OPEN ACCESS Int. J. Phytopathol. 10 (01) 2021. 49-56 DOI: 10.33687/phytopath.010.01.3447

Check for updates

Available Online at EScience Press
International Journal of Phytopathology
ISSN: 2312-9344 (Online), 2313-1241 (Print)
https://esciencepress.net/journals/phytopath

BOTRYOSPHAERIA TREE FUNGAL PATHOGENS AND THEIR DIVERSITY

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ARTICLE INFO

Article History
Received: December 08, 2020
Revised: January 31, 2021
Accepted: March 27, 2021

Keywords
Botryosphaeria dothidea
Ascomycetes
Eucalyptus plant spp.
Stress

ABSTRACT

The genus *Botryosphaeria* identified in 1863 as saprophytes of dead tissue of woody plants have been described as pathogens of economically important plantation trees in agriculture and native forests. The genus is a species-rich, worldwide distributed occurring on diverse host ranges. Species of the *Botryosphaeria* are reported as the pathogens of many plantation trees, including species of *Acacia*, *Eucalyptus,* and *Pinus* causing canker and rapid dieback diseases which often end up in death. *Botryosphaeria* fungal pathogens have cross pathogenicity on different host tree species which enables them important and focus area of research. The taxonomy of *Botryosphaeria* spp. have been under research, identification of these fungi has generally been based on morphological features of the anamorph that usually seen under the microscope. Characters that are used to classify genera in the *Botryosphaeria* have mostly relied on the macroscopic features of the ascospores and the conidial features. Currently, molecular techniques such as DNA sequencing involving amplification of ITS region are important for exact identification of the genera to species level. Recent molecular, phylogenetic and morphological findings showed that order *Botryosphaeriales* is diverse consisting nine families and 33 genera with 23 genera only in the family *Botryosphaeriaceae*. *Botryosphaeria* spp*.* are naturally endophytes associated with tree plants known to cause monocyclic or polycyclic diseases resulting in polyetic epidemics. The factor that makes plants more prone to *Botryosphaeria* fungal species is assumed to be stress or wounding associated with the host plants. Global climate change driven drought is an important factor that initiate stress resulting in nutrient deficiencies. *Botryosphaeria* fungal tree diseases can be best managed by ensuring plants are in optimal health through appropriate integration of cultural, silvicultural and fungicidal applications to effectively prevent and control the diseases.

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INTRODUCTION

The genus *Botryosphaeria* since identified, as saprophytes of dead tissue of woody plants in 1863, repeatedly reported as pathogens, particularly within the nursery and economically important trees utilized in agriculture and forestry (Slippers and Wingfield, 2007). The genus is reported diverse, occurring on a various host starting from monocotyledonous, dicotyledonous, and gymnosperm hosts to woody branches, herbaceous leaves, stems and haulms of grasses, twigs to the thalli of lichens as saprobic, parasitic and endophytic nature usually causing die-back and canker diseases (Crous *et al.*, 2006; Pavlic *et al.*, 2007).

Botryosphaeria fungi were reported as opportunistic pathogens existing symptomless hidden in plant tissues with potential of pathogenicity when plants are under stressing environmental situations like drought, freezing, hot or cold winds, hail wounds or damage which expose to insects pests or other pathogens (Anderson *et al.*, 2004; Slippers and Wingfield, 2007; Gonthier and Nicolotti, 2013; Moral *et al.*, 2019). Research reports reveals that *Botryosphaeria* species are pathogens of many plantation trees, like Acacia, Eucalyptus and Pinus (Mohali *et al.*, 2009). Gezahgne *et al.* (2004) also reported that *Botryosphaeria* species were among the fungi that cause the most damaging canker and dieback disease of *Eucalyptus* spp. in Ethiopia. Jami *et al.* (2014) showed that diverse ecological range and cryptic endophytic property leads these fungi prime for being spread with living material and infect both native and non-native trees. Recent research findings revealed that the species within the genus are now causing new disease outbreaks within the world (Phillips *et al.*, 2013).

