Article

Botryosphaeriaceae: a complex, diverse and cosmopolitan family of fungi

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Abstract

In the last decade, interest in studying the fungi belonging to the Botryosphaeriaceae family has increased due to the diseases that induce in economically important crops, their wide cosmopolitan distribution and the observed association between pathogenesis and host stress. More than ten species associated with symptoms in different parts of the same plant have been reported, indicating that a significant number of species of this family do not have specificity in host range. Besides, several studies have shown the ability of these fungi to ‘jump’ from their original native hosts to agricultural crops that are established in nearby areas, belonging to the same botanical family or to a different family. The objective of this research is to review morphological and molecular markers for taxonomic identification of species in the Botryosphaeriaceae family, their geographical distribution, range of agricultural host and developmental aspects for the disease including dispersal modes. The information presented may be useful in the etiology, identification and diagnosis of Botryosphaeriaceae species as well as the management of the diseases caused by them.

Keywords: hosts, stress, symptoms.

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Introduction

The family Botryosphaeriaceae is represented by 23 genera of cosmopolitan fungi with a wide range of hosts and that can be endophytes, phytopathogenic or saprophytes (Slippers and Wingfield, 2007; Slippers *et al*., 2017). Members of this family induce diseases in plants that are under some form of stress (De Wet *et al*., 2003). They can cause symptoms such as cankers, gummosis, dieback of branches, defoliation and leaf necrosis and plant death; in general, all these symptoms are called decline syndrome (Slippers and Wingfield, 2007).

In recent years, unknown species have been described in various hosts in new geographical regions (Netto *et al*., 2017). This indicates that these fungi are dispersing around the world as a result of commercial globalization mainly, making them a potential threat to agroecosystems, forests, native and introduced plants (Slippers *et al*., 2017).

Identification of Botryosphaeriaceae species

The family Botryosphaeriaceae was introduced by Theissen and Sydow (1918) and belongs to the order Botryosphaeriales (Schoch *et al*., 2006). The genera that have a global geographical distribution and affect a greater number of hosts are *Diplodia*, *Dothiorella*, *Lasiodiplodia* and *Neofusicoccum*, encompassing 70%, with approximately 300 phytopathogenic species (Slippers *et al*., 2017).

The morphological characteristics of mycelium and asexual fruiting bodies are used for identification at the genus and species level (Alves *et al*., 2006; Sandoval-Sánchez *et al*., 2013). However, these characteristics are very variable and sometimes not distinctive, because they share between species; they are also influenced by age and substrate where isolates grow, therefore it is necessary to use molecular tools (Alves *et al*., 2007).

The sequences of genes that encode for elongation factor 1- α (*TEF1- α*), beta tubulin (*β-Tub*) and internal transcribed spacers (ITS) are the molecular regions most commonly used in phylogenetic analyses for the identification of Botryosphaeriaceae species (White *et al*., 1990; Alves *et al*., 2006; Zhou *et al*., 2015). Another gene that is also useful is the second largest subunit of RNA polymerase II (RPB2) (Fernández-Herrera *et al*., 2017).

Recently, Lopes and collaborators (2017) suggested that the genes *MAT1-2-1* and *MAT1-1-1* are efficient in resolution of species within the genus *Neofusicoccum* and were useful in demonstrating that most species are homothallic. One disadvantage of using these markers is that both genes cannot always be obtained or only one isolate of one species is available. The gen *MAT1-2-1* is more accurate and reliable for species differentiation by containing fewer preserved introns and better PCR amplification is obtained.

Another tool for differentiating Botryosphaeriaceae species is the analysis through intern simple sequence repeat (ISSR), which is a simple, reproducible, fast and useful technique when it comes to sequencing a large number of isolates, grouping those of the same species, determining inter-specific variability and differentiating cryptic species as well as detecting intra-specific variability (Zhou *et al*., 2001).

Hybrid species, morphotypes and cryptic species complexes occupying the same ecological niche have been identified in the Botryosphaeriaceae family. In these cases, it is difficult to differentiate species when only one or two loci are used for identification (De Wet *et al*., 2003; Cruywagen *et al*., 2017). Multilocus analysis of DNA sequences and the use of more isolates in analyses is currently the most efficient way to recognize hybrid species, morphotypes and cryptic species complex (Cruywagen *et al*., 2017).

For efficient differentiation of morphotypes, De Wet *et al*. (2003) used the analysis of six coding genes of beta tubulin proteins (*β-Tub*), chitin synthetase (*CHS*), elongation factor 1-α (*TEF1-α*), actin (*ACT*), calmodulin (*CAL*) and glutaraldehyde-6-phosphate (*GPD*), as well as six microsatellite loci (SS5, SS7, SS8, SS9, SS10 and SS11).

