Pathogen profile

**Lecanosticta acicola: A growing threat to expanding global pine forests and plantations**

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**SUMMARY**

*Lecanosticta acicola* causes brown spot needle blight (BSNB) of *Pinus* species. The pathogen occurs mostly in the Northern Hemisphere but has also been reported in Central America and Colombia. BSNB can lead to stunted growth and tree mortality, and has resulted in severe damage to pine plantations in the past. There have been increasingly frequent new reports of this pathogen in Europe and in North America during the course of the past 10 years. This is despite the fact that quarantine practices and eradication protocols are in place to prevent its spread.

**Taxonomy:** Kingdom Fungi; Phylum Ascomycota; Subphylum Pezizomyces; Class Dothideomycetes; Subclass Dothideomycetidae; Order Capnioidales; Family Mycosphaerellaceae; Genus *Lecanosticta*.

**Host range and distribution:** *Lecanosticta* spp. occur on various *Pinus* species and are found in North America, Central America, South America (Colombia), Europe as well as Asia.

**Disease symptoms:** Small yellow irregular spots appear on the infected pine needles that become brown over time. They can be surrounded by a yellow halo. These characteristic brown spots develop to form narrow brown bands that result in needle death from the tips down to the point of infection. Needles are prematurely shed, leaving bare branches with tufts of new needles at the branch tips. Infestation is usually most severe in the lower parts of the trees and progresses upwards into the canopies.

**Useful websites:** The EPPO global database providing information on *L. acicola* (https://gd.eppo.int/taxon/SCIRAC)
Reference genome of *L. acicola* available on GenBank (https://www.ncbi.nlm.nih.gov/genome/?term=Lecanosticta+acicola)
JGI Gold Genome database information sheet of *L. acicola* sequenced genome (https://gold.jgi.doe.gov/organism?xmlid=Go0047147)

**Keywords:** brown spot needle blight, *Lecanosticta acicola*, *Lecanosticta* species, Mycosphaerella dearnessii, pine pathogen, *Pinus* spp.

**INTRODUCTION**

*Lecanosticta acicola* is an ascomycete fungus that causes a disease of *Pinus* spp. known as brown spot needle blight (BSNB). The pathogen was first described by de Thümen (1878) and it owes its notoriety to a disease problem that arose in the southeastern USA on *Pinus palustris*, better known as long leaf pine in that area (Siggers, 1932). This tree species, which is highly susceptible to infection, is peculiar in having a so-called ‘grass’ stage during the first five years of its growth. This mass of young needles provides a favourable environment for infection to occur.

The BSNB pathogen completes its life cycle (Fig. 1) on pine needles that are shed prematurely. This leads to reduced or stunted growth that can result in significant yield losses (Wakeley, 1970) or tree death. In some cases, pine plantations have been sufficiently damaged that they have needed to be cleared (Huang et al., 1995; Lévy, 1996; Markovskaja et al., 2011).

*Lecanosticta acicola* has been recorded on 53 different *Pinus* species and hybrids in native and non-native pine stands in the USA, Canada, several European countries and Asia as well as in Central America and Colombia (Table 1). Due to the severity of the disease, the pathogen has been afforded an A1 quarantine status in Africa, Argentina, Chile, Uruguay, Bahrain, Kazakhstan, Ukraine and Russia, and A2 quarantine status in Europe (https://gd.eppo.int/taxon/SCIRAC/categorization). However, reports of new outbreaks of the disease in various European countries have increased significantly since 2008 (Adamson et al., 2015, 2018; Anonymous, 2012; Cleary et al., 2019; Hintsteiner et al., 2012; Jankovský et al., 2009a; Markovskaja et al., 2011; Mullett et al., 2018; Ortiz de Urbina et al., 2017).

Quarantine measures rely on accurately identifying the presence of pathogens on symptomatic tissues. This is complicated in the case of *L. acicola* where the symptoms of BSNB closely resemble those of Dothistroma needle blight (DNB). DNB is caused by two species: *Dothistroma septosporum* and *D. pini* (Barnes et al., 2016). Due to their similar symptoms,
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Field diagnoses of the causal agent based on symptoms and/or on morphology alone have commonly been incorrect (Shishkina and Tsanava, 1967; Siggers, 1944; Thyr and Shaw, 1964). Consequently, past reports of L. acicola based only on morphological descriptions and symptoms must be treated with caution and verified using molecular identification techniques (van der Nest et al., 2019).

