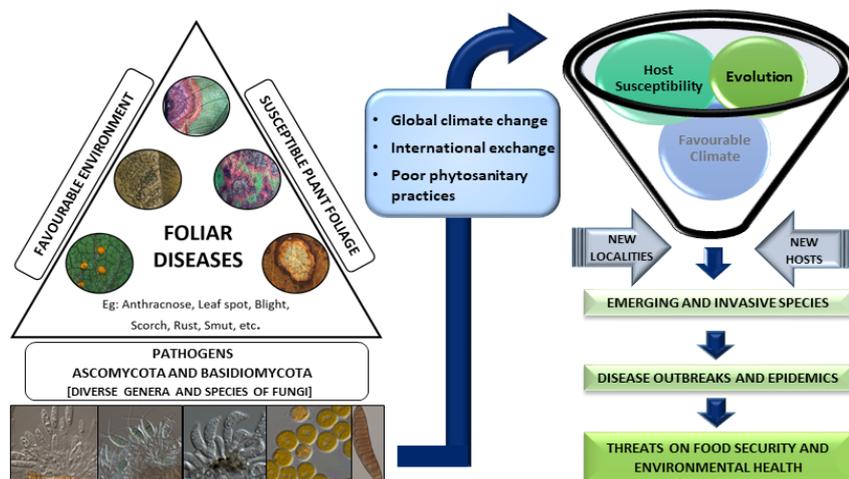


## Foliar pathogenic fungi: growing threats to global food security and ecosystem health

D. Udayanga, S.D. Miriyagalla, I.S. Herath, L.A. Castlebury, H.S. Fernandez and D.S. Manamgoda



### Highlights

- Foliar pathogens represent a diverse assemblage of species in the fungal kingdom.
- Global climate change, increasing international trade of plant material, and poor phytosanitary practices lead to the spread of destructive diseases.
- Non-indigenous, invasive foliar pathogens cause threats to food security and ecosystem health.
- Therefore, emerging foliar diseases should not be ignored, especially when encountered on the new hosts and localities.
- Understanding evolutionary relationships, diversity, and biology of organisms are vital to avert disease epidemics.

## Foliar pathogenic fungi: growing threats to global food security and ecosystem health

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**Abstract:** Globally, foliar pathogenic fungi cause serious losses of annual and perennial crops, ornamentals, landscape plants and forest trees. Plant pathogens that infect foliage are a diverse assemblage of fungi representing both phyla: Ascomycota and Basidiomycota. Although most of the species found on living leaves have been well studied by mycologists and plant pathologists, recent studies have remarkably enhanced the current understanding of species numbers and their evolutionary relationships. The impact of global climate change, the increasing international exchange of plant material and the lack of proper phytosanitary practices have resulted in the potential re-emergences of formerly known destructive fungi, infecting new hosts in new geographic locations. Routinely inspecting diseased plants and accurately identifying and naming causative agents are vital for mitigating the impact of invasive and other non-indigenous pathogens on crops and native flora. It is also necessary to characterise foliar pathogenic fungi based on molecular phylogeny, morphology, pathogenicity and the comparative analysis of fungal genomic data. This review provides an overview of prevalent groups of foliar pathogenic fungi, their diversity and economic impact, while emphasising emerging and destructive species that threaten global food security and ecosystem health.

**Keywords:** Climate change, Emerging pathogens, Epidemics, Invasive fungi, Leaf diseases.

### INTRODUCTION

Plant pathogenic species comprise a diverse array of taxa in the kingdom of fungi (Hawksworth, 2001; Arnold, 2007; Naranjo-Ortiz and Gabaldón, 2019). Plant diseases have resulted in significant losses of yield in crops, leading to serious economic and social issues (Klinkowski, 1970; McDonald and McDermott, 1993; Alam and Rolfe, 2006; Marin-Felix *et al.*, 2017). The fungi that cause foliar diseases have received special attention because they are frequently encountered in nature and are biologically and ecologically significant (Howard and Valent, 1996; Marin *et al.*, 2003).

Many foliar pathogens are recognised as ‘obligate biotrophs’, which implies that their growth and

reproduction totally depend on the host, while others are opportunistic species or secondary invaders (Chaure *et al.*, 2000). Foliar diseases decrease primary production by reduction of photosynthetic area and function (Barón *et al.*, 2012). In severe foliar fungal infections, plant defoliation and death may occur. Non-indigenous, invasive fungi have had a significant effect on native flora, due to their severity of infection and difficulty to control (Allen and Humble, 2002; Rossman, 2008).

Foliar fungal diseases are traditionally named for the symptoms observed or for the common phytopathological term used to refer to the group of fungi causing the disease. For example, informal categories of common foliage diseases, which are regularly found in the literature, include: anthracnose, leaf spots, leaf blights, tip blight, leaf scorch, leaf blotch, wilting, powdery mildews, rusts, and smuts (Callan and Carris, 2004). These phytopathological terms, however, do not always reflect the nature and evolutionary relationships of the causative agents or the disease (Figure 1). Routine collections of foliar fungi and morphological identification of fungal species have been traditionally practiced by both plant pathologists and mycologists and characterised based on disease incidence and microscopic characteristics, coupled with pathogenicity data. These contributions have resulted in numerous disease reports, morphological descriptions and checklists. However, over the last few decades, the development of fungal molecular systematics has revolutionised the identification, species delimitation and phylogenetic placement of pathogenic species (Nilsson *et al.*, 2014; Crous *et al.*, 2015; Hibbett *et al.*, 2016). Therefore, it is now possible to place pathogenic fungi in a natural classification system via molecular data linked to vouchered specimens and cultures (Shenoy *et al.* 2007; Damm *et al.*, 2010; Udayanga *et al.*, 2011; 2012; Kõljalg *et al.*, 2013). Accurate species identification based on DNA sequences and phylogenetic reconstructions have now become routine approaches in evolutionary phytopathology, supporting plant pathologists in detection, diagnostics, diversity estimation, disease surveillance and management. Additionally, historical disease collections made by numerous mycologists and plant pathologists

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are available in several international herbaria around the world. These collections are excellent sources for the sampling of taxa collected in the past from different geographic regions of the world. The pieces of evidence gathered based on these specimens provide a significant contribution to epidemiological efforts of predicting disease origins, modeling of dispersal patterns, and foreshadowing potential invasions.

