


Review Article

A review of citrus anthracnose caused by *Colletotrichum* speciesMousa Najafiniya 

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ABSTRACT

The cultivation of citrus trees is affected by many plant pathogenic fungi, which can cause various diseases and reduce citrus production. The members of *Colletotrichum* genus are the causal agent of anthracnose in a broad range of host plants, including *Citrus* species. More than 35 *Colletotrichum* species have been reported on *Citrus* species worldwide. So far, five species of *C. fructicola*, *C. gloeosporioides*, *C. karstii*, *C. novae-zelandiae*, and *C. siamense*, have been identified in association with citrus trees in the north and south parts of Iran. The diversity of *Colletotrichum* species and the wide range of anthracnose symptoms on citrus indicate a lack of specific pathogen-host relationships. These pathogens can induce various symptoms, including fruit and leaf spots, necrosis, post-flowering fruit drop, dieback, twig blight, and post-harvest rots, leading to significant yield and market value losses. In this review article, we provide an overview of the most prominent *Colletotrichum* species associated with citrus, their geographical distribution, lifestyle, symptoms, pathogenicity, host resistance and management.

KEYWORDS

Anthracnose, blight, *Colletotrichum*, fruit drop, lifestyle.

INTRODUCTION

Citrus species are economically important fruit trees that are widely grown in over 140 countries around the world (FAO 2020). According to the FAO database, the estimated area of citrus cultivation worldwide is 11.42 million ha with 179.0 million tons of production (FAO 2020), and the top 10 major citrus-producing countries are China, Brazil, India, Mexico, the United States, Spain, Egypt, Turkey, Nigeria, and Iran, respectively. Citruses include plant species belonging to the genera of *Citrus*, *Eremocitrus*, *Fortunella*, *Microcitrus* and *Poncirus*, native to South, East and Southeast Asia, Melanesia and Australia (Wu et al. 2018). The international production of citrus fruits encompasses mainly sweet oranges (65%), mandarins (19%), lemons and limes (11%), and grapefruits (5%) (FAO 2020). The citrus cultivation is affected by several phytopathogenic fungi, such as *Colletotrichum* and many other fungal genera, which can cause diseases and reduce their production. The genus *Colletotrichum* belongs to the family *Glomerellaceae* (*Glomerellales*, *Sordariomycetes*), and is the sole member of this family (Jayawardena et al. 2016b). The *Colletotrichum* species have been

introduced in the list of 10 most economically important fungal plant pathogens in the world (Dean et al. 2012), could infect many plant hosts (Bhunjun et al. 2021, Liu et al. 2022). They can produce heavy losses in all citrus-producing areas (Guarnaccia et al. 2021). Anthracnose symptoms of citrus have been reported on leaf, flower, fruit, twig and young branches, which are sometimes along with gum and may be observed during transportation, storage as a post-harvest disease (Damm et al. 2012, Guarnaccia et al. 2021). Some *Colletotrichum* species may cause keratitis in humans, such as *C. gigasporum*, *C. dematium*, and *C. truncatum*. Therefore, it is very important for citrus growers and laborers to take precautions during horticultural operations such as pruning and harvesting (Liu et al. 2014, Liu et al. 2022). The association and interaction of *Colletotrichum* species with citrus have been reported as pathogen, saprobe and endophyte. This interaction is strongly related to host situation and environmental conditions (Liu et al. 2014, Mascarin et al. 2016, Talhinhos and Baroncelli 2021). In Iran, limited information is available regarding the diversity and pathogenicity of *Colletotrichum* species on citrus,

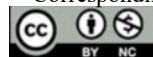
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highlighting the need for further studies on citrus anthracnose. In this paper, we provide an overview of the current understanding and research on the impact of *Colletotrichum* on citrus, geographical distribution, life style, type of symptoms on citrus organs, the frequency of *Colletotrichum* species on *Citrus* in Iran and world, mechanisms of pathogenicity, host resistance and its management.

***Colletotrichum* species lifestyle, life cycle and mechanism of pathogenicity**

Based on present knowledge, *Colletotrichum* is a cosmopolitan genus in fungi (Gomdola et al. 2025). In *Colletotrichum* species, the lifestyle is different and variable, including necrotrophic, hemibiotrophic, latent or endophytic, of which hemibiotrophic is the most common (Jayawardena et al. 2021, Talhinhas and Baroncelli 2021). In citrus and other plant hosts, the differences in lifestyle depend on the *Colletotrichum* species, the host species, the physiological maturity of the host and environmental conditions (De Silva et al. 2017). While *Colletotrichum* species are infecting citrus as their hosts, they need to complete several pathogenesis phases such as pre-penetration, penetration and invasion, colonization and necrotrophic phase, symptom development, sporulation and finally dissemination (Jayawardena et al. 2021) (Fig. 1). In the pre-penetration phase, spore adhesion and germination occur (Jayawardena et al. 2021). Conidia (asexual spores) land on citrus surfaces (fruit, leaves, or twigs) and adhere using mucilaginous secretions (Talhinhas and Baroncelli 2021). Species of *Colletotrichum* are known for their ability to colonize plant tissues of citrus through various infection strategies, including intracellular hemibiotrophy, subcuticular necrotrophy, and intramural necrotrophy (Norphanphoun et al. 2025). Under high humidity conditions, the conidia germinate to form germ tubes, then they differentiate into melanized appressoria, specialized structures that generate high turgor pressure to mechanically penetrate the host cuticle (Talhinhas and Baroncelli 2021). Necrotrophic species actively attack the citrus host and typically produce lytic enzymes or toxins to degrade or kill plant tissues, then will survive on dead plant cells to complete their life cycle (Jayawardena et al. 2021, Talhinhas and Baroncelli 2021). For direct penetration, appressoria secrete enzymes (cutinases, esterases) to degrade the citrus cuticle and wax layers, via a mechanical force by turgor pressure, which drives a penetration peg through the epidermal cell wall (Wharton and Schilder 2008, Talhinhas and Baroncelli 2021). Alternatively, some strains invade citrus via natural openings (stomata, wounds) or produce infection cushions for deeper tissue entry (Timmer et al. 2000, Zakaria 2025). Except for entirely endophytic species, most of *Colletotrichum* species may show a necrotrophic phase in a part of their life cycle (De Silva et al. 2017). *Colletotrichum* species normally are not real bio-trophy; however,

some *Colletotrichum* may show a bio-trophic phase in their life style, then turn to a necrotrophic phase, and thus are considered as hemibiotrophs (Barimani et al. 2013, Jayawardena et al. 2021b). *Colletotrichum acutatum* and *C. gloeosporioides* may show a latent period before causing post-harvest disease of citrus fruits, in which the conidia germinate, form appressoria and then remain dormant in the leaf or branches of the citrus host until the fruit development and ripening stage (Jayawardena et al. 2021, Talhinhas and Baroncelli 2021). In citrus as well as many other plant hosts, several *Colletotrichum* species may exist as endophytes (at least for part of the life cycle) (Cannon et al. 2007). Most *Colletotrichum* species, which have been identified as endophytes, are grouped in the Boninense, Graminicola and Gloeosporioides species complexes (Damm et al. 2012, Weir et al. 2012). The pathogenic *Colletotrichum* species can produce melanin-pigmented appressoria, intracellular and subcuticular colonization (Wharton and Schilder 2008, Ryder and Talbot 2015). Mature appressoria are characterized by the formation of a penetration pore in the base of the cell and by deposition of new cell wall layers and melanin (Ryder and Talbot 2015). Melanized appressoria of *Colletotrichum* species that are non-quiescent are capable of non-enzymatic, forcible penetration of host tissue (Latunde-Dada 2001). In citrus trees, the unripe fruits are rich of high concentrations of antimicrobial compounds to enhance the defense mechanism of the host, so in such conditions, the best thing a fungus can do is to bide its time (Dean et al. 2012). Some species of *Colletotrichum*, such as *C. acutatum* and the *C. gloeosporioides* complexes, have this mechanism and are known as quiescent fungi (Latunde-Dada 2001). Appressoria produced by endophytes grow through citrus tissues and are predominantly intercellular with little or no impact on host cells, whereas appressoria produced by pathogenic fungi are capable of breaching the intact cuticles of citrus hosts (Dean et al. 2012). Comparative genomic analysis reveals that pathogenic *Colletotrichum* species possess a larger repertoire of virulence factors, such as plant cell wall-degrading enzymes, secondary metabolite biosynthetic enzymes, and effectors than related non-pathogenic species (Liang et al. 2018). The coordinated expression of these genes is critical for successful colonization, with different factors being upregulated at specific infection stages, from pre-penetration through the switch to necrotrophy (O'Connell et al. 2012). Key genes involved in plant cell wall degradation and secondary metabolism, particularly effectors, show highly dynamic expression profiles during these stages, and several have been identified and characterized (Zhang et al. 2018). Infection of *Citrus sinensis* by *C. gloeosporioides* induced rapid physiological and transcriptomic changes (Zhang et al. 2024). The pathogen caused epicarp necrosis, reduced total flavonoid content, and suppressed the activity of key

antioxidant enzymes (catalase, peroxidase, and superoxide dismutase) (Zhang et al. 2024). Transcriptomic analysis revealed a massive, early transcriptional response, with 4,600 genes differentially expressed within six hours, which sharply declined to only 580 genes in the subsequent six hours (Zhang et al. 2024). It has been found that *C. gloeosporioides* infection also disrupted key metabolic pathways, including those for flavonoids and reactive oxygen species (Zhang et al. 2024)