Lecanosticta acicola has been well-known in the southeastern USA since the early 1900s, but is rapidly spreading in northern parts of the USA, Canada and in some parts of Europe (Broders et al., 2015). Its complete host range is not known but appears to be expanding (Mullett et al., 2018). A recent taxonomic re-evaluation of isolates previously identified as L. acicola, applying phylogenetic analyses based on DNA sequences, has led to various isolates being recognized as distinct species (Quaedvlieg et al., 2012; van der Nest et al., 2019). This and a number of recent publications (Adamson et al., 2018; Cleary et al., 2019; Mullett et al., 2018; Ondrušková et al., 2018; Ortiz de Urbina et al., 2017; Sadiković et al., 2019; Schneider et al., 2019; Wyka et al., 2017) justifies the need for a review of current knowledge regarding BSNB and the Lecanosticta species that cause this disease. This is the first review of the topic to be presented in 75 years subsequent to that of Siggers (1944).

**LECANOSTICTA SPECIES**

The genus Lecanosticta, which includes nine species with the type species being L. acicola (previously known as Mycosphaerella dearnessii, Table 2), is characterized by stromata and septate, pigmented conidia. The genus was erected by Sydow and Petrak in 1922 (Sydow and Petrak, 1922). The taxonomic history and nomenclature of Lecanosticta acicola has been succinctly presented previously (Evans, 1984; Siggers, 1944) and is summarized and updated in Table 2.

**Lecanosticta acicola** is the oldest known species in the genus and owes its notoriety to the disease of long leaf pine, which it was first associated with, in the southeastern USA (Chapman, 1926; Hedgcock, 1929). Although the pathogen was identified in...
Table 1  Host and geographical range of *Lecanosticta* species.

| Country, region, locality | Year collected | Host | Identification method and additional notes | Identification verified using molecular methods (*) | Reported severity of infections and applied eradication methods | Report references |
|---------------------------|----------------|------|------------------------------------------|---------------------------------------------------|------------------------------------------------------------|------------------|
| Austria, Lower Austria, Valley of the river Ybbs | 1996–2000 | *P. mugo*, *P. sylvestris* | Morphological identifications of the pathogen were performed. | | | Brandstetter and Cech (2003) |
| Austria, Lower Austria, Hollenstein/Ybbs | 2008–2009 | *P. sylvestris* | The pathogen was recognized during a forest survey. | | | Cech and Krehan (2008), Kessler (2009) |
| Austria, Lower Austria, Hollenstein/Ybbs | 2009–2010 | *P. mugo* subsp. *mugo*, *P. mugo* subsp. *uncinata* | Symptoms were observed in a survey. | | | Kessler and Krehan (2011) |
| Austria, Lower Austria | 1996 | *P. mugo* | Fruiting bodies were observed on pine needles. | | | Cech (1997) |
| Austria, Lower Austria, Hollenstein/Ybbs | 1998 | *Pinus sp.* | Symptoms were observed in the field. | | | Brandstetter and Cech (1999) |
| Austria, Lower Austria | 2004 | *P. mugo*, *P. sylvestris* | *TEF 1* sequencing used for identification, both mating types were detected. | * | | Janoušek et al. (2016) |
| Austria, Lower Austria | 2010 | *P. mugo* | *TEF 1* sequencing used for identification, both mating types were detected. | * | | Janoušek et al. (2016) |
| Austria, Upper Austria | 2010 | *P. mugo* | *TEF 1* sequencing used for identification. Mating type 1 was detected. | * | | Janoušek et al. (2016) |
| Austria, Upper Austria, Bregenz (Vorarlberg) | 2011 | *P. mugo* subsp. *mugo* | Symptoms were observed in a survey. | | | Kessler and Krehan (2011) |
| Austria, Upper Austria, Gmunden | 2011 | *P. nigra var. nigra*, *P. mugo* subsp. *mugo* | *ITS* sequencing used for identification. | * | | Hintsteiner et al. (2012) |
| Austria, Upper Austria, Tyrol | 2011 | *P. mugo* subsp. *uncinata* | Symptoms were observed in a survey. | | | Kessler and Krehan (2011) |
Table 1 (Continued)

