





# Quiescence as a strategic stage for the infective process of *Colletotrichum* species

## La quiescencia como estado estratégico del proceso infectivo de especies de *Colletotrichum*

Alberto Páez-Redondo<sup>1\*</sup> ; Dov Prusky<sup>2</sup> ; Lilliana Hoyos-Carvajal<sup>3</sup> 

<sup>1</sup>Universidad de Magdalena, Programa de Ingeniería Agronómica. Santa Marta - Magdalena, Colombia; e-mail: apaez@unimagdalena.edu.co

<sup>2</sup>Institute of Postharvest and Food Sciences, The Volcani Center, Agricultural Research Organization. Rishon LeZion, Israel; e-mail: dovprusk@volcani.agri.gov.il

<sup>3</sup>Universidad Nacional de Colombia, sede Medellín, Departamento de Ciencias Agronómicas. Medellín - Antioquia, Colombia; e-mail: limhoyosca@unal.edu.co

\*corresponding author: apaez@unimagdalena.edu.co

**How to cite:** Páez-Redondo, A.; Prusky, D.; Hoyos-Carvajal, L. 2022. Quiescence as a strategic stage for the infective process of *Colletotrichum* species. Rev. U.D.C.A Act. & Div. Cient. 25(2):e2073. <http://doi.org/10.31910/rudca.v25.n2.2022.2073>

Open access article published by Revista U.D.C.A Actualidad & Divulgación Científica, under Creative Commons License CC BY-NC 4.0

Official publication of the Universidad de Ciencias Aplicadas y Ambientales U.D.C.A, University, Accredited as a High-Quality Institution by the Colombian Ministry of Education.

**Received:** August 30, 2021

**Accepted:** September 22, 2022

**Edited by:** Helber Adrian Arévalo Maldonado

### ABSTRACT

*Colletotrichum*, a genus of Ascomycota fungi with a diversity of species grouped into several species complexes, or clades, is associated with diseases known as “Anthracnose”. It affects significantly different tropical and subtropical fruit species. Infections occur in the field and postharvest; quiescent stages are mainly responsible for postharvest losses. An analysis of this pre-infective stage is made based on consulted papers. The infective process is modulated by the length of the quiescent period of the fungus during the vegetative or pre-productive stages of trees. Quiescent stage is determined by the host’s biochemical responses and the pathogen’s activity. Once the pathogen is activated, it develops an infectious necrotrophic process. *Colletotrichum* quiescence has been studied mainly in subtropical fruits and horticultural species, and the studies highlight the role of volatile compounds, metabolites and enzymes involved in the length and breaking of quiescence, as well as the differential responses according to the phenological stage and the genotype of the plant. Transcriptomic and proteomic analysis of the host-fungus interaction have revealed the role of genes in the occurrence and breaking of quiescence. Knowledge about

the quiescence of *Colletotrichum* in tropical fruits is necessary to improve management efficiency. Detection and induction of quiescent infections has been studied and genomics has allowed to understand the occurrence of quiescence in the infective process; however, in crops in the tropics, such as mango, an important crop in Colombia, questions about associated species and biology of their quiescence are still unanswered.

**Keywords:** Anthracnose; Fruit trees; Hemibiotrophic lifestyle; Infective process; Mango.

### RESUMEN

*Colletotrichum* es un hongo ascomicete, con diversidad de especies agrupadas en complejos o clados y se asocia a enfermedades conocidas, como “Antracnosis” y afecta significativamente especies de frutas tropicales y subtropicales. Las infecciones ocurren en el campo y postcosecha; los estados quiescentes son los principales responsables de pérdidas en postcosecha. Se realizó un análisis de esta etapa pre-infectiva, a partir de publicaciones consultadas. La infección está modulada por la duración del período de quiescencia

del hongo durante las etapas vegetativa o pre-productivas de los árboles y está determinado por las respuestas bioquímicas del hospedante y la actividad del patógeno. Una vez se activa el patógeno, se desarrolla un proceso infeccioso necrotrófico. La quiescencia de *Colletotrichum* se ha estudiado, principalmente, en frutas subtropicales y especies hortícolas y destacan el papel de compuestos volátiles, metabolitos y enzimas en la duración y en la pérdida de la quiescencia, así como las respuestas diferenciales, según la fenología y el genotipo. Análisis transcriptómicos y proteómicos de la interacción hospedante-hongo han revelado el papel de genes en la ocurrencia y pérdida de quiescencia. Conocer la quiescencia de *Colletotrichum* en frutas tropicales es necesario para hacer más eficiente el manejo de la enfermedad. Se ha estudiado la detección e inducción de infecciones quiescentes y estudios genómicos han permitido entender su ocurrencia durante la infección; sin embargo, en cultivos en el trópico, como el mango, un cultivo importante en Colombia, las preguntas sobre las especies asociadas y la biología de la quiescencia de estas, aún están sin respuesta.

Palabras claves: Antracnosis; Árboles frutales; Estilo de vida Hemibiotrófico; Mango; Proceso infeccioso.

## INTRODUCTION

*Colletotrichum* is a genus of the order Glomerellales, family Glomerellaceae that has high diversity and is grouped into several species complexes or clades (Jayawardena *et al.* 2021; Liu *et al.* 2022; Talhinas & Baroncelli, 2021). This genus comprises major plant pathogens that cause Anthracnose diseases in many crops worldwide (Zakaria, 2021; Gañán *et al.* 2015; Ismail *et al.* 2015; Sharma & Kulshrestha, 2015; Honger *et al.* 2014; Liu *et al.* 2014). *Colletotrichum* species present different lifestyles, from non-pathogenic endophyte to necrotrophic pathogen; as a causal agent of diseases, it has been considered a hemibiotrophic microorganism (Freeman *et al.* 2001).

Disease causes significant losses of the marketable production; in mango can cause losses between 39 and 50 % in harvest and 52 % or more in postharvest (Páez Redondo, 2003; Kumari & Singh, 2017). In postharvest, the infective process is regulated by the length of the quiescent stage of the fungus during immature stages of fruits and it is generally activated when organs mature (Prusky *et al.* 2013; Ploetz, 2007).

The infectious process varies among species of *Colletotrichum*, and the occurrence of quiescence is one of those differential aspects. In thale cress (*Arabidopsis thaliana*), *C. higginsianum* cause leaf Anthracnose and once the appressorium is activated, the germinated appressorium forms a biotrophic primary hyphae and the fungus invades the epidermal cells without causing any damage and confined to the first invaded host cell; subsequently, a necrotrophic secondary hypha is formed and hemibiotrophic infective process takes place, invading new cells and intercellular spaces (O'Connell *et al.* 2012). In tomato - *C. gloeosporioides* interaction, melanized appressorium are formed from conidia germinated, and maintain quiescent during some time; after, they develop a penetration peg

and differentiate to a dendritic like structure inside the fruit cuticle, still without penetration of the epidermal cells (Alkan *et al.* 2015); swollen hyphae within the epidermal cell were formed, these structures are also described in leaf infections by *Colletotrichum* species (O'Connell *et al.* 2012; Latunde-Dada, 2001). Usually, as the fruit ripen quiescence ends and infective hyphae extending from the swollen hyphae were observed; at this stage, the fungus shift to a necrotrophic phase (Alkan *et al.* 2015; O'Connell *et al.* 2012; Latunde-Dada, 2001).

Quiescence is part of the colonization process of several *Colletotrichum* species and occurs once the biotrophic phase begins in immature organs or during transition from the biotrophic to the necrotrophic stage (Prusky *et al.* 2013), in different hosts such as mango (Páez Redondo, 2003), tomato (Alkan *et al.* 2015), papaya (Amaral *et al.* 2017), avocado (Fischer *et al.* 2017), guava (Guédez & Rodríguez, 2021) and bananas (De Lapeyre de Bellaire *et al.* 2000), among others. Initial advances in transcriptomic studies have revealed the role of genes that are activated during the interaction between the fungus and some of its hosts, including quiescence. The amount and type of quiescence-related genes vary with the fungus species and the host involved, although some effectors and transcription factors are common (Fu *et al.* 2022; Korn *et al.* 2015; Alkan *et al.* 2015; O'Connell *et al.* 2012). However, the understanding of *Colletotrichum* species quiescence phase requires further research for different hosts, especially under tropical conditions. Therefore, this review aims to update the knowledge about quiescence in some *Colletotrichum* species in tropical fruit trees.