Foliar diseases on crops and ornamentals have caused invasions, severe outbreaks and epidemics in human history. One such outbreak of coffee leaf rust, caused by the fungus *Hemileia vastatrix*, hit the celebrated coffee-production areas of Sri Lanka (then known as Ceylon) circa 1869. The same fungus has been the cause of recent coffee rust disease outbreaks in Colombia (2008 to 2011), Central America and Mexico (2012 to 2013) and Peru and Ecuador (2013), leading to an ongoing crisis in global trade (Avelino *et al.*, 2015; World Coffee Research, 2018; Amico *et al.*, 2020). Due to its significant impact on trade, coffee rust is considered one of the most economically important coffee diseases worldwide (Villarreyna *et al.*, 2020). The dematiaceous hyphomycete, *Bipolaris oryzae*, causes devastating brown spot diseases in rice. This was one of the factors leading to India's Bengal famine of 1943 (Scheffer, 1997). Although it has not caused severe outbreaks in recent times, the same fungus is still being encountered in major rice growing regions worldwide (Manamgoda *et al.*, 2014; Sobanbabu *et al.*, 2018). The rice blast fungus, *Pyricularia oryzae* (syn. *Magnaporthe oryzae*), is considered the most destructive leaf pathogen in rice, causing recurrent outbreaks (Couch and Kohn, 2002). This disease is difficult to control and destroys up to 30% of the world's rice crop each year, resulting in potential economic and humanitarian crises, particularly in Asia (Savary *et al.*, 2000; Saleh *et al.*, 2014; Khan *et al.*, 2016; Nalley, 2016). *Pyricularia oryzae* is widely used to study the molecular basis of diseases and host-pathogen interactions (Dean *et al.*, 2012). Boxwood blight is another invasive disease, which originated in the United Kingdom in 1994 and is currently distributed throughout Asia, Europe, North America, and New Zealand (LeBlanc *et al.*, 2018). As the name suggests, boxwood blight is a disease affecting boxwood (*Buxus* spp.) and causes rapid defoliation and the latent dieback of foliage (Malapi-Wight *et al.*, 2014; Daughtrey, 2019). Recent outbreaks of boxwood blight disease, caused by the fungus *Calonectria pseudonaviculata*, threaten the health and productivity of boxwood in both landscape plantings and nurseries, posing a major threat to the ornamental plant industry (LeBlanc *et al.*, 2018). Plants infected by *C. pseudonaviculata* are eventually weakened, and the resulting plant stress and consequent colonisation by secondary invaders often results in plant death.

Though surveillance and management methods can be effectively applied to prevent severe impacts, many of the fungi causing outbreaks have no cure. The past few decades have witnessed an increasing number of severe fungal infectious diseases in natural populations of humans, animals and plants (Vinatzer *et al.*, 2019). As with the recent global challenge of the novel coronavirus

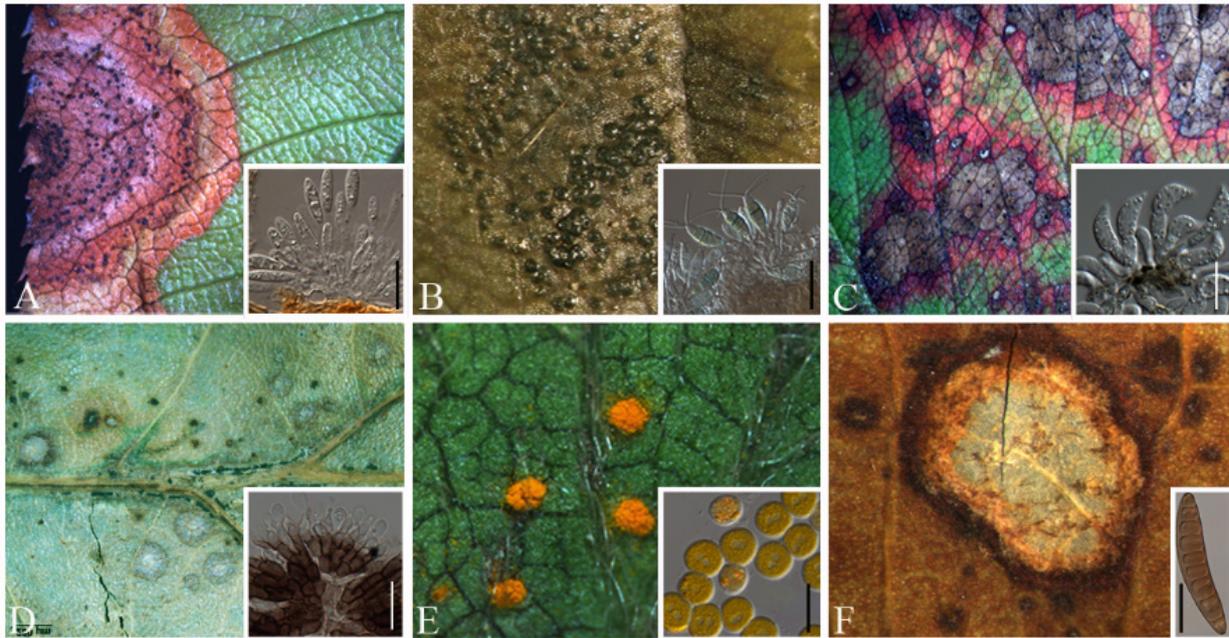
disease (COVID-19) in humans, scientists predict that a potential crop pandemic will occur sooner rather than later. It is highly likely that such an outbreak will be caused by a plant pathogenic fungus (Owings, 2020; Broom, 2020; Horvath, 2020). Potential outbreaks of phytopathogenic fungi could impact food supply systems by crop production in the affected areas. However, with the global population projected to number more than nine billion by 2050, the food supply will need to be protected to satisfy increasing demand.