Several research findings also indicates increasing evidence of identified new species of the Botryosphaeriaceae related to global climate change (Desprez-Loustau *et al.*, 2006; Slippers and Wingfield, 2007; Phillips, 2016). The increasing importance of *Botryosphaeria* due to pressure on plant communities as a result of climate change is a key motivation to focus on and compile existing knowledge about host, symptoms, taxonomy, diversity, distribution, pathogenicity and management options of this group of fungi for better widen awareness and future ease of identification, prevention and control of associated diseases.

TAXONOMY OF *BOTRYOSPHAERIA* TREE FUNGAL PATHOGENS

The family of Botryosphaeriaceae was reported being passed through sere of taxonomic revisions over the past years and now referred to as large family of filamentous fungi within the *Ascomycota* of which first members were described in the 1820s as species of *Sphaeria* (Phillips *et al.*, 2013; Slippers *et al.*, 2013).The genus *Botryosphaeria* was reported by Cesati and De Notaris in 1863 and Theissen and Sydow grouped the family *Botryosphaeriaceae* and therefore the genus *Botryosphaeria* as sub-class of the *Dothideinae* in 1918 (Slippers *et al.*, 2009; Slippers *et al.*, 2017). Taxonomy of *Botryosphaeriaceae* and *Botryosphaeria* are under several revisions to different family and subfamily up to now, but Schoch *et al.* (2006) introduced the order *Botryosphaeriales*, containing single family, *Botryosphaeriaceae* and genera *Botryosphaeria* using multigene based phylogeny for the first time.

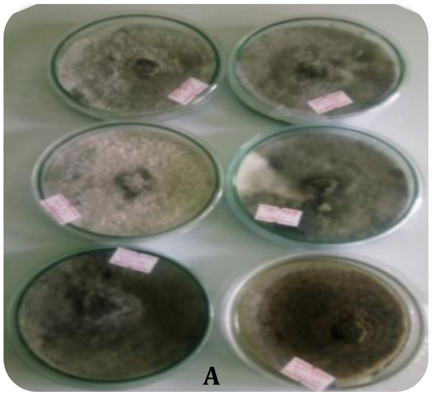
IDENTIFICATION OF *BOTRYOSPHAERIA* SPECIES

Identification of *Botryosphaeria* spp. using morphological method

Botryosphaeria spp. are often easily distinguished from the remainder of fungal groups by their macroscopic features like grey to black aerial mycelium and gray to indigo or grey to black pigment visible from the reverse side of cultures on the petri plates (Crous *et al.*, 2006; Phillips *et al.*, 2008). Asexual morphs are reported to be easily observed on cultures induced in Water Agar (WA), or pine needles and regularly used for identification because of minor differences across the taxon (Figure 1) while, sexual morphs have little taxonomic importance due to their variation in response to different substrate or growth conditions (Phillips *et al.*, 2013). In recent years, identification of genus *Botryosphaeria* to species level is accurately done in combination of DNA sequence data with the morphological characteristics (Denman *et al.*, 2003; Phillips *et al.*, 2008).

Identification of *Botryosphaeria* species using molecular methods

In recent years, molecular techniques involving analysis of internally transcribed spacer (ITS) of the ribosomal RNA gene region (rRNA) is quicker and accurate identification method to differentiate between closely related *Botryosphaeria* species of overlapping features than traditional morphological methods (Phillips, 2002; Slippers *et al.*, 2017). DNA sequence analysis of the ITS region are often more accurate and informative if it involves other explanatory gene regions: introns of protein-encoding genes, β-tubulin, actin, EF1-α and the RNA polymerase II (rpb2) to differentiate among very closely related genera to species of *Botryosphaeria* like *B. dothidea* and *Neofusicoccum parvum* (Phillips *et al.*, 2013; Slippers *et al.*, 2017). The minimal DNA sequence of the ITS region required for the identification of *Botryosphaeria* species is to be 200 base pairs (bp) sequence as reported by Vilas-Boas *et al.* (2007).