## MATERIALS AND METHODS

The present paper consists of a literature review and provides information about the quiescence of *Colletotrichum* spp. in fruit species, and factors associated with its occurrence and breaking are explicitly highlighted, mainly under subtropical conditions. Additionally, concepts that could be the basis of questions or hypotheses for future research are raised, especially for tropics where advances on the subject are still limited.

The information consulted was taken from different scientific articles, review articles and chapter of books available in different bibliographic databases such as Science Direct, Elsevier, Scopus and Google Scholar, emphasizing the aspects related to the occurrence of quiescence in the *Colletotrichum*-host interactions. Some keywords used were quiescence, *Colletotrichum*, quiescent infections, tropical fruit trees, Anthracnose, plant diseases, plant pathogens, management and endophytes, in different combinations of searches. No specific time period was defined for the search for information, to identify advances in knowledge on the topic; however, papers from the last 35 years were consulted, in English and Spanish.

## RESULTS AND DISCUSSION

**General aspects of quiescence.** Quiescence is considered part of pre-colonizing process in some species of plant pathogens and is

usually considered a resting stage of the microbe following the onset of infection, but before the necrotrophic colonization is initiated (Prusky *et al.* 2013). Quiescence is strategic for some phytopathogenic fungi, and occurs among biotrophic and necrotrophic stages of some hemibiotrophic pathogens (Figure 1); for some phytopathogenic fungi, it is not easy to distinguish whether their lifestyle is hemibiotrophic or totally necrotrophic (Rajarammohan, 2021) and in this situation, quiescence can be the difference between both lifestyles. Quiescence is reported for other pathogens fungi-host interactions, such as grapevine (*Vitis vinifera*) - *Neofusicoccum parvum* (Czemmel *et al.* 2015), apple (*Malus domestica*) - *Phlyctaena vagabunda* (Lattanzio *et al.* 2001), pistachio (*Pistacia vera*) - *Botryosphaeria dothidea* (Ahimera *et al.* 2003), *V. vinifera* - *B. cinerea* (Haile *et al.* 2017), papaya (*Carica papaya*) - *Lasiodiplodia theobromae* (Amaral *et al.* 2017), mango (*Mangifera indica*) - *Lasiodiplodia theobromae* and *Alternaria alternata* (Diskin *et al.* 2017), mango - *Botryosphaeria*, *Phomopsis* and *Pestalotiopsis* (Johnson *et al.* 1992). This article will only focus on *Colletotrichum*-host interactions.

Quiescent stages of *Colletotrichum* are reported in various fruit trees (Sharma & Kulshrestha, 2015; Prusky *et al.* 2013), such as banana and others Musaceae (Photita *et al.* 2005), guava (*Psidium guajava*) (Fischer *et al.* 2019), avocado (*Persea americana*) (Binyamini & Schiffmann-Nadel, 1972), mango (*Mangifera indica*) (Paramasivan *et al.* 2009), papaya (*Carica papaya*) (Siddiqui & Ali, 2014), passion fruit (*Passiflora edulis* f. *flavicarpa* and *P. edulis* f. *edulis*) (Joy & Sherin, 2016) and citrus trees (*Citrus* spp.) (Peres *et al.* 2005). Quiescence in the genus *Colletotrichum* is reported for some species, mainly in *C. gloeosporioides* specie (Prusky *et al.* 2013).

Quiescence is modulated by the availability of nutrients, metabolic changes, and presence of antifungal compounds in the host (Prusky *et al.* 2013), as well as to the insufficient enzyme potential of the fungus to invade unripe fruit (Adikaram *et al.* 2015). Furthermore, quiescence can be a strategy of *Colletotrichum* to avoid toxic levels of antifungal compounds present in unripe fruits (Adikaram *et al.* 2015). In this way, the fungus escapes the action of management strategies, and remains as an inoculum to infect at any time during harvest and postharvest.

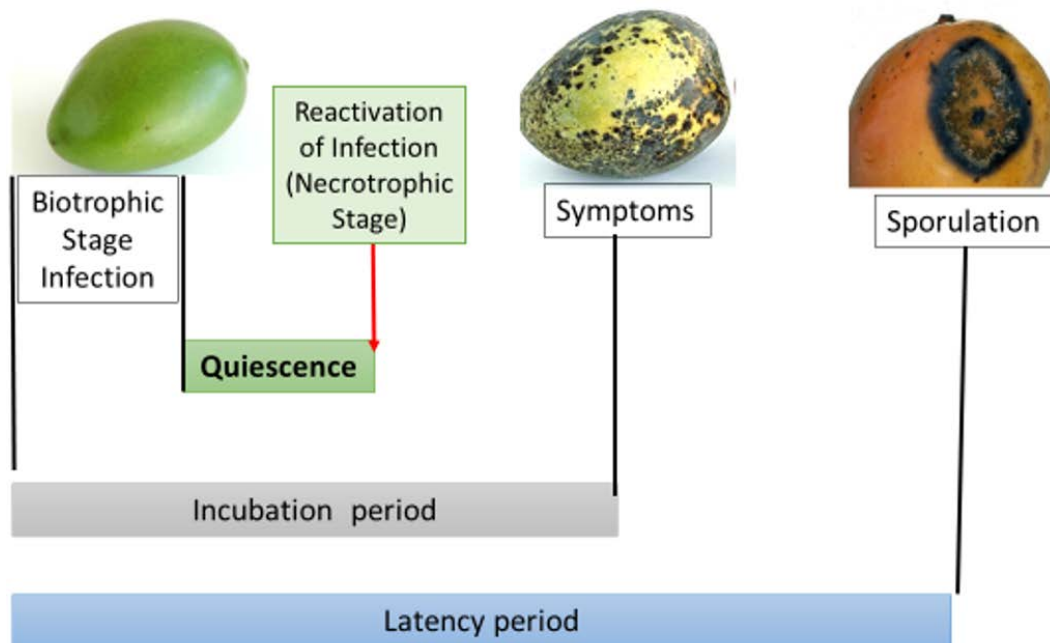


Figure 1. Scheme of an infective process by *Colletotrichum* sp. Quiescence after the biotrophic infective process has started; infection is reactivated and the fungus in its necrotrophic stage causes symptoms (incubation period) and subsequently produces a new inoculum (latency period).

The significant changes in metabolic synthesis and biochemical responses of the host fruit are regulated by differential genes expression that has been reported during the quiescent stage (Korn *et al.* 2015; Alkan *et al.* 2015; O'Connell *et al.* 2012). Genes that regulate infectious process of *Colletotrichum* are expressed differentially at each stage (Alkan *et al.* 2015; O'Connell *et al.* 2012; Latunde-Dada, 2001). The genes related to quiescence also differ according to the fungus species and infected host (Liu *et al.* 2022; Li *et al.* 2017; Korn *et al.* 2015; Alkan *et al.* 2015; Gan *et*

*al.* 2013; O'Connell *et al.* 2012). During appressoria development, a significant up-regulation of factors modulating the melanization of fungal cell wall is expressed and is concomitant with the accumulation of glycerol, factors that contribute to appressorial strength and the process of highly localized turgor pressure (Alkan *et al.* 2015). Also, cyclic adenosine monophosphate (*AMP*) and the mitogenic activation protein kinase (*MAPK*) signaling and other pathways, known to play a role in inducing appressoria formation and melanin biosynthesis in *Colletotrichum*, are up-regulated

(Shnaiderman *et al.* 2013). During quiescence of *C. gloeosporioides*, 178 genes could be defined as quiescent-specific, and are related with cell cycle components that regulated the DNA synthesis, genes encoding for a *G1/S-specific* cyclin, histone modifiers, and ATP-dependent chromatin remodeling complexes regulating DNA accessibility needed for gene activation/repression (Alkan *et al.* 2015). The production of ammonia during *Colletotrichum* colonization and alkalization of the environment has been previously reported as factors that break quiescence (Shnaiderman *et al.* 2013; Alkan *et al.* 2013a; Miyara *et al.* 2010).

In simultaneous analysis of tomato – *C. gloeosporioides* interaction, fruit transcripts were highly up-regulated during the quiescent stage. Defense pathways were further up regulated, including the phenylpropanoid pathway for phytoalexin and lignin. Pathways for the synthesis of phenylpropanoid derivatives as potential substrates for peroxidase activity, was also increased in the expression. These results have shown that phytoalexin biosynthesis and lignification comprise a major ongoing defense pathway used by the fruit in response to the quiescent fungi (Alkan *et al.* 2015). Transcript expression changes from rishtin to the  $\alpha$ -tomatine biosynthetic pathway, suggesting an effective response to *C. gloeosporioides*, creating a hostile environment that would signal the fungus to enter an extended quiescent stage (Alkan *et al.* 2015).