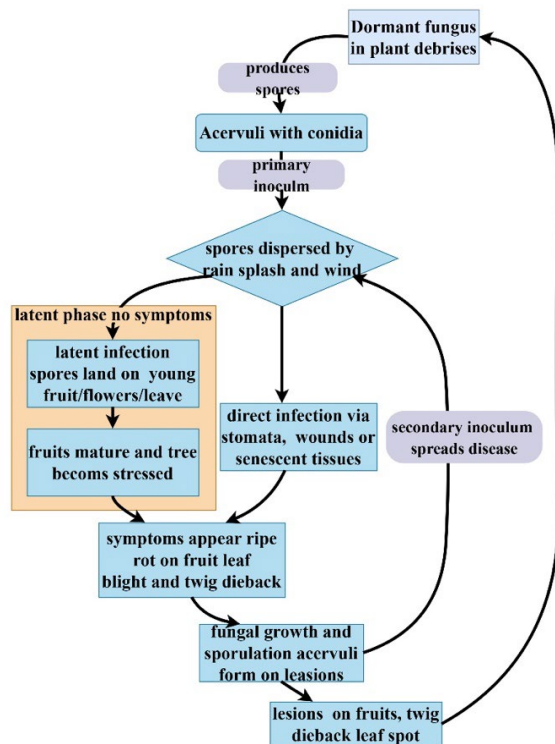


Fig 1. General diagram of *Colletotrichum* life cycle on Citrus trees (created using Drawio software)

Although clear host specificity has been documented within the *C. graminicola* species complex, whose members are typically restricted to Poaceae hosts, most *Colletotrichum* species are not host-specific. Therefore, host specificity is not always present in *Colletotrichum* species, although host preferences may sometimes be observed (Guevara-Suarez et al. 2022). So it is very important in those countries that have high plant biodiversity, in which crops are present in a field all year long and may share their pathogens (Guevara-Suarez et al. 2022). Sometimes a single *Colletotrichum* species may cause disease on several hosts, while one host can be infected by multiple *Colletotrichum* species (de Silva et al. 2019). Some of its species may be associated with symptomless hosts as endophytes in living plants, as saprobes on dead plant material (Jayawardena et al. 2021). A single species may show different nutritional modes based on the environmental conditions in which they occur (Jayawardena et al. 2016a). It has also been

reported that some *Colletotrichum* species are associated with only one host while others can attack and infect many hosts, and this can affect the success rate of disease management (da Silva et al. 2020). Based on the literature reviewed, there was high variability in terms of inoculation methods for confirmation of pathogenicity, such as wounded or unwounded, mycelial plugs or conidial suspension, and it is very important because it will affect the results of considering host range in *Colletotrichum* species (Guevara-Suarez et al. 2022). In the case of citrus and its allied genera (*Atlantia*, *Fortunella*, *Microcitrus*, *Murraya*, *Poncirus*) it has been reported that *Colletotrichum* species are associated as epiphytes, saprobes, important pre-harvest and post-harvest pathogens, as well as endophytes (Huang et al. 2013). According to Liu et al. (2015), six species from the *C. gloeosporioides* complex were found in both healthy and diseased leaf tissue of *Citrus* spp., indicating they can switch from an endophytic to a pathogenic lifestyle. Consequently, more studies are required to understand what causes these typically endophytic taxa to become pathogenic on *Citrus* (Liu et al. 2023). Previous research indicates that endophytic fungal colonization can differ significantly among a plant's tissues, with genera showing specific preferences (Huang et al. 2015). Liu et al. (2023) in case of *Citrus maxima*, isolated endophytes from leaves and twigs and found a higher number of *Colletotrichum* species in leaves. The reasons for these variations are not yet clear; however, potential influencing factors include tissue organization, nutrient availability, the specific lifestyle of the fungal genus, as well as locality and seasonal effects (Liu et al. 2023). The pathogenic species of *Colletotrichum* can cause some important citrus diseases, such as blight and wither-tip of twigs, fruit and leaf spots, leaf necrosis, post-flowering fruit drop, dieback, and postharvest rots in fruits, which lead to a significant decrease in both yields and market value (Pérez-Mora et al. 2021). The study and knowledge of pathogens management of citrus as one of the most important fruit industries worldwide, is very important. To provide useful information for appropriate management strategies of high-risk pathogens, accurately resolving and delimiting species of *Colletotrichum*, the knowledge of lifestyle, biology, epidemiology and knowledge of their pathogenic ability are critical (Jayawardena et al. 2021).

***Colletotrichum* taxonomy and species frequency in general, and in the case of citrus**

Recent changes in the understanding of species concepts in *Colletotrichum* resulted in many taxa being considered as species complexes rather than individual species (Bhunjun et al. 2021). To date, at least 16 species complexes (Fig. 2) include *Acutatum* (41 species), *Agaves* (5 species), *Boninense* (26 species), *Caudatum* (8 species), *Dematium* (17 species),

Destructivum (20 species), Dracaenophilum (8 species), Gigasporum (8 species), Gloeosporioides (57 species), Graminicola (16 species), Magnum (8 species), Orbiculare (8 species), Orchidearum (8 species), Spaethianum (9 species), and Truncatum (4 species) have been identified in *Colletotrichum* (Talhinhas and Baroncelli 2021, Liu et al. 2022, Gomdola et al. 2025). Bhunjun et al. (2021), proposed the combination of two complexes of *C. caudatum* and the *C. graminicola* within the *C. graminicola-caudatum* species complex (Bhunjun et al. 2021, Gomdola et al. 2025). In *Colletotrichum*, by July 2025, over 1000 epithets are listed in Index Fungorum. This genus has 874 named species, of which 764 are currently accepted in the Species Fungorum database (<https://www.speciesfungorum.org>; July 28, 2025) (Wang et al. 2024, Gomdola et al. 2025, Norphanphoun et al. 2025). The overall study of pathogenicity assays and genetic diversity of *Colletotrichum* spp. on citrus trees reported that *C. gloeosporioides* is the most virulent species on *Citrus* spp. (Guarnaccia et al. 2017b). According to scientific literature (Table 1) and based on the multilocus phylogeny approach, around 39 distinct *Colletotrichum* species belong to eight species complexes (Fig. 3) that were reported with *Citrus* from the main citrus-producing region around the world (Riolo et al. 2021, Liu et al. 2023, Wang et al. 2024, Gomdola et al. 2025). The most prominent species complexes associated with citrus are Gloeosporioides (15 species) followed by Acutatum (9 species), Boninense (7 species), Orchidearum (2 species), Magnum (3 species), Dracaenophilum, Graminicola (*C. endophytum* as endophyte), Truncatum (each with one species) and *C. citrus-medicae* (only one record) (Talhinhas and Baroncelli 2021, Gomdola et al. 2025, Norphanphoun et al. 2025). Based on present knowledge, at least five species, including *C. karstii* and *C. novae zelandiae* (from Boninense species complex), *C. fructicola*, *C. gloeosporioides*, and *C. siamense* (from Gloeosporioides species complex) have been reported to be associated with citrus species in the north and south parts of Iran and are responsible for citrus anthracnose on sweet orange, mandarin, grapefruit, and Mexican lime (Alizadeh et al. 2015, Arzanlou et al. 2015, Taheri et al. 2016, Heidari et al. 2018). The anthracnose disease is widespread in citrus orchards of the Mazandaran Province and causes heavy losses to some citrus commercial tree varieties (Taheri et al. 2016). Citrus anthracnose disease in Australia is associated with at least six *Colletotrichum* species (Wang et al. 2024). In the case study of associated *Colletotrichum* species with citrus in Thailand, it has been reported that isolates of *Colletotrichum* species

