



Phytopathogenic discomycetes, their economic impacts and control applications

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Abstract

Discomycetes is an artificial group in Ascomycota, comprising fungal species bearing saucer-, cup- or disc-like ascoma. There are many records of phytopathogenic discomycetes causing diseases in a wide range of vascular and non-vascular plants worldwide. In this review, we present phytopathogenic, discomycetous fungal taxa and provide notes on representative species, their economic importance and available management strategies. Phytopathogenic discomycetes are found in six classes of fungi, *Dothideomycetes* (distributed across three orders, two families and seven genera), *Eurotiomycetes* (across two orders, two families and two genera), *Lecanoromycetes* (across three orders, three families and four genera), *Leotiomycetes* (across nine orders, 23 families and 104 genera) and *Pezizomycetes* (across one order, seven families and 18 genera). The survival and completion of the life cycle of these discomycetes depend on their mode of parasitism on plant hosts in terrestrial habitats, including man-made landscapes (i.e., agricultural areas) and natural environments (i.e., forests). Agricultural and forest plant commodities are impacted by biotrophic, hemibiotrophic and necrotrophic discomycetes. Due to the complexity of their life cycles, many species have not yet been discovered and documented. Thus, this study can provide the foundation for comprehensive future studies into their taxonomy, physiology and host interactions.

Keywords – epidemiology – food security – fungal diseases – parasitic fungi – virulence

Introduction

The increasing human population and reduction of agricultural landscapes have a direct impact the global food security. For agricultural crops, fungal diseases pose one of the most significant challenges, with climate change aggravating the infection on various crops (Harvell et al. 2002). It is estimated that 16% of crop losses are due to microbial pathogens, among which approximately 75% are caused by fungal diseases (Oerke 2006).

Fungal diseases on food crops negatively impact food availability and economic losses. One of the most devastating fungal pathogens, *Pyricularia oryzae* (basionym: *Magnaporthe oryzae*) causes the blast disease not only on rice but also on barley, millet and wheat (Couch et al. 2005, Dean et al. 2012). Blast disease caused by *Pyricularia oryzae* lowers the yield by 10–13% or around 50 million tonnes (Talbot et al. 2003, Boddy 2016). *Fusarium oxysporum* is another

phytopathogen targeting ornamental and horticultural crops, causing an economic loss of over 130 million USD to the banana industry in Australia (Cook et al. 2015). Phytopathogenic fungi not only affect food crops but also leads to substantial losses in forestry. *Ceratocystis fagacearum* is a fungal pathogen of oak that cause significant economic losses by infecting more than 260,000 oak trees in Anoka County, Minnesota, resulting in a mitigation cost of over 18 million USD (Haight et al. 2011). Annually, in the USA, fungal diseases caused more than 200 billion Euro of financial loss on pre- and post-harvest agricultural commodities, including the cost of fungicides, which exceeds 600 million USD (Arora et al. 2004).

Phytopathogenic discomycetes

Discomycetes is an artificial group of ascomycetes characterized by their teleomorphic discs, cups or saucer-like apothecia or ascomatal structures, composing a hymenium, with or without paraphyses and outlined by excipular cells (Pfister & Kimbrough 2001, Ekanayaka et al. 2017). Discomycetes inhabit terrestrial and aquatic environments as saprobes, symbionts (bryosymbionts, ectomycorrhizae and lichens), endophytes, fungicolous taxa, nematode trappers and phytopathogens (Hosoya & Otani 1995, Künkele et al. 2005, Wang et al. 2011, Doveri 2012, Gueidan et al. 2014, Hyde et al. 2014, Lücking et al. 2016). In their life cycle, discomycetes fungi have shown hyphomycetous, coelomycetous, pycnidial and yeast asexual forms (Redhead 1977a, Hansen & Pfister 2006, Lantz et al. 2011, Crous et al. 2014). Those asexual forms are recognized for some taxa, but some are not available due to the isolation difficulties which hinder further studies on the understanding of discomycetes' life cycle (Spooner 1987).

Previous records classified phytopathogenic discomycetes in various fungal taxa within *Ascomycota* from many host plants and regions (Dowson 1913, Funk 1962, 1967, Childs 1968, Funk 1982, Fitt et al. 1988, Batra 1991, Annesi et al. 1997, Cho et al. 2016, Egertová et al. 2016, Elad et al. 2016, Çolak & Kaygusuz 2017, Crous et al. 2019). Many phytopathogenic discomycetes parasitize host plants in their apothecial forms, such as *Pezizomyces*, while some *Leotiomyces* infect in their asexual forms (i.e., *Botrytis cinerea*, *Monilinia fructigena*, *Sclerotinia sclerotiorum*, etc.) (Groves & Drayton 1939, Schwartz & Steadman 1978, Batra & Harada 1986). Induction of apothecial formation in phytopathogenic discomycetes depends on specific conditions, such as mimicking natural habitats that vary within regions and species even within a similar genus (Bergquist & Lorbeer 1973, Spiers & Hopcroft 1986, Moore-Landecker 1992, Norvell & Redhead 1994, Terhem 2015). For example, apothecia of *Drepanopeziza brunnea* (anamorph: *Marssonina brunnea*) were reported in Europe but not in New Zealand, Japan and Korea (Spiers & Hopcroft 1986).

Phytopathogenic discomycetes are noteworthy to be further explored because of their economic importance and need for management strategies (Elad & Freeman 2002, Bogacheva 2005, Baral 2016). However, the number of studies on these phytopathogens is not proportionately similar to those that centralized on certain taxa due to their massive economic impacts on a wide range of crops (Batra 1991, Boland & Hall 1994, Elad et al. 2004). *Botrytis cinerea*, for example, gained tremendous research interest throughout the world, resulting in new records (on hosts, regions), host-pathogen interactions, disease incidences and management strategies (Elad & Shtienberg 1995, Legard et al. 2000, Dean et al. 2012, Williamson et al. 2007, Sowley et al. 2010, Duan et al. 2014, Elad et al. 2016, Yang et al. 2018, Ebrahimzadeh & Abrinbana 2019, Petrasch et al. 2019). Furthermore, *Monilinia fructigena*, several other *Monilinia* species and *Sclerotinia sclerotiorum* also received immense research interest due to their negative economic impact on food crops (Boland & Hall 1994, Kim et al. 2008, Ivanović & Ivanović 2001, Hily et al. 2010, Hu et al. 2014, De Miccolis Angelini et al. 2018). In addition, *Diplocarpon rosae*, *Oculimacula yallundae* and other phytopathogenic discomycetes are also gaining research interest and are still in need of more investigations (Blein et al. 2009, Marin-Felix et al. 2019).

Phytopathogenic discomycetes are diverse and unique but reported separately in individual studies. Current information on discomycete taxa, their impacts and updates on available approaches for disease mitigation are disjointed, thus, required to be revisited as a whole. The main

purpose of this review is to extract and compile information from miscellaneous resources about fungal taxa, their diseases, their economic significance, and the available mitigation strategies to provide an overview of phytopathogenic discomycetes.

Discomycete species are distributed across 11 classes: *Arthoniomycetes*, *Coniocybomycetes*, *Dothideomycetes*, *Eurotiomycetes*, *Geoglossomycetes*, *Lecanoromycetes*, *Leotiomycetes*, *Lichinomycetes*, *Neoleotomycetes*, *Orbiliomycetes* and *Pezizomycetes* (Ekanayaka et al. 2017), inhabiting terrestrial and aquatic environments with various ecological roles. Among these, some are phytopathogens that cause various plant fungal diseases (Hosoya & Otani 1995, Künkele et al. 2005, Wang et al. 2011).

Phytopathogenic discomycetes in *Dothideomycetes*

Phytopathogenic discomycetes in *Dothideomycetes* are characterized by semi-immersed to erumpent, black, hysteriform apothecia, bitunicate or fissitunicate asci and ellipsoid, fusiform, long clavate and septate ascospores (Samuels & Müller 1979, Inácio et al. 2012, Guatimosim et al. 2015, Jayasiri et al. 2016, Tian et al. 2016). The sexual forms of phytopathogenic discomycetes in *Dothideomycetes* are grouped in *Catinellales*, *Eremithallales*, *Hysteriales*, *Mytilinidiales*, *Patellariales* and *Pleosporales* (Ekanayaka et al. 2017). Many phytopathogenic *Dothideomycetes* were noted (Hongsanan et al. 2020), but very few belong to discomycetes (Table 1).

Rhytidhysteron rufulum is a phytopathogenic species in *Dothideomycetes* recognized as a weak parasite on unidentified dicotyledon plants despite most studies finding this species as saprobes (Samuels & Müller 1979, Thambugala et al. 2016). No further studies have been conducted to explore the weak pathogenicity of *Rhytidhysteron rufulum* on its hosts. Tian et al. (2016) reported *Aldona stella-nigra*, *Aldonata pterocarpi* and *Viegasella pulchella* to cause leaf necrosis by penetrating host cells and obtaining nutrients via structures under ascomata (Inácio & Canon 2008). *Antoniomyces loranthicola* and *Dothidasteromella parvispora* also cause leaf spot diseases on *Gaiadendron punctatum* and *Olox wightiana*, respectively (Luttrell & Muthapa 1974, Inácio et al. 2012). Guatimosim et al. (2015) reported the biotrophic pathogen, *Inocyclus angularis* to cause the black tar spot disease on fern species (*Pleopeltis atrolepis*). Further studies on life cycles, infection modes, and pathogenicity factors of *Antoniomyces loranthicola*, *Dothidasteromella parvispora* and *Inocyclus angularis* are limited and need to be studied in detail (Luttrell & Muthapa 1974, Inácio et al. 2012). The number of species of phytopathogenic discomycetes is shown in Table 1, but the number can be more since it only represents one species for each reported genus.

Phytopathogenic discomycetes in *Eurotiomycetes*

Eurotiomycetes is a prominent class of saprobes that switches to pathogens in humans, animals, plants and symbionts (lichens, ectomycorrhizae and myrmecophytes) (Henkel et al. 2006, Blatrix et al. 2013, Gueidan et al. 2014). *Eurotiomycetes* include cleistothecial and perithecial bearing phytopathogens (Döbbeler 1997, Thambugala et al. 2014), among which most are filamentous, such as *Aspergillus* sp. (Cotty et al. 1994), while few are discomycetes (Table 2) (Döbbeler & Hertel 2013). Phytopathogenic discomycetes in *Eurotiomycetes* are characterized by short to long stalked-apothecia, unitunicate, clavate asci, and fusiform to ellipsoid, hyaline to dark brown, septate ascospores (Marsh et al. 2010, Döbbeler & Hertel 2013).

Stenocybe nitida is a biotroph on *Plagiochilla punctata*, causing systemic infections in its host by developing hyphae on cell walls and producing stipitate apothecia from the leafless stem of the host (Döbbeler & Feuerer 2004). *Stenocybe nitida* was parasitic mostly on *Plagiocilla punctata* but sometimes found on other *Plagiochilla* species (Döbbeler & Hertel 2013). In contrast to *S. nitida*, *Dactylospora heimerlii* not only infect axil leaves and perianth of *Plagiocillaceae* (Marsh et al. 2010) but also other genera of hepatic bryophytes (Döbbeler & Triebel 1985). For both species, detailed studies on life cycles and pathogenic factors are still lacking (Davey & Currah 2006). Phytopathogenic discomycetes in *Eurotiomycetes* were reported mostly on bryophytes from different regions (Döbbeler & Hertel 2013).

Phytopathogenic discomycetes in *Lecanoromycetes*

Lecanoromycetes consists of mostly lichenized symbionts (lichens) in addition to saprobes and phytopathogens (Sherwood et al. 1980, Huneck & Yoshimura 1996, Lawrey & Diederich 2003, Wedin & Wiklund 2004). Based on ascomatal morphologies, *Lecanoromycetes* divided into plectomycetes, pyrenomycetes and discomycetes (Luttrell 1955). Phytopathogenic discomycetes in *Lecanoromycetes* are defined by interlamellar, sessile apothecia, unitunicate, claviform to cylindrical asci, and hyaline, ellipsoid, elongated ovate to fusiform, aseptate to septate ascospores (Vězda 1965, Ceynowa-Giełdon 2003, Söchting et al. 2008, Stenroos et al. 2009, Döbbeler & Hertel 2013). In this study, we found records of phytopathogenic discomycetes distributed across two orders and four genera in *Lecanoromycetes* (Table 3). Table 3 represents phytopathogenic genera with one or two species and some with more species, such as *Potriphila* (Döbbeler 2002).