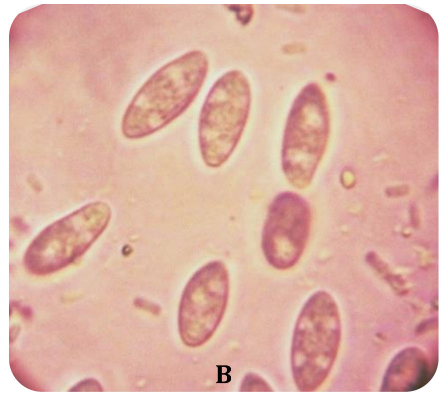


Figure 1. Macroscopic (A) and microscopic (B) morphology of *Botryosphaeria* specie (*Neofusicoccum parvum*) from *Eucalyptu*s plants on Malt Extract Agar in Ethiopia (CEE-FRC, 2017).

GENUS AND SPECIES OF *BOTRYOSPHAERIA* SPECIES DESCRIBED SO FAR

Currently the taxonomy of *Botryosphaeria* is reported under Fungi, Phylum *Ascomycota*, Class *Dothideomycetes*, order *Botryosphaeriales*, family *Botryosphaeriaceae* and genus *Botryosphaeria* (Denman *et al.*, 2003; Crous *et al.*, 2006; Yang *et al.*, 2017). Recent molecular, phylogenetic and morphological findings revealed that order *Botryosphaeriales* generally consists 9 families and 33 genera of which 23 genera are within the family *Botryosphaeriaceae* and genus *Botryosphaeria* now encompassing, *B. agaves*, *B. corticis*, *B. dothidea*, *B. fabicerciana*, *B. fusispora*, *B. ramose*, *B. eucalyptorum* and *B. scharifii* (Ahumada, 2005; Abdollahzadeh *et al.*, 2013; Phillips *et al.*, 2013; Slippers *et al.*, 2013).

BIOLOGY OF *BOTRYOSPHAERIA* TREE FUNGAL PATHOGENS

Botryosphaeria species were reported to survive frequently on bark and other parts like evergreen leaves as endophytes, latent or opportunists and overwinter as fruiting bodies on dead tissue, germinate epiphytically, penetrate and grow intercellularly and transmitted horizontally in plant tissues (Slippers *et al.*, 2009). Gonthier and Nicolotti (2013) reported *Botryosphaeria* fungi penetrate the trees using powerful enzymes actively or via the stomata, natural openings, wounds passively and absorb nutrients by producing an appressorium-like hyphal masses.

REPRODUCTION IN *BOTRYOSPHAERIA* SPP.

Reproduction in *Botryosphaeria* fungal species

Botryosphaeria spp. have clear sexual (teleomorph) and asexual (anamorph) stages that produce mass of spores from a central ostiole within the pycnidium or perithecium (Phillips *et al.*, 2013). The sexual morphs are not intrinsically important for identification and classification since it varies within a species in several growth conditions (Phillips *et al.*, 2013).Characters aid to differentiate between genera and species of *Botryosphaeria* have largely relied on the morphological features of the anamorph like conidial shapes, pigmentation, wall thickness, and septation (Phillips *et al.*, 2013). Conidia of the *Botryosphaeria* are often distinguished by thin-walled, narrow and fusicoccum-like, and thick-walled, wider, diplodia-like conidia (Moral *et al.*, 2019).

EPIDEMIOLOGY, LIFE CYCLE, PATHOGENICITY, AND SYMPTOMS OF *BOTRYOSPHAERIA* TREE DISEASES

Species of the *Botryosphaeria* survive adverse environmental conditions as pycnidia (small dark 'pimple-like' structure) often endophytically, on infected and/or pruned wood and barks while (Phillips *et al.*, 2013; Slippers *et al.*, 2013). The virulent nature of the fungi typically occurs when trees are subjected to stress (Jami *et al.*, 2014). Mechanism of spread for *Botryosphaeria* species from one plant species to another different is by conidia or ascospores dispersed via wind and rain splashes (Gonthier and Nicolotti, 2013). *Botryosphaeria* spp. use appressorium, enzymes and toxins for active mechanical penetration and directly through natural openings like stomata and lenticels for colonization of host tissues (Mancero-Castillo *et al.*, 2018). After active mechanical penetration fungal mycelium continually grow, advancing after arrival and rupture the leaf epidermis while in the case of wounds, openings like stomata and lenticels, the cell walls of xylem vessels and tracheids adjacent to the injuries are extensively lignified becoming necrotic ending up in canker development (Gonthier and Nicolotti, 2013; Moral *et al.*, 2019).