belong to Gloeosporioides and the Orchidearum complex (Najafiniya et al. 2024). The results of the same study showed that in Thailand, *C. siamense* was the most dominant species associated with symptomatic citrus, followed by *C. gloeosporioides*, *C. fructicola*, *C. endophytica* and *C. Plurivorum* (as a new report on citrus). *Colletotrichum gigasporum*, *C. kokhaense* sp. nov. and *C. tropicicola* have also been reported on citrus from Thailand (Wang et al. 2025). Pathogenicity testing confirmed that multiple *Colletotrichum* species, including *C. siamense*, *C. gloeosporioides*, *C. gigasporum*, *C. kokhaense* sp. nov., and *C. plurivorum*, incited disease across citrus tissues and their pathogenicity was consistent on fruits, seedlings, and in planta shoots, with *C. gigasporum* exhibiting superior aggressiveness (Wang et al. 2025). These isolates have been obtained from mandarin (*Citrus reticulata*), pomelo (*Ci. maxima*), Persian lime (*Ci. latifolia*), Thai lime (*Ci. hystrix*) and acid lime (*Ci. aurantifolia*) in Thailand (Najafiniya et al. 2024, Wang et al. 2025). In China, at least nine species of *C. boninense*, *C. brevispora*, *C. citricola*, *C. citri*, *C. fructicola*, *C. gloeosporioides*, *C. karstii*, *C. murrayae*, *C. simmondsii* have been reported on citrus species (Huang et al. 2013). Several *Citrus* species, such as bergamot orange (*Ci. bergamia*), pomelo, mandarin, sweet orange (*Ci. sinensis*), and kumquat (*Fortunella margarita*), are known hosts of *C. fructicola* infection during preharvest and postharvest periods (Zakaria 2025). The *Colletotrichum abscisum* has been reported on citrus only from the American continent (Braganca et al. 2016), restricted to Rutaceae family and the American continent, so it should be considered as a candidate quarantine organism for other countries (Crous et al. 2015, Talhinhas and Baroncelli 2021). In Europe (case study in Italy, Greece, Malta, Portugal, and Spain), it has been reported that *Colletotrichum* species associated with citrus are belong to three species complexes of Gloeosporioides, Boninense and Acutatum, and in terms of economic importance, two species of *C. gloeosporioides* and *C. karstii* were the predominant species (Guarnaccia and Crous 2017). In Iran, the citrus anthracnose disease is economically important in rainy and humid areas such as north part of Iran, as well as in Khuzestan and Hormozgan provinces, but it is less important in other southern parts of Iran, such as Kerman and Fars provinces, which are less rainy. In terms of citrus sustainable production and durable management of citrus anthracnose in Iran, it is necessary to monitor *Colletotrichum* species, which are still under external quarantine for Iran (Table 1). Any imported citrus plant materials in the borderlines must be checked for possible infection. There is a possible risk of shifting

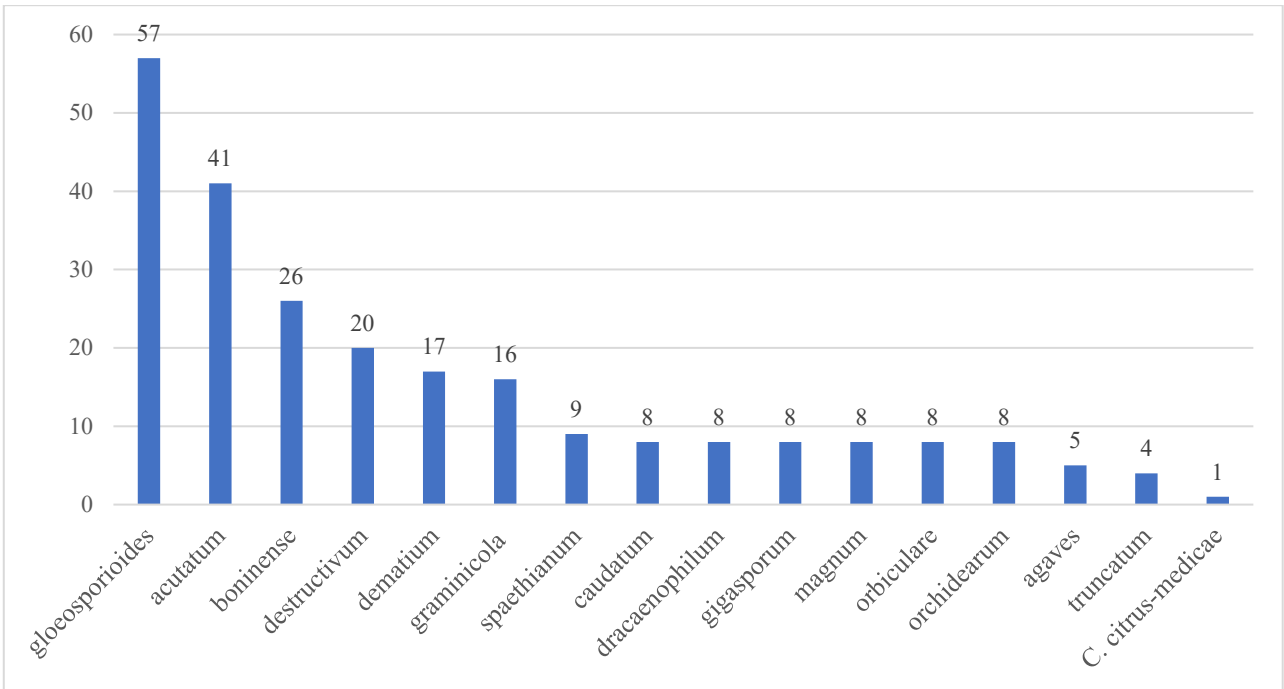


Fig 2. The *Colletotrichum* species complexes and the number of their species accepted by phylogenetic data up to 2025.

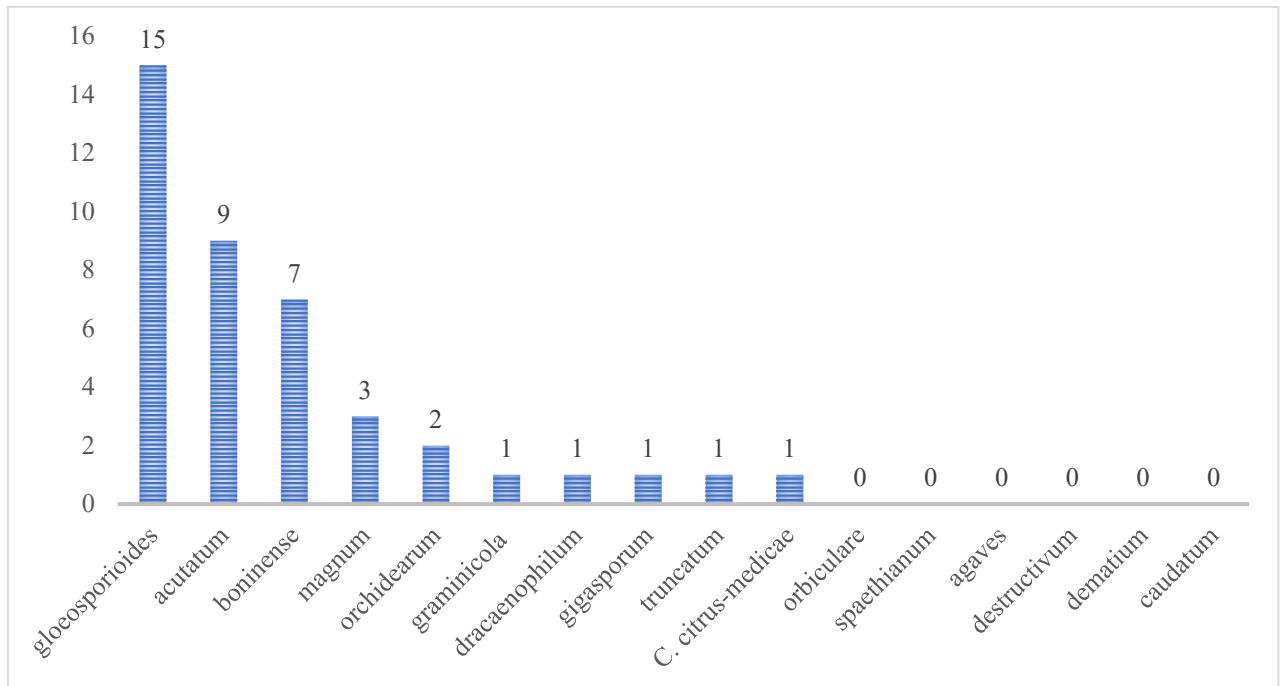


Fig 3. The most important *Colletotrichum* species complex and their frequency associated with *Citrus* spp. around the world up to 2025.

Colletotrichum species from other crops to citrus trees, so it needs to be monitored continuously and specifically while doing intercropping with other plant hosts.