Absconditella sphagnum, *Caloplaca nivalis*, *Potriphila navicularis* and *Puttea margaritella* are pathogenic discomycetes infecting various bryophytic families (*Andreaeaceae*, *Grimmiaceae*, *Polytrichaceae*, *Ptilidiaceae* and *Sphagnaceae*) (Söchting et al. 2008, Döbbeler & Hertel 2013). *Absconditella sphagnum* infects *Sphagnum* sp, an important bryophyte that provides the raw material for horticulture (Stenroos et al. 2010, Ludwig 2019). In Guizhou province, China, the net revenue of *Sphagnum* farming reached € 15000 per ha annually and is considered an exported commodity to overseas countries, such as Europe, Indonesia, Japan, North America, Malaysia, Taiwan, Thailand and Vietnam (Zhu 2019). *Potriphila navicularis* infect bryophyte species, such as *Dendroligotrichum squamosum* but is found mainly on *Polytrichastrum alpinum* (Döbbeler 1996). Infection of *P. navicularis* is systemic and develops haustoria in each host cell of trichomes, following the emergence of pycnidia on upper leaves and apothecia on lower leaves (Döbbeler 1996, Döbbeler & Hertel 2013). These biotrophic associations with hosts prevail in the environment (Döbbeler 1997). *Puttea margaritella* is most likely a necrophyte found mostly on diseased and decaying *Ptilidium pulcherrimum*, a bryophyte that exhibits antimicrobial and moderate cytotoxicity properties against subcutaneous tumor cells in laboratory trials (Guo et al. 2009, Stenroos et al. 2009, Veljić et al. 2010), and also found on *Lophocolea heterophylla* as a facultative host (Stenroos et al. 2009, Czarnota & Hernik 2013). *Caloplaca nivalis* was also reported as a pathogen on *Andreaea* sp. and *Grimmia* sp. (Söchting et al. 2008).

Studies on phytopathogenic discomycetes in *Lecanoromycetes* are lacking (Davey & Currah 2006). Döbbeler (2002) reported micro-niches favored by bryophylous ascomycetes and briefly discussed the niche of *P. navicularis* but does not provide details on their life cycle and virulence factors. There are no studies on infection modes, life cycles and pathogenic factors of *A. sphagnum*, *C. nivalis* and *P. margaritella*. Most studies reported their incidence in different regions and on various bryophytes (Döbbeler 2002, Söchting et al. 2008, Czarnota & Hernik 2013). However, to date, no economic losses and control strategies against these pathogens on their related aforementioned bryophytic species are reported.

Phytopathogenic discomycetes in *Leotiomyces*

Leotiomyces include teleomorphic fungi bearing various shapes of minute to medium-sized apothecia, cleistothecia and perithecia with anamorphic forms of hyphomycetes and coelomycetes (Quandt & Haelewaters 2021). *Leotiomyces* are found in terrestrial and aquatic habitats mostly as saprobes, sometimes as endophytes, symbionts (lichen, ectomycorrhiza), and animal and plant pathogens (Tedersoo et al. 2009, Queloz et al. 2011, Blehert 2012, Zhang & Wang 2015). Phytopathogenic discomycetes in *Leotiomyces* are characterized by sessile to stipitate, immersed to superficial apothecia, inoperculate, clavate to cylindrical asci interspersed with paraphyses, and hyaline to brown, filiform, pyriform, fusoid to ellipsoid ascospores (Jones 1919, Redhead & Spicer 1981, Jülich & de Vries 1982, Nannfeldt 1984a, Petersen & Pfister 2010, Stenroos et al. 2010, Döbbeler & Hertel 2013, Johnston et al. 2013, Guatimosim et al. 2016). Phytopathogenic discomycetes in *Leotiomyces* cause various diseases and significant financial impacts on economically important plant commodities (Knight & Wheeler 1977, Boland & Hall 1994, Nutter et al. 2002, Parnell et al. 2008, Dean et al. 2012, Elad et al. 2016). More than 100 genera of

phytopathogenic discomycetes within nine *Leotiomyces* orders were listed in Table 4. The table displays that this class has the most members of phytopathogenic discomycetes among others. Perhaps, this is due to their thriving mode in man-made environments, such as agricultural lands, while other discomycetes, for example, *Pezizomycetes* are mostly found in forest habitats.

In *Leotiomyces*, phytopathogenic species are exclusively found in *Cyttariaceae*, *Drepanopezizaceae*, *Erysiphaceae*, *Medeloriaceae* and *Sclerotiniaceae* (Baral 2016). However, among these, discomycetes cannot be found in *Erysiphaceae* as their sexual morph characters are restricted to perithecia and cleistothecia (Salmon 1900). Hence, this family is excluded from the current study. Phytopathogenic discomycetes in *Cyttariaceae* and *Medeolariaceae* generally affect host plants in forests, and their existence is restricted to particular regions (Petersen & Pfister 2010, Pfister et al. 2013). *Drepanopezizaceae* and *Sclerotiniaceae* infect valuable plant commodities mostly grown in man-made habitats (Horst 1990, Schuster 2004, Denton-Giles et al. 2019). Phytopathogenic species, representing *Cyttariaceae*, *Drepanopezizaceae*, *Godroniaceae*, *Medeloriaceae*, *Ploettnerulaceae* and *Sclerotiniaceae* that cause an economic impact on agricultural and forestry commodities (i.e., ornamental plants, seed crops, orchards, staple and cover crops and forestry) are selected and described here. Host plants affected by phytopathogenic *Leotiomyces* are exceptionally broader compared to other discomycetous classes. These hosts range from non-vascular plants (bryophytes and pteridophytes) to agricultural and forestry commodities, including nursery material (Table 4) (Townsend 1951, Redhead 1977b, Jülich & de Vries 1982, Williamson et al. 2007, Bezerra et al. 2008, Melzer et al. 1997, Guatimosim et al. 2016, Marin-Felix et al. 2019, Baral et al. 2022). The species number of phytopathogenic discomycetes in Table 4 is an underestimate since it only represents one or few species for each reported genus.

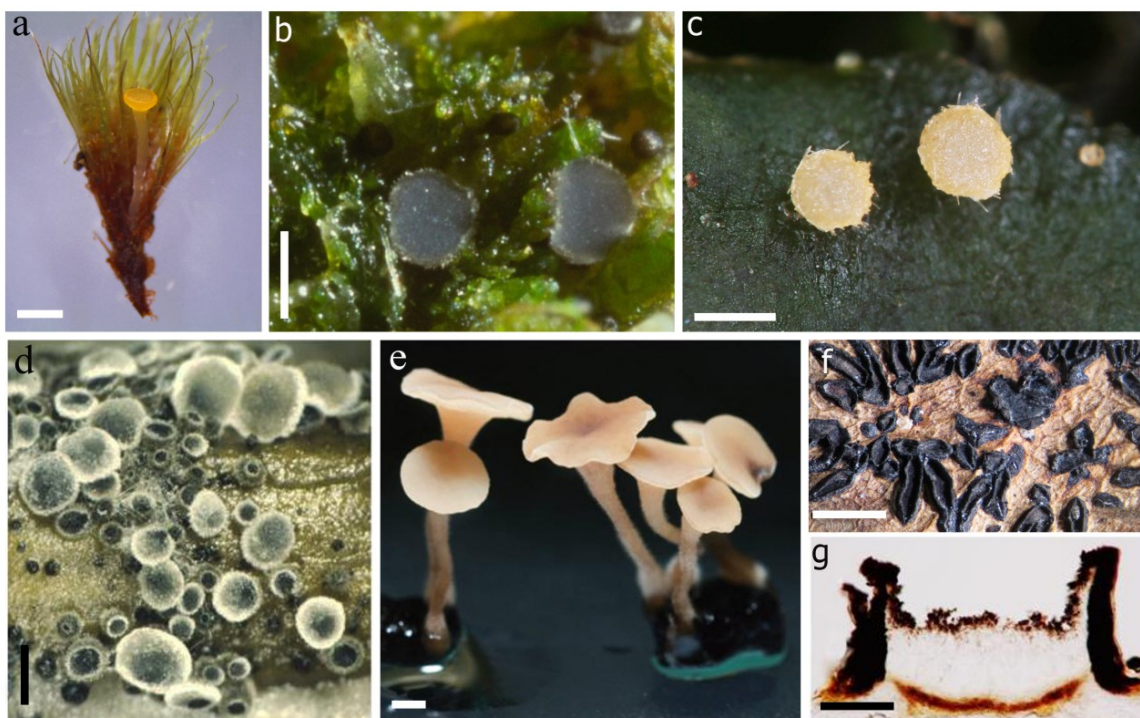


Fig. 1 – Apothecial characters of phytopathogenic discomycetes. a *Bryoclavivulus campylopi* (Johnston et al. 2013). b *Hyaloscypha hepaticola* (Baral et al. 2009). c *Octosporopsis erinacea* (Egertová et al. 2018). d *Oculimacula yallundae* (Marin-Felix et al. 2019). e *Botrytis cinerea* (Rodenburg et al. 2018). f *Aldona stella-nigra* (Tian et al. 2016). g Close section of *Aldona stella-nigra*'s apothecium (Tian et al. 2016). Scale bars: a, d, e, f = 1 mm, b = 200 μ m, c = 500 μ m, g = 100 μ m.

Table 1 Phytopathogenic discomycetes in *Dothideomycetes*.

Fungal taxa	Diseases	Nutritional mode	Host	Region	References
<i>Rhytidhysterium rufulum</i> (<i>Hysteriales</i> , <i>Hysteriaceae</i>)	Black spot	Weak pathogen	Woods of dicotyledon	South and North America, Indonesia, Jamaica, Costa Rica, Dominican Republic	Samuels & Müller (1979)
<i>Aldona stella-nigra</i> (<i>Parmulariales</i> , <i>Parmulariaceae</i>)	Leaf spot		<i>Pterocarpus</i> spp.	Indonesia, The Philippines	Tian et al. (2016)
<i>Aldonata pterocarpii</i> (<i>Parmulariales</i> , <i>Parmulariaceae</i>)	Leaf spot		<i>Pterocarpus draco</i>	India	Tian et al. (2016)
<i>Antoniomyces loranthicola</i> (<i>Parmulariales</i> , <i>Parmulariaceae</i>)	Black spot		<i>Gaiadendron punctatum</i>	Panama	Inácio et al. (2012)
<i>Dothidasteromella parvispora</i> (<i>Parmulariales</i> , <i>Parmulariaceae</i>)	Yellowish spot		<i>Olax wightiana</i>	India	Luttrell & Muthapa (1974)
<i>Viegasella pulchella</i> (<i>Parmulariales</i> , <i>Parmulariaceae</i>)	Leaf spot		<i>Sapotaceae</i>	Paraguay	Tian et al. (2016)
<i>Inocyclus angularis</i> (<i>Dothideomycetes</i> order <i>incertae sedis</i> , <i>Asterinales</i> genera <i>incertae sedis</i>)	Tar spot		<i>Pleopeltis astrolepis</i>	Florida, Southern Brazil	Guatimosim et al. (2015)

Table 2 Phytopathogenic discomycetes in *Eurotiomycetes*.

Fungal taxa	Nutrition mode	Host	Region	References
<i>Dactylospora heimerlii</i> (<i>Sclerococcomycetidae</i> , <i>Sclerococcales</i> , <i>Dactylosporaceae</i>)	Bryophytes parasitic	<i>Plagiochila asplenioides</i>	Alaska, Europe, Japan, Tasmania	Marsh et al. (2010)
<i>Stenocybe nitida</i> (<i>Mycocaliciomycetidae</i> , <i>Mycocaliciales</i> , <i>Mycocaliciaceae</i>)	Cell wall infection	<i>Plagiochila punctata</i>	Europe	Döbbeler & Hertel (2013)

Table 3 Phytopathogenic discomycetes in *Lecanoromycetes*.

Fungal taxa	Nutrition mode	Host	Region	References
<i>Abconditella sphagnum</i> (<i>Ostroporales</i> , <i>Stictidaceae</i>)	Bryophytic necrotrophs	<i>Sphagnum compactum</i> , <i>Sphagnum fuscum</i> , <i>Sphagnum magellanicum</i>	Europe	Vězda (1965), Ceynowa-Gieldon (2003)

Table 3 Continued.

Fungal taxa	Nutrition mode	Host	Region	References
<i>Caloplaca nivalis</i> (<i>Teloschistales, Teloschistaceae</i>)	Bryophytic necrotrophs	<i>Andreaea</i> sp., <i>Grimmia</i> sp.	Europe, USA, Scotland	Søchting et al. (2008)
<i>Potriphila navicularis</i> (<i>Ostroporales, Odontotremataceae</i>)	Bryophytic parasitic	<i>Polytrichastrum alpina</i>	Antarctica, Asia, Australia, Europe, USA, South America	Döbbeler & Hertel (2013)
<i>Puttea margaritella</i> (<i>Lecanorales genera incertae sedis</i>)	Liverwort parasitic	<i>Ptilidium pulcherrimum</i>	Europe	Stenroos et al. (2009)

Table 4 Phytopathogenic discomycetes in *Leotiomyces*.