In *C. fructicola* – pear leaves interaction, the key regulators of plant Salicylic Acid-mediated defense response, were mainly upregulated at QS (Fu *et al.* 2022).

These findings indicate that quiescence is not a simple resting stage of the pathogen, also host gene response may contribute to activate some pathways before the necrotrophic colonization is initiated.

**Effect of host physiological changes on *Colletotrichum* quiescence.** Hormone ethylene is a factor that modulates appressoria formation in the host; during quiescence pathogen stimulate fruit ethylene production and defensive responses, so will also enhance the ripening process and accelerate the release from quiescence (Prusky & Sionov, 2021). Exposure of the spores of *C. gloeosporioides* and *C. musae* to ethylene, at  $\leq 1$  microl/liter, caused germination, branching of the germ tube, and formation of multiple appressoria from a single spore; propylene can induce spore germination and the formation of multiple appressoria, as well; ethylene induced germination and appressorium formation in the *Colletotrichum* sp. climacteric fruit but not in non-climacteric ones as citrus (Flaishman & Kolattukudy, 1994). While these results strongly suggest that this fruit fungal interaction have coevolved to develop a mechanism to use the host's ripening hormone as a signal to differentiate structure of infection; the fact is that processes do not occur concurrently and all appressoria formation for quiescence occurs in the orchard, away from the climacteric process where major ethylene quantities are produced (Prusky *et al.* 1996).

The breaking of quiescent stages includes a series of reactions that synchronize a decrease in the host's defense with the acceleration of the infective process by the fungus. This includes cuticle

degradation, cell wall degradation, fruit softening, increase in total soluble solids, changes in pH, decrease in preformed antifungal and inducible compounds, increase in reactive oxygen species (ROS) and hormones changes (Prusky & Sionov, 2021; Prusky *et al.* 2013). All these physiological changes associated with the fruit ripening create specific signals of fungal recognition for the initiation of the necrotrophic stage. Postharvest pathogens produce and secretes proteins and enzymes, which modify host cell walls, to overcome the physical constraints imposed by the wall and to release sugars to sustain its own energy needs. These processes might facilitate the intercellular expansion of hyphae and, thus, enhance the pathogen's ability to access cellular resources. On the other hand, use of the wall's sugar constituents for energy might require the complete breakdown of a variety of polysaccharides into monosaccharides (Prusky *et al.* 2016b). The degradation of the plant cell wall matrix by pathogens may affect the proteins embedded in the cell wall and are likely to activate PAMP-triggered immunity (Mengiste, 2012), which often leads to callose deposition at sites of penetration, accumulate phenolic compounds and various toxins in the cell wall and synthesize lignin-like polymers to reinforce the wall (Hückelhoven, 2007). Because fruit cell wall degrading enzymes (CWDEs) are normally activated during ripening, it was commonly assumed that fruit softening contributes to the transition to susceptibility to pathogens (Paniagua *et al.* 2014; Blanco-Ulate *et al.* 2013). However, in some cases fungal colonization occurs also in unripe fruits (Wang *et al.* 2007), suggesting the complexity of the changes modulating quiescence. Also, plants *PG* inhibiting proteins (*PGIPs*) may reduce the pathogen pectin degradation (De Lorenzo *et al.* 2001). For this reasons inhibition of cell wall softening usually delay fruit susceptibility.

The alkalization of the environment tissue round the quiescent infection by ammonia may contribute to breaking quiescence by activation of fungal transcription factors that modulate the synthesis of pectolytic enzymes. These pH changes are modulated by nutritional availability in unripe or ripening fruits (Prusky & Ziv, 2019; Ment *et al.* 2015; Prusky *et al.* 2016a).

**Chemical Compounds regulates quiescence in *Colletotrichum*-host interaction.** Quiescence in *Colletotrichum* could be regulated by the production of antimicrobial compounds, production of phytoalexins, new enzymes and even the formation of physical resistance structures (Sanzani *et al.* 2012). Chemical compounds from immature organs of bananas (De Lapeyre de Bellaire *et al.* 2000), avocados (Ahimera *et al.* 2003) and mangoes (Kienzle *et al.* 2014) determine the maintenance of quiescence of some *Colletotrichum* species. Relationship between quiescence and high levels of antifungal compounds in the peel of immature fruits of some fruit trees such as mango and avocado has been described (Beno-Moualem & Prusky, 2000; Droby *et al.* 1986; Cojocarú *et al.* 1986).

The accumulation and reduction of antifungal compounds, mainly derived from natural lipids such as 1-acetoxo-dihydroxy-n-heptadecane-16-ene and others with single or triple double bonds, are responsible for the occurrence of quiescence or breakdown of it

(Prusky & Ziv, 2019; Prusky *et al.* 2013); Recently, it has been shown that in the skin of Hass avocado fruits during ripening and storage, the persin and epicatechin contents decrease significantly (Bowen *et al.* 2018), which is related to the loss of quiescence of pathogens at maturity. These compounds have been specifically identified in immature avocado fruits, and inhibited germ tube elongation of *Colletotrichum* sp. conidia (Guetsky *et al.* 2005). The synthesis of resorcinols, gallotannins and chitinases in immature fruits is related to the quiescence of the pathogen; mango unripen fruits have shown a low susceptibility to *Colletotrichum* (Parthasarathy *et al.* 2015; Karunanayake *et al.* 2011; Paramasivan *et al.* 2009). In addition, the presence of potential sources of secondary metabolites such as n-hexane in the peel of immature fruits and latex of mango helps maintain the fungal quiescence (Sinniah *et al.* 2012).

Reactive oxygen species (ROS) synthesized by the host play a fundamental role in limiting the development of pathogens and maintaining their quiescence, because they modulate host's resistance; generally, their increment is associated with hydrogen peroxide increase or addition in the epidermis of immature fruits, where the levels of phenylalanine ammonia lyase (PAL) and epicatechin are also higher (Prusky *et al.* 2013). Accumulation of ROS are the result of the balance between ROS production and antioxidant activity. In grape and tomato, ROS, lipid peroxidation, and protein oxidation were increased at breaker stage conditions where the fungus was still in a quiescent stage; in many fruits, storage is associated with an increase in ROS, which results either from increased ROS production or from a decrease in antioxidative activity (Hodges, 2003). Antioxidants may inhibit fruit ripening and senescence (Lester, 2003), while high O<sub>2</sub> or application of H<sub>2</sub>O<sub>2</sub> leads to increase ROS and senescence (Tian *et al.* 2013). However post-harvest pathogens may modulate host ROS production by the secretion of elicitors, toxins, and antioxidants to modify the plant ROS production (Aver'Yanov *et al.* 2012; Alkan *et al.* 2013a; Alkan *et al.* 2013b).

**Pathogen development and break of quiescence.** The breaking of the quiescence is synchronically regulated by fungal effector proteins that manipulate their hosts for effective colonization. The pathogen must maintain host viability during initial biotrophic and quiescent interaction, but after needs to elicit host death for subsequent necrotrophic development. This elicitation process occurs in ripening fruits concurrently or as result of host ripening. Most fungal effector genes are host-induced and expressed in consecutive waves associated with pathogenic transitions, indicating distinct effector suites are deployed at each stage. Kleemann *et al.* (2012) demonstrated that antagonistic effectors either induce or suppress plant cell death. Based on these results obtained in an interaction with a non-host plant such as *Arabidopsis thaliana*, it can be concluded that the quiescence of a hemibiotrophic species of *Colletotrichum* is guided through a coordinated expression of antagonistic effectors that support cell viability or death that is probably modulated by metabolic changes in the host.

Internal metabolic factors of the pathogen that modulate appressorial formation and colonization, also induce breakdown

of quiescence. Ammonium secreted and or its accumulation by *C. gloeosporioides* during spore germination and host colonization contribute to pathogenicity (Prusky & Sionov, 2021; Prusky & Ziv, 2019; Ment *et al.* 2015; Prusky *et al.* 2016a; Prusky *et al.* 2016b; Miyara *et al.* 2010). *AMET* and *MEPB* genes modulate the secretion and accumulation of ammonia by the pathogen; in an investigation, the disruption of these genes resulted in 45 % less colonization of *C. gloeosporioides* in avocado fruits (Shnaiderman *et al.* 2013). The factors that active this nitrogen metabolism are still unknown, but it has been reported that nitrogen-metabolism genes *GDH2*, *GS1*, *GLT*, and *MEP* are differentially expressed during colonization by *C. gloeosporioides* in avocado (Miyara *et al.* 2010).