Morphological and molecular identification of *Colletotrichum* species (in general)

Species identification in *Colletotrichum* was initially based on morphology and the host association; however, morphological characters are variable, and many species are not host-specific (Jayawardena et al. 2021). With the development of molecular methods, the identification and species delimitation of *Colletotrichum* has changed by multi-gene

phylogenetic analyses, along with the morphological characters (Cai et al. 2009). Morphological characters such as conidial morphology (both shape and size dimension), colony characters, growth rate, conidiogenous cell, conidiophore, presence or absence of chlamydospore, seta, and appressoria morphology (see Fig 4. Which obtained from mandarin fruit and characterized before by Najafiniya et al. 2024) are being used for primary identification of *Colletotrichum* (Jayawardena et al. 2021). Molecular methods, primarily using ITS, followed by multilocus phylogeny methods, increased the finding of phylogenetic relationships of *Colletotrichum* species (Jayawardena

et al. 2021, Gomdola et al. 2025). Internal transcribed spacer is normally useful to separate species complexes within the genus (Jayawardena et al. 2016a, Marin-Felix et al. 2019). Application of a combination set of *act*, *ApMat*, *apn2*, *cal*, *chs-1*, *gapdh*, *gs*, *his3*, *sod2*, or *tub2* genes (Table 2) is required for the sharp identification of most *Colletotrichum* species (Jayawardena et al. 2016a, Marin-Felix et al. 2019, Jayawardena et al. 2021). In nature, the most common form of *Colletotrichum* species on citrus is the asexual phase, although the teleomorph stage may also occur in some species (Gomdola et al. 2025).

Table 1. *Colletotrichum* species associated with citrus, host range, distribution, lifestyle and disease type symptoms.

<i>Colletotrichum</i> species	Species complex	Citrus hosts and type symptoms	distribution	Life style	References
<i>C. abscisum</i>	Acutatum	post-bloom fruit drop of <i>Ci. sinensis</i> , and key lime, anthracnose on leaves, petal necrosis and flowers	USA, Brazil (restricted to the American continent)	Pathogen, endophyte	(Crous et al. 2015, Braganca et al. 2016, Jayawardena et al. 2016)
<i>C. acutatum</i>	Acutatum	anthracnose of fruit, flower, leaves and twigs, post-flowering fruit drop on Tahiti lime, <i>Citrus sinensis</i> , <i>Ci. limon</i> , <i>Ci. aurantium</i>	Brazil, Italy, South Africa, Spain, Thailand, Mediterranean regions	Pathogen	(Peres et al. 2008, Lima et al. 2011, McGovern et al. 2012, Guarnaccia et al. 2017b)
<i>C. aenigma</i>	Gloeosporioides	Anthracnose on <i>Ci. sinensis</i>	Italy	Pathogen	(Guarnaccia et al. 2017b)
<i>C. artocarpicola</i>	Gloeosporioides	<i>Citrus</i> spp.	Australia	Pathogen, endophyte	(Gomdola et al. 2025)
<i>C. asianum</i>	Gloeosporioides	<i>Ci. reticulata</i> ,	China, Indonesia, Thailand	Pathogen, endophyte, epiphyte	(Prihastuti et al. 2009, Lijuan et al. 2012, Benatar and Wibowo 2021)
<i>C. australianum</i>	Gloeosporioides	leaf and fruit diseases	Australia	Pathogen	(Wang et al. 2021a)
<i>C. boninense</i>	Boninense	<i>Ci. tachibana</i> , <i>C. maxima</i>	China, Japan, Europe	Pathogen	(Lijuan et al. 2012, Guarnaccia et al. 2017b)
<i>C. brevispora</i>	Magnum	Anthracnose of <i>Citrus</i> spp, <i>Ci. maxima</i>	China	Pathogen, endophyte	(Huang et al. 2013, Benatar and Wibowo 2021)
<i>C. catinaense</i>	Boninense	Fruit tear stain on <i>Ci. sinensis</i> , leaf lesion on <i>C. reticulata</i> , dieback on <i>Citrus</i> spp.	Italy, Portugal	Pathogen	(Guarnaccia et al. 2017b)
<i>C. ciggaro</i>	Gloeosporioides	<i>Ci. reticulata</i>	Italy	Pathogen (potential quarantine for Iran)	(Guarnaccia et al. 2017a)
<i>C. citri</i> (syn= <i>C. nymphaeae</i>)	Acutatum	Shoot dieback on <i>Ci. sinensis</i> , <i>Ci. reticulata</i> , <i>Ci. paradise</i> , <i>Ci. aurantifolia</i> ,	China, Egypt, India, South Africa	Pathogen	(Damm et al. 2012, Huang et al. 2013, Benatar and Wibowo 2021)
<i>C. citricola</i>	Boninense	<i>Ci. unshiu</i> ,	China	Pathogen, endophyte, saprobe	(Prihastuti et al. 2009, Huang et al. 2013)
<i>C. clivicola</i>	Orchidearum	<i>Ci. limon</i>	Vietnam	pathogen	(Douanla-Meli et al. 2018)
<i>C. constrictum</i>	Boninense	<i>Ci. limon</i>	New Zealand	pathogen	(Damm et al. 2012)
<i>C. endophytica</i>	Gloeosporioides	<i>Citrus</i> spp.	Thailand	Pathogen, endophyte, saprobe,	(Udayanga et al. 2013, Wang et al. 2016, Najafiniya et al. 2024)

Table 1. Continued.

<i>C. endophytum</i>	Graminicola	<i>Ci. maxima</i>	Thailand	Endophyte, pathogen (potential quarantine for Iran)	(Hyde et al. 2014)
<i>C. fructicola</i>	Gloeosporioides	leaf and fruit diseases, dieback on <i>Ci. sinensis</i> , <i>C. bergamia</i>	China, Iran, Thailand	Pathogen, endophyte	(Prihastuti et al. 2009, Arzanlou et al. 2015, Taheri et al. 2016, Benatar and Wibowo 2021, Najafiniya et al. 2024)
<i>C. gigasporum</i> <i>C. gloeosporioides</i>	Gigasporum Gloeosporioides	Leaf and fruit pre-harvest symptoms such as wither-tip on twigs, tear-stain and stem-end rot on fruit, twig and shoot dieback, sweet fruit anthracnose, post-bloom fruit drop on <i>Ci. sinensis</i> , <i>Ci. reticulata</i> , <i>Ci. aurantium</i> , <i>Ci. paradisi</i>	Thailand Albania, Australia, Brazil, California, China, Mediterranean, Mexico, Iran, Italy, South Africa, Spain, Thailand, Tunisia, Turkey	pathogen Pathogen, epiphyte, sometimes endophyte	(Wang et al. 2025) (Benyahia et al. 2003, Kaur et al. 2007, Lima et al. 2011, Lijuan et al. 2012, Taheri et al. 2016, Riolo et al. 2021, Najafiniya et al. 2024)
<i>C. godetiae</i>	Acutatum	Fruit rot on <i>Ci. aurantium</i>	China	pathogen	(Jayawardena et al. 2021)
<i>C. guangdongense</i>	Magnum	<i>Ci. maxima</i>	China	pathogen	(Norphanphoun et al. 2025)
<i>C. helleniense</i>	Gloeosporioides	Wither tip twig on <i>Ci. reticulata</i> , dieback on <i>Poncirus trifoliata</i>	Italy, Greece	Pathogen (potential quarantine for Iran)	(Guarnaccia et al. 2017a)
<i>C. hystrix</i>	Gloeosporioides	Leaf lesion of <i>Ci. hystrix</i>	Australia, Italy	Pathogen (potential quarantine for Iran)	(Guarnaccia et al. 2017a)
<i>C. johnstonii</i>	Acutatum	Fruit rot on <i>Citrus</i> sp	New Zealand (quarantine potential for Iran)	pathogen	(Damm et al. 2012)
<i>C. kokhaense</i> sp. nov	Magnum	Seedling, fruit and leaf	Thailand	Pathogen	(Wang et al. 2025)
<i>C. karstii</i>	Boninense	leaf and fruit diseases, wither-tip on <i>Ci. aurantium</i> , <i>Ci. reticulata</i> , <i>Ci. sinensis</i> , <i>Ci. limon</i>	Australia, Brazil, China, South Africa, Iran, Italy, Mediterranean region, Tunisia, Turkey	pathogen	(Taheri et al. 2016, Heidari et al. 2018, Benatar and Wibowo 2021, Riolo et al. 2021, Wang et al. 2024)
<i>C. limetticola</i>	Acutatum	Wither tip and dieback, anthracnose, on leaves, young twig, flowers and fruits of <i>Ci. aurantifolia</i>	Cuba, USA (potential quarantine for Iran)	pathogen	(Damm et al. 2012)
<i>C. limonicola</i>	Boninense	Wither tip, twig blight on <i>Ci. limon</i> , <i>Ci. sinensis</i>	Europe (only one record), Iran	pathogen	(Guarnaccia et al. 2017b)
<i>C. musae</i> <i>C. novae-zelandiae</i>	Bloeosporioides Boninense	Dieback and twig blight on orange, mandarin, lemon, grapefruit fruit	Australia, Iran, New Zealand,	pathogen pathogen	(Alizadeh et al. 2015) (Damm et al. 2012, Taheri et al. 2016, Guarnaccia et al. 2017b, Wang et al. 2024)
<i>C. nymphaeae</i>	Acutatum	Leaf anthracnose on <i>Ci. sinensis</i> , <i>Ci. aurantium</i> , <i>Ci. aurantifolia</i> , <i>Ci. limon</i> , entomopathogen on <i>Citrus orthezia</i> scale	Australia, Brazil, China, Iran, Italy, USA	Pathogen	(Damm et al. 2012, Huang et al. 2013, Mascarin et al. 2016, Heidari et al. 2018)

Table 1. Continued.