Distribution

Slippers *et al*. (2017) indicate that phytopathogenic fungi belonging to Botryosphaeriaceae generally affect plants in subtropical and tropical zones, however, in recent years its presence has been reported worldwide, an example of the above are the species of *Neofusicoccum* that are known to colonize 46 hosts from 18 botanical families in ten countries including all continents (Sakadilis *et al*., 2011).

This ability to infect multiple hosts and migrate between them facilitates the establishment and spread of species and genotypes of Botryosphaeriaceae in new areas (Mehl *et al*., 2017). Some members of this family may have some specificity, which is influenced by the host and its habitat (Slippers and Wingfield, 2017). Human activities that influence phytopathogen dispersion and its interactions with its hosts are: the introduction of non-native plants in new areas, changes in land use and intensive deforestation (Pavlic-Zup *et al*., 2015).

In addition, when these fungi infect plants in conditions of high temperatures and drought, they can become very aggressive pathogens and result in a potential threat to agroecosystems, natural forests, native and introduced plants (Piskur *et al*., 2011). This has led to an increase in interest in studying these fungi due to their presence in multiple hosts, new geographical areas and their aggressiveness in hosts under stress (Slippers *et al*., 2017).

Host range

The phytopathogenic species of Botryosphaeriaceae attack woody plants (Sakalidis *et al*., 2011). They are considered to attack mainly angiosperms, although in the case of *Diplodia* species which are restricted to gymnosperms, it has been suggested that it comes from an ancestor of Botryosphaeriaceae that evolved in angiosperms (De Wet *et al*., 2008). There are studies that demonstrate the ability of these fungi to move from native to non-native hosts and between plants close or distant phylogenetically (Sakadilis *et al*., 2013; Pavlic-Zup *et al*., 2015).

Some of the new species that have been identified are restricted to a single host and are not very pathogenic, suggesting that they are recently introduced or that they are only associated endophytically (Perez *et al*., 2010). However, cases of host infected by only one or more than ten species associated with symptoms in different parts of the plant have been reported, indicating that they can infect more than one organ indistinctly (Delgado-Cerrone *et al*., 2016; Mayorquin *et al*., 2016; Tedihou *et al*., 2017).

Some authors indicate that the most frequently isolated species in a host is usually not the most aggressive (Mayorquin *et al*., 2016). Due to the lack of consistency to delimit *Botryiosphaeria species*, it is difficult to quantify how many plants they attack, however, in a recent study approximately 1 692 hosts worldwide were determined (Batista *et al*., 2012). These pathogens attack ornamental forest plants and various agricultural hosts, including tropical fruit trees (Fernández-Herrera *et al*., 2017; Lawrence *et al*., 2017) (Table 1), deciduous shrubs, herbaceous plants and palms (Table 2).

Table 1. Distribution of Botryosphaeriaceae species associated with canker, gummosis, decline and rot in evergreen fruit trees.

Host	Species	Country	Reference
Citrus x *cinensis*	*Lasiodiplodia theobromae*, *Neoscytalidium dimidiatum*	Italy, Mexico	Polizzi *et al*. (2009); Polanco-Florián *et al*. (2019)
Citrus latifolia	*Lasiodiplodia citricola*, *Lasiodiplodia iraniensis*, L. *pseudotheobromae*, L. *theobromae*, *Lasiodiplodia subglobosa*, L. *citricola.*	Mexico	Bautista-Cruz *et al*. (2018); Valle-De la Paz *et al*. (2019)
Citrus x *limon*	L. *pseudotheobromae*, L. *theobromae*, *Neofusicoccum australe*, *Neofusicoccum parvum*, *Neoscytalidium hyalinum*, *Spencermartinsia viticola*	Brazil, USA, Turkey	Adesemoye and Eskalen (2011); Mayorquin *et al.* (2012); Awan *et al*. (2016); Guajardo *et al*. (2018)
Citrus spp.	*Diplodia mutila*, *Diplodia seriata*, *Dothiorella viticola*, *Diplodia iberica*, L. *citricola**, *Lasiodiplodia hormozganensis*, *Lasiodiplodia iraniensis* L. *theobromae*, *Lasiodiplodia parva*, *N. australe*, *Neofusicoccum dimidiatum*, *Neofusicoccum luteum*, *Neofusicoccum mediterraneum*, *N. parvum.*	USA, United Arab Emirates, Iran, Oman	Abdollahzadeh *et al*. (2010); Al-Sadi *et al*. (2013); Adesemoye *et al*. (2014)
Dimocarpus longan	L. *hormozganensis*, L. *iraniensis*, L. *pseudotheobromae*, L. *theobromae*	Puerto Rico	Serrato-Díaz *et al*. (2019)
Mangifera indica	*Botryosphaeria fabicerciana*, *Diplodia allocellula*, *Lasiodiplodia brasiliense*, *Lasiodiplodia crassispora*, *Lasiodiplodia gonubiensis*, *Lasiodiplodia egyptiacae*, L. *hormozganensis**, L. *iraniensis**, *Lasiodiplodia mahajangana* L. *pseudotheobromae*, L. *theobromae*, *Lasiodiplodia viticola*, *N. mediterraneum*, *N. parvum*, *Neofusicoccum umdonicola*, *Neofusicoccum vitifusiforme*, *Pseudofusicoccum olivaceum*	Iran, Egypt, United Arab Emirates, Mexico, Peru, South Africa, Thailand	Abdollahzadeh *et al*. (2010); Ismail *et al*. (2012); Al-Sadi *et al*. (2013); Sandoval-Sánchez *et al*. (2013); Trakunyingcharoen *et al*. (2014); Mehl *et al*. (2017)