Foliar fungal diseases have received much attention in recent history because they cause rapid losses in crop production. Some plant pathogenic fungi have intricate or poorly understood lifecycles, and few discriminatory morphological characteristics (Wikee *et al.*, 2011; Aime *et al.*, 2018). Therefore, understanding the biology, ecology, diversity and evolution of foliar pathogenic fungi is key to predicting threats and implementing mitigation strategies. This review outlines the diversity and impact of foliar pathogenic fungi based on key examples of prevalent fungal groups associated with economically important plants, with emphasis on emerging and potentially invasive species. Furthermore, we highlight the potential threats by foliar pathogenic fungi in the future on global food security and ecosystem health, based on their records of known historical impact on food crops or other economically important plants.

#### Diversity of foliar pathogens in the fungal kingdom

Foliar pathogenic species are a diverse assemblage of fungi belonging to both Ascomycota and Basidiomycota. These include many well-known pathogenic groups. The fungal classes Dothideomycetes, Sordariomycetes and Leotiomycetes, in Ascomycota are composed of ecologically diverse species, including many foliar pathogens that affect high value crops, ornamentals and forest trees (Table 1). Similarly, fungi belonging in Basidiomycota are well-known causative agents of a large number of severe fungal plant diseases. For instance, rust fungi, belonging in the Basidiomycota, class Pucciniomycetes, are widely distributed parasites found in various geographic locations worldwide (Arthur, 1934; Savile, 1971; Smith *et al.*, 2004; Padamsee *et al.*, 2012; Aime *et al.*, 2014). Smut fungi make up a second well-known group, consisting of a few severe foliar pathogens that parasitize cereals and fibre crops. Another well-known basidiomycetous foliar pathogenic genus, *Exobasidium*, which includes the causative agent of blister blight in tea (*E. vexans*) belongs to the class Exobasidiomycetes (Sinniah *et al.*, 2016; Weerasooriya *et al.*, 2018). *Exobasidium vexans* is a relatively poorly studied obligate biotrophic pathogen, but it has serious ramifications for the quality of tea production (Chaliha *et al.*, 2019).

Apart from well-known foliar fungi, a large number of novel leaf diseases and host associations occurring in crops, ornamental plants and forest trees are being reported in recent phytopathological and mycological literature (Chen *et al.*, 2018; Rodriguez-Salamanca, 2018; Tsai *et al.*, 2018; Salgado-Salazar *et al.*, 2019; Liang *et al.*, 2019). These previously undescribed fungi are commonly encountered



**Figure 1 :** Microscopic images of some foliar diseases and their causative agents.

A) Leaf blight on *Prunus serrulata* (Japanese cherry) caused by *Botryosphaeria dothidea* B) Leaf blight of *Fragaria* × *annassa* (cultivated strawberry) caused by *Neopestalotiopsis* sp. C) Leaf scorch of *Fragaria* × *annassa* caused by *Diplocarpon fragariae* D) Oak blight of *Quercus macrocarpa* (Bur Oak) caused by *Tubakia iowensis* E) Orange rust on *Duchesnea indica* (mock strawberry) caused by *Phragmidium tormentillae* F) Bird's eye spot of *Hevea brasiliensis* (Pará rubber) caused by *Bipolaris heveae*. Scale bars: A-F: 10 µm. Images were captured using a Discovery V20 stereomicroscope and AxioCam HrC digital camera (Carl Zeiss Microscopy, Thornwood, New York, USA) imaging system.

in relatively unexplored habitats, and numerous cryptic species are also being revealed in molecular mycological studies. According to Hawksworth and Rossman (1997), many fungal species have been collected, but remain lost or hidden as named species or ignored because they lack modern characterisations. Although a large number of genera and species of plant pathogenic fungi have been documented in the extant body of literature, most names are either not in use or the fungi are otherwise poorly known (Marin-Felix *et al.*, 2017). Therefore, it is not surprising that the foliar pathogenic continuum of fungi has yet to be fully explored, particularly among many poorly studied groups.

#### Host, pathogen and environment for the emergence of foliar diseases

Although fungi are commonly associated with leaf diseases, most fungal diseases minimally affect the plant's overall leaf area, causing minor biotic stress in terms of overall growth and development. Annual crops are infected with leaf pathogens mostly at the latent stage of growth or near harvest; thus, they may minorly impact production in most cases. However, environmental changes can directly influence the development and survival rates of foliar pathogens, modify host susceptibility and subsequently alter the effects of the diseases on host plants (Fisher, 2012; Elad and Pertot, 2014; Velásquez *et al.*, 2018). In hot and humid conditions, when infection pressures for fungal pathogens are high, leaf pathogens can cause severe defoliation and plant death. Therefore, climate factors, pathogen virulence and the dynamics of foliar disease add

an extra level of complexity to plant protection. In addition, pathogen growth rates and the production and germination of propagules strongly depend on temperature, relative humidity and, in the case of foliar pathogens, often leaf wetness (Colhoun, 1973; Huber and Gillespie, 1992).

Plant foliage is the often the first line of contact for invasive and non-indigenous fungal species. Most foliar pathogens, when successfully colonised on leaves, have the advantage of being able to be dispersed by the wind, making them widely distributed across geographical borders. Some foliar fungal species asymptotically hitchhike within the plant tissues as endophytic fungi and can become latent pathogens on the same or different hosts when the environmental conditions are favourable (Petrini *et al.*, 1991; Slippers and Wingfield, 2007; Gomes *et al.*, 2013).

Crops heavily sprayed with fungicides might never show infections from some common foliar pathogens (Haq *et al.*, 2020). However, leaf diseases are often taken seriously only if they result in a sudden outbreak or cause moderate to complete defoliation a few years in a row. Leaf loss over several consecutive growing seasons in plants infected with destructive foliar fungi can result in increased levels of inoculum, reduced growth, and increased susceptibility to pests and other diseases, leading to severe economic losses or environmental threats.

**Table 1:** Examples of destructive foliar pathogenic fungal species causing diseases on crops and ornamentals, their current classification, prevalent host(s), disease and supporting literature.