<i>C. phormii</i>	Acutatum	<i>Ci. sinensis, reticulata</i>	<i>Ci.</i>	Mediterranean region	Pathogen		(Guarnaccia et al. 2017b)
<i>Table 1. Continued</i>							
<i>C. plurivorum</i>	Orchidearum	<i>Ci. aurantifolia</i>		Thailand	pathogen		(Najafiniya et al. 2024)
<i>C. siamense</i>	Gloeosporioides	leaf and fruit diseases, dieback on <i>Ci. reticulata</i> , <i>Ci. sinensis</i> , <i>aurantifolia</i> , <i>paradise</i> , <i>pennivesiculata</i>	<i>Ci.</i>	Australia, China, India, Iran, Italy, Mexico, Thailand	Pathogen, endophyte, epiphyte		(Prihastuti et al. 2009, Taheri et al. 2016, Benatar and Wibowo 2021, Wang et al. 2021b, Najafiniya et al. 2024)
<i>C. simmondsii</i>	Acutatum	<i>Citrus spp.</i> , <i>reticulata</i>	<i>Ci.</i>	Australia, China, Italy,	Pathogen, endophyte (potential for Iran)	quarantine	(Damm et al. 2012, Benatar and Wibowo 2021)
<i>C. tainanense</i>	Gloeosporioides	<i>Ci. maxima</i>		China	endophyte		(Liu et al. 2023)
<i>C. theobromicola</i>	Gloeosporioides	leaf and fruit diseases		Australia	Pathogen		(Wang et al. 2021a)
<i>C. tomentosae</i>	Gloeosporioides	<i>Ci. maxima</i>		China	endophyte		(Liu et al. 2023)
<i>C. tropicicola</i>	Dracaenophilum	Leaves of <i>Ci. maxima</i>		Thailand, Mexico	Endophyte, pathogen		(Noireung et al. 2012, Wang et al. 2025)
<i>C. truncatum</i>	Truncatum	Dieback on <i>Ci. flamea</i> , <i>Ci. limon</i> and <i>Ci. reticulata</i>	<i>Ci.</i>	China	Pathogen, endophyte (potential for Iran)	quarantine	(Huang et al. 2013, Guarnaccia et al. 2017b)
<i>C. citrus-medicae</i>	One record only	Leaf spot on <i>Ci. maxima</i>	<i>Ci.</i>	China	pathogen		(Hyde et al. 2020)

Table 2. Commonly used loci, primer name, sequences, and references for *Colletotrichum* species (Weir et al. 2012, Wang et al. 2025).

locus	Product name	Primer name	direction	Sequences (5'→3')	References
<i>Act</i>	actin	ACT-512F ACT783R	Forward Reverse	TGTGCAAGGCCGGTTTCGC TACGAGTCCTTCTGGCCCAT	Carbone and Kohn, 1998
<i>Apn2</i>	Mat1 and adjacent DNA lyase gene	Apn1W1F Apn1W1R	Forward Reverse	ATGGAGCACAAAAACGAACA GCGGAGCAGAGGATGTAGTC	Crouch et al 2009b
<i>Cal</i>	Calmodulin	Cl1C Cl2C	Forward Reverse	GARTWCAAGGAGGCCTTCTC TTTTTGCATCATGAGTTGGAC	Weir et al. 2012
<i>Chs-1</i>	Chitin synthase	CHS-79F CHS-345R	Forward Reverse	TGG GGC AAG GAT GCT TGG AAG AAGGG AAG AAC CAT CTG TGA GAG TTG	Carbone and Kohn, 1998
<i>gapdh</i>	glyceraldehyde-3-phosphate dehydrogenase	GDF1 GDR1	Forward Reverse	CCGTCAACGACCCCTTCATTGA GGGTGGAGTCGTACTTGAGCATGT	Peres et al., 2008
<i>GS</i>	Glutamin synthetase	GSF1 GSR1	Forward Reverse	ATG GCC GAG TAC ATC TGG GAA CCG TCG AAG TTC CAG	Stephenson et al. 1997
<i>His3</i>	Hyston 3	CYLH3F CYLH3R	Forward Reverse	AGGTCCATGGTGGCAAG AGCTGGATGTCCTTGGACTG	Crous et al. 2004
ITS	Internal transcribed spacer	ITS4 ITS5	Forward Reverse	TCCTCCGCTTATTGATATGC GGAAGTAAAAGTCGTAACAAGG	White et al., 1990
<i>Sod2</i>	Manganese-superoxide dismutase	SODglo2-F SODglo2-R	Forward Reverse	CAG ATC ATG GAG CTG CAC CA TAG TAC GCG TGC TCG GAC AT	Moriwaki and Tsukiboshi 2009
<i>Tub2</i>	B-tubulin2	Bt2a Bt2b	Forward Reverse	GGTAACCAAATCGGTGCTGCTTTC ACCCTCAGTGTAGTGACCCTTGGC	Glass and Donaldson, 1995

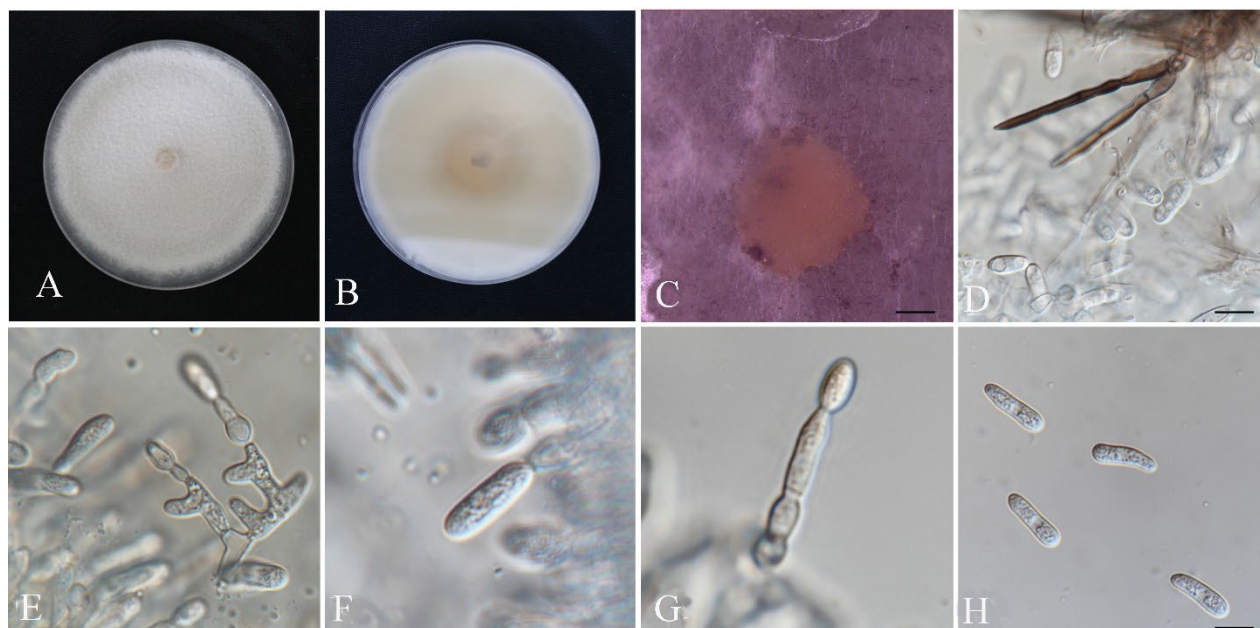


Fig. 4. Some morphological and microscopical characters of *Colletotrichum gloeosporioides* (strain MN-4, obtained from mandarin fruit showing anthracnose symptoms and characterized by Najafiniya et al. 2024). (A, B) upper and reverse view of colony on PDA, (C) mass spore in orange color, (D) seta, (E–H) conidiophore, conidiogenous cell, and conidia. Scale bars: (D) 10 μ m, (E–H) 5 μ m.