Fungal taxa	Diseases or nutritional modes	Host	Region	References
<i>Allantophomopsis cytisporae</i> (<i>Phacidiales, Phacidiaceae</i>)	Black rot	<i>Pinus</i> sp., <i>Vaccinium</i> sp.	Latvia, USA	Crous et al. (2014, 2015)
<i>Ascocalyx pinicola</i> (<i>Helotiales, Godroniaceae</i>)	Canker	<i>Pinus taeda</i>	Japan	Kondo & Kobayashi (1984)
<i>Ascocorticium anomalum</i> (<i>Helotiales, Ascocortiaceae</i>)	Whitish, corticoid patches	<i>Pinus</i> sp., <i>Picea</i> sp., <i>Juniperus</i> sp., <i>Larix</i> sp., <i>Acacia</i> sp., <i>Betula</i> sp., <i>Calluna</i> sp.	Europe, North Africa, USA	Jülich & de Vries (1982)
<i>Ascodichaena rugosa</i> (<i>Helotiales, Ascodichaenaceae</i>)	Cork wall inhibition	<i>Fagus sylvatica</i>	Germany	Butin & Pamarewaran (1980)
<i>Ascosorus floridanus</i> (<i>Helotiales, Ascocortiaceae</i>)	Corticoid patches	<i>Quercus laurifolia</i>	USA	Jülich & de Vries (1982)
<i>Atropellis piniphila</i> (<i>Helotiales, Godroniaceae</i>)	Canker	<i>Pinus</i> sp.	USA	Lohman & Cash (1940)
<i>Belonioscyphella hypnorum</i> (<i>Helotiales genera incertae sedis</i>)	Yellowish decoloration	<i>Bryum moravicum</i> , <i>Anomodon</i> sp., <i>Hypnum</i> sp.	Czech Republic, Finland, Canada, Germany	Egertová et al. (2016)
<i>Bifusella linearis</i> (<i>Rhytismatales, Rhytismataceae</i>)	Brown spot needle blight	<i>Pinus radiata</i>	USA	Broders et al. (2015)
<i>Bloxamia cyatheicola</i> (<i>Helotiales, Bloxamiaceae</i>)	Frond spot	<i>Cyathea delgadii</i> , <i>Cyathea atrovirens</i>	Brazil	Guatimosim et al. (2016)
<i>Blumeriella jaapii</i> (<i>Helotiales, Drepanopezizaceae</i>)	Leaf spot	<i>Prunus</i> spp.	Europe, UK, USA	Annesi et al. (1997), Schuster (2004)

Table 4 Continued.

Fungal taxa	Diseases or nutritional modes	Host	Region	References
<i>Botrytis cinerea</i> (<i>Helotiales, Sclerotiniaceae</i>) Teleomorph: <i>Botryotinia fuckeliana</i>	Gray mold	Over 200 crop plants species	Worldwide	Williamson et al. (2007)
<i>Botrytis pseudocinerea</i> (<i>Helotiales, Sclerotiniaceae</i>)	Gray mold	<i>Brassica napus</i> , <i>Lycopersicon esculenta</i> , strawberries, <i>Vitis vinifera</i>	China, France, Germany, Hungary, New Zealand, USA	Walker et al. (2011), Li et al. (2015)
<i>Bryoclaviculus campylopi</i> (<i>Helotiales, Bryoglossaceae</i>)	Small lesion on the base of leaf axil cells	<i>Campylopus acuminatus</i>	New Zealand	Johnston et al. (2013)
<i>Bryoglossum gracile</i> (<i>Helotiales, Bryoglossaceae</i>)	Death patches	Tundra moss	Canada, Europe, Greenland, Iceland, USA	Kankainen (1969), Redhead (1977a)
<i>Bryoscyphus atromarginatus</i> (<i>Helotiales, Helotiaceae</i>)	Thallus parasitic	<i>Marchantia polymorpha</i>	The Netherlands	Verkley et al. (1997)
<i>Calycellina leucella</i> (<i>Helotiales, Pezizellaceae</i>)	Defoliation, leaf withering	<i>Betula</i> spp.	Japan	Bennell & Millar (1984)
<i>Cenangium ferruginosum</i> (<i>Helotiales, Cenangiaceae</i>)	Pine dieback	<i>Pinus sylvestris</i>	USA, South Korea, Spain	Santamaria et al. (2007)
<i>Ciboria carunculoides</i> (<i>Helotiales, Sclerotiniaceae</i>)	Popcorn disease	Mulberry	Korea, Japan	Hong et al. (2007)
<i>Ciborinia camelliae</i> (<i>Helotiales, Sclerotiniaceae</i>)	Petal blight	<i>Camellia</i> spp.	World wide	Sarachi et al. (2019)
<i>Cistella japonica</i> (<i>Helotiales genera incertae sedis</i>)	Stem canker	Hinoki cypress	Japan	Yamada et al. (2003)
<i>Clarireedia paspali</i> (<i>Helotiales, Sclerotiniaceae</i>)	Dollar spot	<i>Axonopus compressus</i> , <i>Paspalum vaginatum</i>	China, USA	Hu et al. (2019)
<i>Coccomyces strobi</i> (<i>Rhytismatales, Rhytismataceae</i>)	Bark death, canker	<i>Pinus strobus</i>	USA	Reid & Cain (1961), McMullin et al. (2019)
<i>Collophorina hispanica</i> (<i>Leotiales, Tympanidaceae</i>)	Branch canker	Almond	USA, Iran, Spain	Holland et al. (2018)
<i>Cristulariella depraedans</i> (<i>Helotiales, Sclerotiniaceae</i>)	Leaf spot	<i>Acer</i> spp.	Europe, Japan, Korea, USA, Poland	Redhead (1975), Cho et al. (2016)

Table 4 Continued.

Fungal taxa	Diseases or nutritional modes	Host	Region	References
<i>Crumenulopsis sororia</i> (<i>Helotiales, Cenangiaceae</i>)	Canker	<i>Pinus</i> spp.	Europe	Vuorinen (2000)
<i>Cudoniopsis pussila</i> (<i>Helotiales, Sclerotiniaceae</i>)	Parasitic on branch	<i>Eugenia proba</i>	Argentina	Spegazzini (1925)
<i>Cyclaneusma minus</i> (<i>Marthamycetales, Marthamycetaceae</i>)	Needle cast	<i>Pinus radiata, Pinus nigra</i>	USA	Frederick et al. (1980)
Basionym: <i>Naemacyclus minor</i> <i>Cyttaria darwinii, C. espinosae, C. exigua, C. gunni, C. nigra, C. pallida</i> (<i>Cyttariales, Cyttariaceae</i>)	Tree canker and galls	<i>Nothofagus</i> spp.	Australia, New Zealand, South America	Petersen & Pfister (2010)
<i>Darkera abietis</i> (<i>Phacidiales, Phacidiaceae</i>)	Needle blight	<i>Abies balsamae</i>	USA	Whitney (1975)
<i>Davisomycella ampla</i> (<i>Rhytismatales, Rhytismataceae</i>)	Jack pine needle blight	<i>Pinus</i> spp.	Brazil, New Zealand, USA	Minter & Gibson (1978a)
<i>Dermea abietinum, D. prunastri, D. pruni, D. pseudotsugae</i> (<i>Helotiales, Dermateaceae</i>)	Dieback	Helmlock, plum	China, UK, USA	Dowson (1913), Dodge (1932), Funk (1967), Jiang & Tian (2019)
<i>Didymascella tetraspora</i> (<i>Helotiales genera incertae sedis</i>)	Needle blight	<i>Juniperus communis</i>	Scotland	Phillips & Burdek (1992)
<i>Diplonaevia luzulina</i> (<i>Helotiales, Calloriaceae</i>)	Leaf parasitic	<i>Luzulae</i> spp.	Finland, Norway, Sweden	Nannfeldt (1984a)
<i>Diplocarpon rosae</i> (<i>Helotiales, Drepanopezizaceae</i>)	Leaf spot, leaf scorch	<i>Rosa</i> spp.	Canada, Pakistan, UK	Knight & Wheeler (1977)
Anamorph: <i>Marssonina rosae</i> <i>Discinella schimperi</i> (<i>Helotiales, Discinellaceae</i>)	Circumpolar parasitic	<i>Sphagnum squarrosum</i>	Canada, Slovakia	Redhead & Spicer (1981)
Synonym: <i>Helotium schimperi</i> <i>Drepanopeziza brunnea</i> (<i>Helotiales, Drepanopezizaceae</i>)	Leaf blight	<i>Populus</i> sp.	USA	Spiers & Hopcroft (1998)
Synonym: <i>Marssonina brunnea</i>				

Table 4 Continued.

Fungal taxa	Diseases or nutritional modes	Host	Region	References
<i>Drepanopeziza ribis</i> (<i>Helotiales, Drepanopezizaceae</i>)	Leaf spot	<i>Ribes</i> spp.	Europe, USA, Japan, Australia and New Zealand	Booth & Waller (1979)
<i>Dumontinia tuberosa</i> (<i>Helotiales, Sclerotiniaceae</i>)	Root rot	<i>Hepatica nobilis</i>	Japan	Uzuhashi et al. (2010)
<i>Durandiella pseudotsugae</i> (<i>Leotiales, Tympanidaceae</i>)	Dime canker	Douglas fir	Canada	Funk (1962)
<i>Elliotiana kernerii</i> (<i>Helotiales, Sclerotiniaceae</i>)	Parasitic on branch	<i>Abies alba</i>	France	Van Vooren et al. (2009)
<i>Elytroderma deformans</i> (<i>Rhytismatales, Rhytismataceae</i>)	Needle cast	<i>Pinus ponderosa</i>	USA	Childs (1968)
<i>Fabrella tsugae</i> (<i>Helotiales, Cenangiaceae</i>)	Needle blight	<i>Tsuga</i> sp.	Canada	Korf (1962)
<i>Felisbertia melastomacearum</i> (<i>Helotiales, Drepanopezizaceae</i>) Basionym: <i>Fabraea melastomacearum</i>	Parasitic on leaves	<i>Melastomaceae</i>	Spain	Spegazzini (1889)
<i>Gloeotinia temulenta</i> (<i>Helotiales, Helotiaceae</i>)	Blind seed	<i>Lolium perenne, Secale cereale</i>	Ireland, Scotland, New Zealand, USA	Hardison (1962)
<i>Gremmeniella abietina</i> (<i>Helotiales, Godroniaceae</i>) Anamorph: <i>Brunchorstia pinea</i>	Stem cancer, death of crown and seedlings	<i>Abies</i> spp., <i>Pinus</i> spp.	Turkey, Europe, USA	Özkazanç & Maden (2013)
<i>Grovesiana pyramidalis</i> (<i>Helotiales, Sclerotiniaceae</i>)	Zonate leaf spot	Soursop, avocado	Brazil, Japan, USA	Cline et al. (1983), Bezerra et al. (2008)
<i>Grovesiella abieticola</i> (<i>Helotiales, Godroniaceae</i>)	Stem canker	<i>Abies</i> sp.	USA	Chastagner et al. (2017)
<i>Godronia cassandrae</i> (<i>Helotiales, Godroniaceae</i>) Anamorph: <i>Topospora myrtilli</i>	Canker	Blubberies	Canada	Sabaratham (2018)
<i>Hyaloscypha hepaticola, Hyaloscypha albocarpa</i> (<i>Helotiales, Hyaloscyphaceae</i>)	Rhizoid infection	<i>Cephaloziella</i> spp.	Belgium, Finland, Germany	Baral et al. (2009)
<i>Hymenoscyphus fraxineus</i> (<i>Helotiales, Helotiaceae</i>) Synonym: <i>Chalara fraxinea</i>	Ash dieback	Ash trees	Europe	Baral et al. (2014)

Table 4 Continued.