| Country, region, locality | Year collected | Host | Identification method and additional notes | Identification verified using molecular methods (*) | Reported severity of infections and applied eradication methods | Report references |
|---------------------------|---------------|------|---------------------------------------------|-----------------------------------------------|-------------------------------------------------|------------------|
| Austria, Upper Austria    | 2012          | P. nigra | TEF 1 sequencing used for identification. Mating type 2 was detected. | Janoušek et al. (2016) | | |
| Austria, Upper Austria    | 2015          | P. mugo, P. mugo subsp. mugo, P. mugo subsp. uncinata, P. sylvestris | The pathogen was detected during a forest survey and confirmed with laboratory tests (method not specified). | EPPO (2015) | | |
| Austria, Graz             | 2016          | P. mugo | Infected needles were collected by I. Barnes. Isolations were made by I. Barnes and A. van der Nest, and identified by ITS sequencing. Mating type 2 was detected. | I. Barnes, FABI, Pretoria, South Africa, personal communication | | |
| Austria, Lower Austria    | 2016          | P. mugo | Infected needles were collected by T. Cech. Isolations were made by I. Barnes and A. van der Nest, and identified by ITS sequencing. Mating type 2 was detected. | I. Barnes, FABI, Pretoria, South Africa, personal communication | | |
| Austria, Salzburg         | 2016          | P. uncinata | Infected needles were collected by T. Cech. Isolations were made by I. Barnes and A. van der Nest, and identified by ITS sequencing. Mating type 2 was detected. | I. Barnes, FABI, Pretoria, South Africa, personal communication | | |
| Austria, Upper Austria    | 2016          | P. mugo | Infected needles were collected by T. Cech. Isolations were made by I. Barnes and A. van der Nest, and identified by ITS sequencing. Mating type 1 was detected. | I. Barnes, FABI, Pretoria, South Africa, personal communication | | |
| Belize                    | 1981          | P. caribaea, P. oocarpa | Morphological identifications were made. Confirmation is needed as molecular identification did not reveal L. acicola in Central America (van der Nest et al., 2019). | Evans (1984) | | |
| Bulgaria, near Sofia      | 1938          | P. nigra | The pathogen was identified based on morphological characteristics. However, the conidial descriptions are not typical of L. acicola and therefore this record is doubtful and should be verified. | Kovačevski (1938) | | |
| Canada, Manitoba          | 1965          | P. banksiana, P. contorta var. latifolia | Symptoms were observed in the field and the presence of the pathogen was confirmed with morphological identifications. | Laut et al. (1966) | | |
| Canada, New Brunswick, Quebec and Ontario | 2009          | P. strobus | L. acicola was reported to occur with Canavergella banfieldii on all trees sampled and confirmed based on morphological characteristics. | Laflamme et al. (2010) | | |
| Country, region, locality | Year collected | Host | Identification method and additional notes | Identification verified using molecular methods (*) | Reported severity of infections and applied eradication methods | Report references |
|--------------------------|---------------|------|-------------------------------------------|--------------------------------------------------|-------------------------------------------------|-----------------|
| Canada, Quebec           | 2011          | P. strobus, P. mugo | TEF 1 sequencing used for identification, both mating types detected.  | *  | Janoušek et al. (2016) |
| China, Jiangsu           | 1958          | P. thunbergii | Identification method not specified.  | Insignificant damage was reported. | Ye and Wu (2011) |
| China, Fujian province   | 1982–1985     | P. elliottii | Morphological identifications of the pathogen.  |  | Li et al. (1987) |
| China, Anhui, Fujian, Guangdong, Guangxi, Jiangsu, Jiangxi and Zhejiang provinces | 1986 | P. caribaea, P. clausa, P. echinata, P. elliottii, P. palustris, P. taeda, P. thunbergii | Morphological characteristics were used to identify the pathogen.  |  | Li et al. (1986), Ye and Wu (2011) |
| China, Fujie             | 1988          | P. elliottii | Morphological characteristics and RAPD analysis were used to identify the pathogen. TEF 1 sequencing was further used for identification and mating type 2 was detected by Janoušek et al. (2016).  | *  | Huang et al. (1995), Janoušek et al. (2016) |
| China, Zhejiang          | 1991          | P. thunbergii | Morphological characteristics and RAPD analysis were used to identify the pathogen.  | *  | Huang et al. (1995) |
| China, Jiangxi           | 1992          | P. elliottii, P. thunbergii | Morphological characteristics and RAPD analysis were used to identify the pathogen.  | *  | Huang et al. (1995) |
| China, Guanxi            | 1992          | P. caribaea, P. elliottii | Morphological characteristics and RAPD analysis were used to identify the pathogen.  | *  | Huang et al. (1995) |
| Colombia, Piedras Blancas and Pereira | 1978 | P. radiata, P. elliottii, P. patula | Identification method not specified.  |  | Gibson (1980) |
| Colombia, Albán          | 1981          | P. radiata | Morphological identification, sexual and asexual state were identified.  |  | Plantations were severely defoliated.  | Evans (1984) |