Another factor reported as an inducer of appressoria formation was the surface wax of the host; avocado (*Persea americana*) fruit wax induced germination and appressorium formation from the spores of *C. gloeosporioides* (Flaishman *et al.* 1995; Podila *et al.* 1993). On the other hand, the infective process of *Colletotrichum* species includes the degradation of the cuticle and cuticular waxes through cutinases, favoring the establishment of the pathogen and its penetration into the host's tissues (Villafana & Rampersad, 2020; Alkan *et al.* 2015).

#### **Quiescence and endophytic behavior of *Colletotrichum* species.**

Endophytic stage refers to a behavior or habitat type of a microbe, which does not generate apparent damage or symptom expression within its plant host despite being active in the tissues during part of its life cycle (Hyde & Soyong, 2008) and they are generally located in the intercellular spaces behaving as endosymbionts (Rodriguez *et al.* 2009). On the other hand, quiescence corresponds to a biotrophic stage of halted infection in which induction of symptoms does not occur, waiting for the right time of host response (Prusky *et al.* 2013). *Colletotrichum* as endophytic or quiescent pathogen is related to asymptomatic tissues, but subsequently may change to necrotrophic pathogen due to signals in the host, with the consequent expression of symptoms in them (Ranathunge & Sandani, 2016; Delaye *et al.* 2013; Kogel *et al.* 2006). It has been suggested that quiescence may be a form of endophytic behavior or survival strategy on non-host species.

Pathogenicity of the species *C. asianum*, *C. cliviae*, *C. dianesei* (synonym *C. melanocaulon*), *C. fructicola*, *C. karstii*, *C. tropicale* and *C. endomangiferae* corresponding to endophytic isolates from asymptomatic mango tissues, was confirmed on leaves and fruits of this same plant species (Vieira *et al.* 2014), indicating that endophytic stage may be a quiescence-like strategy. In others research, it has been shown that several strains of *Colletotrichum* spp. obtained as endophytes in several plant species have resulted pathogenic by artificial inoculations, such as *Phaseolus vulgaris* (Gonzaga *et al.* 2015) and tropical grasses (Manamgoda *et al.* 2013).

These reports raise the discussion if the quiescent stage could be part of endophytic style of some *Colletotrichum* species, since they do not generate visible infections during phenological stages where the tissues are immature. Recent studies indicate that *C. tropicale* isolated from symptomless leaves and stems of mango cultivar

Azúcar was pathogenic on ripen fruits (Quintero-Mercado *et al.* 2019). The study of endophytic species and the relationship of quiescence with this lifestyle of pathogenic species of *Colletotrichum* are part of the new focus of research, which will improve efficiency in the management of “Anthracnose”.

#### **Management of *Colletotrichum* spp. as quiescent fungi.**

Quiescent structures constitute a hidden source of inoculum that remains invisible mainly in flowers and fruits (Ploetz, 2007). In recent research, it was found that quiescent structures of *Colletotrichum* sp., were present in asymptomatic tissues of leaves and stems of mango cv. Azúcar (Quintero-Mercado *et al.* 2019). This way, the fungus can escape the action of chemical molecules and even the effect of cultural practices. When conditions are favorable for infection, the fungus leaves the quiescent stage and start necrotrophic phase in plant tissues; thus, that any management measure is unsuccessful (Páez Redondo, 2003).

Traditionally, the technological options implemented for the management of fruit Anthracnose consist in reducing the active inoculum in the field, avoiding conditions for re-infections through sanitation, pruning, the use of drainages in the soil, and application of fungicides (Páez Redondo, 2003). Conventional postharvest management based on hot water, fungicides, and lately chitosan, affect the inoculum from the field located on the surface of the fruits (Kumari & Singh, 2017; Chowdappa *et al.* 2014; Prusky *et al.* 2013); however, the quiescent or endophyte inoculum is not significantly affected. Therefore, this article highlights strategies focused on affecting quiescent structures of the fungus, and that can be applied in field and postharvest.

The use of a wrapper impregnated with a mixture of chitosan-vanillin and zeolite is proposed as packaging for fruits, which allows the excess of ethylene to be absorbed. Although the results in mango Nam Dok Mai were positive, its use must be validated commercially (Jaimun & Sangsuwang, 2019).

The combination of chitin, microbial suspensions and thermal treatments could reduce the expression of Anthracnose in postharvest; in mango cv. Azúcar, heat treatment, microbial activity and storage at 13 °C of the fruits, allowed a reduction of quiescent infections between 83 and 89 % (Zapata-Narváez *et al.* 2021).

The use of preformed antifungal compounds is an option that should be considered for postharvest management of Anthracnose; these compounds are naturally synthesized in early phenological stages of the fruit (Adikaram *et al.* 2017). In mango, higher levels of gallotannins, resorcinols and chitinases have been found in resistant genotypes; gallotannins activity decreased with fruit ripening but this decreased is 10 % less in resistant cultivars (Paramasivan *et al.* 2009). Recent research focuses on evaluating the effect of volatile compounds produced by microorganisms and plants (Cheng *et al.* 2022; Huang *et al.* 2021; Shi *et al.* 2021), which need to be evaluated under field and postharvest conditions.

Treatments of mango fruits with microorganisms is an option that is being evaluated in postharvest, specially bacteria that could prevent the activation of quiescent stage. *Pseudomonas fluorescens*, *Bacillus subtilis*, *Saccharomyces cerevisiae*, *Brevundimonas diminuta*, *Stenotrophomonas maltophilia*, *Candida membranifaciens* and yeasts induce the synthesis of lytic enzymes, chitinase and glucanase, which has resulted in a longer quiescence period and reduction of Anthracnose severity during storage (Vivekananthan *et al.* 2004). However, the use of biological control is still uncertain. On the other hand, the search for metabolites that affect the synthesis of compounds by the pathogen or that degrade cellular components of the fungus must be deepened.

*The induction of resistance can be considered in the control of infections from quiescent stages.* Banana fruits harvested from plants treated with salicylic acid (SA) and acibenzolar-S-methyl, showed reduced Anthracnose severity and delayed onset of disease symptom expression (Wanigasekara *et al.* 2014). Another compound that has been used in post-harvest treatments is Butyl Hydroxyanisole (BHA), which was evaluated in mango fruits through vacuum infiltration 72 hours prior to *C. gloeosporioides* inoculation; a significant reduction in the incidence and size of the lesion was observed, which was correlated with an improvement in the contents of peroxidases, polyphenoloxidases, chitinases, phenyl-amin-liases, glucanases, hydrogen peroxide and phenolic compounds in fruits (Zhu *et al.* 2008).

*Colletotrichum* as well as *Alternaria alternata*, secrete ammonium and alkalize the medium for the infective process. The immersion of mango fruits in hydrochloric acid (50 mM) alone delays the activation of quiescent *Alternaria* infections (Prusky *et al.* 2006). Acidification of the cell matrix is an option to consider in the short term for the treatment of infections from the quiescence of the fungus, however the use of fungicides in acidic solutions requires further investigation.

In conclusion, publications to date are clear and deep on infectious processes focused on the necrotrophic phase of the fungus, with good support from genomic studies on the interaction with the host. But, many aspects of the biology of quiescence and its expression in different *Colletotrichum* species, especially in mangoes and other tropical fruit crops, are still unknown. It is necessary to deepen the study of the relationship between endophytism and quiescence. In pathogenic endophytic species, such as *C. gloeosporioides*, the occurrence of quiescence can be considered a form of transition from endophytism to the necrotrophic phase, or could quiescence be considered a form of endophytism?

Holistic management of Anthracnose requires that we focus on how to manage the pathogenesis of an endophytic and quiescent fungus.

**Conflict of interests:** The manuscript was prepared and reviewed with the participation of all authors, who declare that no conflict of interest is present that might question the validity of the results presented in the article.