Fungal taxa	Diseases or nutritional modes	Host	Region	References
<i>Hypodermella laricis</i> (<i>Rhytismatales, Rhytismataceae</i>)	Needle cast	<i>Larix</i> spp.	Asia, Europe, USA	Minter (1988)
<i>Hysteronaevia luzulicola</i> (<i>Helotiales genera incertae sedis</i>)	Leaf infection	<i>Luzula arcuata</i>	Canada, Sweden	Nannfeldt (1984b)
<i>Isthmiella quadrispora</i> (<i>Rhytismatales, Rhytismataceae</i>)	Needle blight	<i>Abies lasiocarpa</i>	USA	Ziller (1968)
<i>Kohninia linnaeicola</i> (<i>Helotiales, Sclerotiniaceae</i>)	Parasitic on petioles	<i>Linnaea borealis</i>	Norway	Holst-Jensen et al. (2004)
<i>Lachnellula willkommii</i> , <i>Lachnellula decidua</i> (<i>Helotiales, Lachnaceae</i>)	Canker	<i>Larix</i> spp.	Asia, Europe, USA	Yde-Andersen (1979)
<i>Lachnopsis catarinensis</i> (<i>Helotiales, Lachnaceae</i>)	Fronde blight	<i>Dicksonia sellowiana</i>	Brazil	Guatimosim et al. (2016)
<i>Lachnum spartina</i> (<i>Helotiales, Lachnaceae</i>)	Dead shoot	<i>Spartinae alterniflora</i>	USA	Cantrell et al. (1996)
<i>Lambertella corni-maritima</i> (<i>Helotiales, Rutstroemiaceae</i>)	Mummified fruits	<i>Malus prunicola, Prunus domestica, Sorbus aucuparia</i>	Czech Republic, Europe	Palmer et al. (1994)
<i>Lahmia kunzei</i> (<i>Lahmiales, Lahmiaceae</i>)	Branch dieback	<i>Populus</i> sp.	USA	Enebak et al. (1996)
<i>Leptotrochila medicaginis</i> (<i>Helotiales, Drepanopezizaceae</i>)	Yellow leaf blotch	Alfalfa	USA, Canada	Malvick (1988)
<i>Lirula macrospora</i> (<i>Rhytismatales, Rhytismataceae</i>)	Needle blight	<i>Picea</i> sp.	USA	Walla (2016)
<i>Lophodermella concolor</i> (<i>Rhytismatales, Rhytismataceae</i>)	Needle cast	<i>Pinus</i> sp.	USA	Minter & Millar (1993)
<i>Lophodermium seditiosum</i> (<i>Rhytismatales, Rhytismataceae</i>)	Pine blight	<i>Pinus sylvestris</i>	USA, Europe	Minter & Millar (1980), Sinclair (1987)
<i>Lophophacidium dooksii</i> (<i>Rhytismatales, Rhytismataceae</i>)	Needle cast	<i>Pinus radiata</i>	USA	Broders et al. (2015)
<i>Marthamyces emerginatus</i> (<i>Marthamycetales, Marthamycetaceae</i>)	Leaf spot	Eucalyptus	Australia	Crous et al. (2019)
<i>Medeolaria farlowii</i> (<i>Medeolariales, Medeolariaceae</i>)	Leaf whorl, leaf brown	<i>Medeola virginiana</i>	USA	LoBuglio & Pfister (2010)

Table 4 Continued.

Fungal taxa	Diseases or nutritional modes	Host	Region	References
<i>Meloderma desmazieri</i> (<i>Rhytismatales, Rhytismataceae</i>)	Needle cast	<i>Pinus strobus</i>	Europe	Bednářová et al. (2013)
<i>Micraspis acicola</i> (<i>Micraspidales, Micraspidaceae</i>)	Snow blight	<i>Picea mariana</i>	Canada	Darker (1963), Quijada et al. (2020)
<i>Mniaecia jungermanniae</i> (<i>Leotiales, Mniaeciaceae</i>)	Swollen rhizoid, malformed spores	<i>Cephalozia, Diplophyllum, Scapania</i>	Belgium	Raspé & Sloover (1998), Pressel & Duckett (2011)
<i>Monilinia fructigena</i> (<i>Helotiales, Sclerotiniaceae</i>) Anamorph: <i>Monilia fructigena</i>	Brown rot, mummy fruit	<i>Actinidiaceae, Berberidaceae, Betulaceae, Cornaceae, Ebenaceae, Ericaceae, Myrtaceae, Moraceae, Rosaceae, Solanaceae, Vitaceae</i>	Egypt, Morocco, east and south Asia, Europe, USA, Brazil, Chile, Uruguay	CABI/EPPO (2000), Leeuwen et al. (2002)
<i>Myriosclerotinia curreyana</i> (<i>Helotiales, Sclerotiniaceae</i>)	Black spot on stems	<i>Juncus</i> spp.	Denmark, Croatia, Norway, UK, USA	Schumacher & Kohn (1985)
<i>Naemacyclus fimbriatus</i> (<i>Marthamycetales, Marthamycetaceae</i>)	Needle cast	<i>Pinus</i> spp.	Europe, USA	Vujanovic et al. (2007)
<i>Neofabraea perenans</i> (<i>Helotiales, Dermateaceae</i>)	Bull's eye rot	<i>Malus domestica</i>	USA	Aguillar et al. (2018)
<i>Oculimacula yallundae</i> (<i>Helotiales, Ploettnerulaceae</i>)	Eye spot	Poaceae, winter wheat	Africa, Australia, Europe, South America, New Zealand, USA	Marin-Felix et al. (2019)
<i>Ovulinia azaleae</i> (<i>Helotiales, Sclerotiniaceae</i>)	Petal blight	Azalea, rhododendron	USA, Japan, Europe, New Zealand, Australia	Backhaus (1994)
<i>Pezicula cinnamomea</i> (<i>Helotiales, Dermateaceae</i>)	Canker	Red oak	Europe	Kehr (1991), Ooki et al. (2003)
<i>Pezicula corticola</i> (<i>Helotiales, Dermateaceae</i>) Anamorph: <i>Cryptosporiopsis corticola</i>	Bull's eye rot	Japanese pear	Japan	Nitta et al. (2002)
<i>Phacidium lacerum</i> (<i>Phacidiales, Phacidiaceae</i>) Anamorph: <i>Ceuthospora pinastri</i>	Fruit rot, leaf spot	Apple, pear	USA	Wiseman et al. (2016), Crous et al. (2019)

Table 4 Continued.

Fungal taxa	Diseases or nutritional modes	Host	Region	References
<i>Phaeosclerotinia nipponica</i> (<i>Helotiales, Sclerotiniaceae</i>) Basionym: <i>Sclerotinia phaeospora</i>	Fruit rot	<i>Malus</i> sp.	Japan	Hori (1916)
<i>Ploioderma lethale</i> (<i>Rhytismatales, Rhytismataceae</i>)	Pine needle blight	<i>Pinus</i> sp.	USA	Minter & Gibson (1978b)
<i>Potebniomyces piri</i> (<i>Phacidiales, Phacidiaceae</i>) Anamorph: <i>Phacidiopycnis piri</i>	Fruit rot (Phacidiopycnis rot)	Pear	USA	Xiao & Boal (2007)
<i>Potridiscus polymorphus</i> (<i>Helotiales genera incertae sedis</i>)	Bryophytes parasitic	<i>Dendrologotrichum</i> sp.	Australia, New Zealand	Döbbeler & Hertel (2013)
<i>Pragmopora pithya</i> (<i>Leotiales, Tympanidaceae</i>)	Canker	Douglas fir	USA	Funk (1975)
<i>Pseudopeziza medicaginis</i> (<i>Helotiales, Ploettnerulaceae</i>)	Common leaf spot	Alfalfa	Europe, USA, Oceania	Jones (1919), Townsend (1951)
<i>Pseudophacidium diselmae</i> (<i>Phacidiales, Phacidiaceae</i>)	Stem canker	<i>Diselma archeri</i>	Australia	Yuan et al. (2000)
<i>Pyrenopeziza brassicae</i> (<i>Helotiales, Mollisiaceae</i>)	Light leaf spot	<i>Brassicae napus</i>	Europe, UK	Boys et al. (2007)
<i>Redheadia quercus</i> (<i>Helotiales, Sclerotiniaceae</i>)	Brown leaf spots	<i>Quercus acutissima</i>	Japan	Suto & Suyama (2005)
<i>Rhabdocline pseudotsugae</i> , <i>Rhabdocline parkeri</i> (<i>Helotiales, Cenangiaceae</i>)	Needle cast	<i>Larix</i> sp., <i>Pseudotsugae menziesii</i>	USA	Gernandt et al. (1997)
<i>Rhytisma acerinum</i> , <i>Rhytisma punctatum</i> (<i>Rhytismatales, Rhytismataceae</i>)	Tar spot	<i>Acer platanoides</i> , <i>A. pseudoplatanus</i>	Europe, USA	Horst (2008), Held et al. (2018)
<i>Sarcotrochila alpina</i> (<i>Helotiales, Cenangiaceae</i>)	Needle cast	<i>Larix</i> spp.	Europe, USA	Jalkanen (2016)
<i>Schroeteria decaisneana</i> (<i>Helotiales, Sclerotiniaceae</i>)	Seed infection	<i>Veronica hederifolia</i> , <i>Veronic aarvensis</i>	Germany	Baral et al. (2022)
<i>Schizothyrioma ptarmicae</i> (<i>Helotiales, Dermateaceae</i>)	Leaf lesion	<i>Achillea ptarmica</i>	France, Germany, Holland, Poland	Holm (1971), Adamska (2004)
<i>Sclerencoelia pruinosa</i> (<i>Helotiales, Sclerotiniaceae</i>)	Sooty bark canker	<i>Populus tremuloides</i> , <i>Populus grandidentata</i> , <i>Populus tremula</i>	Northern America and Northern Europe	Pärtel et al. (2017)

Table 4 Continued.

Fungal taxa	Diseases or nutritional modes	Host	Region	References
<i>Scleromitrua shiraiana</i> (<i>Helotiales, Sclerotiniaceae</i>)	Popcorn disease	Mulberries	China, Japan, Korea	Schumacher & Holst-Jensen (1997)
<i>Sclerotinia minor</i> (<i>Helotiales, Sclerotiniaceae</i>)	Rot root	More than 90 plant species	Europe, Asia, USA, South America, Oceania	Melzer et al. (1997), CABI/EPPO (2003)
<i>Sclerotinia sclerotiorum</i> (<i>Helotiales, Sclerotiniaceae</i>)	Watery soft rot, cottony soft rot	More than 400 plant species and pteridophytes	USA, South America, Oceania, Asia, Canada	Boland & Hall (1994), CABI/EPPO (2005)
Anamorph: <i>Sclerotium compactum</i>				
<i>Scolecobolus pteridii</i> (<i>Helotiales, Lachnaceae</i>)	Frond spot	<i>Pteridium arachnoideum</i>	Brazil	Guatimosim et al. (2016)
<i>Seaverinia geranii</i> (<i>Helotiales, Sclerotiniaceae</i>)	Rhizome parasitic	Geranium	USA	Whetzel (1945)
<i>Septotinia podophyllina</i> (<i>Helotiales, Sclerotiniaceae</i>)	Leaf lesion, leaf blotch	<i>Podophyllum peltatum</i>	Asia, Europe, USA	Whetzel (1937), Kam (1973)
<i>Spilopodia ranunculi</i> (<i>Helotiales, Drepanopezizaceae</i>)	Parasitic on epigeal stolon	<i>Ranunculi repens</i>	UK	Graddon (1984)
<i>Spilopodiella arxii</i> (<i>Helotiales, Drepanopezizaceae</i>)	Parasitic on leaves	<i>Caricis sempervirens</i>	Switzerland	Müller (1989)
<i>Stamnaria americana</i> (<i>Helotiales genera incertae sedis</i>)	Fern parasitic	<i>Equisetum hyemale</i>	USA	Seaver (1932), Künkele et al. (2005)
<i>Streptotinia caulophylli</i> (<i>Helotiales, Sclerotiniaceae</i>)	Target spot	<i>Caulophyllum thalictroides</i> , <i>Menispermum dauricum</i>	Canada, China	Elliott (1962), Bai et al. (2014)
<i>Stromatinia narcissi</i> (<i>Helotiales, Sclerotiniaceae</i>)	Bulb rot	<i>Narcissus</i> , <i>Zephyranthes</i>	Canada	Drayton & Groves (1952)
<i>Symphyosirinia clematidis</i> (<i>Helotiales, Helotiaceae</i>)	Seed pathogen	<i>Clematis</i> spp.	Germany, Spain	Baral (1994), Gams et al. (2009)
<i>Therrya piceae</i> (<i>Rhytismatales, Rhytismataceae</i>)	Canker	<i>Picea glauca</i>	USA	Funk (1982)
<i>Trochila laurocerasi</i> (<i>Helotiales, Cenangiaceae</i>)	Leaf spot	<i>Prunus laurocerasus</i>	UK, Europe, Australia, Poland	Stoykov & Assyov (2009)
<i>Valdensinia heterodoxa</i> (<i>Helotiales, Sclerotiniaceae</i>)	Leaf spot	<i>Vaccinium corymbosum</i>	Japan, Canada, USA, Europe	Norvell & Redhead (1994)
Teleomorph: <i>Valdensia heterodoxa</i>				

Cyttariceae accommodates 13 species of biotrophic discomycetes (Index Fungorum 2023). *Cyttaria* species are endemic to South America (Argentina and Chile) (Minter et al. 1987) and Oceania (southern Australia, Tasmania and New Zealand) (Petersen & Pfister 2010). They were documented for their associations with specific host trees (*Nothofagus* spp.) and their phylogenetic affinities (Petersen & Pfister 2010). The disease development of three *Cyttaria* species (*Cyttaria gunnii*, *Cyttaria nigra* and *Cyttaria pallida*) was described by Gadgil (2009). Their infection started with the germination of ascospores in the young shoot of *Nothofagus* spp. The penetrated fungi secrete specific substances responsible for the functioning of cell proliferation and gall formation. The spines comprise a combination of fungal hypha and host tissues, from which the apothecia arise. The extent of mycelial colonization determines the longevity of gall existence and is varied among *Cyttaria* species. Gadgil (2009) described that due to short hyphal colonization distances of *C. gunnii* and *C. nigra* localized galls are formed, whereas, for *C. pallida*, fungal hyphae grow down to the branch, resulting over the years-gall.