<b>Foliar pathogenic species (current name)</b>	<b>Current classification (Phylum, Class &amp; Order)</b>	<b>Prevalent Host(s)*</b>	<b>Foliar disease</b>	<b>Supporting Literature</b>
<i>Austropuccinia psidii</i>	Phylum: Basidiomycota Class: Pucciniomycetes Order: Pucciniales	<i>Myrtaceae</i> hosts	Myrtle rust	du Plessis (2019)
<i>Bipolaris oryzae</i>	Phylum: Ascomycota Class: Dothideomycetes Order: Pleosporales	<i>Oryza sativa</i> (rice)	Brown spot of rice	Manamgoda <i>et al.</i> , (2014); Sobanbabu <i>et al.</i> , (2018)
<i>Bipolaris maydis</i>	Phylum: Ascomycota Class: Dothideomycetes Order: Pleosporales	<i>Zea mays</i> (maize)	Southern leaf blight of corn	Manamgoda <i>et al.</i> , (2014); Macedo <i>et al.</i> , (2016)
<i>Bipolaris sorokiniana</i>	Phylum: Ascomycota Class: Dothideomycetes Order: Pleosporales	<i>Triticum aestivum</i> (wheat)	Leaf spot	Wang and Wei (2016); Li <i>et al.</i> , (2019)
<i>Cercospora sojina</i>	Phylum: Ascomycota Class: Dothideomycetes Order: Capnodiales	<i>Glycine max</i> (soybean)	Frog eye leaf spot	Zhang and Bradley (2014); Shreshta <i>et al.</i> , (2017)
<i>Calonectria pseudonaviculata</i>	Phylum: Ascomycota Class: Sordariomycetes Order: Hypocreales	<i>Buxus</i> sp.	Boxwood blight	Gauthier and Dockery (2018)
<i>Colletotrichum</i> spp.	Phylum: Ascomycota Class: Sordariomycetes Order: Glomerellales	<i>Hevea brasiliensis</i> (Pará rubber)	Colletotrichum Leaf Disease / CLD	Hunupolagama <i>et al.</i> , (2017); Cao <i>et al.</i> , (2019)
<i>Colletotrichum</i> spp.	Phylum: Ascomycota Class: Sordariomycetes Order: Glomerellales	multiple genera of plants	Anthracnose	Cao et al (2019); Nascimento et al (2019)
<i>Diaporthe ampelina</i>	Phylum: Ascomycota Class: Sordariomycetes Order: Diaporthales	<i>Vitis</i> spp., <i>Ampelopsis</i> spp.	Cane and leaf spot	Guarnaccia <i>et al.</i> , (2018)
<i>Diplocarpon fragariae</i>	Phylum: Ascomycota Class: Leotiomycetes Order: Helotiales	<i>Fragaria</i> sp. (strawberry)	Leaf scorch	Sivanesana and Gibson (1976); Johnston <i>et al.</i> , (2014)
<i>Discula destructiva</i>	Phylum: Ascomycota Class: Sordariomycetes Order: Diaporthales	<i>Cornus</i> spp.	Dogwood anthracnose	Redlin (1991); Trigiano <i>et al.</i> , (2016)
<i>Entyloma helianthi</i>	Phylum: Basidiomycota Class: Exobasidiomycetes Order: Entylomatales	<i>Helianthus annuus</i> (sunflower)	Sunflower leaf smut	Rooney-Latham <i>et al.</i> , (2017)
<i>Entyloma oryzae</i>	Phylum: Basidiomycota Class: Exobasidiomycetes Order: Entylomatales	<i>Oryza sativa</i> (rice)	Rice leaf smut	Mulder and Holliday (1971); Vanky (2012)
<i>Exobasidium vexans</i>	Phylum: Basidiomycota Class: Exobasidiomycetes Order: Exobasidiales	<i>Camellia sinensis</i> (tea)	Blister blight	Mabbett (2016)
<i>Exserohilum turcicum</i>	Phylum: Ascomycota Class: Dothideomycetes Order: Pleosporales	<i>Zea mays</i> (maize)	Northern leaf blight of corn	Hernandez-Restrepo <i>et al.</i> , (2018); Nieuwoudt <i>et al.</i> , (2018)
<i>Hemileia vastatrix</i>	Phylum: Basidiomycota Class: Pucciniomycetes Order: Pucciniales	<i>Coffea</i> spp.	Coffee rust	Talhinhas <i>et al.</i> , (2017); Santana <i>et al.</i> , (2018)
<i>Melampsora medusae</i>	Phylum: Basidiomycota Class: Pucciniomycetes Order: Pucciniales	<i>Populus</i> spp.	Poplar leaf rust	Feau <i>et al.</i> , (2009); Newcombe and Chastagner (1993)

<i>Phakopsora pachyrhizi</i>	Phylum: Basidiomycota Class: Pucciniomycetes Order: Pucciniales	<i>Glycine max</i> (soybean)	Asian soybean rust	Rincão <i>et al.</i> , (2018)
<i>Podosphaera xanthii</i>	Phylum: Ascomycota Class: Leotiomycetes Order: Erysiphales	multiple genera of plants.	Powdery mildew	Chen <i>et al.</i> , (2017); Cho <i>et al.</i> , (2017)
<i>Pseudocercospora fijiensis</i>	Phylum: Ascomycota Class: Dothideomycetes Order: Capnodiales	<i>Musa</i> spp. (banana)	Black Sigatoka disease (black leaf streak)	Manzo-Sanchez <i>et al.</i> , (2019); Fullerton and Casonato (2019)
<i>Puccinia triticina</i>	Phylum: Basidiomycota Class: Pucciniomycetes Order: Pucciniales	<i>Triticum</i> spp.	Wheat leaf rust	Terefe <i>et al.</i> , (2014) Kolmer (2015)
<i>Pyricularia oryzae</i>	Phylum: Ascomycota Class: Sordariomycetes Order: Magnaporthales	<i>Oryza sativa</i> (rice)	Rice blast disease	Klaubauf <i>et al.</i> , (2014); Milazzo <i>et al.</i> , (2019)
<i>Spilocaea oleagina</i>	Phylum: Ascomycota Class: Dothideomycetes Order: Pleosporales	<i>Olea</i> spp. (Olive)	Peacock leaf spot	González-Lamothe <i>et al.</i> , (2002)
<i>Teratosphaeria</i> spp.	Phylum: Ascomycota Class: Dothideomycetes Order: Capnodiales	<i>Eucalyptus</i> spp.	Leaf blight	Crous <i>et al.</i> , (2009); (2019)
<i>Urocystis cumminsii</i>	Phylum: Basidiomycota Class: Ustilaginomycetes Order: Urocystidales	<i>Dichelostemma capitatum</i>	Leaf smut	Savchenko <i>et al.</i> , (2020)
<i>Urocystis tritici</i>	Phylum: Basidiomycota Class: Ustilaginomycetes Order: Urocystidales	<i>Triticum</i> spp. (wheat)	Flag smut	Savchenko <i>et al.</i> , (2016)
<i>Ustilago cynodontis</i>	Phylum: Basidiomycota Class: Ustilaginomycetes Order: Ustilaginales	<i>Cynodon dactylon</i>	Leaf stripe smut	Kruse <i>et al.</i> , (2018)
<i>Ustilago serpens</i>	Phylum: Basidiomycota Class: Ustilaginomycetes Order: Ustilaginales	<i>Elymus repens</i>	Leaf stripe smut	Kruse <i>et al.</i> , (2018)
<i>Zymoseptoria tritici</i>	Phylum: Ascomycota Class: Dothideomycetes Order: Capnodiales	<i>Triticum aestivum</i> (wheat)	Leaf spot or speckled leaf blotch	Allioui <i>et al.</i> , (2016); Harrat <i>et al.</i> , (2017)