DISEASES AND SYMPTOMS

Botryosphaeria being opportunistic pathogens trigger several pre-infection processes like adhesion, spore germination, and host recognition once land on susceptible tissues of as pycnidiospores or ascospores, (Slippers *et al.*, 2009; Sammonds *et al.*, 2015).

Symptoms of the disease are usually die-back and canker on twigs, branches and trunks of trees, and more rarely cause diseases like seed-capsule abortion, leaf diseases, seedling diseases and root cankers, blight of shoots, gummosis, in severe cases (Pillay *et al.*, 2013).

HOST RANGES DISTRIBUTION AND CROSS PATHOGENICITY

Botryosphaeria fungal species exists across all geographical and climatic areas of the planet**,** except the Polar Regions (Abdella, 2004; Slippers and Wingfield, 2007; Taylor *et al.*, 2009). The fungal species are frequently introduced to new area via imported infected planting or nursery material and jump hosts to cause devastating diseases on native plant species (Slippers *et al.*, 2005). *Botryosphaeria* spp. are reported to cause diseases on important forest tree species worldwide particularly on Acacia spp., *Pinus* spp., *Olea* spp., *Prunus* spp., *Syzygium* species and *Eucalyptus* spp. (Abdollahzadeh *et al.*, 2013). Pavlic *et al.* (2007), Pillay *et al.* (2013), and Jami *et al.* (2014) reported the cross pathogenicity of *Botryosphaeria* spp. specially *Botryosphaeria dothidea*, among *Syzygium*, *Eucalyptus* spp. and *Acacia* spp. (Figure 2).