Drepanopezizaceae accommodates eight phytopathogenic discomycete genera, namely *Blumeriella*, *Diplocarpon*, *Drepanopeziza*, *Felisbertia*, *Leptotrochila*, *Pseudopeziza*, *Spilopodia* and *Spilopodiella* (Spegazzini 1889, Müller 1989, Graddon 1984, Johnston et al. 2019, Quandt & Haelewaters 2021). There are records of *Felisbertia*, *Spilopodia* and *Spilopodiella* pathogenic species, but their disease symptoms, life cycles and virulence factors are not yet reported (Spegazzini 1889, Müller 1989, Graddon 1984). Most species in *Drepanopezizaceae* infect dicotyledon leaves and scarcely herbaceous plants (Johnston et al. 2019). One species in *Drepanopezizaceae* that is important for floriculture (especially for cut roses) is *Diplocarpon rosae*. *Diplocarpon rosae* (anamorph: *Marssonina rosea*) is a hemibiotrophic pathogen causing defoliation, plant weakening and even the death of susceptible rose varieties planted outdoors (Black et al. 1994, Drewes-Alvarez 2003, Gachomo et al. 2006). A significant factor affecting the disease severity of *D. rosae* is the low humidity maintenance in greenhouses, which results in minimal infections (Horst 1983). A large amount of free water in outdoor landscapes stimulates massive germination of *D. rosae* conidia, leading to substantial infections in host plants (Horst & Cloyd 2007). Following the conidial germination, up to 3 germ tubes are grown from distal ends and differentiate to appressoria for cell penetration (Gachomo & Kotchoni 2007). However, some germ tubes invade host plants regardless of appressoria formation (Gachomo & Kotchoni 2007). Germ tubes and/or appressoria penetrate the host cuticle and develop infection vesicles that contain subcuticular and intercellular hyphae (Gachomo 2005). Subcuticular and intercellular hyphae penetrate epidermal cells, develop an initial haustorium, and then more haustoria were formed towards the leaf periphery (Aronescu 1934, Gachomo 2005). Acervuli are then formed along the length of the subcuticular hyphae and are visible on leaves, petioles, stems and twigs with the disease (Gachomo & Kotchoni 2007). The formation of apothecia is suggested to be dependent on weather conditions. If the weather is suitable, apothecia can be formed at the end of winter or spring on old leaves, however, if not, asexual morphs will be developed (Aronescu 1934, Knight & Wheeler 1977). The assumption is that cold temperatures in the snowy winter trigger the apothecial formation of *D. rosae* (Dodge 1931). However, the optimized weather conditions for apothecial formation are not clearly understood as the germination trial on conidia and ascospores from overwintered infected leaves in different seasons had failed (Knight & Wheeler 1977). Another hypothesis is that it might be related to a specific *D. rosae* strain as all strains do not produce apothecia (Dodge 1931), but this hypothesis required further studies. Studies on virulence factors of *D. rosae* were conducted by Neu & Debener (2019), in which they revealed that some pectin-degrading enzymes and effector candidate genes are related to haustoria formation and penetration, but further studies are necessary.

Medeolariaceae is a leotiomyce family comprising only *Medeolaria farlowii*, an obligate pathogen of *Medeola virginiana* with limited occurrence in the northeastern US (Thaxter 1922, Pfister 1984). Morphologically, *M. farlowii* lacks ascospores, excipular cells and ascospore characterization (LoBuglio & Pfister 2010). Disease symptoms of this fungus include shortened internodes and swollen tissues, with brown and woolly characters (Thaxter 1922, LoBuglio &

Pfister 2010). Infected plants were visible with lesions on stems, rhizomes and tubers, and infections spread throughout plants. However, symptoms at the onset of the disease remain unclear (Pfister et al. 2013). It was suggested that its ascospore dispersal is related to the foraging insects on infected plants (Pfister 1984). Therefore, more studies are required, especially on its life cycle and virulence factors.

Sclerotiniaceae comprises 31 genera of parasitic fungi (Johnston et al. 2019, Quandt & Haelewaters 2021, Wijayawardene et al. 2022), and their teleomorphs are recognized, except for some genera, such as *Amphobotrys* (Hennebert 1973), *Haradamyces* (Masuya et al. 2009) and *Myrioconium* (Davidson & Cash 1933) which are known only from their asexual morphs. Due to their massive fungal infections on agricultural and horticultural commodities (Smith 1900, Boland & Hall 1994, Leeuwen et al. 2002, Elad et al. 2016, De Miccolis Angelini et al. 2018), *Sclerotiniaceae* became the most studied group among all the families in *Leotiomyces*, especially *Botrytis cinerea* (Whetzel 1945, Holst-Jensen et al. 1997, Dean et al. 2012, Navaud et al. 2018). *Botrytis cinerea* infects more than 500 host genera ranging from agricultural to horticultural, ornamental, cover crops and non-vascular plants (Elad et al. 2016). Fungal diseases caused by *Botrytis cinerea*, such as gray mold and blight canker that damage valuable economic commodities immensely, gained attention from phytopathologists (Dean et al. 2012). The life cycle of *Botrytis cinerea* was described by Williamson et al. (2007). Infection of *Botrytis cinerea* begins under wet conditions with over 9.3% humidity, allowing conidia to germinate (Williamson et al. 1995). Conidia spread mostly by wind but also via water droplets, insects, and unsanitized agricultural tools and clothes (Jarvis 1977). Conidial germination may also be affected by ethylene gas production from host plants (Elad & Volpin 1988). Two to five germ tubes produced during conidial germination and appressoria are useful for host cell penetration and infection (Williamson et al. 2007). On the plant surface, conidial penetration of *Botrytis cinerea* is facilitated by the cutinolytic enzyme activities (Salinas & Verhoeff 1995), while the infections on injured tissues started by direct penetration through the injured tissues (Van Kan 2005). The fungus produces several substances in the host tissue, such as botrydial, cellulases, polygalacturonases (ecto and endo) and oxalic acid, which are detrimental and act as virulence factors (Nakajima & Akutsu 2014). As a host defense, plants trigger programmed cell death and hypersensitive responses upon pathogen recognition and kill the infected host tissues to prevent infection (Govrin & Levin 2000). Vegetative mycelia, conidia and sclerotia are asexual forms of *Botrytis cinerea* used for dispersal and survival. In temperate regions, sclerotia grow in early spring and produce conidiophores and multinucleate conidia. Spermatization of sclerotia leads to the production of apothecia and later ascospore formation (Williamson et al. 2007).

Oculimacula yallundae belongs to *Ploettnerulaceae* and parasitises barley, oats, rye, some grasses and wheat (Murray et al. 1994, Chapman et al. 2008). *Oculimacula yallundae* is a soil-borne fungus causing eye spot disease or elliptical-shaped lesions on leaf sheath at the stem base (Lucas et al. 2000). Conidial germination of *Oculimacula yallundae* on coleoptile facilitated by rain splashes (Bateman & Taylor 1976). Conidial germ tubes develop into appressoria, which directly penetrate coleoptile tissues inter- and intracellularly via colonizing leaf sheath cells and ultimately invading the stem via successive leaf sheath (Soulié et al. 1985, Daniels et al. 1991). Blein et al. (2009) report *O. yallundae* as a necrotrophic fungus (Groenewald et al. 2003) and showed that the fungus exhibits both asymptomatic and symptomatic stages in its infection cycle, which is a characteristic of a hemibiotroph (Lucas et al. 2000). The asymptomatic stage is shown during conidial colonization on coleoptile (Lucas et al. 2000, Blein et al. 2009), while the symptomatic phase is shown after the pathogen penetrates leaf sheath epidermal cells and develops in a confined space, leading to death cells (Blein et al. 2009). Apothecia of *O. yallundae* were spotted on post-harvest wheat stubble during spring and autumn (Dyer et al. 1994, Vera & Murray 2016). However, further studies are needed to determine initial apothecia development and the environmental factors that influence it (Vera & Murray 2016).

Gremmeniella abietina (synonym: *Scleroderris lagerbergii*) is one of the most devastating phytopathogenic discomycetes in *Leotiomyces*, infecting forest and nursery commodities

(Özkazanç & Maden 2013). Initially, the pathogen is indigenous to Europe, widespread to North America, and is the causative agent of dieback and cankers on various ages of coniferous trees in Europe and North America (Setliff et al. 1975, Kaitera et al. 2000, Porta et al. 2008). Infected plants are characterized by necrotic lesions formed on needles and branches with distorted terminal twigs (Santamaría et al. 2003). A study conducted in Southern Sweden showed that the life cycle of *G. abietina* is completed within two years (Hellgren & Barklund 1992). The infection mode of *G. abietina* in red pine seedlings was reported by Ylimartimo et al. (1996). Infection begins with the germination of conidia attached to the outermost bracts, subtending the short shoots and the inner bracts at the needle base (Ylimartimo et al. 1996). The emerging hyphae from conidia are enveloped by fibrillar extracellular sheath containing chitin, galactose, lipids, polygalacturonic acids and proteins (Benhamou & Ouellette 1987a, b). The hypha then penetrates stromata and colonizes the underlying bract tissues (Ylimartimo et al. 1996). Colonization by *G. abietina* occurs from the outward growth of hypha through the epidermis into intercellular spaces of cell junctions and middle lamellae, partly or completely embedded in host cell walls. Hypha then reached the lumen and periderm cell walls, isolating the bract from the shoot. Hyphal tips that are attached to host cell walls secrete extracellular enzymes, such as exoglucanases, laccases, peroxidases and polygalacturonases, to degrade the host cell wall (Ylimartimo et al. 1996, Simard et al. 2005, 2012). In the field, conidia (produced by pycnidia) and ascospores (released by apothecia) are the infection sources of *G. abietina* on coniferous trees (Kaitera et al. 1997). In Sweden, conidia commonly disperse from April to July and sporulate until the end of August, and ascospores are released a while later after the summer (Laflamme & Archambault 1990, Hellgren & Barklund 1992). Conidia and ascospores initiate the infection in the summer but penetrate further until the periderm and living tissues of pine shoots in the next winter (Lang & Schütt 1974, Patton et al. 1984). Apothecia and pycnidia grow on dead shoots of living infected trees for at least two years (Hellgren & Barklund 1992, Kaitera et al. 1997). Environmental factors, such as high humidity and water source availability, aid the infection of *G. abietina* (Skilling 1972), while mild temperature increases its symptom development (Marosy et al. 1989).

Besides infecting vascular plants, discomycetes in *Leotiomyces* also infect non-vascular plants, such as bryophytes and pteridophytes (Redhead & Spicer 1981, Künkele et al. 2005, Baral et al. 2009, Döbbeler & Hertel 2013). Some discomycete *Leotiomyces* form biotrophic associations with bryophytes, such as *Discinella schimperi* on *Sphagnum squarrosum* (Redhead & Spicer 1981) and *Mniaecia jungermanniae* on *Cephalozia bicuspidata* (Raspé & Sloover 1998). Redhead & Spicer (1981) described the action mode of *Discinella schimperi* on mucilaginous cells of the hosts. Once a single hypha contacts the apical papilla of the host cell, it develops an appressorium, which then grows in branches forming a dorm, covering most of the cells (Redhead & Spicer 1981). Penetration into apical papilla cells is followed by the formation of a branched haustorium-like structure inside the host cell wall. The haustorium-like structure grows excessively and spreads out until it reaches mucilaginous cells. Infected mucilaginous cells are often used to diagnose the presence of *D. schimperi* on *Sphagnum squarrosum* (Redhead & Spicer 1981). However, further studies are needed on the virulence factors of *D. schimperi*. In contrast to *D. schimperi*, the action mode of *Mniaecia jungermanniae* as a biotroph was not described in detail, and the formation of either appressoria or haustoria on *Cephalozia bicuspidate* was never asserted (Raspé & Sloover 1998). The biotrophic association between *M. jungermanniae* and its host is unclear as it was described merely on the swollen tip of bryophyte rhizoid responsible for rhizoid penetration (Killian 1926). Among bryophyte species, *Marchantia polymorpha* is reported to be the most valuable due to its thallus paste for treatment of insect bites and external inflammation (Chandra et al. 2017). However, there are no economic losses have not been reported due to fungal damage caused by *Bryoscyphus atomarginatus* on this host.

Four discomycetes in *Leotiomyces*, such as *Bloxamia cyatheicola*, *Lachnopsis catarinensis*, *Scolecocladium pteridii* and *Stannaria americana*, are reported to infect pteridophytes (Guatimosim et al. 2016, Haelewaters et al. 2018). *Bloxamia cyatheicola* causes frond spots, characterized by irregular chlorotic to pale brown necrotic lesions on *Cyathea delgadii* pinnulae.