\*Other hosts can be retrieved at Fungal Databases of USDA-ARS: <https://nt.ars-grin.gov/fungaldatabases/> (Farr and Rossman, 2020)

### ***Colletotrichum*, the cause of foliar anthracnose**

*Colletotrichum* is a genus of plant pathogenic fungi (phylum: Ascomycota; class: Sordariomycetes) with worldwide distribution (Hyde *et al.*, 2009; Cannon *et al.*, 2012). Anthracnose caused by *Colletotrichum* species is primarily defined as sunken necrotic spots or blights on leaves, stems, flowers or fruits (Udayanga *et al.*, 2013; Shivas *et al.*, 2016; De Silva *et al.*, 2017; Sangpueak *et al.*, 2018). Foliar anthracnose is commonly found in tropical and subtropical environments, affecting wide ranges of crops, including cereals, grasses, vegetables, ornamentals and forest trees (Alahakoon *et al.*, 1994; Crouch *et al.*, 2009; Lobato *et al.*, 2010; Nair, 2010; Rojas *et al.*, 2010; Damm *et al.*, 2012a, 2012b). Therefore, the foliar *Colletotrichum* species are considered to be a major cause of pre- and post-harvest loss of a wide range of high-value crops, and these species are also commonly encountered in plant biosecurity interceptions (Udayanga *et al.*, 2013; Shivas *et al.*, 2016; De Silva *et al.*, 2017).

*Collectotrichum* species are frequently encountered in routine collections of leaf necrotic symptoms. These species usually co-occur with other ascomycetes, either as primary pathogens or as secondary invaders. Amongst prevailing foliar diseases, anthracnose caused by *Colletotrichum* species is one of the most severe diseases among cultivated rubber trees (*Hevea brasiliensis*) (Liu *et al.*, 2018). *Colletotrichum* Leaf Disease (CLD) is a major cause of declining rubber yields in South East Asia. In Sri Lanka, CLD reached an epidemic magnitude in February and March 1996 due to unusually wet weather (Jayasinghe *et al.*, 1997). In many parts of the world, *Colletotrichum gloeosporioides* is the causative agent of CLD in rubber. Apart from the species in the *C. gloeosporioides* species complex, *C. acutatum* is also a major causative agent of CLD, particularly in Sri Lanka (Jayasinghe *et al.*, 1997). The most common CLD symptom in rubber is small to large circular lesions on mature and immature leaves. CLD development may also significantly reduce rubber yield by secondary leaf fall. In severe epidemics, CLD also affects

young twigs with premature leaves, causing the tips to blacken and the typical brown to black anthracnose lesions to form on the green stems (Hunupolagama *et al.*, 2017).

Accurately identifying the species causing CLD is critical for understanding the epidemiology and developing effective control measures. However, the genus *Colletotrichum* contains many species with overlapping morphological characteristics, which may vary due to environmental conditions and geography, thus making species delimitation difficult. Therefore, an approach involving both morphological characteristics and multi-loci phylogenetic analysis is recommended for accurately identifying these *Colletotrichum* species (Cai *et al.*, 2009). According to Marin-Felix *et al.*, (2017), there are approximately 11 distinct *Colletotrichum* species complexes: gloeosporioides, boninense, truncatum, acutatum, dematium, gigasporum, orbiculare, graminicola, spaethianum, destructivum and caudatum. Each complex contains numerous phylogenetically closely related species, some of which are rich in species numbers. For example, the gloeosporioides clade alone consists of at least 30 different species, associated with numerous host plants causing minor to severe diseases. This enormous diversity and the frequent occurrence of foliar *Colletotrichum* pathogenic species in nature highlights the need for repeated collection and identification, particularly from unexplored ecosystems, to understand patterns of pathogen distribution and disease incidence. The rapidly growing species numbers, new disease reports and novel host associations of *Colletotrichum* species in the last two decades illustrate the unprecedented impact of these fungi in agriculture and ornamental trade. Thus, the timely responses to initial outbreaks are essential to prevent a possible impact on high-value crops and native flora.

#### Diaporthalean fungi causing foliar diseases

Species of Diaporthales (Ascomycota) have been extensively studied and the order is one of the largest and most well-defined orders in the Sordariomycetes class of Ascomycota (Castlebury *et al.*, 2002; Zhang *et al.*, 2006; Rossman *et al.*, 2007). The order Diaporthales contains a large number of notable fungi causing serious diseases in a wide range of plant hosts, including landscape trees and field crops, across both tropical and temperate natural ecosystems (Zhang and Blackwell, 2001; Adams *et al.*, 2006; Gryzenhout *et al.*, 2006; Udayanga *et al.*, 2014, 2015). An early twentieth century outbreak of the chestnut blight pathogen, *Cryphonectria parasitica* (Cryphonectriaceae), which belongs to the Diaporthales, caused the defoliation and death of chestnut trees in North America (Anagnostakis 1987; Brewer 1995). Thus, due to their wide occurrence and enormous diversity, the diaporthalean fungi cause devastating diseases in economically important host plants, resulting in sudden outbreaks, local losses and quarantine issues affecting international trade.