Host	Species	Country	Reference
Nephelium lappaceum	L. *brasiliensis*, L. *hormozganensis*, L. *iraniensis*, L. *pseudotheobromae*, L. *theobromae*, *Neofusicoccum batangarum*, *N. parvum*	Puerto Rico	Serrato-Díaz *et al*. (2019)
Persea americana	*D. mutila*, *D. seriata*, *Dothiorella iberica*, *Fusicoccum aesculi*, L. *theobromae*, *N. australe*, *N. luteum*, *Neofusicoccum nonquaesitum*, *N. parvum*, *Neofusicoccum* sp.	Chile, USA, Mexico	McDonald *et al*. (2011); Molina-Gayosso *et al*. (2012); Valencia *et al*. (2019)
Pouteria sapota	*L. theobromae*	Mexico	Tovar-Pedraza *et al*. (2012)

*= species described recently.

Table 2. Distribution of Botryosphaeriaceae species associated with canker, gummosis, decline and rot in shrub, deciduous, herbaceous and palm hosts.

Host	Species	Country	Reference
Anacardium occidental	*Lasiodiplodia brasiliense*, *Lasiodiplodia euphorbicola*, *Lasiodiplodia gonubiensis*, L. *iraniensis*, *Lasiodiplodia jatrophicola*, *Lasiodiplodia gravistriata**, L. *pseudotheobromae*, L. *theobromae*, *Neofusicoccum batangarum*, *Pseudofusicoccum stromaticum*	Brazil	Netto *et al*. (2017)
Actinidia chinensis	*Botryosphaeria dothidea*, *N. parvum*, L. *theobromae*	China	Zhou *et al*. (2015)
Carica papaya	L. *brasiliense**, L. *hormozganensis*, *Lasiodiplodia marypalme**, L. *pseudotheobromae*, L. *theobromae*.	Brazil	Netto *et al*. (2014)
Cocos nucifera	L. *brasiliense*, L. *egyptiacae*, L. *pseudotheobromae*, L. *theobromae*	Brazil, China	Rosado *et al*. (2016); Zhang and Niu (2019)
Fragaria x *ananassa*	*Macrophomina phaseolina*	Chile, Spain, Republic of Tunisia	Avilés *et al*. (2008); Sánchez *et al*. (2013); Hajlaoui *et al*. (2015)
Malus domestica	*B. dothidea*, *Diplodia intermedia*, *D. seriata*, *Diplodia pseudoseriata*, *L. pseudotheobromae* , L. *theobromae*, *N. australe*, *N. luteum*, *N. parvum*	China, Uruguay	Delgado-Cerrone *et al*. (2016); Xue *et al*. (2019)