Lachnopsis catarinensis causes frond blight, characterized by a necrotic area at the apex of *Dicksonia sellowiana* pinnulae and *Scolecocladium pteridii* causes frond spots, characterized by pale brown necrotic area on individual pinnulae of *Pteridium arachnoideum* (Guatimosim et al. 2016). *Stammaria americana* was documented by Haelewaters et al. (2018) as a pathogen on *Equisetum hyemale*, but further studies on disease symptoms were not reported. This study found that reports on the action modes of aforementioned discomycetes are lacking, and even the species records of discomycetous fungi associated with fern species are still limited (Guatimosim et al. 2016). Similar to their biotrophic associations with bryophytes, their associations with pteridophytes depend largely on the prevalence of their hosts (Döbbeler 1997, Davey & Currah 2006). Due to the lack of hosts and the rarity of some plants resulting from deforestation, these pathogenic leotiomycetous taxa can be categorized as endangered species, regardless of their phytopathogenic status (Windisch 2002).

Phytopathogenic discomycetes in *Neolectomyces*

Being the only order in *Neolectomyces* (Landvik et al. 1993), *Neolectales* accommodates *Neolecta*, the only discomycetous genus in *Taphrinomycotina* (Eriksson & Winka 1997). Most *Neolecta* species are saprobes, and the only pathogen reported is *Neolecta vitellina* (Table 5). Phytopathogenic discomycetes in *Neolectomyces* are characterized by their yellow, club-like apothecia, unitunicate, cylindrical asci with no paraphyses, and hyaline, fusoid to globose ascospores (Landvik et al. 2003, Friebe 2015). *Neolecta vitellina* was reported as a pathogen on rootlets of conifers (Redhead 1979), despite the lack of evidence on its nutrition mode (Landvik et al. 2003). To date, detailed research on the life cycle and pathogenicity factors of *N. vitellina* has not yet been studied (Healy et al. 2013).

Phytopathogenic discomycetes in *Pezizomyces*

Phytopathogenic discomycetes in *Pezizomyces* are characterized by bright or dull colored, superficial, sessile, apothecia, sometimes with setae, unitunicate, operculate or inoperculate, long to short, cylindrical, claviform asci with paraphyses, and hyaline to brown, fusoid to ellipsoid ascospores (Fitzpatrick 1917, Wolf 1958, Çolak & Kaygusuz 2017, Döbbeler et al. 2018, Egertová et al. 2018). Phytopathogenic *Pezizomyces* cause diseases in various host plants, such as pine seedlings (Egger & Paden 1986a, b), hardwood trees (Davidson 1950, Hughes 1960, Gibson 1979, Wingfield & Swart 1994, Cha et al. 2009) and bryophytes (Döbbeler et al. 2018, Egertová et al. 2018, Vega et al. 2019). In this study, we compiled 19 genera within eight families recognized as phytopathogenic discomycetes (Table 6). Table 6 is an underestimation since each genus is listed with at least one representative species in contrast to the actual pathogenic species numbers. The listed discomycetes infect plants with various disease symptoms, such as chlorosis, phloem degeneration (Egger & Paden 1986a, b), canker (Davidson 1950, Hughes 1960), root rot (Gibson 1979) and are recorded in various regions (Table 6) (Wingfield & Swart 1994, Wu 2001, Cha et al. 2009).

The most prominent pathogenic discomycete in *Pezizomyces* is *Rhizina undulata*, which causes root rot on coniferous plantations in Asia, Europe, South Africa and North America (Gibson 1979, Wingfield & Swart 1994). As a pyrophilous fungus, ascospore germination of *R. undulata* was stimulated by heat shock at 35–45 °C (Jalaluddin 1967a). *Rhizina undulata* favors acidic soil to grow, and its mycelia spread through soil, infecting conifer roots that come in contact (Jalaluddin 1967a, Murray & Young 1961). The colonization of *R. undulata* impacts coniferous seedlings and mature trees negatively (Murray & Young 1961, Weir 1915). *Rhizina undulata* infects and kills vascular tissues of pine seedlings (Egger & Paden 1986a, b). Annually, *R. undulata* infected conifer fields vary in their devastation lengths in different regions. In Japan and Korea, *R. undulata* infects 3–6 m irregular rings of coniferous fields (Sato et al. 1974, Lee & Kim 1990), while in the USA and Europe, 0.6–1 m of radial fields were affected (Phillips & Burdekin 1982, Tainter & Baker 1996). Besides abiotic factors such as alkaline soil (pH 7–8) (Jalaluddin 1967b), biotic factors such as the presence of broad leaves and conifer absence can be limiting factors for *R. undulata*

(Semashko 2014). Detailed studies on the life cycle, infection mode and virulence factors of *R. undulata* are still lacking. Perhaps, it is due to the difficulties of inducing the disease on the hardwood (Lee et al. 2005) and culturing ascospores and conidia from *R. undulata* mycelia in the laboratory (Semashko 2014).

In addition to *Rhizina undulata*, several pathogens from various families in *Pezizomycetes* are causing diseases in pine seedlings. *Caloscypha fulgens* and *Pyropyxis rubra* cause seedling death, while *Geopyxis carbonaria*, *Tricharina praecox*, and *Trichophaea hemisphaerioides* trigger moderate disease symptoms. Other pezizomycetous pathogens, such as *Anthracobia maurilabra* and *Gyromitra infula*, cause weak infections in root seedlings (Egger & Paden 1986a). Further detailed descriptions of biotrophic associations between the aforementioned *Pezizomycetes* with pine seedlings were discussed by Egger & Paden (1986a, b). However, more studies are needed to confirm their pathogenicity status, especially the life cycle and virulence factors responsible for fungal diseases.

Discomycete *Pezizomycetes* are found mostly in humid forests, which provide suitable habitats for various host plants, including bryophytes. Six genera of phytopathogenic *Pezizomycetes*, namely *Lamprospora*, *Neottiella*, *Octospora*, *Octosporopsis*, *Filicupula* and *Octosporella*, infect bryophytes (Table 6) and develop biotrophic associations with their related hosts. Most recent records on *Lamprospora* species were documented, including a brief description regarding its biotrophic infection on bryophytes. Vega et al. (2019) documented *Lamprospora dictydiola* as one of the three bryophyllous described. *Lamprospora dictydiola* develops appressoria enveloped by a hyphal layer to infect and grow on rhizoids of *Tortula muralis*. Appressoria are connected with thin-walled, irregular-shaped, aseptate haustoria. From the middle part of appressoria, infection pegs emerge and invade the rhizoid wall. Appressoria and haustoria are important structures in bryophyte infection (Döbbeler 1980) and also reported in *Octosporella* species (Döbbeler et al. 2018).

Economic importance of selected phytopathogenic discomycetes

Phytopathogenic discomycetes in different classes show various degrees of economic impacts. Phytopathogenic species in *Dothideomycetes* (e.g., *Mycosphaerella graminicola*) and *Eurotiomycetes* (e.g., *Aspergillus flavus* and *A. parasiticus*) were reported to reduce the yield and product quality by causing diseases on agricultural and horticultural commodities (Cotty et al. 1994, Hofmann 2010, Orton et al. 2011, Ohm et al. 2012). However, the damage caused by discomycetes in *Dothideomycetes* and *Eurotiomycetes* (Tables 1, 2) are not significant on their related hosts, hence no records were found for their economic losses (Inácio & Canon 2008, Guatimosim et al. 2015). Discomycetes in *Lecanoromycetes* mostly parasitize lichens (Lawrey & Diederich 2003), and some infect bryophytes (Döbbeler & Hertel 2013), but none have been reported as pathogens on valuable agricultural dicots and monocots (Hibbet et al. 2007, Søchting et al. 2008, Gueidan et al. 2015). Economic losses are also not documented for phytopathogenic *Neolectomycetes* (Healy et al. 2013), while the loss for one discomycete in *Pezizomycetes* was noted (Thies et al. 1979), but the financial damage is apparent for pathogenic discomycetes in *Leotiomycetes* (Dean et al. 2012). Host plants affected by pathogenic *Leotiomycetes* are exceptionally wider compared to other discomycete classes. Plants affected range from non-vascular plants (bryophytes and pteridophytes) to agricultural and forestry commodities (i.e. orchard, spice, staple, ornamental, cover and oil seed crops), including nursery material (Table 4) (Boland & Hall 1994, Künkele et al. 2005, Williamson et al. 2007, Pressel & Duckett 2011).

Control strategies for selected phytopathogenic discomycetes

Diplocarpon rosae causes black spot disease on *Rosa* spp. planted in outdoor landscapes (Knight & Wheeler 1977). *Rosa* spp. are high-valued ornamental plants with cultivation areas of more than 800 ha, and around 18 million stems are harvested annually worldwide (Blom & Tsujita 2003). In the USA, roses are considered one of the floricultural crops worth approximately \$ 24–28 million in 2018–2019 (USDA 2020a).

Table 5 Phytopathogenic discomycetes in *Neolectomyces*.

Fungal taxa	Nutritional modes	Host	Region	References
<i>Neolecta vittelina</i> (<i>Neolectales</i> , <i>Neolectaceae</i>)	Rootlet parasitic	Conifers	USA, Norway	Redhead (1977b, 1979), Landvik et al. (2003)

Table 6 Phytopathogenic discomycetes in *Pezizomycetes*.

Fungal taxa	Diseases or nutritional modes	Host	Region	Notes	References
<i>Anthracobia maurilabra</i> , <i>Anthracobia tristis</i> (<i>Pezizales</i> , <i>Pyrenomataceae</i>)	Radicle elongation reduction	Pine seedlings	Canada	Under certain temperature in monoxenic culture caused disease symptom	Egger & Paden (1986a, b)
<i>Ascobolus carbonarius</i> , <i>Ascobolus epimyces</i> (<i>Pezizales</i> , <i>Ascobolaceae</i>)	Radicle elongation reduction	Pine seedlings	Canada	Under certain temperature in monoxenic culture caused disease symptom	Egger & Paden (1986a, b)
<i>Caloscypha fulgens</i> (<i>Pezizales</i> , <i>Caloscyphaceae</i>)	Seed germination decline	Lodge pole pine	Canada		Egger & Paden (1986a)
<i>Filicupula suboperculata</i> (<i>Pezizales</i> genera <i>incertae sedis</i>)	Parasitic on phyllodia	<i>Frullania</i> <i>tamarisci</i>	Scotland		Yao & Spooner (1996)
<i>Geopyxis carbonaria</i> (<i>Pezizales</i> , <i>Tarzettaceae</i>)	Chlorotic seedlings	<i>Pinus contorta</i>	Canada, Norway		Egger & Paden (1986b), Vrålstad et al. (1998)
<i>Gyromitra infula</i> (<i>Pezizales</i> , <i>Discinaceae</i>)	Chlorotic seedlings	Pine seedlings	Canada	Under certain temperature in monoxenic culture caused disease symptom	Egger & Paden (1986b)
<i>Lamprospora dictydiola</i> (<i>Pezizales</i> , <i>Pyrenomataceae</i>)	Haustoria infection	<i>Tortula</i> <i>muralis</i>	Czech Republic, Georgia, Germany, Italy, Portugal, Spain, Ukraine		Vega et al. (2019)
<i>Neottiella ricciae</i> (<i>Pezizales</i> , <i>Pyrenomataceae</i>)	Thallus and rhizoid infection	<i>Riccia</i> spp.	Canary island, Europe, India, USA		Németh et al. (2017)
<i>Octosporella microtricha</i> , <i>O. nematospora</i> (<i>Pezizales</i> genera <i>incertae sedis</i>)	Biotrophic parasites	<i>Frullania</i> spp.	New Zealand, Spain		Döbbeler et al. (2018)

Table 6 Continued.

