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; Köjalg 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 (Villarreyena 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; Sobanabu 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 pathogen 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
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 asymptptomatically 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 (Pettrini 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.

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

Podosphaera xanthii
Phylum: Ascomycota
Class: Leotiomycetes
Order: Erysiphales
multiple genera of plants.
Powdery mildew
Chen et al., (2017); Cho et al., (2017)

Pseudocercospora fijiensis
Phylum: Ascomycota
Class: Dothioromycetes
Order: Ustilaginomycetes
Musa spp. (banana)
Black Sigatoka disease (black leaf streak)
Manzo-Sanchez et al., (2019); Fullerton and Casonato (2019)

Puccinia triticina
Phylum: Pucciniomycota
Class: Pucciniales
Order: Pucciniales
Triticum spp.
Wheat leaf rust
Terefe et al., (2014) Kolmer (2015)

Pyricularia oryzae
Phylum: Ascomycota
Class: Sordariomycetes
Order: Magnaporiales
Oryza sativa (rice)
Rice blast disease
Klaubauf et al., (2014); Milazzo et al., (2019)

Spilocaea oleagina
Phylum: Ascomycota
Class: Dothioromycetes
Order: Pleosporales
Olea spp. (Olive)
Peacock leaf spot
González-Lamothe et al., (2002)

Teratosphaeria spp.
Phylum: Ascomycota
Class: Dothioromycetes
Order: Capniales
Eucalyptus spp.
Leaf blight
Crous et al., (2009); (2019)

Urocystis cumminsi
Phylum: Ascomycota
Class: Ustilaginomycetes
Order: Ustilaginales
Dicholostemma capitatum
Leaf smut
Savchenko et al., (2020)

Urocystis tritici
Phylum: Ascomycota
Class: Ustilaginomycetes
Order: Ustilaginales
Triticum spp. (wheat)
Flag smut
Savchenko et al., (2016)

Ustilago cynodontis
Phylum: Ascomycota
Class: Ustilaginomycetes
Order: Ustilaginales
Cynodon dactylon
Leaf stripe smut
Kruse et al., (2018)

Ustilago serpens
Phylum: Ascomycota
Class: Ustilaginomycetes
Order: Ustilaginales
Elymus repens
Leaf stripe smut
Kruse et al., (2018)

Zymoseptoria tritici
Phylum: Ascomycota
Class: Dothioromycetes
Order: Capniales
Triticum aestivum (wheat)
Leaf spot or speckled leaf blotch
Alliou et al., (2016); Harrat et al., (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; Shivav 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; Shivav 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 causal 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 (Hunupalagama 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 (Kačergiūs 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 lifecycle (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, Golovinomycetaceae, Cystothecaceae, Erysiphaceae and Phyllactinieae (Braun, 2010; Takamatsu et al., 2015). The Erysiphaceae 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 Golovinomyceae 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 Cystothecaceae 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 Phyllactinieae 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 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. tritici (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 Africa 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**

Smut (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 shedding 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 (Vánky et al., 2011, Vánky, 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, sapropores, 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 (Köljalg 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’Conell et al., 2012), diaporthalean 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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