alienum* and *C. fioriniae* from avocados and treated them with cold plasma for 180 s or 360 s in open and sealed environments. In some treatments, the colony growth was reduced, and the conidial germination was inhibited, suggesting that cold plasma treatment may be an effective control for *C. alienum* and *C. fioriniae* in avocado. Cold plasma has also been used to decontaminate fruit containers and packaging. Misra et al. (2014) [161] used two gas mixtures (65% O_2 + 16% N_2 + 19% CO_2 and 90% N_2 + 10% O_2) to decontaminate packaged and sealed strawberries, which reduced the microflora level from 5 to 3.0 $\log_{10}$ CFU/g in 300 s with no post-treatment changes to the packaging material.

Alternative methods to reduce post-harvest fruit crop losses are ongoing. Biocontrol agents, edible fruit coatings, and GRAS salt, cold plasma, and nanomaterial treatments have shown promising results, but they are not without challenges. The performance varies among fruit crops, and the formulations and costs need further investigation. Moreover, some methods are combined to improve efficacy, creating other issues, such as public and industry acceptance, product registration, and commercial viability.

9. Conclusions and Future Directions

Previously, anthracnose pathogens are often referred to as *C. gloeosporioides* or *C. acutatum* because, in many cases, the identification procedures did not include the use of multiple markers, and frequently, only the ITS region was analyzed. Thus, the data obtained may not reflect the true causal pathogens. Moreover, it is now accepted that *C. gloeosporioides* is not the most common anthracnose pathogen in tropical fruit crops, as previously thought.

Various *Colletotrichum* species can cause anthracnose in tropical fruit crops, thus becoming serious limiting factors in the production and marketing of these commodities. Table 2 shows diverse species of *Colletotrichum* associated with anthracnose of banana, papaya, mango, dragon fruits, guava, and avocado. Some of the *Colletotrichum* species not only infected the fruits but the stem and leaves as well indicated that other parts of the plants harbor inoculum sources for anthracnose infection on fruit crops. Several species including *C. siamense*, *C. asianum*, *C. scovillei*, *C. gloeosporioides, C. karstii, C. fructicola,* and *C. tropicale* can infect multiple hosts, demonstrated the possibility of cross infection to various types of fruit crops as well as other crops.

Since molecular phylogenetic analysis was applied for identification and characterization of *Colletotrichum* species, diverse species were reported to be associated with anthracnose of tropical fruits (Table 2). Many of the *Colletotrichum* species listed in Table 2 belong to different species complexes including *C. gloeosporioides*, *C. acutatum* and *C. boninense* complexes. Species in a species complex are closely related, and have similar behavior of host infection and colonization [12,13,46]. Thus, infection and colonization of various *Colletotrichum* spp. on different tropical fruit crops are also similar. In terms of virulence, anthracnose symptoms on different fruits may vary depending on the variety of the fruits, inoculum concentration, humidity and temperature [5]. Moreover, pathogenic variation of *Colletotrichum* spp. infected fruit crops has been demonstrated [162,163].

Diverse species of *Colletotrichum* causing anthracnose of fruit crops are also a quarantine concern. Banana, papaya, mango, dragon fruits, guava and avocado are exported and imported worldwide, and latent infection is part of the disease cycle of anthracnose pathogens. There are possibilities that the anthracnose pathogens can be distributed to other areas or regions. Therefore, it is important to document all the *Colletotrichum* spp. associated with anthracnose on different types of fruit crops.

Accurate identification and scientific name assignment of anthracnose pathogens are vital issues because precise taxonomic information enables us to classify a given species as a pathogen, saprophyte, or endophyte. The species involved in tropical fruits anthracnose may also have different presentations. It is well-known that effective disease management often depends on the proper identification of the causative pathogen.

The use of multiple markers allowed the recognition of an increasing number of *Colletotrichum* phylogenetic species, including species that cause anthracnose. However, for some of these phylogenetic species, information on the host range, pathogenicity, virulence variability, sensitivity to fungicides, and geographical distribution are still scarce. This situation may create a problem for plant pathologists, as many members of *Colletotrichum* are among the fungal species of quarantine concern in several countries. Keeping up to date with recently reported *Colletotrichum* species affecting tropical fruit crops is central to identify the risks posed by them.

Table 2. Diversity of *Colletotrichum* spp. and the infected plant parts.

Fruit Crop	***Colletotrichum* spp.**	**Infected Parts**
Banana (*Musa* spp.)	*C. scovillei,C. gloeosporioides,C. siamense, C. tropicale, C. chrysophilum, C. paxtonii C. theobromicola*	Fruit
	C. musae	Ripe fruit, but has been reported from leaves and root of *Musa* spp.
Mango (*Mangifera indica* L.)	*C. fructicola, C. tropicale, C. fragariae sensu stricto, C. jasmine-sambac, C. melanocaulon, C. alienum*	Fruit
	C. asianum, C. karstii, C. scovillei, C. scovillei, C. fructicola, C. siamense, C. cliviicola, C. musae C. cordylinicola, C. endophytica, C. gigasporum, C. liaoningense, C. tropicale	Fruit and leaves
	C. gloeosporioides	Fruit, leaves, and inflorescence
Papaya (*Carica papaya* L.)	*C. magna, C. gloeosporioides, C. dematium, C. acutatum, C. simmondsii, C. karstii, C. queenslandicum, C. siamense, C. salsolae, C. magnum, C. brevisporum, C. fructicola, C. plurivorum, C. okinawense, C. siamense*	Fruit
Dragon fruits (*Hylocereus* spp.)	*C. gloeosporioides sensu lato, C. truncatum, C. aenigma, C. siamense*	Fruit and stem
	C. gloeosporioides	Young stem
	C. boninense	Fruit
	C. karstii	Stem
Guava (*Psidium guajava* L.)	*C. gloeosporioides sensu lato, C. psidii, C. guajavae, C. simmondsii, C. abscissum, C. siamense*	Fruit
	C. gloeosporioides	Fruit and leaves
Avocado (*Persea americana* Mill.)	*C. gloeosporioides sensu lato, C. nymphaeae C. gloeosporioides, C. gigasporum, C. karstii, C. godetiae, C. alienum, C. fructicola, C. siamense, C. aenigma, C. alienum, C. perseae C. nupharicola, C. theobromicola, C. tropicale. C. kahawae* subsp. *cigarro, C. jiangxiense, C. cigarro, C. chrysophilum*	Fruit

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Abbreviations

ACT	actin
ApMat	mating type (Mat1-2)
CHS1	chitin synthase
CAL	calmodulin
CFU	colony forming unit
GAPDH	glyceraldehyde-3-phosphatedehydrogenase
GRAS	generally recognized as safe
GS	glutamine synthetase
HIS3	histone
ITS	internal transcribed spacer

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