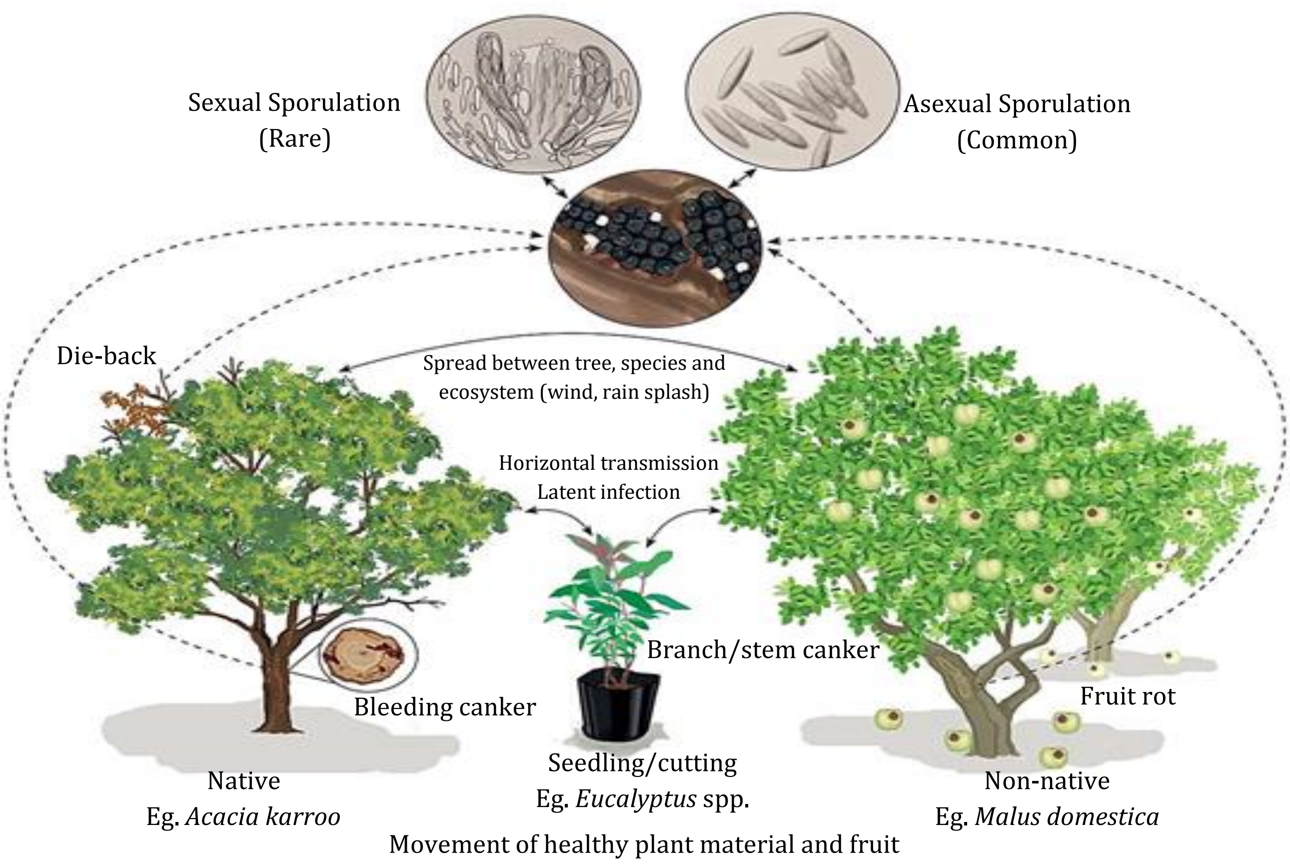


Figure 2. An illustrative example of typical disease symptoms, host associations, sporulation and cross pathogenicity of *Botryosphaeria dothidea* fungus on three hosts, including native (*Acacia* sp.) and non-native (*Eucalyptus* and *Malus* spp.) hosts (Marsberg *et al.*, 2016).

FACTORS CONTRIBUTING TO DISEASES INITIATION AND SYMPTOM DEVELOPMENTS

Botryosphaeria spp. penetrate trees through wounds from mechanical damage or natural openings (Jami *et al.*, 2014). Insects, animals, hail, windstorms and cultural practices can cause damage or wounds are prime infection sites for fungal species increasing the chance for the infection to develop and cause diseases in trees (Slippers and Wingfield, 2007; Abdella, 2004). Conidial dispersal of *Botryosphaeria* species and initiation of spore release were reported to be correlated with rainfall, fog, dew, overhead irrigation, as water dissolves the mucilage to free the conidia (Gonthier and Nicolotti, 2013). Early spring and summer, late summer and autumn are assumed ideal periods for primary and secondary infections respectively while the former the result of high relative humidity which initiate conidia release and germination (Úrbez-Torres *et al.*, 2016). Increasing temperatures, droughts, floods, range expansions for pests and pathogens and pressure on mutualistic partners are stress aggravating factors on plant communities exposing to serious damaging diseases (Desprez-Loustau *et al.*, 2006; Slippers and Wingfield, 2007). Marsberg *et al.* (2016), Gonthier and Nicolotti (2013), Slippers and Wingfield (2007) reported that various stresses are causing irreversible or reversible physical damage to tree physiology which enable *Botryosphaeria* spp., leading causes of diseases which usually manifests affecting both cuticle penetrability and therefore the persistence of the fungi in plant part.

DISEASES AND SYMPTOMS CAUSED BY *BOTRYOSPHAERIA* ON ECONOMICALLY IMPORTANT TREE SPECIES

Botryosphaeria dothidea causing diseases of Eucalyptus species

Botryosphaeria dothidea (Moug. ex Fr) Ces. & De Not, 1863,were considered as wound-infecting stress related pathogens and therefore the recent global climate change is predicted to be the main factor for the occurrence of the strain on many plant communities, including trees in the natural woody ecosystems, managed forests and agriculture offering opportunity for a pathogen to infect new hosts (Burgess *et al.*, 2006). The present wide spread distribution of *B. dothidea* globally has most likely resulted from anthropogenic long-distance dispersal via the worldwide trade of plants and plant products and disease expression is typically attributed to a biotic stress like drought, physical damage, water logging, frost and unsuitable growing environments (Slippers and Wingfield, 2007). *Botryosphaeria dothidea* is among important quarantine fungi in many countries since it is often easily transported with plant tissues and seeds among countries and regions without showing any visible disease symptoms (Abdella, 2004; Pavlic *et al.*, 2007). The limited host specificity nature of the fungal pathogen enables the fungi to be cross pathogenic once introduced into new area (Marsberg *et al.*, 2016). *Botryosphaeria* were reported among the pathogens critically influencing *Eucalyptus* grown in plantations or woodlot causing cankers and dieback followed by production of kino, a dark-red tree sap, and in severe cases mortality of trees (Figure 3) (Denman *et al.*, 2000; Gezahgne *et al.*, 2004; Slippers *et al.*, 2009). These fungi also exist asymptomatically with healthy Eucalyptus leaves, twigs and stems, typically causing disease when there are suitable environmental conditions (Gezahgne *et al.*, 2004; Pérez *et al.*, 2008).