## REFERENCES

1. ADIKARAM, N.; KARUNANAYAKE, C.; SINNIHAH, G.; VITHANAGE, I.K.; YAKANDAWALA, D. 2015. Fungal quiescence in fruit: an attempt to avoid toxic substances? *Journal of Mycopathological Research*. 53:1-7.
2. ADIKARAM, N.K.B.; KARUNANAYAKE, L.C.; SINNIHAH, G.D.; ABAYASEKARA, C.L.; KOMALA VITHANAGE, S.; YAKANDAWALA, D.M.D. 2017. A review of the role for natural defenses in the management of *Colletotrichum* rotting of ripe mangoes. *Acta Horticulturae*. 1183:229-232. <https://doi.org/10.17660/actahortic.2017.1183.32>
3. AHIMERA, N.; DRIEVER, G.F.; MICHAILIDES, T.J. 2003. Relationships among propagule numbers of *Botryosphaeria dothidea*, latent infections, and severity of panicle and shoot blight in pistachio orchards. *Plant Disease*. 87(7):846-853. <https://doi.org/10.1094/PDIS.2003.87.7.846>
4. ALKAN, N.; ESPESO, E.A.; PRUSKY, D. 2013a. Virulence regulation of phytopathogenic fungi by pH. *Antioxidants & Redox Signaling*. 19(9):1012-1025. <https://doi.org/10.1089/ars.2012.5062>
5. ALKAN, N.; FRIEDLANDER, G.; MENT, D.; PRUSKY, D.; FLUHR, R. 2015. Simultaneous transcriptome analysis of *Colletotrichum gloeosporioides* and tomato fruit pathosystem reveals novel fungal pathogenicity and fruit defense strategies. *New Phytologist*. 205(2):801-815. <https://doi.org/10.1111/nph.13087>
6. ALKAN, N.; MENG, X.; FRIEDLANDER, G.; REUVENI, E.; SUKNO, S.; SHERMAN, A.; THON, M.; FLUHR, R.; PRUSKY, D. 2013b. Global aspects of pacC regulation of pathogenicity genes in *Colletotrichum gloeosporioides* as revealed by transcriptome analysis. *Molecular Plant-Microbe Interactions*. 26(11):1345-1358. <https://doi.org/10.1094/MPMI-03-13-0080-R>
7. AMARAL, D.D.; MONTEIRO, A.L.R.; DA SILVA, E.I.; DE OLIVEIRA LINS, S.R.; ALVES DE OLIVEIRA, S.M. 2017. Frequency of quiescent fungi and post-harvest alternative management of stem end rot in papaya. *Revista Caatinga*. 30(3):786-793. <https://doi.org/10.1590/1983-21252017v30n327rc>
8. AVER'YANOV, A.A.; BELOZERSKAYA, T.A.; GESSLER, N.N. 2012. Fungus Development and Reactive Oxygen: Phytopathological Aspects. En: Witzany, G. (ed.). *Biocommunication of Fungi*. Springer (Berlin). p.261-271.
9. BENO-MOUALEM, D.; PRUSKY, D. 2000. Early events during quiescent infection development by *Colletotrichum gloeosporioides* in unripe avocado fruits. *Phytopathology*. 90(5):553-559. <http://dx.doi.org/10.1094/PHTO.2000.90.5.553>
10. BINYAMINI, N.; SCHIFFMANN-NADEL, M. 1972. The utilization in vitro of different avocado fruit constituents by *Colletotrichum gloeosporioides*. *Mycologia*. 64(4):916-919.
11. BLANCO-ULATE, B.; VINCENTI, E.; POWELL, A.L.T.; CANTU, D. 2013. Tomato transcriptome and mutant analyses suggest a role for plant stress hormones in the interaction between fruit and *Botrytis cinerea*. *Frontiers in Plant Science*. 4:142. <https://doi.org/10.3389/fpls.2013.00142>
12. BOWEN, J.; BILLING, D.; CONNOLLY, P.; SMITH, W.; COONEY, J.; BURDON, J. 2018. Maturity, storage and ripening effects on anti-fungal compounds in the skin of "Hass" avocado fruit. *Postharvest Biology and Technology*. 146:43-50. <https://doi.org/10.1016/j.postharvbio.2018.08.005>
13. CHENG, Y.-J.; WU, Y.-J.; LEE, F.-W.; OU, L.-Y.; CHEN, C.-N.; CHU, Y.-Y.; KUAN, Y.-C. 2022. Impact of storage condition on chemical composition and antifungal activity of pomelo extract against *Colletotrichum gloeosporioides* and anthracnose in Post-harvest mango. *Plants*. 11(15):2064. <https://doi.org/10.3390/plants11152064>
14. CHOWDAPPA, P.; GOWDA, S.; CHETHANA, C.S.; MADHURA, S. 2014. Antifungal activity of chitosan-silver nano-particle composite against *Colletotrichum gloeosporioides* associated with mango anthracnose. *African Journal of Microbiology Research*. 8(17):1803-1812. <https://doi.org/10.5897/AJMR2013.6584>
15. COJOCARU, M.; DROBY, S.; GLOTTER, E.; GOLDMAN, A.; GOTTLIEB, H.E.; JACOBY, B.; PRUSKY, D. 1986. 5-(12-Heptadecenyl)-resorcinol, the major component of the antifungal activity in the peel of mango fruit. *Phytochemistry*. 25(5):1093-1095. [https://doi.org/10.1016/S0031-9422\(00\)81560-5](https://doi.org/10.1016/S0031-9422(00)81560-5)
16. CZEMMEL, S.; GALARNEAU, E.R.; TRAVADON, R.; MCELDRONE, A.J.; CRAMER, G.R.; BAUMGARTNER, K. 2015. Genes expressed in grapevine leaves reveal latent wood infection by the fungal pathogen *Neofusicoccum parvum*. *PloS One*. 10:e0121828. <https://doi.org/10.1371/journal.pone.0121828>
17. DE LAPEYRE DE BELLAIRE, L.; CHILLET, M.; MOURICHON, X. 2000. Elaboration of an early quantification method of quiescent infections of *Colletotrichum musae* on bananas. *Plant Disease*. 84(2):128-133. <http://dx.doi.org/10.1094/PDIS.2000.84.2.128>
18. DELAYE, L.; GARCÍA-GUZMÁN, G.; HEIL, M. 2013. Endophytes versus biotrophic and necrotrophic pathogens-are fungal lifestyles evolutionarily stable traits? *Fungal Diversity*. 60:125-135. <https://doi.org/10.1007/s13225-013-0240-y>