Common field symptoms of citrus anthracnose

The symptoms of citrus anthracnose caused by different *Colletotrichum* species are different around the world and highly dependent on the pathogen species, host conditions, and the stage of infection (Wang et al. 2025). *Colletotrichum* species cause disease of leaves, fruit, twigs, and branches of several citrus species. The anthracnose symptoms on citrus are leaf spot and leaf necrosis, which may be observed on different citrus species in either home garden or commercial orchards (Fig. 5). Chlorosis in the canopy, crown thinning, twig and shoot dieback or wither-tip of citrus, which sometimes results in gumming on apical twigs and old branches (Fig. 6) are other important symptoms of citrus anthracnose caused by *Colletotrichum* species, and among them, *C. gloeosporioides* is the most aggressive species on citrus twigs (Guarnaccia et al. 2017b, Riolo et al. 2021, Najafiniya et al. 2024, Wang et al. 2024). Outbreaks of citrus shoot dieback have increased in Europe and the Mediterranean region, notably in Albania and southern Italy, a trend associated with climate change and the rising frequency of extreme weather events (Guarnaccia et al. 2017b). Well-known examples of host and organ specificity have been reported in the USA for two members of the *Colletotrichum acutatum* complex, *C. abscissum* (known to cause post-bloom fruit drop in sweet orange) and *C. limetticola*, (affecting exclusively key lime and causing shoot blight anthracnose) (Riolo et al. 2021, Wang et al. 2024).

Important *Colletotrichum*-related diseases of citrus fruit include post-bloom fruit drop and pre- and post-

harvest anthracnose (Fig. 7) (Huang et al. 2013, Guarnaccia et al. 2017b, Najafiniya et al. 2024). The most common species responsible for these conditions are *C. abscissum* and *C. gloeosporioides* (Lima et al. 2011). This species can cause decay of citrus flowers, brown lesions on petals, and severe damage to fruits, leading to rotting, discoloration, and premature fruit drop, sometimes resulting in significant yield loss. For example, in Brazil, premature fruit drop may reach up to 93% when flowering coincides with the rainy season (Timmer et al. 2000, Lima et al. 2011). In cases where flowers are not present on trees, the pathogen survives on leaves and twigs for long periods without visible symptoms and it is difficult to detect it (de Gasparoto et al. 2023). In addition, sometimes natural flower fall-off tree because of abiotic agents, which may be mistakenly identified as anthracnose by growers and this is a very important thing for issuing health certificates for citrus nurseries, which may need more acute identification by experts (de Gasparoto et al. 2023). Although it has been reported that *C. acutatum* may be introduced from strawberry nurseries to citrus orchards but there is less information regarding the shifting of *C. abscissum* from citrus nurseries to citrus orchards (Peres et al. 2008, de Gasparoto et al. 2023). In the case study of Thailand, it has been proven that the main citrus species, including mandarin, acid lime, pomelo, Thai lime (kaffir lime), and Tahiti lime, are the hosts of different *Colletotrichum* spp., and they could be a potential threat for economic loss in citrus (Najafiniya et al. 2024).

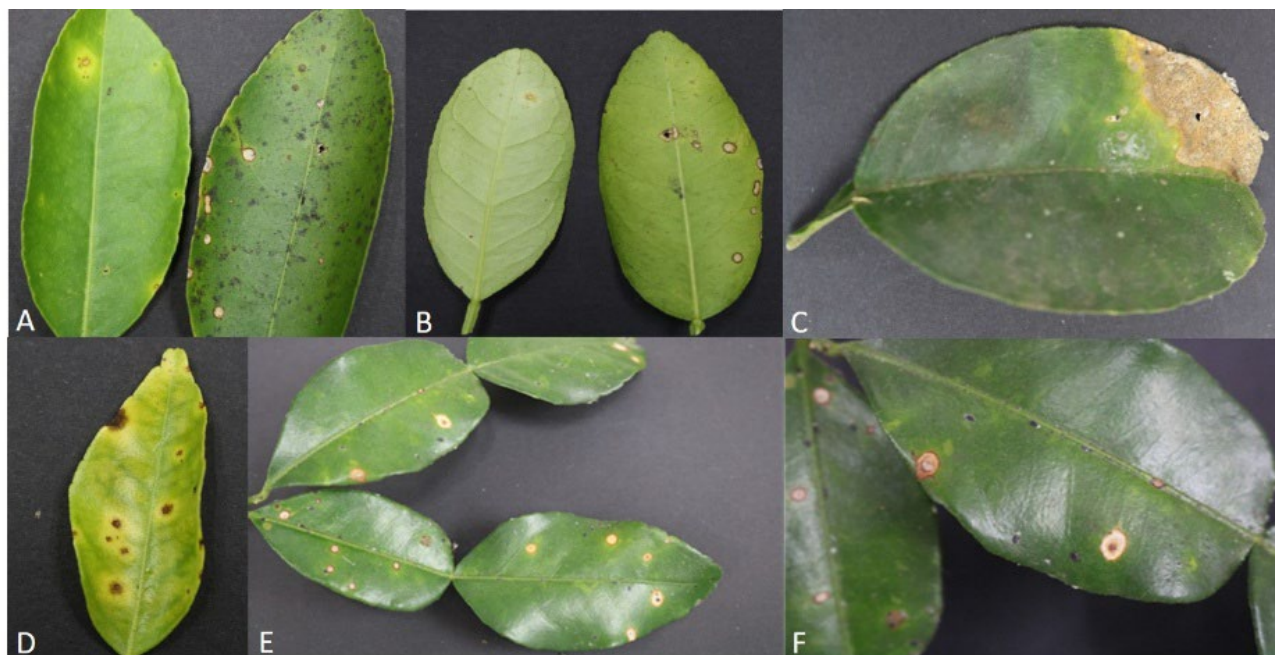


Fig. 5. Leaf spot and leaf necrosis of Citrus caused by *Colletotrichum*. (A, B) leaf spot on acid lime, (C) leaf necrosis on Pomelo, (D) leaf spot on mandarin, (E, F) leaf spot on Thai lime.



Fig. 6. Anthracnose symptoms on citrus trees. (A, B) wither-tip and dieback on acid lime, (C) dieback on Pomelo, (D–F) wither tip and twig blight affecting the mandarin tree.



Fig. 7. The anthracnose, melanoses, rough leaf spot, and twig blight caused by *Colletotrichum* on mandarin (A–E) and pomelo (F).

Biology and epidemiology of *Colletotrichum* on citrus

Colletotrichum spp. are ascomycete fungi that can survive as saprophytes or pathogens, produce asexual spores that serve as a source for disease spread, and can also form sexual structures called perithecia, which can act as a source for genetic recombination (Jayawardena et al. 2021). They can cause pre- and postharvest diseases when the environmental conditions are suitable (Lima et al. 2011). The pathogen survives between seasons in infected plant debris (mummified fruit, fallen leaves, dead twigs) as mycelium or appressoria (Zakaria 2021). Many *Colletotrichum* species are latent plant pathogens as its unique intracellular hemibiotrophic lifestyle (Jayawardena et al. 2021). Species essentially being symptomless endophytes in living plant tissues and switch their lifestyle from endophytic to pathogenic depending on host development stage and environmental conditions (Hyde et al. 2009, Jayawardena et al. 2021). The outbreaks of *Colletotrichum* twig and shoot dieback of citrus can be observed during the growing seasons on both young and mature trees (Guarnaccia et al. 2017b). Generally, after prolonged drought stress and possible mechanical wounds following strong winds, the incidence rate of citrus anthracnose will increase on affected trees (Riolo et al. 2021). Environmental variables such as rainfall have been positively correlated with the proportions of diseased flowers in *Ci. sinensis* anthracnose caused by *C. acutatum* (Timmer and Zitko 1996, Newfeld et al. 2025). In *Colletotrichum*, it has also demonstrated that pH can affect the virulence and alter the fungus's ability to