Figure 3. Diseases symptoms associated with *Botryosphaeria* (*Botryosphaeria dothidea*) on *Eucalyptus grandis* plant species (Picture taken from plantation fields, CEE-FRC, 2010).

MANAGEMENT OF TREE DISEASES CAUSED BY *BOTRYOSPHAERIA* FUNGAL PATHOGENS

There are no effective fungicide controls for *Botryosphaeria* diseases, the best management option is to keep plants in optimal health by providing the appropriate cultural management options such as silviculture, avoiding plant stress and injury, and employing appropriate sanitation measures (Slippers and Wingfield, 2007; Úrbez-Torres *et al.*, 2016). Research findings showed that several strategies and their integration can help to effectively manage tree diseases caused by *Botryosphaeria* fungal species.

Plant selection avoidance and exclusion

Proper plant surveillance for signs of stress during purchase and planting trees at an appropriate landscape can help to minimize *Botryosphaeria* diseases (Gonthier and Nicolotti, 2013). In commercial forestry species-site matching, appropriate planting densities and spacing, soil treatment involving fumigation, soil solarization or sanitation to reduce inoculum can be used to minimize exposure of trees to *Botryosphaeria* diseases (Slippers *et al.*, 2009; Little *et al.*, 2003). Maintenance of soil fertility by addition of fertilizers or compost to avoid nutrient stress, and appropriate irrigation to avoid moisture stress, reducing humidity available for spore release, mycelial growth and infection can minimize host susceptibility and infection (Michailides *et al.*, 2004).

Coating wounds with a fungicidal paint may reduce infection by these and other pathogens (Epstein *et al.*, 2008). Neighboring trees health is also important in nursery settings so that young plants may not get infected by inoculum from surrounding diseased plants (Stanosz *et al.*, 2005).

Resistance

The use of clonal material with similar genetic features raises likelihood of disease outbreaks in large areas of the world (Pérez *et al.*, 2008). Plant breeding using appropriate screening for resistance and tolerance to species of the *Botryosphaeria* in forestry and agriculture prior to commercialization and transplanting can be an effective management option against the diseases (Slippers *et al.*, 2009). Research findings of Wingfield *et al.* (2001) show that breeding for resistance has reduced the impact of diseases such as *Cryphonectria* stem canker of *Eucalyptus* spp.to the extent of among the least threatening diseases.

Integrated disease management

In nurseries, strategies include sanitation, hygiene practices such as the disinfection of grafting shears and pruning tools, wound treatment with a fungicidal paint, pruning at an appropriate time and at a moderate level, and irrigation strategies that minimize exposure to the water or humidity that are available for spore release and mycelial growth can be best approaches to manage diseases due to *Botryosphaeria* spp. (Epstein *et al.*, 2008; Cysne *et al.*, 2010; Gonthier and Nicolotti, 2013).

CONCLUSIONS

- *Botryosphaeria* fungal spp. evolved from saprophytes to endophytes then to opportunistic pathogens of tree plants.
- Current global climate change is providing an opportunity for *Botryosphaeria* spp. to cause substantial losses on the plantation tree species in the world.
- Reliable identification of isolates to species level needs advanced molecular technology.
- The infection cycle and epidemiology of *Botryosphaeria* tree diseases needs further detailed research.
- There is limited information on management of *Botryosphaeria* tree plantation diseases using fungicides and biocontrol approaches.
- There is little information on mechanism for species overlap and gene flow between native and introduced *Eucalyptus* and other hosts.
- *Botryosphaeria* species are well suited to being accidentally moved internationally together with germplasm. The patterns and extent of such movements are not known for most of the species in the world.

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CONFLICT OF INTEREST

The authors declare that they have no conflicts of interest.

AUTHORS CONTRIBUTIONS

All the authors contributed equally to this work.