Fungal taxa	Diseases or nutritional modes	Host	Region	Notes	References
<i>Octospora leucoloma</i> (<i>Pezizales, Pyrenomataceae</i>)	Parasitic on bryophytes	<i>Bryum</i> sp., <i>Funaria</i> sp., <i>Leptobryum</i> sp.	Bulgaria, Turkey, USA		Çolak & Kaygusuz (2017)
<i>Octosporopsis erinacea</i> (<i>Pezizales, Pyrenomataceae</i>)	Parasitic on bryophytic thalli	<i>Dumortiera hirsuta</i> , <i>Riccardia</i> sp.	Malaysia		Egertová et al. (2018)
<i>Peziza pratervis</i> (<i>Pezizales, Pezizaceae</i>)	Seed germination decline	Lodge pole pine	Canada		Egger & Paden (1986a)
<i>Pithya cupressi</i> (<i>Pezizales, Sarcoscyphaceae</i>)	Twig wilting disease	<i>Juniperus</i> , <i>Cupressus</i> , <i>Thuja</i> , <i>Sequoia</i>	China, Europe, Japan, USA, Taiwan		Sawada (1931), Wu (2001)
<i>Plicaria endocarpoides</i> (<i>Pezizales, Pezizaceae</i>)	Seed germination decline	Lodge pole pine	Canada		Egger & Paden (1986a)
<i>Pyropyxis rubra</i> (<i>Pezizales, Pyrenomataceae</i>)	Seed germination decline	Oak	Canada		Egger & Paden (1986a)
<i>Rhizina undulata</i> (<i>Pezizales, Rhizinaceae</i>)	Root rot	<i>Pinus sylvestris</i> , <i>Pseudotsuga mensiesii</i> , <i>Larix cajanderi</i>	Northern Asia, Europe, USA, South Africa		Gibson (1979), Wingfield & Swart (1994), Cha et al. (2009)
<i>Tricharina praecox</i> (<i>Pezizales, Pyrenomataceae</i>)	Phloem degeneration	Pine seedlings	Canada	Under certain temperature in monoxenic culture caused disease symptom	Egger & Paden (1986a, b)
<i>Trichophaea hemisphaerioides</i> (<i>Pezizales, Pyrenomataceae</i>)	Moderate chlorotic symptom	Pine seedlings	Canada	Under certain temperature in monoxenic culture caused disease symptom	Egger & Paden (1986b)
<i>Urnula craterium</i> (<i>Pezizales, Sarcosomataceae</i>)	Canker	Oak, hardwood trees	Europe, USA		Davidson (1950), Wolf (1958), Ayer et al. (2000)

Infection of *D. rosae* does not cause mortality in the plant host, but the host weakening, such as weight loss, is apparent (Gachomo et al. 2007). Lyle (1960) found that infection of *D. rosae* may cause weight loss for *Rosa* spp. up to 73–98%. Control strategies available for *D. rosae* include several cultural practices, such as proper sanitation (pruning stems bearing infected leaves and removing them from the planted area), avoiding excessive water and providing sufficient distance between each plant (Horst 1983). However, if those sanitation efforts are insufficient or too late, fungicide applications can be used (Behe et al. 1993). Recent research found that synthetic fungicides, such as penconazole or boscalid plus pyraclostrobin combined with inducers (a stimulant beneficial in inducing host defense responses) provide control against *Diplocarpon rosae* (Percival & Graham 2021). Another control effort to suppress *D. rosae* infection was by studying potential resistant genes in new rose cultivars. The *Rdr1*, *Rdr2*, *Rdr3* and *Rdr4* genes were identified as the potential loci against *D. rosae* black spot in the latest research, and further studies on these genes are vital in building up genetic resistance in rose cultivars (Menz et al. 2017, Zurn et al. 2018).

Pseudopeziza medicaginis is a discomycete species causing common leaf spots on economically important legume crops, especially alfalfa (*Medicago sativa*) (Townsend 1951). Alfalfa is a plant commodity cultivated in temperate regions for pasture, silage, seed, and cover crops (Bouton 2021). Infection of *P. medicaginis* on alfalfa triggers leaf spot disease that reduces dry matter up to 40% (Morgan & Parberry 1977). A recent study estimated a yield reduction of 62% at the highest disease severity on alfalfa (Nutter et al. 2002). Growers must cut infected alfalfa in severe disease cases (Frate & Davis 2007). A recommended control strategy against *P. medicaginis* is the use of resistant cultivars (Kehr et al. 1984, Summers 1998). Alfalfa cultivars exhibited various degrees of resistance against leaf spot disease, but a study showed the incidence of *P. medicaginis* infection in a highly resistant cultivar (Inch et al. 1993). The available method to increase alfalfa resistance was by increasing plant resistance via crossing the transgenics expressing a hydrogen peroxide/reactive oxygen species producing enzyme or an oxalate degrading enzyme in pathogen tolerant lines or inbreds obtained through conventional genetic manipulations or by the transformation of tolerant plants or plant tissues with a hydrogen peroxide/reactive oxygen species producing gene or by altering the expression of an endogenous hydrogen peroxide/reactive oxygen species producing gene (Bidney et al. 2000). The latest research on alfalfa resistance revealed that *MsPGIP2* is a gene responsible for limiting common leaf disease caused by *P. medicaginis* and further research are necessary to enhance and transform this gene on alfalfa cultivars (Gui et al. 2016).

Neofabraea perenans (anamorph: *Cryptosporiopsis perennans*) is a pathogenic species on valuable orchard crops, such as apples and pears (Dugan et al. 1993). In the USA, the production of apples and pears worth more than 2.9 billion USD and 300 million USD in 2020, respectively (USDA 2020b, c). *Neofabraea perenans* causes bull's eye rot, a post-harvest disease and cankers on the bark of apples and pears, despite other *Neofabraea* species infecting similar fruit crops (Garipey et al. 2005, Aguillar et al. 2018). In British Columbia, depending on the apple cultivar, *Neofabraea* bull eye rot resulted in 5 % to 40% yield loss (Sholberg & Haag 1996), while the yield loss of pear production in the USA due to bull eye rot was estimated to be around 5–50% (Lennox et al. 2004). The available control strategies to alleviate *Neofabraea* cankers include conducting thorough inspections and removal of infected plant parts to minimize the spread of disease inoculum and reduce infection rates of cankers on barks (Garipey et al. 2005). As for bull's rot disease, the latest study showed fungicide applications during pre- and post-harvest periods on fruit crops were available for domestic use but might not be for international transportation (Aguillar et al. 2018). However, each *Neofabraea* species has specific sensitivity and may develop resistance to certain fungicides (Weber & Palm 2010), hence, new experiments for novel modes of action of fungicides were suggested (Garton et al. 2019).

Oculimacula yallundae is the causal agent of eyespot disease on staple crops, such as wheat and other cereals (Crous et al. 2003). Winter wheat, the third most popular crop cultivated in the USA (Vocke & Ali 2013), represents up to 80% of overall wheat in the USA, with an economic

value of more than 5 billion USD in 2020 (Vocke & Ali 2013, USDA 2020d). However, *Oculimacula* eyespot disease reduces grain yield, especially in the Pacific Northwest (Clarkson 1981). *Oculimacula* pathogens damaged wheat production up to 40–50% in the UK and, in 1998, an approximate estimation of loss due to *Oculimacula yallundae* and *Oculimacula acutiformis* reached £24 million (Fitt et al. 1988, Al-Azri et al. 2015, Palicová et al. 2018). In Europe and the Pacific Northwest, infection severity depends on the weather, especially during heavy rainfall and mild winter conditions, as they increase fungal infections (Serfling et al. 2016). Effective management strategies for controlling *Oculimacula* eyespot on wheat are currently being investigated despite the recommended approaches for disease mitigation. Cultural practices, such as crop rotation and tillage, are available besides pesticide applications (Wei et al. 2011). The use of fungicides, such as prochloraz, was deemed ineffective due to the developing resistance reported in Germany, France and the UK (Parnell et al. 2008), however, prochloraz is still proven to be effective during the field tests conducted in Japan against *Oculimacula* eyespot (Takeuchi et al. 2018). The latest study on pesticide applications against more than 100 *Oculimacula* isolates showed that 58% had low to medium resistance, one isolate had strong resistance while 42% of isolates were still sensitive to prochloraz (Palicová & Matušinsky 2019). Fungicide applications are effective at the beginning of the stem elongation period (Dumalasoová et al. 2015). Planting resistant cultivars are the other option to mitigate *Oculimacula* infection and is currently being studied. In the Pacific Northwest, resistant cultivars are developed against *Oculimacula* infection (Jones et al. 1995). Even though the resistant cultivars do not provide 100% protection against eye spot disease, field tests on wheat cultivars bearing the resistance gene *Pch1* showed lower damage against *Oculimacula* infection in the Czech Republic (Palicová et al. 2018).

Drepanopeziza brunnea (anamorph: *Marssonina brunnea*) is a phytopathogenic discomycete in *Drepanopezizaceae* reported as the causative agent of leaf blight on *Populus* spp., affecting 15–45% of wood losses on harvested poplar in Europe (Spiers & Hopcroft 1986, Castellani 1970). Poplar trees (*Populus* spp.) are valuable as energy crops used as lignocellulosic feedstock for biofuel production, with a target production of 61 billion litres in the USA (Sissine 2007). Hence, any diseases on *Populus* spp. may result in devastating impacts on the harvested poplar products (Netzer et al. 2002). The available control strategies do not entirely protect *Populus* sp from *Drepanopeziza* leaf blight since they are mainly preventive measures, such as fungicide applications on poplar seeds, to reduce leaf blight infection at the seedling stage (Spiers & Wenilam 1983). Research efforts focusing on the co-evolution of pathogenicity between *D. brunnea* and poplar to develop resistant varieties as an alternative control strategy had been initiated (Zhu et al. 2012) while the latest research highlighted the gene expression profiles and the roles of effectors in host specificity (Ren et al. 2020).

Gremmeniella abietina infection is widespread in Europe, North America and Asia, killing young trees and causing growth reduction in old trees (EFSA et al. 2017). In Quebec, the percentage of *G. abietina* infection in red pines reaches 86–100% and causes > 40% mortality without any treatments or control strategies (Laflamme 1999). In 2001, the *G. abietina* epidemic covered over 400 K ha of *Pinus sylvestris* with estimated financial damage of approximately 250 million Euro in Sweden (Hansson et al. 2004, Wulff et al. 2006). Control strategies against *G. abietina* infection are being assessed, including pruning, fungicide application and endophytic inoculations. It was noted that cutting up to two-thirds of tree crown reduces *G. abietina* infection rates by 22–47% (Laflamme 1999). Preventive measures to contain the disease on coniferous trees were studied by Hudler & Neal (1990). They documented that the sanitation method of immersing diseased seedlings of *Pinus sylvestris* and *Pinus resinosa* in water at 50 °C was able to eradicate *G. abietina* propagules. This control strategy was based on the high possibility that overwintered *G. abietina* spores in cut Christmas trees might spread the disease to new areas where they were discarded (Magasi & Manley 1974). Certain preventive measures to avoid *G. abietina* infection, such as pine site selections, spacing between plants, chemical applications and biological control were listed in EFSA et al. (2017). In the worst case of *G. abietina* infection, pesticide utilization has been allowed in the nursery (Hopkin & McKenney 1995) but not recommended in the forest,

especially in Europe (EC 2009). Biological control is the other recommended control strategy against *G. abietina*. The latest research on biological control against *G. abietina* in the greenhouse revealed that the infection was reduced in endophyte-inoculated pine seedlings (Romeralo et al. 2015).

As a biotrophic species, *Cyttaria* caused gall formation, leading to twisted branches and often breaking due to high wind. However, no studies were conducted on the impact of *Cyttaria* infection on timber production of *Nothofagus menziesii* nor their control strategies (Gadgil 2009). Besides *Cyttaria*, *Medeolaria farlowii* infection on its host *Medeola virginiana* has never been reported to cause the host death or any financial damages. Biotrophic discomycetes in *Leotiomyces* that cause fungal diseases on bryophytes and pteridophytes also lack studies on economic losses (Guatimosim et al. 2016).

Among other phytopathogenic discomycetes, *Botrytis cinerea* is the most destructive pathogen on valuable agricultural, ornamental and forestry commodities, including non-vascular plants (Dean et al. 2012, Elad et al. 2016). The global annual financial damage caused by *B. cinerea* is more than \$10–100 billion (Jin & Wu 2015). Economic and yield losses vary in different regions on various agricultural commodities. Yield loss caused by *B. cinerea* infection is about 20% and reached 50% as environmental conditions favour the widespread of the disease (Hu et al. 2017). Fruit rot on strawberries caused by *B. cinerea* was estimated to be 13–18% in the USA (Mertely et al. 2000), while gray mold reduces zucchini yield by 20% in Korea (Cheon & Jeon 2013). In New Zealand, the annual loss caused by *B. cinerea* infection on wine grapes was estimated at NZ\$ 2578/hectare (Hill et al. 2019). In Croatia, the estimated loss of apple price during storage was approximately € 5–53/ton for *B. cinerea*, *Monilia fructigena* and *Colletotrichum* spp. (non-discomycete phytopathogens) infections (Ivić et al. 2013).

Control strategies to manage gray mold caused by *B. cinerea* varies, and many studies have been conducted (Elad & Shtienberg 1995, Bika et al. 2021). *Botrytis cinerea* can infect pre- and post-harvest agricultural, horticultural and ornamental commodities, thus, various and specific methods to reduce disease infection were tried and documented. Bika et al. (2021) reported several potential methods to manage *B. cinerea* infection on ornamental crops. Those strategies include using resistant cultivars (Takatsu et al. 1999), practicing sanitation (by removing diseased plant parts, disinfecting cutting tools and containers in the greenhouse), dipping cut roses in hot water (50 °C) (Elad & Vopin 1991), irradiation treatment using UV and gamma rays on cut flowers (Chu et al. 2015), monitoring temperature and humidity (Holz et al. 2007), nutrient adjustment (Alvarez 2012), and biological control or employing antagonistic organisms against *B. cinerea*, such as *Trichoderma* sp. (Elad & Shtienberg 1995), *Clonostachys rosea* (Sutton 1997), *Exophiala jeanselmei* (Zapata et al. 2016) and *Pseudomonas* sp. (Gao et al. 2018). Other control methods against *B. cinerea* include the utilization of plant growth regulators, for e.g., benzothiodiazole and gibberellins (Shaul et al. 1995, Friedrich et al. 1996), natural chemical coating (e.g., plant extract and essential oils for post-harvest treatment) (Wilson et al. 1997), nanotechnology (He et al. 2011), chemical control (Fernández-Ortuño et al. 2015) and strategies using a combination of biological control, cultural, growth regulators, chemical via ‘a system-based approach’ (Parke & Grünwald 2012).