19. DE LORENZO, G.; D'OVIDIO, R.; CERVONE, F. 2001. The role of polygalacturonase-inhibiting proteins (PGIPs) in defense against pathogenic fungi. Annual review of phytopathology. 39:313-335.  
<https://doi.org/10.1146/annurev.phyto.39.1.313>
20. DISKIN, S.; FEYGENBERG, O.; MAURER, D.; DROBY, S.; PRUSKY, D.; ALKAN, N. 2017. Microbiome alterations are correlated with occurrence of postharvest Stem-end rot in mango fruit. Phytobiomes. 1(3):117-127.  
<https://doi.org/10.1094/PBIOMES-05-17-0022-R>
21. DROBY, S.; PRUSKY, D.; JACOBY, B.; GOLDMAN, A. 1986. Presence of antifungal compounds in the peel of mango fruits and their relation to latent infections of *Alternaria alternata*. Physiological and Molecular Plant Pathology. 29(2):173-183.  
[https://doi.org/10.1016/S0048-4059\(86\)80019-4](https://doi.org/10.1016/S0048-4059(86)80019-4)
22. FISCHER, I.H.; DE MORAES, M.F.; FIRMINO, A.C.; AMORIM, L. 2019. Detection and epidemiological progress of quiescent avocado diseases. Ciência Rural. 49(8):e20180731.  
<http://dx.doi.org/10.1590/0103-8478cr20180731>
23. FISCHER, I.H.; SOARES-COLLETTI, A.R.; PALHARINI, M.C.D.A.; PARISI, M.C.M.; AMORIM, L. 2017. Temporal progress and spatial patterns of quiescent diseases inguava influenced by sanitation practices. Scientia Agricola. 74(1):68-76.  
<http://dx.doi.org/10.1590/1678-992X-2015-0425>
24. FLAISHMAN, M.A.; HWANG, C.S.; KOLATTUKUDY, P.E. 1995. Involvement of protein phosphorylation in the induction of appressorium formation in *Colletotrichum gloeosporioides* by its host surface wax and ethylene. Physiological and Molecular Plant Pathology. 47(2):103-117.  
<https://doi.org/10.1006/pmpp.1995.1046>
25. FLAISHMAN, M.A.; KOLATTUKUDY, P.E. 1994. Timing of fungal invasion using host's ripening hormone as a signal. Proceedings of the National Academy of Sciences. 91:6579-6583.  
<https://doi.org/10.1073/pnas.91.14.6579>
26. FREEMAN, S.; HOROWITZ, S.; SHARON, A. 2001. Pathogenic and nonpathogenic lifestyles in *Colletotrichum acutatum* from strawberry and other plants. Phytopathology. 91(10):986-992.  
<https://doi.org/10.1094/PHYTO.2001.91.10.986>
27. FU, M.; BAI, Q.; ZHANG, H.; GUO, Y.; PENG, Y.; ZHANG, P.; SHEN, L.; HONG, N.; XU, W.; WANG, G. 2022. Transcriptome analysis of the molecular patterns of pear plants infected by two *Colletotrichum fructicola* pathogenic strains causing contrasting sets of leaf symptoms. Frontiers in Plant Science. 13:761133.  
<https://doi.org/10.3389/fpls.2022.761133>
28. GAN, P.; IKEDA, K.; IRIEDA, H.; NARUSAKA, M.; O'CONNELL, R.J.; NARUSAKA, Y.; TAKANO, Y.; KUBO, Y.; SHIRASU, K. 2013. Comparative genomic and transcriptomic analyses reveal the hemibiotrophic stage shift of *Colletotrichum* fungi. New Phytologist. 197(4):1236-1249.  
<https://doi.org/10.1111/nph.12085>
29. GAÑÁN, L.; ÁLVAREZ, E.; CASTAÑO ZAPATA, J. 2015. Identificación genética de aislamientos de *Colletotrichum* spp. causantes de Antracnosis en frutos de aguacate, banano, mango y tomate de árbol. Revista Academia Colombiana de Ciencias Exactas Física y Naturales. 39(152):339-347.  
<http://dx.doi.org/10.18257/raccefyn.192>
30. GONZAGA, L.L.; COSTA, L.E.O.; SANTOS, T.T.; ARAÚJO, E.F.; QUEIROZ, M.V. 2015. Endophytic fungi from the genus *Colletotrichum* are abundant in the *Phaseolus vulgaris* and have high genetic diversity. Journal of Applied Microbiology. 118(2):485-496.  
<https://doi.org/10.1111/jam.12696>
31. GUÉDEZ, C.; RODRÍGUEZ, D. 2021. Infecciones quiescentes por *Colletotrichum gloeosporioides* en las diferentes etapas de desarrollo del fruto de guayaba (*Psidium guajava* L.) en dos épocas de producción. Revista de la Facultad de Agronomía de la Universidad del Zulia. 38(4):751-770.  
[https://doi.org/10.47280/RevFacAgron\(LUZ\).v38.n4.01](https://doi.org/10.47280/RevFacAgron(LUZ).v38.n4.01)
32. GUETSKY, R.; KOBILER, I.; WANG, X.; PERLMAN, N.; GOLLOP, N.; AVILA-QUEZADA, G.; HADAR, I.; PRUSKY, D. 2005. Metabolism of the flavonoid epicatechin by laccase of *Colletotrichum gloeosporioides* and its effect on pathogenicity on avocado fruits. Phytopathology. 95(11):1341-1348.  
<https://doi.org/10.1094/PHYTO-95-1341>
33. HAILE, Z.M.; PILATI, S.; SONEGO, P.; MALACARNE, G.; VRHOSEK, U.; ENGELEN, K.; TUDZINSKY, P.; ZOTTINI, M.; BARALDI, E.; MOSER, C. 2017. Molecular analysis of the early interaction between the grapevine flower and *Botrytis cinerea* reveals that prompt activation of specific host pathways leads to fungus quiescence. Plant, Cell & Environment. 40(8):1409-1428.  
<https://doi.org/10.1111/pce.12937>
34. HODGES, D.M. 2003. Chapter 1. Overview: Oxidative stress and postharvest produce. En: Postharvest oxidative stress in horticultural crops. CRC Press (New York). p.1-12.
35. HONGER, J.O.; OFFEI, S.K.; ODURO, K.A.; ODAMTTE, G.T.; NYAKU, S.T. 2014. Identification and species status of the mango biotype of *Colletotrichum gloeosporioides* in Ghana. European Journal of Plant Pathology.



- 140:455-467.  
<https://doi.org/10.1007/s10658-014-0480-z>
36. HUANG, X.; LIU, T.; ZHOU, C.; HUANG, Y.; LIU, X.; YUAN, H. 2021. Antifungal activity of essential oils from three *Artemisia* species against *Colletotrichum gloeosporioides* of mango. *Antibiotics*. 10(11):1331.  
<https://doi.org/10.3390/antibiotics10111331>
37. HÜCKELHOVEN, R. 2007. Cell wall-associated mechanisms of disease resistance and susceptibility. *Annual Review of Phytopathology*. 45:101-127.  
<https://doi.org/10.1146/annurev.phyto.45.062806.094325>
38. HYDE, K.D.; SOYTONG, K. 2008. The fungal endophyte dilemma. *Fungal Diversity*. 33:163-173.
39. ISMAIL, A.M.; CIRVILLERI, G.; YASEEN, T.; EPIFANI, F.; PERRONE, G.; POLIZZI, G. 2015. Characterization of *Colletotrichum* species causing Anthracnose disease of mango in Italy. *Journal of Plant Pathology*. 97(1):167-171.  
<http://dx.doi.org/10.4454/JPP.V97I1.011>
40. JAIMUN, R.; SANGSUWAN, J. 2019. Efficacy of chitosan-coated paper incorporated with vanillin and ethylene adsorbents on the control of anthracnose and the quality of Nam Dok Mai mango fruit. *Packaging Technology and Science*. 32(8):383-394.  
<https://doi.org/10.1002/pts.2446>
41. JAYAWARDENA, R.S.; BHUNJUN, C.S.; HYDE, K.D.; GENTEKAKI, E.; ITTHAYAKORN, P. 2021. *Colletotrichum*: lifestyles, biology, morpho-species, species complexes and accepted species. *Mycosphere*. 12(1):519-669.  
<https://doi.org/10.5943/mycosphere/12/1/7>
42. JOHNSON, G.I.; MEAD, A.J.; COOKE, A.W.; DEAN, J.R. 1992. Mango stem end rot pathogens-Fruit infection by endophytic colonization of the inflo-rescence and pedicel. *Annals of Applied Biology*. 120(2):225-234.  
<https://doi.org/10.1111/j.1744-7348.1992.tb03420.x>
43. JOY, P.P.; SHERIN, C.G. 2016. Diseases of passion fruit (*Passiflora edulis*) and their management. In: Pandey, A.K.; Mall, P. (eds.). *Insect pests management of fruit crops*. Biotech. p.453-470.
44. KARUNANAYAKE, L.C.; ADIKARAM, N.; KUMARIHAMY, B.M.; BANDARA, B.M.; ABAYASEKARA, C. 2011. Role of antifungal gallotannins, resorcinols and chitinases in the constitutive defence of immature mango (*Mangifera indica* L.) against *Colletotrichum gloeosporioides*. *Journal of Phytopathology*. 159(10):657-664.  
<https://doi.org/10.1111/j.1439-0434.2011.01818.x>
45. KIENZLE, S.; CARLE, R.; SRUAMSIRI, P.; TOSTA, C.; NEIDHART, S. 2014. Occurrence of Alk(en)ylresorcinols in the fruits of two mango (*Mangifera indica* L.) cultivars during on-tree maturation and postharvest storage. *Journal of Agricultural and Food Chemistry*. 62(1):28-40.  
<https://dx.doi.org/10.1021/jf4028552>
46. KLEEMANN, J.; RINCON-RIVERA, L.J.; TAKAHARA, H.; NEUMANN, U.; VAN THEMAAT, E.V.L.; VAN DER DOES, H.C.; HACQUARD, S.; STÜBER, K.; WILL, I.; SCHMALENBACH, W.; SCHMELZER, E.; O'CONNELL, R.J. 2012. Sequential delivery of host-induced virulence effectors by appressoria and intracellular hyphae of the phytopathogen *Colletotrichum bigginsianum*. *PLoS Pathogens*. 8:e1002643.  
<https://doi.org/10.1371/journal.ppat.1002643>
47. KOGEL, K.H.; FRANKEN, P.; HÜCKELHOVEN, R. 2006. Endophyte or parasite—what decides? *Current Opinion in Plant Biology*. 9(4):358-363.  
<https://doi.org/10.1016/j.pbi.2006.05.001>
48. KORN, M.; SCHMIDPETER, J.; DAHL, M.; MÜLLER, S.; VOLL, L.M.; KOCH, C. 2015. A genetic screen for pathogenicity genes in the hemibiotrophic fungus *Colletotrichum bigginsianum* identifies the plasma membrane proton pump Pma2 required for host penetration. *PLoS One*. 10:e0125960.  
<https://doi.org/10.1371/journal.pone.0125960>
49. KUMARI, R.; SINGH, R. 2017. Anthracnose of mango incited by *Colletotrichum gloeosporioides*: A comprehensive review. *International Journal Pure & Applied Bioscience*. 5(1):48-56.  
<http://dx.doi.org/10.18782/2320-7051.2478>
50. LATTANZIO, V.; DI VENERE, D.; LINSALATA, V.; BERTOLINI, P.; IPPOLITO, A.; SALERNO, M. 2001. Low temperature metabolism of apple phenolics and quiescence of *Phlyctaena vagabunda*. *Journal of Agricultural and Food Chemistry*. 49(12):5817-5821.  
<https://doi.org/10.1021/jf010255b>
51. LATUNDE-DADA, A.O. 2001. *Colletotrichum*: tales of forcible entry, stealth, transient confinement and breakout. *Molecular Plant Pathology*. 2(4):187-198.  
<https://doi.org/10.1046/j.1464-6722.2001.00069.x>
52. LESTER, G. 2003. *Oxidative stress affecting fruit senescence. Postharvest oxidative stress in horticultural crops*. CRC Press (New York). p.113-129.
53. LI, X.; WU, Y.; LIU, Z.; ZHANG, C. 2017. The function and transcriptome analysis of a bZIP transcription factor CgAP1 in *Colletotrichum gloeosporioides*. *Microbiological Research*. 197:39-48.  
<https://doi.org/10.1016/j.micres.2017.01.006>