shift from biotrophy to necrotrophy in the host plant (Soares et al. 2014). Another environmental variable, such as the atmospheric humidity, soil moisture, soil nutrient content, or presence of other microbes, may also be important in plant–microbe interaction (Newfeld et al. 2025). The incidence rate and disease severity in a single home garden or commercial citrus orchard may be varied (Najafiniya et al. 2024). On the top of the canopy of mature citrus plants, and also in those trees that face drought stress, the anthracnose symptoms are often severe (Riolo et al. 2021). In case of post-bloom fruit drop, the crucial infection period is during flowering (Riolo et al. 2021) and cool, wet weather during bloom is a highly favorable condition for disease incidence. The *Colletotrichum* infection usually occurs through wounds or cracks in the fruit peel or through natural openings such as the calyx or stem (Zakaria 2021, 2025), it can also infect the young leaves, causing leaf spot symptoms (Najafiniya et al. 2024). Citrus anthracnose is common in humid, rainy climates and is more severe on stressed trees (Jayawardena et al. 2021). The epidemiology of *Colletotrichum* on citrus fruits is complex and depends on several environmental factors such as humidity, temperature, and rainfall, which can influence disease development (Riolo et al. 2021). High humidity levels and warm temperatures favor the growth and spread of the pathogen (Zakaria 2021, 2025). Rainfall and water droplets can also facilitate the spread of the pathogen from infected to healthy fruits, and prolonged leaf wetness (12+ hours) is critical for infection (Jayawardena et al. 2021). Citrus trees weakened by drought, nutrient imbalance, frost damage, or other

pests/diseases are far more susceptible to severe symptoms (Jayawardena et al. 2021). Citrus orchards with a history of anthracnose and poor sanitation have higher inoculum levels, increasing disease risk (Riolo et al. 2021). *Colletotrichum* species on citrus were likely introduced and dispersed into new areas through several pathways, such as the agricultural trade of latent-infected plants, transportation, and other human-aided means (Liebhold et al. 2012). These pathways for introducing and dispersing fungal pathogens, collectively termed "hitchhiking," typically involve fungi traveling latent within plant tissues as small propagules (Fisher et al. 2012, Gladieux et al. 2016). Hitchhiking through international plant trade is a documented pathway for the introduction of fungal pathogens such as *Diaporthe* spp. into new regions (Hilário and Gonçalves 2023). Subsequent establishment in these areas, as demonstrated by the case of *C. fructicola* in certain EU countries, is contingent upon two key factors: the presence of a susceptible host and a favorable climate, which enable the fungal propagules to successfully infect and colonize (Health et al. 2021).

General mechanisms of citrus trees' defense against *Colletotrichum*

During infection and colonization by *Colletotrichum* species, citrus host plants mount several defense responses (Zakaria 2025). Citrus defense against anthracnose is a multifaceted phenomenon and relies on pre-existing physical and chemical barriers combined with a rapid, potent, and multi-pronged inducible defense response (Zakaria 2021). The physical and chemical barriers present in the plant before pathogen attack form the first line of defense (Zakaria 2021). The cuticle, a waxy layer on the surface of leaves, stems, and fruit, acts as a critical physical barrier (Wang et al. 2024). A thicker and more robust cuticle can prevent the initial adhesion and penetration of *Colletotrichum* appressoria (Wang et al. 2024). Some resistant citrus genotypes have been observed to have a denser cuticular structure, making direct penetration more difficult (Zakaria 2021, 2025). The structural composition of the cell wall, including the density of cellulose, hemicellulose, and pectin, can influence resistance (De Silva et al. 2017). Thicker cell walls or those with more cross-linking can provide a stronger physical impediment to the invading hyphae (De Silva et al. 2017). Citrus plants contain a range of pre-formed antifungal metabolites, such as Limonoids and Flavonoids (Duarte-Sierra et al. 2019). Compounds like limonin and nomilin, as well as various flavonoids, have demonstrated antifungal activity against *Colletotrichum* species (Duarte-Sierra et al. 2019). Their presence in tissues at the time of challenge can inhibit spore germination and mycelial growth (De Silva et al. 2017). Components of citrus essential oils, such as d-limonene, linalool, and citral, are known to have potent antifungal properties and

while concentrated in the peel, their presence in leaf and stem tissues can contribute to pre-formed resistance (Duarte-Sierra et al. 2019).

In a research work in Italy, it has been reported that there are different levels of resistance among citrus groups against *Colletotrichum* species (Vitale et al. 2021). The results of the same study showed that Tarocco, a blood orange group, is highly susceptible to anthracnose on leaf and fruit, pre-harvest fruit drop, and twig dieback and defoliation, but the lemon group showed the least susceptibility reaction. Valencia orange, Navel oranges, and Mandarin, Satsuma, showed generally an intermediate susceptible response. The Femminello Zagara Bianca lemon was the only tolerant citrus cultivar to pre-harvest fruit drop disease (Vitale et al. 2021).

The plant immune system recognizes *Colletotrichum* through conserved molecules like chitin in the fungal cell wall and this recognition triggers defense signaling pathways, primarily the Salicylic Acid (SA) and Jasmonic Acid (JA)/Ethylene (ET) pathways (Boller and Felix 2009). In resistant interactions, this recognition is faster and stronger, leading to a more robust activation of downstream defenses (Boller and Felix 2009). In citrus, scoparone and scopoletin are two well-studied coumarin phytoalexins, and their accumulation at the infection site has been directly correlated with resistance, as they effectively inhibit the growth of *Colletotrichum* hyphae (Boller and Felix 2009). The induction of PR genes is a hallmark of systemic acquired resistance (Zakaria 2025). Key PR proteins involved in citrus-*Colletotrichum* interactions include: Chitinases enzymes (PR-3, PR-4, PR-8), which hydrolyze chitin, a major component of the fungal cell wall, directly damaging the invading hyphae, β -1,3-Glucanases enzymes (PR-2), can break down β -1,3-glucans, another key structural polymer of the fungal cell wall. The synergistic action of chitinases and glucanases is highly effective in lysing fungal tips (Zakaria 2021). Thaumatin-like proteins (PR-5) and peroxidases (PR-9) also play roles in antifungal activity and cell wall strengthening (Zakaria 2021). Resistant genotypes are characterized by their ability to efficiently recognize the pathogen, activate key defense signaling pathways (SA/JA/ET), and deploy a synergistic arsenal of antimicrobial phytoalexins, cell wall-degrading enzymes (chitinases, glucanases), and structural reinforcements (lignification, callose) to confine and eliminate the *Colletotrichum* pathogen (da Silva et al. 2020).

Management strategies of *Colletotrichum* spp.

In terms of lifestyle, as it was mentioned in previous parts, *Colletotrichum* spp. may be grouped as a latent pathogen, endophyte, hemibiotroph or necrotroph (De Silva et al. 2017). Identification and management of anthracnose caused by *Colletotrichum* spp. may be difficult because of their potential to show

different lifestyles and their ability to make it change, and possible cross-infection among their hosts (da Silva et al. 2020). Management of *Colletotrichum* on citrus fruits involves a combination of cultural, biological, and chemical control methods (Rovetto et al. 2024).

Cultural control methods: The principal cultural approach for the management of *Colletotrichum* anthracnose focuses on measures that limit the inoculum levels and dissemination of the pathogen (Rovetto et al. 2024). For most fruit crops, removing diseased and mummified fruit and symptomatic vegetative tissue is generally recommended (Dowling et al. 2020). Cultural control measures involve generating and using clean planting stock, proper sanitation, removing and destroying of fallen fruits, leaves and dead plant materials in association with chemical spraying, limiting rain-splash and overhead irrigation, adjusting soil nutrients, managing weeds, and using cultivars with limited susceptibility to the disease, are critical operations to reduce the primary inoculum sources (Hamada and May De Mio 2017, Rovetto et al. 2024, Zakaria 2025). Proper and on-time pruning improves air circulation within the canopy to reduce humidity and leaf wetness duration (Rovetto et al. 2024). Water management, such as drip irrigation instead of overhead sprinklers, will keep foliage dry. Proper nutrition and balanced fertility will avoid any unwanted stress on citrus trees (Rovetto et al. 2024). In a cross-infection study of five *Colletotrichum* species on various hosts, *C. fructicola* and other members of the gloeosporioides complex were found to be capable of infecting all tested fruits, namely papaya, citrus orange, rose apple, mango, guava, and chili (Phoulivong et al. 2012). The phenomena of cross-pathogenicity and latent infection in *Colletotrichum* species are of particular concern in mixed-cropping systems (Zakaria 2025). Here, asymptomatic host crops can act as reservoirs for the pathogen, harboring latent infections that amplify the risk of disease outbreaks (Freeman and Shabi 1996). Understanding the host range through cross-infection studies provides critical data for developing effective disease management strategies in the field and postharvest, as well as for breeding resistant cultivars (Zakaria 2021, 2025). The use of resistant citrus cultivars can help reduce disease incidence and spread. Understanding the host range through cross-infection studies provides critical data for developing effective disease management strategies in the field and postharvest, as well as for breeding resistant cultivars (Zakaria 2025).