Though diaporthalean species are primarily known to cause various stem blights, cankers, root rots and fruit disease, many are also known to cause severe foliar diseases in economically important crops and forest trees. For instance, dogwood anthracnose (*Discula destructiva*),

strawberry leaf blotch (*Gnomoniopsis fructicola*), and Bur Oak blight (*Tubakia iowensis*) have caused notable disease incidents. Of these, *D. destructiva* has significantly impacted wild and ornamental *Cornus* species in the United States, proving itself to be a potentially devastating fungal disease, in both landscapes and forests throughout the eastern and northwestern United States since the late 1970's. Many genera in the Diaporthales are species-rich and widely encountered as asexual morphs on the leaves and stems of living plants. Diaporthalean fungi are also commonly encountered during quarantine inspections, leading to various issues affecting international trade of plant material (Kačergius *et al.*, 2010; Duan *et al.*, 2016). The wide occurrence and the unexpected diversity of pathogenic species in the Diaporthales have made it possible to cause devastating diseases on economically important host plants, resulting in sudden outbreaks and yield losses.

#### Foliar pathogenic graminicolous hyphomycetes

Hyphomycetes are a type of mitosporic fungi, which lack closed fruiting bodies and directly produce conidia via conidiophores during their asexual lifecycles (Ellis, 1971). Graminicolous hyphomycetes are associated with grasses and related crops in the Poaceae plant family (Sivanesan, 1987). Most graminicolous hyphomycetes are helminthosporoid species, which are now divided into six genera – *Bipolaris*, *Curvularia*, *Drechslera*, *Exserohilum*, *Johnalcornia* and *Porocercospora* – belonging to the Pleosporales (Dothideomycetes, Ascomycota) (Sivanesan, 1987; Manamgoda *et al.*, 2012; Amaradasa *et al.*, 2014; Tan *et al.*, 2014; Hernandez-Restrepo *et al.*, 2018). In addition to helminthosporoid graminicolous hyphomycetes, several other fungal genera, encountered as graminicolous hyphomycetes (e.g., alternarioid and cercosporoid fungal species) also have detrimental effects on plants.

Graminicolous hyphomycetes associated with cereal crops and their wild relatives have been reported as destructive phytopathogens, leading to significant yield losses and starvation worldwide. Severe crop losses have been reported in the United Kingdom and the United States, due to Southern corn leaf blight, caused by *Bipolaris maydis* (Manamgoda *et al.*, 2011), and Northern corn leaf blight, caused by *Exserohilum turcicum* (Smith *et al.*, 1988). *Bipolaris sorokiniana* is another common leaf spot pathogen in wheat and barley (Duveiller and Gilchrist, 1994). Though graminicolous hyphomycetes are primarily identified via morphology, successful species-level delimitation is always followed by comprehensive phylogenetic analyses incorporating molecular data (Manamgoda *et al.*, 2014, 2015; Tan *et al.*, 2014, 2016, 2018; Marin-Felix *et al.*, 2017, 2020). For instance, species discrimination of the genus *Curvularia*, solely based on morphological characteristics, is difficult as they share similar characteristics therefore, multi-locus, combined analyses are required in phylogenetic reconstruction (Manamgoda *et al.*, 2015; Tan *et al.*, 2018; Marin-Felix *et al.*, 2017, 2020). However, the diversity, wide distribution and impact of graminicolous hyphomycetes on food and fibre security emphasise the need for the study of these

fungi, as they can emerge as outbreaks anywhere in the world.

### Fungi causing powdery mildew

Powdery mildew is a common, serious, economically significant disease, which affects various crops (e.g., cereal plants, vegetables, fruit trees and ornamental plants) and has been reported to have an exclusively angiosperm host range (Mori *et al.*, 2000). However, characterised by the formation of a white, powdery film on leaf surfaces, stems or fruits (Mori *et al.*, 2000), powdery mildew is, to a greater degree, considered a foliar pathogen, given the extent of the foliar damage it causes, compared with damage to other plant organs. Powdery mildew is caused by obligate biotrophic pathogenic fungi belonging to the Erysiphaceae family, the sole family in the Erysiphales (class: Leotiomycetes, phylum: Ascomycota) (Ito and Takamatsu, 2009). By reducing leaf surface area for photosynthesis, and thus reducing crop quality and yield, Erysiphales pathogens turn themselves into a major economic concern.

The Erysiphaceae contains 16 genera, including approximately 873 species (Takamatsu *et al.*, 2015). In accordance with molecular-level investigations, all 16 genera are divided into five main tribes: Blumerieae, Golovinomyceteae, Cystothecae, Erysipheae and Phyllactiniaee (Braun, 2010; Takamatsu *et al.*, 2015). The Erysiphales order is reported to house both tree-parasitic and herb-parasitic species. The early divergent species are mostly tree-parasitic, indicating the occurrence of host shifts from trees to herbs over the course of evolution (Takamatsu, 2004). Early speculations concerning the phylogeny and host relationships of Erysiphales were based on critical morphological features (e.g., number of asci, number of ascospores, morphology of appendages, nature of conidiogenesis and mycelium features), whereas more recent taxonomic studies using molecular characteristics have given better insights into the phylogenetic aspects of the order and have helped restructure the taxonomic groups vastly (Takamatsu, 2013). Most of the tribes are well defined by molecular analyses, except Erysipheae, which contains the sole genus *Erysiphe* – the largest of all genera in the family, accounting for more than half of its species (Takamatsu *et al.*, 2015).