Host	Species	Country	Reference
Olea sp.	*L. hormozganensis*[*]	Iran	Abdollahzadeh *et al*. (2010)
Prunus persica	*B. dothidea*, *D. seriata*, *D. intermedia*, *N. parvum*, *N. luteum*, *D. pseudoseriata*, *N. australe*, *L. theobromae*	China	Tian *et al*. (2018); Wang *et al*. (2011)
Pyrus communis	*B. dothidea*, *Botryosphaeria rhodina*, *Botryosphaeria obtusa*, *B. parva*	China	Zhai *et al*. (2014)
Rubus idaeus	*Neofusicoccum algeriense*	Mexico	Serret-López *et al*. (2017)
Rubus subgenero Eubatu	L. *theobromae,* L. *parva*	Mexico	Contreras-Pérez *et al*. (2019)
Saccharum officinarum	*M. phaseolina*	Mexico	Leyva-Mir *et al*. (2015)
Vaccinium spp.	*B. dothidea*, *L. theobromae*, *N. parvum*, *N. australe*, *Neofusicoccum eucalyptorum*	China, Mexico, Portugal	Mondragón-Flores *et al*. (2012); Xu *et al*. (2015); Boyzo-Marín *et al*. (2016); Hilário *et al*. (2019)
Vitis vinifera	*D. seriata*, *D. mutilata*, *N. australe*, *N. luteum*, *N. parvum*	New Zealand	Billones-Baaijens *et al*. (2015)

[*]= species described recently.

Factors that condition the disease

The phytopathogenic species of Botryosphaeriaceae have a great diversity of hosts, are opportunistic fungi capable of colonizing a large number of botanical species and causing disease in those that are under some type of stress, mainly water stress (De Wet *et al*., 2003). This could be explained because in response to the lack of water, the plant increases levels of abscisic acid and its defenses regulated by jasmonic acid, ethylene and salicylic acid are suppressed and as a result susceptibility to pathogens is increased (Asselbergh *et al*., 2008).

This is important given the emerging climate change conditions that not only increases stress in plant communities but also promotes pathogen development and their survival rates (Slippers and Wingfield, 2017). Stress in plants modifies their susceptibility to pathogens which causes changes in the impact of diseases on crops (Elad and Pertot, 2014).

Symptoms

Diseases of consideration in various crops of agricultural importance are associated with members of Botryosphaeriaceae (Eskalen *et al*., 2013; Bautista-Cruz *et al*., 2018). Some studies carried out by Rosado *et al*. (2016) indicate that often multiple species of the same genus, as well as different genera, are associated with the symptoms and it is difficult to differentiate them for each species (Delgado-Cerrone *et al*., 2016).

In some cases, it has been possible to associate symptoms with the pathogen species due to certain characteristics such as the presence of rings in injuries (Tian *et al*., 2018). Symptoms associated with these fungi are: canker in branches and trunk, decline, gummosis, dieback of branches, necrosis in leaves, rots of seeds, fruits, peduncle, root and blight of shoots and inflorescences (Slippers *et al*., 2005; Sandoval-Sánchez *et al*., 2013; Dugan *et al*., 2015; Hajlaoui *et al*., 2015; Netto *et al*., 2017; Rodríguez-Gálvez *et al*., 2017).

Transmission and dispersion

According to Bihon *et al*. (2011), these fungi are transmitted horizontally from mature plants to young plants by means of spores; however, vertical transmission has not yet been proven. The release of spores is more frequent during the rainy period than in other seasons, and these are mainly dispersed by splashing rainwater (Skalen *et al*., 2013).

Research indicates that in addition to their potential as pathogens, they can be associated with fungi of other families and transmitted by bark beetle (*Hypocryphalus mangiferae*), which acts as a vector in the dispersion between hosts (Adawi *et al*., 2006). On the other hand, it is believed that the dieback caused by these fungi could serve as a mitigating of other major diseases such as the sudden oak death, by killing branches that would otherwise produce leaves that easily become infected with *Phytophthora ramorum* and that are spread through splashes of rainwater (Lawrence *et al*., 2017).

When fruit trees are subjected to cultural practices, pruning wounds are a source of stress for the plant and provide an entry point to pathogens that colonize tissues in a basipetal form (Rodríguez-Gálvez *et al*., 2017). There are reports that indicate that the presence of a wound is not necessary for fungi to infect the host’s organs, however, they do contribute to increasing the severity of symptoms (Zhou *et al*., 2015).

Abiotic factors such as the increase of temperature, high relative humidity, droughts, frosts, high planting densities and poor pruning practices favor the development of the disease increasing the incidence that ranges from 20 to 97% in some crops (De la Mora-Castañeda *et al*., 2014; Fernández-Herrera *et al*., 2017; Bautista-Cruz *et al*., 2018).

Conclusions

The Botryosphaeriaceae family is of great importance for the diseases that cause in crops of agricultural importance in all temperate, tropical and subtropical areas around the world. Their ability to move from endophyte to pathogen in plants under stress means a threat in crops subjected to suboptimal developmental conditions, water stress, for example.

Due to the lack of information on aspects of reproduction, survival, dispersion and accurate detection and identification techniques, more studies on these pathogens to establish appropriate disease control and management measures are required globally.

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