54. LIU, F.; CAI, L.; CROUS, P.W.; DAMM, U. 2014. The *Colletotrichum gigasporum* species complex. *Persoonia-Molecular Phylogeny and Evolution of Fungi*. 33:83-97. <http://dx.doi.org/10.3767/003158514X684447>
55. LIU, F.; MA, Z.Y.; HOU, L.W.; DIAO, Y.Z.; WU, W.P.; DAMM, U.; SONG, S.; CAI, L. 2022. Updating species diversity of *Colletotrichum*, with a phylogenomic overview. *Studies in Mycology*. 101(1):1-56. <https://doi.org/10.3114/sim.2022.101.01>
56. MANAMGODA, D.S.; UDAYANGA, D.; CAI, L.; CHUKEATIROTE, E.; HYDE, K.D. 2013. Endophytic *Colletotrichum* from tropical grasses with a new species *C. endophytica*. *Fungal Diversity*. 61:107-115. <https://doi.org/10.1007/s13225-013-0256-3>
57. MENGISTE, T. 2012. Plant immunity to necrotrophs. *Annual review of phytopathology*. 50:267-294. <https://doi.org/10.1146/annurev-phyto-081211-172955>
58. MENT, D.; ALKAN, N.; LURIA, N.; BI, F.-C.; REUVENI, E.; FLUHR, R.; PRUSKY, D. 2015. A role of AREB in the regulation of PACC-dependent acid-expressed-genes and pathogenicity of *Colletotrichum gloeosporioides*. *Molecular Plant-Microbe Interactions*. 28(2):154-166. <https://doi.org/10.1094/MPMI-09-14-0252-R>
59. MIYARA, I.; SHAFRAN, H.; DAVIDZON, M.; SHERMAN, A.; PRUSKY, D. 2010. pH regulation of ammonia secretion by *Colletotrichum gloeosporioides* and its effect on appressorium formation and pathogenicity. *Molecular Plant-Microbe Interactions*. 23(3):304-316. <https://doi.org/10.1094/MPMI-23-3-0304>
60. O'CONNELL, R.J.; THON, M.R.; HACQUARD, S.; AMYOTTE, S.G.; KLEEMANN, J.; TORRES, M.F.; DAMM, U.; BUIATES, E.A.; EPSTEINS, L.; ALKAN, N.; ALTMÜLLER, J.; ALVARADO-BALDERRAMA, L.; BAUSER, C.A.; BECKER, C.; BIRREN, B.W.; CHEN, Z.; CHOI, J.; CROUCH, J.A.; DUVICK, J.P.; FARMAN, M.A.; GAN, P.; HEIMAN, D.; HENRISSAT, B.; HOWARD, R.J.; KABBAGE, M.; KOCH, C.; KRACHER, B.; KUBO, Y.; LAW, A.D.; LEBRUN, M.-H.; LEE, Y.-H.; MIYARA, I.; MOORE, N.; NEUMANN, U.; NORDSTRÖM, K.; PANACCIONE, D.G.; PANSTRUGA, R.H.; PLACE, M.; PROCTOR, R.H.; PRUSKY, D.; RECH, G.; REINHARDT, R.; ROLLINS, J.A.; ROUNSLEY, S.; SCHARDL, C.L.; SCHWARTZ, D.C.; SHENOY, N.; SHIRASU, K.; SIKHAKOLLI, U.R.; STÜBER, K.; SUKNO, S.A.; SWEIGARD, J.A.; TAKANO, Y.; TAKAHA-RA, H.; TRAIL, F.; VAN DER DOES, H.C.; VOLL, L.M.; WILL, I.; YOUNG, S.; ZENG, Q.; ZHANG, J.; ZHOU, S.; DICKMAN, M.B.; SCHULZE-LEFERT, P.; VAN THEMAAT, E.V.L.; MA, L.-J.; VAILLANCOURT, L.J. 2012. Lifestyle transitions in plant pathogenic *Colletotrichum* fungi deciphered by genome and transcriptome analyses. *Nature Genetics*. 44:1060-1065. <https://doi.org/10.1038/ng.2372>
61. PÁEZ REDONDO, A.R. 2003. Tecnologías sostenibles para el manejo de la antracnosis (*Colletotrichum gloeosporioides* (Penz.) Penz. y Sacc.) en papaya (*Carica papaya* L.) y mango (*Mangifera indica* L.). Corporación colombiana de investigación agropecuaria-AGROSAVIA (Bogotá, Colombia). 18p.
62. PANIAGUA, C.; POSÉ, S.; MORRIS, V.J.; KIRBY, A.R.; QUESADA, M.A.; MERCADO, J.A. 2014. Fruit softening and pectin disassembly: an overview of nanostructural pectin modifications assessed by atomic force microscopy. *Annals of botany*. 114(6):1375-1383. <https://doi.org/10.1093/aob/mcu149>
63. PARAMASIVAN, M.; MOHAN, S.; SYED ALI, G.; MATHIYAZHAGAN, S.; MUTHUKRISHNAN, N. 2009. Detection of latent infections in mango fruit with herbi-cides. *Archives of Phytopathology and Plant Protection*. 42(4):318-326. <https://doi.org/10.1080/03235400601069696>
64. PARTHASARATHY, S.; MOHAMMAD FAISAL, P.; PRABAKAR, K.; THIRIBHUVANAMALA, G.; RAJALAKSHMI, J. 2015. Profiling of antifungal compounds from n-hexane extracts of mango fruits against major post-harvest pathogens. *Annals of Plant and Soil Research*. 17:311-316.
65. PERES, N.A.; TIMMER, L.W.; ADASKAVEG, J.E.; COR-RELL, J.C. 2005. Lifestyles of *Colletotrichum acutatum*. *Plant Disease*. 89(8):784-796. <https://dx.doi.org/10.1094/PD-89-0784>
66. PHOTITA, W.; TAYLOR, P.W.J.; FORD, R.; HYDE, K.D.; LUMYONG, S. 2005. Morphological and molecular characterization of *Colletotrichum* species from herbaceous plants in Thailand. *Fungal Diversity*. 18:117-133.
67. PLOETZ, R.C. 2007. Diseases of tropical perennial crops: challenging problems in diverse environments. *Plant Disease*. 91(6):644-663. <https://doi.org/10.1094/PDIS-91-6-0644>
68. PODILA, G.K.; ROGERS, L.M.; KOLATTUKUDY, P.E. 1993. Chemical signals from avocado surface wax trigger germination and appressorium formation in *Colletotrichum gloeosporioides*. *Plant Physiology*. 103(1):267-272. <https://doi.org/10.1104/pp.103.1.267>
69. PRUSKY, D.; ALKAN, N.; MENGISTE, T.; FLUHR, R. 2013. Quiescent and necrotrophic lifestyle choice during postharvest disease development. *Annual Review of Phytopathology*. 51:155-176. <https://doi.org/10.1146/annurev-phyto-082712-102349>