Essential oils: Essential oils, which are plant-extracted concentrates of bioactive compounds, are used as an alternative method to control postharvest diseases in fruit crops (Zakaria 2025). The application of essential oils (EOs) for postharvest disease control is often enhanced by combining them with edible coatings like

chitosan, which act as effective carriers, improving the antimicrobial efficacy of the EOs and extending produce shelf life (da Costa Gonçalves et al. 2021). Specific compounds, including carvacrol, honokiol, magnolol, and thymol, derived from sources such as lemongrass and mint, have demonstrated the potential to inhibit *C. fructicola* growth and reduce anthracnose lesion development (da Costa Gonçalves et al. 2021).

Biocontrol method: Numerous biocontrol agents, such as avirulent *Colletotrichum* strains, bacteria, filamentous fungi, and yeasts, have been investigated for the management of postharvest anthracnose in fruit crops (Shi et al. 2021). Two bacterial strains, *Lysobacter enzymogenes* OH11 and *Bacillus tequilensis* YYC 155, have shown potential to control anthracnose caused by *C. fructicola* in pears and *Camellia oleifera* leaves, respectively (Zhao et al. 2021, Zhou et al. 2022). Despite progression to field testing, the most promising bio-fungicides and systemic acquired resistance (SAR) inducers have demonstrated variable efficacy, which persists even in combination with traditional chemical treatments (Dowling et al. 2020). Similar to essential oils, the application of biocontrol agents against *Colletotrichum* spp. requires further research into their mechanisms of action, toxicity, storage stability, and cost-effectiveness (Shi et al. 2021). Alternative methods evaluated for controlling *C. fructicola* in fruit crops include neutral electrolyzed water, hot water, chitosan, and Natamycin, and these treatments have demonstrated potential in suppressing anthracnose development on hosts such as strawberries, papaya, and apples (Hirayama et al. 2016, Valencia-Chamorro et al. 2021, Cao et al. 2023).

Chemical control using fungicides with different modes of action is frequently applied to control anthracnose in various crops (Zakaria 2021, 2025). While methyl benzimidazole carbamates (MBCs), dithiocarbamates, and quinone outside inhibitors (QoIs) are the most common fungicides against anthracnose, MBCs and QoIs have largely lost their efficacy due to widespread fungal resistance (Hu et al. 2015, Dowling et al. 2020). While multisite protectants (e.g., mancozeb, captan, chlorothalonil) have historically demonstrated moderate to good efficacy against *Colletotrichum* spp., their utility is now limited by increasingly stringent regulations (Dowling et al. 2020). This constraint, alongside the challenge of wetter, longer growing seasons, has driven the adoption of locally systemic fungicides for disease management (Dowling et al. 2020). It is, therefore, essential to adopt alternative or complementary control methods to minimize the use of fungicides (Hu et al. 2015).

Challenges and limitations: The diverse lifestyles of *Colletotrichum* species and their dynamic interactions with host plants present a significant challenge to global plant biosafety (Jayawardena et al. 2021). Their ability to switch life cycle stages makes accurate detection and effective control difficult (De Silva et al. 2017). Compounding this issue, international trade serves as a pathway for the long-distance dispersal of these fungi via asymptomatic hosts, potentially introducing new pathogens (Jayawardena et al. 2021). Consequently, a deeper understanding of *Colletotrichum* lifestyles is not merely academic but is essential for informing robust quarantine protocols and managing the risks associated with world trade (Jayawardena et al. 2021).

CONCLUSION

According to various research studies, different species of *Colletotrichum* have been reported to cause citrus anthracnose worldwide (Riolo et al. 2021). The most important species are *C. acutatum*, *C. gloeosporioides*, *C. asiaticum*, *C. citri* and *C. siamensis* (Guarnaccia et al. 2017b, Najafiniya et al. 2024). *Colletotrichum gloeosporioides* has several plant hosts and is the prominent *Colletotrichum* species caused citrus anthracnose (Huang et al. 2013, Guarnaccia et al. 2017b). As a matter of fact, *Colletotrichum* species may show a variable mode of lifestyle such as dormant pathogens, saprobes, epiphytes or endophytes (Jayawardena et al. 2021). Abiotic tension agents have a key role in starting the infection by *Colletotrichum* species and may shift to a pathogenic lifestyle when their hosts are facing unfavorable conditions (Jayawardena et al. 2016a). Given the climate-induced drought stress affecting most citrus orchards in southern Iran, monitoring the status of citrus anthracnose in these areas is essential. In Europe, improper conditions of drought stress were introduced as the factors resulted in infection by *Colletotrichum* spp. and provided a favorable condition for fungi to shift from a latent or endophytic to a pathogenic mode (Riolo et al. 2021), while in the United States, abiotic factors which are resulted in triggering of anthracnose in citrus have not yet been identified (Mayorquin et al. 2019). Study, finding the diversity of *Colletotrichum* species and the factors enhancing the distribution of this disease are a principal necessity for conducting any control measure program (Rovetto et al. 2024). Some *Colletotrichum* species, such as *C. abscisum* and *C. hystricis* are a potential quarantine in Iran (Table 3). A more durable management work plane, adaptable with organic agriculture, should be focused at both preventing or reducing the effect of predisposing agents and decreasing the primary sources of inoculum of *Colletotrichum* in the garden, such as enough and right time irrigation regime to avoid water stress, application of wind- breaks to protect the plants against winds and pruning of infected branches and trigger new flushing in canopy (Riolo et

al. 2021). *Colletotrichum* remains one of the significant postharvest diseases affecting citrus fruits worldwide (Riolo et al. 2021). Effective management of the disease involves a combination of cultural, biological, and chemical control methods (Rovetto et al. 2024). The integration of different control strategies can create a sustainable disease management system that reduces the impact of the pathogen on citrus fruit production (Rovetto et al. 2024). However, further research is necessary to understand the biology and epidemiology of *Colletotrichum* on citrus and identify effective control methods to manage the disease (Riolo et al. 2021). It was found that some isolates of *C. gloeosporioides* were not pathogenic and considered endophytes, it can be due to the different climatic conditions in different countries and apparently, some changes are going to happen in pathogenic fungi (Jayawardena et al. 2021, Najafiniya et al. 2024). Climate changes, long drought stress, may provide favorable conditions for the development of *Colletotrichum* dieback (Riolo et al. 2021).

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ADATA AVAILABILITY

All data are available in the manuscript.

DECLARATION

In this manuscript, there is nothing to declare and the authors declare no conflicts of interest.

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ETHICS APPROVAL

This article does not contain any studies with human participants or animals performed by any of the authors.

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مروری بر آنتراکنوز مرکبات ناشی از گونه‌های *Colletotrichum*

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بخش تحقیقات بیماریهای گیاهی، موسسه تحقیقات گیاهپزشکی کشور، سازمان تحقیقات، آموزش و ترویج کشاورزی، تهران، ایران

چکیده

کشت درختان مرکبات تحت تأثیر بسیاری از قارچ‌های بیماری‌زای گیاهی قرار دارد که می‌توانند باعث بیماری‌های مختلف و کاهش تولید مرکبات شوند. اعضای جنس *Colletotrichum* عامل بیماری آنتراکنوز در طیف وسیعی از گیاهان میزبان، از جمله گونه‌های مرکبات هستند. بیش از ۳۵ گونه *Colletotrichum* روی گونه‌های مرکبات در سراسر جهان گزارش شده است. تاکنون، پنج گونه *C. fructicola*، *C. gloeosporioides*، *C. karstii*، *C. novae-zelandiae* و *C. siamense* در ارتباط با درختان مرکبات در مناطق شمال و جنوب ایران شناسایی شده‌اند. تنوع گونه‌های *Colletotrichum* و طیف گسترده علائم آنتراکنوز روی مرکبات نشان دهنده عدم وجود روابط اختصاصی پاتوژن-میزبان است. این عوامل بیماری‌زا می‌توانند علائم مختلفی از جمله لکه‌های میوه و برگ، نکروز برگ، ریزش میوه پس از گلدهی، سرخشیدگی، سوختگی سرشاخه و پوسیدگی پس از برداشت را ایجاد کنند که منجر به کاهش قابل توجه عملکرد و ارزش بازارپسندی می‌شود. در این مقاله، مروری بر مهم‌ترین گونه‌های *Colletotrichum* مرتبط با مرکبات، پراکندگی جغرافیایی، سبک زندگی، علائم، بیماری‌زایی، مقاومت میزبان و مدیریت آنها ارائه شده است.

کلمات کلیدی: آنتراکنوز، ریزش میوه، سبک زندگی، سوختگی، کولتوتریکوم.