Most economic implications are caused by the herb-parasitic, rather than the tree-parasitic, species. Most monocot hosts of powdery mildews (such as wheat, barley, rye, oats, etc.) belonging to the family Poaceae, are valued food crops. These are often associated with a single pathogenic genus, *Blumeria*, within the Blumerieae tribe (Inuma *et al.*, 2007). The genus *Golovinomyces* housed within the Golovinomyceteae tribe, comprises the causative agents of powdery mildew in common ornamental plants, such as Asteraceae (daisies), Boraginaceae (borages) and Lamiaceae (mints) (Takamatsu *et al.*, 2013). The most commonly reported cases of Cucurbit Powdery Mildew (CPM) disease affect economically important crops in the Cucurbitaceae family (including cantaloupes, melons, squash and pumpkins). Causative agents of CPM include *Podosphaera xanthii* of the Cystothecae tribe and *Golovinomyces orontii* (syn. *Erysiphe cichoracearum*);

these are considered the major threats to the worldwide cultivation of cucurbits (Pirondi *et al.*, 2015; Rebelo *et al.*, 2017). The three genera – *Leveillula*, *Phyllactinia*, and *Pleochaeta* – in the Phyllactiniaee tribe generally infect hosts in the Ulmaceae (elm) and Fabaceae (pea) families. Increasingly incorporating molecular data and new morphological characteristics into taxonomic studies has helped researchers describe new species, as well as asexual morphs of known sexual morphs (Braun, 2010). Several sources record epidemics that resulted from powdery mildews being introduced into regions in which it had not been previously reported. Some historical examples include the introduction of *Erysiphe necator*, the grape powdery mildew pathogen, into Europe from North America during the nineteenth century and the introduction of *Sphaerotheca mors-uvae*, or the American gooseberry mildew, into Europe and Asia from North America (Kiss, 2005). *Erysiphe flexuosa*, which infects horse chestnuts, and *E. elevata*, which infects Indian beans, are some recent examples of the alien introduction of powdery mildew pathogens into the European region (Ale-Agha *et al.*, 2000). The obligate biotrophic nature of powdery mildews enables them to grow and reproduce exclusively on specific host plants. Additionally, the prodigious production of spores and quick dispersal patterns allow these fungi to infect a wide area of agricultural fields, leading to rapid losses of high-value crops and hindering ornamental trade of plant material.

### Rust fungi

Placed in the order Pucciniales (phylum: Basidiomycota, class: Pucciniomycetes), ‘rust fungi’ are a species-rich group of parasitic, foliar fungal pathogens, which are capable of inducing extensive economic and ecological damage (Aime *et al.*, 2018). With more than 7,800 species recorded, these obligate biotrophic pathogens belong to approximately 115 to 163 genera (Aime *et al.*, 2006; Figueroa *et al.*, 2020), but the family classifications remain doubtful and require further clarification. Rust fungi have complex life cycles, sometimes involving unrelated but specific plant hosts and (at most) five different spore types. These pathogens can reduce crop yields by depositing rusty-brown/orange, powdery spores on leaf surfaces, reducing the photosynthetic capacities of their hosts and diverting photosynthates into their own biomass (Aime *et al.*, 2018). Important cereal crops, legumes, and trees such as poplar, pine and *Eucalyptus* spp., are at high risk of infection from rust fungi (Figueroa *et al.*, 2020).

Many different *Puccinia* species have been major culprits of numerous wheat rust epidemics worldwide, owing to their ability to spread over thousands of kilometres, across continents and oceans, via the wind (Kolmer, 2005). The first major epidemic of wheat stem rust, caused by *Puccinia graminis*, occurred in Ethiopia during 1993 and 1994. Since then, many other wheat rusts, like *P. tritricina* (wheat leaf rust) and *P. striiformis* (stripe/yellow rust) have become more frequent in Africa, the Middle East, Asia, Australia, New Zealand, Europe and America, in the major wheat cultivating regions of the world (Singh *et al.*, 2008). Another recent alien invasion into the Western hemisphere

occurred in South and North America. *Phakopsora pachyrhizi*, the causal agent of Asian soybean rust, arrived from Asia, with Brazil bearing the highest losses – as great as an estimated US\$2 billion in 2003 (Yorinori *et al.*, 2005). Coffee rust, caused by *Hemileia vastatrix* was first reported in Sri Lanka circa 1869 (Monaco, 1977) and subsequently spread across Southern India and Java, causing coffee cultivation to be terminated entirely. Another outbreak in Angola in 1966 initiated the spread of *H. vastatrix* across the Atlantic, reaching Brazil (Bowden *et al.*, 1971). Myrtle rust, caused by *Austropuccinia psidii*, is a widely distributed rust disease, which infects Myrtaceae and Heteropyxidaceae plants. *Austropuccinia psidii* was first identified in 1884 from guava in Brazil before it spread into Central and South America, South Florida and, later, to Australia, Japan, China and South Africa, infecting numerous economically important hosts (Yamaoka, 2014). White pine blister rust, caused by *Cronartium ribicola* has also caused decades of epidemic conditions, decimating most of the white pine forests in the United States and Canada (Kinloch, 2003).

The current rate of climate change, which is continuously altering global temperatures, moisture levels, solar radiation levels and wind turbulence, can intensify the potential of rust fungi epidemics by influencing disease establishment and dispersal and, thereby, extending the infection range (Desprez-Loustau *et al.*, 2007). Thus, ideal environmental conditions (especially increased moisture levels on leaf surfaces) lead to new suitable climate spaces for rust diseases. Host plant homogenisation is another inductive factor, which creates greater numbers of susceptible host individuals (Helfer, 2013). The virulence of rust pathogens can depend on temperature (Evans *et al.*, 2007), and pathogen aggressiveness (e.g., speed and reproduction success) may also increase as hosts become more susceptible due to climate-change-induced stresses (Helfer, 2013). The global plant trade can also regularly expand the range of host plants and their rusts, while the movement of rust species globally can provide the opportunity for novel hybrid species to be generated, which can eventually give rise to new, even more destructive, host–rust relationships.

### Smut fungi

Smuts (Ustilaginomycotina) belong to a heterogeneous group of fungi that parasitize plant hosts and produce teliospores as a means of reproduction (Schafer, 1987; Vánky, 2004; Bauer *et al.*, 2008). Smut fungi are the second largest group of plant parasitic Basidiomycota. The species commonly known as smuts share similar lifecycles and cellular organisation. Smuts affect a number of economically important cereal crops, their relatives in the Poaceae family as well as some economically important non-poaceous hosts like sunflower (Asteraceae). Although smuts primarily infect panicles and seeds of cereal crops, some species infect leaves of crops and ornamental herbs, resulting in severe damage. The fungus produces slightly raised, angular, black spots (sori) on both sides of the leaves, causing severe loss of photosynthetic pigmentation. Similarly, many smuts infect commercially important

crops, considerably impacting yield as well as the aesthetic nature of ornamentals.