70. PRUSKY, D.B.; BI, F.; MORAL, J.; BARAD, S. 2016a. How does host carbon concentration modulate the lifestyle of postharvest pathogens during colonization? *Frontiers in Plant Science*. 7:1306.  
<https://doi.org/10.3389/fpls.2016.01306>
71. PRUSKY, D.; KOBILER, I.; AKERMAN, M.; MIYARA, I. 2006. Effect of acidic solutions and acidic prochloraz on the control of postharvest decay caused by *Alternaria alternata* in mango and persimmon fruit. *Postharvest Biology and Technology*. 42(2):134-141.  
<https://doi.org/10.1016/j.postharvbio.2006.06.001>
72. PRUSKY, D.; WATTAD, C.; KOBILER, I. 1996. Effect of ethylene on activation of lesion development from quiescent infections of *Colletotrichum gloeosporioides* in avocado fruits. *Molecular Plant-Microbe Interactions*. 9(9):864-868.
73. PRUSKY, D.; ZIV, C. 2019. Mechanisms of fungal quiescence during development and ripening of fruits. In: Palou, L.; Smilanick, J.L. (eds.). *Postharvest pathology of fresh horticultural produce*. CRC Press. p.407-436.
74. PRUSKY, D.; BARAD, S.; MENT, D.; BI, F. 2016b. The pH modulation by fungal secreted molecules: a mechanism affecting pathogenicity by postharvest pathogens. *Israel Journal of Plant Sciences*. 63:22-30.  
<https://doi.org/10.1080/07929978.2016.1151290>
75. PRUSKY, D.B.; SIONOV, E. 2021. Special Issue "Interplay between Fungal Pathogens and Harvested Crops and Fruits". *Microorganisms*. 9(3):553.  
<https://doi.org/10.3390/microorganisms9030553>
76. QUINTERO-MERCADO, A.; DANGON-BERNIER, F.; PÁEZ-REDONDO, A. 2019. Endophytic isolation of *Colletotrichum* spp. from the leaves and branches of mango (*Mangifera indica* L.) cultivar Azúcar in the municipality of Ciénaga, Magdalena, Colombia. *Revista de la Academia Colombiana de Ciencias Exactas, Físicas y Naturales*. 43(166):65-77.  
<https://doi.org/10.18257/raccefyn.788>
77. RAJARAMMOHAN, S. 2021. Redefining plant-necrotroph interactions: the thin line between hemibiotrophs and necrotrophs. *Frontiers in Microbiology*. 12:673518.  
<https://doi.org/10.3389/fmicb.2021.673518>
78. RANATHUNGE, N.P.; SANDANI, H.B.P. 2016. Deceptive behaviour of *Colletotrichum truncatum*: strategic survival as an asymptomatic endophyte on non-host species. *Journal of Plant Protection Research*. 56(2):157-162.  
<https://doi.org/10.1515/jppr-2016-0026>
79. RODRIGUEZ, R.J.; WHITE JR, J.F.; ARNOLD, A.E.; REDMAN, R.S. 2009. Fungal endophytes: diversity and functional roles. *New phytologist*. 182(2):314-330.  
<https://doi.org/10.1111/j.1469-8137.2009.02773.x>
80. SANZANI, S.M.; REVERBERI, M.; PUNELLI, M.; IPPOLITO, A.; FANELLI, C. 2012. Study on the role of patulin on pathogenicity and virulence of *Penicillium expansum*. *International Journal of Food Microbiology*. 153(3):323-331.  
<https://doi.org/10.1016/j.ijfoodmicro.2011.11.021>
81. SHARMA, M.; KULSHRESTHA, S. 2015. *Colletotrichum gloeosporioides*: an anthracnose causing pathogen of fruits and vegetables. *Biosciences Biotechnology Research Asia*. 12(2):1233-1246.  
<http://dx.doi.org/10.13005/bbra/1776>
82. SHI, X.-C.; WANG, S.-Y.; DUAN, X.-C.; WANG, Y.-Z.; LIU, F.-Q.; LABORDA, P. 2021. Biocontrol strategies for the management of *Colletotrichum* species in postharvest fruits. *Crop Protection*. 141:105454.  
<https://doi.org/10.1016/j.cropro.2020.105454>
83. SHNAIDERMAN, C.; MIYARA, I.; KOBILER, I.; SHERMAN, A.; PRUSKY, D. 2013. Differential activation of ammonium transporters during the accumulation of ammonia by *Colletotrichum gloeosporioides* and its effect on appressoria formation and pathogenicity. *Molecular Plant-Microbe Interactions*. 26(3):345-355.  
<https://doi.org/10.1094/MPMI-07-12-0170-R>
84. SIDDIQUI, Y.; ALLI, A. 2014. Chapter 11-*Colletotrichum gloeosporioides* (Anthracnose). In: Bautista-Baños, S. (ed.). *Postharvest Decay. Control Strategies*. Academic Press. p.337-371.  
<https://doi.org/10.1016/B978-0-12-411552-1.00011-9>
85. SINNIHAH, G.D.; ADIKARAM, N.K.B.; ABAYASEKARA, C. L. 2012. Differential defense responses expressed in mango (*Mangifera indica* L.) cultivars resistant and susceptible to *Colletotrichum gloeosporioides*. *Indian Phytopathology*. 65(4):2-6.
86. TALHINHAS, P.; BARONCELLI, R. 2021. *Colletotrichum* species and complexes: geographic distribution, host range and conservation status. *Fungal Diversity*. 110:109-198.  
<https://doi.org/10.1007/s13225-021-00491-9>
87. TIAN, S.; QIN, G.; LI, B. 2013. Reactive oxygen species involved in regulating fruit senescence and fungal pathogenicity. *Plant Molecular Biology*. 82:593-602.  
<https://doi.org/10.1007/s11103-013-0035-2>
88. VIEIRA, W.A.S.; MICHHEREFF, S.J.; DE MORAIS JR, M.A.; HYDE, K.D.; CÂMARA, M.P.S. 2014. Endophytic species of *Colletotrichum* associated with mango in northeastern Brazil. *Fungal Diversity*. 67:181-202.  
<https://doi.org/10.1007/s13225-014-0293-6>

89. VILLAFANA, R.T.; RAMPERSAD, S.N. 2020. Diversity, structure, and synteny of the cutinase gene of *Colletotrichum* species. *Ecology and evolution*. 10(3):1425-1443. <https://doi.org/10.1002/ece3.5998>
90. VIVEKANANTHAN, R.; RAVI, M.; RAMANATHAN, A.; SAMIYAPPAN, R. 2004. Lytic enzymes induced by *Pseudomonas fluorescens* and other biocontrol organisms mediate defense against the anthracnose pathogen in mango. *World Journal of Microbiology and Biotechnology*. 20:235-244. <https://doi.org/10.1023/B:WIBI.0000023826.30426.f5>
91. WANG, A.; TAN, D.; TAKAHASHI, A.; ZHONG LI, T.; HARADA, T. 2007. MdERFs, two ethylene-response factors involved in apple fruit ripening. *Journal of Experimental Botany*. 58(13):3743-3748. <https://doi.org/10.1093/jxb/erm224>
92. WANIGASEKARA, U.W.N.P.; ADIKARAM, N.K.B.; ABAYASEKARA, C.L. 2014. Pre-harvest chemical elicitor treatment enhances induced resistance in harvested banana fruit cv. 'Embul' and reduces Anthracnose caused by *Colletotrichum musae*. *Journal of the National Science Foundation of Sri Lanka*. 42(2):101-110. <https://doi.org/10.4038/jnsfsr.v42i2.6994>
93. ZAKARIA, L. 2021. Diversity of *Colletotrichum* species associated with anthracnose disease in tropical fruit crops- A review. *Agriculture*. 11(4):297
94. ZAPATA-NARVÁEZ, Y.A.; IZQUIERDO-GARCÍA, L.F.; BOTINA-AZAÍN, B.L.; BELTRÁN-ACOSTA, C.R. 2021. Efficacy of microbial antagonists and chitin in the control of *Colletotrichum gloeosporioides* in postharvest of mango cv. Azúcar. *Revista mexicana de fitopatología*. 39(2):248-265. <https://doi.org/10.18781/r.mex.fit.2102-1>
95. ZHU, X.; CAO, J.; WANG, Q.; JIANG, W. 2008. Postharvest infiltration of BTH reduces infection of mango fruits (*Mangifera indica* L. cv. Tainong) by *Colletotrichum gloeosporioides* and enhances resistance inducing compounds. *Journal of Phytopathology*. 156(2):68-74. <https://doi.org/10.1111/j.1439-0434.2007.01320.x>