For *Pezizomyces*, economic losses were reported for *Rhizina undulata*, a pyrophilous fungus whose apothecia emerge after forest fires (Lee et al. 2005). South Korea reported huge economic losses, resulting from *R. undulata* infections in pine seedlings after the forest fires in 1996–2000 (Lee et al. 2005). In the Pacific Northwest USA, Thies et al. (1979) reported that 64 out of 277 burned Douglas fir cuts were infected with *R. undulata* after burning practices in Washington and Oregon, and its effect on pine seedling growth afterwards. In Africa, 1.2 million ha of forest plantations were also threatened by *R. undulata* infection since its first report in 1944 (Wingfield & Swart 1994). Along with *Sphaeropsis sapinea*, *R. undulata* infection caused significant losses to forest plantations in South Africa (Germishuizen 1984).

Control strategies to mitigate *R. undulata* infections, such as avoiding slash-burning practices for cleaning up agricultural wastes, have been applied (Germishuizen 1984). However, this strategy

led to the emergence of other forest pathogens, such as pine bark beetles, as they survive easily without fire and develop their offspring. Hence, the application of chemical sprays is necessary (Wingfield & Swart 1994). Finding new and effective strategies to control rot root disease has been a challenge since multiple efforts to induce disease infection on various trees failed (Lee et al. 2005). Therefore, mitigating fungal diseases while suppressing beetle infestation required integrated pest management strategies. Slash burning avoidance is mandatory and should be coupled with the immediate removal of dead trees and debris from forest fields to avoid creating nesting grounds for bark beetles (Wingfield & Swart 1994). Fungicide application can be substituted for on-site burning to avoid *Rhizina* infections. In case of accidental fires, several plant baiting techniques can be used and also careful monitoring of *R. undulata* infection patterns in the field is required (Wingfield & Swart 1994).

Genome and –omic studies of phytopathogenic discomycetes

The use of various analytical tools and modern technologies, such as the utilization of nuclear magnetic resonance (NMR), mass spectrometry (MS) and high-throughput-next generation sequencing (HT-NGS) improve technical analyses on genomic, metabolomic, proteomic and transcriptomic research (Shiratake & Suzuki 2016). Numerous studies using genomic, metabolomic, proteomic and transcriptomic approaches are available on *Botrytis cinerea* (AbuQamar et al. 2016). *Botrytis cinerea* genomes were sequenced by Amselem et al. (2011) and Van Kan et al. (2016), who drafted the genomes of *B. cinerea* strain T4 and B05.10 to be 37.9 Mbp (14,270 genes) and 38.8 Mbp (13,664 genes), respectively. Knowledge of the whole genome sequence of *B. cinerea* provides researchers to identify critical information on pathogenesis, such as virulence factors (Nakajima & Akutsu 2014), secondary metabolites (Collado & Viaud 2016) and susceptibility genes in host plants (Sun et al. 2017). Virulence factors that are responsible for host surface penetration (lipase and cutinase), host cell killing (botcinolid, botcinins derivatives, botrydial metabolites, Cu–Zn-superoxide dismutase, Nep1-like proteins, sesquiterpenoid metabolites and xylanase), host tissue conversion into fungal masses (aspartic protease, *BcPgl*, *BcPG2* and pectin methylesterase), and suppressing host defense (ATP-binding cassette transporters and *BcBirtl*) of *B. cinerea* were identified (Salinas & Verhoeff 1995, Cutler et al. 1993, Have et al. 1998, Duran-Patron et al. 2000, Valette-Collet et al. 2003, Rolke et al. 2004). Another important finding was the silencing of *DND1*, a susceptibility gene toward *B. cinerea* reduced lesion sizes on tomato and potato leaves (Sun et al. 2017). The importance of these molecular studies is related to the control methods, which rely heavily on chemical fungicides, leading to *B. cinerea* resistance, negatively impacting non-target organisms (Leroux et al. 2002, Weber 2011). Thus, a combination of genomic, proteomic, transcriptomic and metabolomic studies will provide valuable information, such as gene cascading of plant defense mechanism for resistant cultivars, an effective and eco-friendly control approach against *B. cinerea*.

In addition to *B. cinerea*, whole genomes have been sequenced for other phytopathogenic discomycetes in *Sclerotiniaceae*, such as *Sclerotinia sclerotiorum* (Amselem et al. 2011), *Sclerotinia borealis* (Mardanov et al. 2014), *Monilinia fructigena* (Landi et al. 2018), *Monilinia fructicola* (De Miccolis Angelini et al. 2018), *Monilinia laxa* (Naranjo-Ortiz et al. 2018) and *Scleromitrella shiraiana* (Lv et al. 2021). Draft genomes have also been provided for *Drepanopeziza brunnea* (Zhu et al. 2012), *Diplocarpon rosae* (Neu et al. 2017), *Oculimacula yallundae* (Sheng & Murray 2017), *Gremmeniella abietina* (Hamelin et al. 1993), and *Coccomyces strobili* (Stajich 2018a). Comparative fungal genome analysis for identifying virulence factors in *Scleromitrella borealis*, *Drepanopeziza brunnea*, *Diplocarpon rosae*, *Monilinia fructicola*, *Monilinia fructigena* and *Monilinia laxa* have been started (Neu & Debener 2019, Ren et al. 2020, Lv et al. 2021), but not yet for *Gremmeniella abietina*, *Coccomyces strobili* and *Oculimacula yallundae* (Hamelin et al. 1993). In *Pezizomycetes*, phytopathogenic discomycetes with whole genome sequences are *Caloscypha fulgens*, *Geopyxis carbonaria*, *Gyromitra infula* and *Rhizina undulata*, however, further analysis of these genomes is still lacking (Stajich 2018b).

Genome sequences are available for 101 fungal phytopathogens in *Dothideomycetes*, and phylogenetic analysis based on newly sequenced genomes indicated that plant pathogenicity in *Dothideomycetes* evolved multiple times (Haridas et al. 2020). However, whole genome sequences have not been reported for phytopathogenic discomycetes in *Dothideomycetes*. It will be interesting to incorporate this group in comparative analysis with other pathogenic taxa that are not discomycetes in a genomic study.

Genomes of 41 fungal species in *Lecanoromycetes* have been sequenced (Pizarro et al. 2019, Resl et al. 2022). Further studies on the loss of mating gene *MAT 1* (responsible for self-fertilization or homothallism) (Pizarro et al. 2019), heterothallic ancestor revelation and carbohydrate-active enzymes gene prediction based on fungal genome analysis were reported (Resl et al. 2022). But no genome has yet been published on phytopathogenic discomycetes in *Lecanoromycetes*. The phylogenetic affinities based on genome sequences between phytopathogenic discomycetes in *Lecanoromycetes* in plants, saprobes and lichens will be intriguing.

In *Neoleotiomycetes*, the genome sequence for *Neoleota irregularis* was documented but not *Neoleota vittelina* (Nguyen et al. 2017). Compared to other members of *Taphrinomycotina*, the genome of *Neoleota irregularis* was less in size and the number of protein-coding genes, even though it has a true teleomorph structure, is similar to fungal species in *Pezizomycotina* (Landvik et al. 2003, Healy et al. 2013). It will be intriguing to compare the current available fungal genome of *Neoleota irregularis* as a saprobe (Redhead 1977a, Nguyen et al. 2017) and *Neoleota vittelina* as a biotroph (Redhead 1979).

Genomes of *Aspergillus*, a medically and industrially important *Eurotiomycete*, had been sequenced (Arnaud et al. 2012), and further studies on genes responsible for spore production structures were revealed (de Vries et al. 2017, Mead et al. 2020). The loss of *abaA* gene in *Aspergillus nidulans* (*Eurotiomycetes*) and other species triggered failures in the formation of phialides and conidiospores (Mead et al. 2020). Additionally, this gene was independently lost in four lineages of *Eurotiomycetes* based on whole genome phylogeny (Mead et al. 2020). Even though fungal genomes of some *Eurotiomycetes* are available, genomes for phytopathogenic discomycetes have not been sequenced. Hence their affinities compared to other *Eurotiomycetes* based on whole genome phylogeny are still unknown.

Conclusions, challenges and future perspectives

Phytopathogenic discomycetes are ecologically essential, and in this paper, we provide a comprehensive account on selected members across discomycetes classes, disease impacts on hosts, economic significances, available and the latest research on control strategies. We listed 133 genera of terrestrial phytopathogenic discomycetes distributed worldwide, representing six classes within two subphyla (*Pezizomycotina* and *Taphrinomycotina*). They are recognized as biotrophs, hemibiotrophs and necrotrophs on spermatophytes, pteridophytes and bryophytes with varied disease symptoms (Tables 1–6).

It was revealed that most of the discomycetous phytopathogens reside in *Leotiomycetes* with approximately 104 fungal genera, infecting economically important plant families, *Brassicaceae*, *Cupressaceae*, *Ericaceae*, *Fagaceae*, *Pinaceae*, *Poaceae*, *Rosaceae* and *Solanaceae*. As hemibiotrophic and necrotrophic discomycetes, *Botrytis cinerea*, *Diplocarpon rosae*, *Drepanopeziza brunnea*, *Gremmeniella abietina*, *Neofabrae perenans*, *Oculimacula yallundae*, *Pseudopeziza medicaginis* and *Rhizina undulata* affect the agriculture and forestry. Three *Cyttaria* species (*Cyttaria gunnii*, *Cyttaria nigra* and *Cyttaria pallida*), *Medeolaria farlowii* and *Neoleota vitellina* were documented as weak pathogens associated with vascular plants. All phytopathogenic discomycete genera in *Eurotiomycetes* and *Lecanoromycetes*, together with some genera in *Leotiomycetes* and *Pezizomycetes* form biotrophic associations with bryophytes and pteridophytes. In *Dothideomycetes*, there are also discomycetous genera reported as pathogens on vascular plants.

In this paper, the economic significance and current phytopathogenic status of *Botrytis cinerea*, *Diplocarpon rosae*, *Diplocarpon brunnea*, *Gremmeniella abietina*, *Neofabrae perenans*, *Oculimacula yallundae*, *Pseudopeziza medicaginis* and *Rhizina undulata* were briefly reported.

The impact caused by phytopathogenic fungi on important agricultural and forestry commodities is massive (10–100 billion USD solely caused by *B. cinerea*). Not to mention the financial loss caused by the other phytopathogenic discomycetes in *Leotiomyces* in Table 4, which were not given in detail such as *Ascocorticium anomalum*, *Ascosorus floridanus*, *Ascodichaena rugosa*, *Monilinia* sp., *Sclerotinia sclerotiorum*, that are reported separately in certain regions are far away from the exact numbers. Hence, more comprehensive studies on host-pathogen relationships, including management strategies, especially on the less known phytopathogenic discomycetes are essential. Chemical applications for managing phytopathogenic discomycetes are still the leading solution to reduce economic damage and yield loss on agricultural products, which are essential for food security. Therefore, studies focusing on enhancing the defense mechanisms on host plants against fungal infections, such as breeding research and biological control are vital.

Research on phytopathogenic discomycetes is focused extensively on *B. cinerea* compared to other discomycetous phytopathogens. The majority of the less focused phytopathogenic discomycete groups were recorded separately, and their classification is still uncertain due to outdated taxonomic placements. Therefore, the phytopathological studies of these taxa are underrated. Whole genome sequences of phytopathogenic discomycetes, such as *Botrytis cinerea*, can be one of the resources for a stable classification as shown in Johnston et al. (2019). Another challenge for discomycete studies is the difficulty to obtain cultures for many discomycetous species on artificial media for advanced research. Despite the difficulty to germinate, some taxa were successfully cultured. However, some of those cultures were easily contaminated and difficult to maintain (Paden 1972). Availability and accessibility to cultures also limit the possibility of successful phytopathological studies on discomycetes. Additionally, host-pathogen interactions on certain discomycetous species are uncertain, which can hinder the research method in virulence-related studies. For example, *Rhizina undulata* is a culturable discomycetous pathogen (Paden 1972) but the disease inductions on roots continuously failed, resulting in impediments in further advanced research (Lee et al. 2005).

Further research on biotrophic discomycetes, such as *Cyttaria* sp and *Medeolaria farlowii* on a laboratory scale, is also challenging due to their restricted and limited obligate nature of the association with the host. Bryophytes and pteridophytes are less popular hosts compared to valuable agricultural and forestry plant commodities, hence, not many studies were conducted in relation to fungal infections or host-pathogenic interactions. A better understanding of the physiological interaction between host plants (either vascular or nonvascular) with phytopathogenic discomycetous fungi *in vivo* and *in vitro* is aimed to tackle ongoing disease incidents and upcoming breakouts. Basic and additional research coupled with new innovative approaches using advanced technologies, such as next-generation sequencing, may provide insights on these phytopathogens, not only on taxonomy and evolutionary but also may deeply unfold host-pathogen interactions (genotype and phenotype revelation) as well as biotic and abiotic factors related to fungal diseases outbreaks.

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