The flag smut disease in wheat produces long, grey and black lesions on leaves and leaf sheaths and causes stunted plants with deformed tillers. The leaves of infected plants are twisted and covered with long, grey lesions, which break open to release black, powdery spores. The fungus causing flag smut, has been referred to as both *Urocystis agropyri* and *U. tritici*. Savchenko *et al.*, (2016) identified *Urocystis agropyri* as a distinct taxon from *U. tritici*, which is the cause of flag smut disease on wheat (Savchenko *et al.*, 2016). In addition to losses in yield, wheat flag smut is quarantined in many countries, and shipments of wheat with flag smut spores can be refused entry (EPPO Global Database, 2020).

Stripe smut in grasses, caused by *Ustilago striiformis* s.l., is a complex of smut fungi widely distributed over both temperate and subtropical regions (Savchenko *et al.*, 2014; Kruse *et al.*, 2018). It is estimated that nearly 100 different grass species, belonging to more than 30 genera, are susceptible to stripe smut (Savchenko *et al.*, 2014). This disease causes shredding and death of leaf tissue, following the rupture of elongated sori (Toh and Perlin, 2016). Rice leaf smut is caused by *Entyloma oryzae*, and it is a widely distributed, but somewhat minor, disease (Vanky *et al.*, 2011, Vanky, 2012).

Among the diseases on non-poaceous hosts, sunflower white leaf smut is caused by a recently described species, *Entyloma helianthi*, from the United States (Rooney-Latham *et al.*, 2017). It is a relatively minor foliar disease, occurring primarily in greenhouse-grown sunflowers, which causes leaf spot, defoliation and reduced crop yield and value (Rooney-Latham *et al.*, 2017).

Relatively fewer numbers of molecular phylogenetic studies are available for smut fungi, therefore much work is required to develop backbone phylogenetic trees and to resolve species complexes (Kruse, 2018). Smuts are significant, not only as prevalent pathogens, but also as models for other basic and practical scientific areas of investigation, including obligate biotrophy, evolution and disease invasion. Thus, the foliar smuts can cause severe loss of cereal crop production, leading to severe threats for food security both regionally and globally. Moreover, the international trade of cereal crops can be affected by unexpected issues due to the sudden emergence of unknown diseases and spread of invasive smuts across the geographic borders.

### Insights in to foliar fungi - impact of molecular systematics and genomics

The past two decades have witnessed exponential growth in understanding the magnitude of fungal diversity, species numbers and their relationships, due to advances in DNA sequencing technologies and state-of-the art analytical methods (Blackwell *et al.*, 2006; Crous *et al.*, 2015). Molecular systematics is using promising tools to reveal the unexplored fungal diversity associated with plants as pathogens, saprobes, endophytes and other mutualistic species. DNA-based taxonomy has allowed mycologists to

resolve cryptic diversity in the species-rich genera of fungi, such as *Alternaria*, *Bipolaris*, *Curvularia*, *Colletotrichum*, *Diaporthe*, *Fusarium* and *Neopestalotiopsis*, which include large numbers of foliar pathogens. Large numbers of available nuclear ribosomal internal transcribed spacer region (ITS) fungal barcode sequences in GenBank, as well as other curated fungal DNA sequence repositories such as UNITE (Kõljalg et al., 2013 <https://unite.ut.ee/>), have facilitated the plant pathology field and other interdisciplinary areas related to fungal research (Nilsson et al., 2014). Multi-gene phylogenies of leaf-inhabiting genera have been used to resolve many species complexes in fungi, combined with a consolidated approach to species recognition criteria, including morphological, biochemical, physiological and pathogenicity data. Phylogenetic reconstructions not only resolve the evolution of pathogens, but can also be used to develop predictive tools for phytosanitary risk analysis in crop protection and biosecurity (Gilbert et al., 2012; Gilbert and Parker, 2016).

The genomic data of plant pathogenic fungi generated by high-throughput DNA sequencing platforms could reveal reliable DNA markers for disease diagnostics, genes related to pathogenicity such as carbohydrate-degrading enzymes, fungal effector proteins, various secondary metabolites and toxins (Islam et al., 2012; McGrann et al., 2016; Juliana et al., 2018). The phylogenetic reconstructions based on the analysis of full genomes or at least large portions of them, have resulted in more robust phylogenies of various genera and higher level taxa of fungi (Kuramae et al., 2006; Luo et al., 2015; Whiston and Taylor, 2016). The genome data of representatives from the key foliar fungal groups, including *Colletotrichum* spp. (O'Connell et al., 2012), diaporthean fungi (Wu et al., 2020), Dothideomycetes (Haridas et al., 2010), powdery mildews (Frantzeskakis et al., 2019), rusts (Hacquard et al., 2012; Gill et al., 2019) and smuts (Benevenuto et al., 2018) are available from several recent studies. Thus, comparative genomic analyses have revealed essential information, which can be used to form epidemiological predictions, to understand host resistance and pathogen evolution related to potential outbreaks (Xue et al., 2012; Kuan et al., 2015). Overall, molecular systematics and genomics have significantly improved the present understanding of foliar pathogens, leading to accurate identification, disease surveillance and implementation of effective disease management.

## CONCLUSIONS

Globally, foliar diseases in plants are growing threats to agriculture, food security, biodiversity and the ecological balance of the natural environment. Pathogenic fungal species that cause foliar diseases are highly taxonomically diverse. Although some foliar pathogens only minorly impact plants, it is highly likely that a similar pathogen may cause destructive diseases, leading to regional and global threats. Therefore, emerging or invasive species of foliar pathogens should not be underestimated, especially when encountered on economically important hosts and new geographic regions. Evolutionary relationships inferred by molecular data, as well as understanding the disease epidemiology and genomics of the pathogens, provide

information about disease spread, which necessitates predictions concerning potential outbreaks and epidemics.

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## DECLARATION OF CONFLICT OF INTEREST

The authors declare no conflict of interest.

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