| Country, region, locality | Year collected | Host | Identification method and additional notes | Identification verified using molecular methods (*) | Reported severity of infections and applied eradication methods | Report references |
|--------------------------|---------------|------|---------------------------------------------|--------------------------------------------------|---------------------------------------------------------------|-------------------|
| Colombia, Refocosta      | 2011          | *P. caribaea* | Infected needles were collected by C.A. Rodas. Isolations were made by I. Barnes. *TEF 1 sequencing was used for identification and mating type 2 was detected by Janoušek et al. (2016).* | * | Janoušek et al. (2016) |
| Costa Rica, Alajuela     | 1980          | *P. oocarpa* | Morphological identification of pathogen. | | Evans (1984) |
| Croatia, Dalmatia        | 1975          | *P. halepensis* | Morphological identification of *L. acicola*. | | Milatović (1976) |
| Croatia, Zadar           | Not specified | *P. halepensis* | Forest surveys were conducted. It is not specified in the English abstract whether morphological identifications were performed. | | Glavaš and Margaletić (2001) |
| Croatia, Zadar           | 2009          | *P. halepensis* | *TEF 1 sequencing was used for identification. Mating type 2 was detected.* | * | Janoušek et al. (2016) |
| Croatia, Kožino          | 2015          | *P. halepensis* | *TEF 1 sequencing was used for identification. Mating type 2 was detected.* | * | Sadiković et al. (2019) |
| Cuba, Baracoa, Guantánamo, Plateau of Mayarí and Master Saw | 1980–1998     | *P. caribaea, P. cubensis, P. maestrensis* | Symptom identification and morphological confirmation of the fungus. | | Mostly seedlings in nurseries were infected. | López Castilla et al. (2002) |
| Country, region, locality | Year collected | Host | Identification method and additional notes | Identification verified using molecular methods (*) | Reported severity of infections and applied eradication methods | Report references |
|--------------------------|----------------|------|---------------------------------------------|--------------------------------------------------|-------------------------------------------------|-----------------|
| Czech Republic, Southern Bohemia, Červené Blato Nature Reserve | 2007 | *P. uncinata subsp. uliginosa* | Morphological identifications were conducted as well as sequencing of the ITS region. The identity of the pathogen was again confirmed with TEF 1 sequencing by Janoušek et al. (2016). Both mating types were detected. | * | Heavy defoliation was reported in 2007. No control measures were taken as the incidence was reported in a natural nature reserve. | Jankovský et al. (2009b), Janoušek et al. (2016) |
| Czech Republic, Southern Bohemia, Soběslav, Borkovická Blata National Nature Reserve | 2008 | *P. uncinata subsp. uliginosa* | Morphological identifications were conducted as well as sequencing of the ITS region. The identity of the pathogen was again confirmed with TEF 1 sequencing by Janoušek et al. (2016). Both mating types were detected. | * | No action was taken as the outbreak was in a natural reserve. | Jankovský et al. (2009a), Janoušek et al. (2016) |
| Estonia, Hiiumaa Island and Kärevere | 2014–2015 | *P. mugo* | Symptom identification was confirmed with conventional PCR directly from pine needles. *Lecanosticta acicola* was isolated from the needles and confirmed with ITS sequencing. Both mating types were detected. | * | | Adamson et al. (2015) |
| Estonia, Tallinn Botanical Garden | 2006–2008 | *P. ponderosa* | Material of *D. mugo* was collected and isolated but in culture it was determined to be *L. acicola* based on culture morphology. The TEF 1 sequences were later determined for representative isolates and mating type 2 was detected (Janoušek et al., 2016). | * | | Drenkhan and Hanso (2009), Janoušek et al. (2016) |
| Estonia, Tallinn Botanical Garden | 2010–2013 | *P. mugo, P. mugo var. pumilio, P. ponderosa, P. uncinata* | Symptom identification was confirmed with conventional PCR directly from pine needles. *Lecanosticta acicola* was isolated from the needles and confirmed with ITS sequencing. Mating type 1 was detected. | * | | Adamson et al. (2015) |
| Estonia, Tartu county | 2016 | *P. sylvestris, P. mugo, Pinus × rhaetica* | Visual symptom identification was confirmed with conventional PCR and selected isolates were identified using an ITS sequencing PCR. Both mating types were detected. | * | | Adamson et al. (2018) |
| Estonia, Tori and Vasula | 2012, 2013 | *P. mugo* | Symptom identification was confirmed with conventional PCR directly from pine needles. *Lecanosticta acicola* was isolated from the needles and confirmed with ITS sequencing. | * | | Adamson et al. (2015) |
Table 1  (Continued)

| Country, region, locality | Year collected | Host | Identification method and additional notes | Identification verified using molecular methods (*) | Reported severity of infections and applied eradication methods | Report references |
|---------------------------|----------------|------|-----------------------------------------|--------------------------------------------------|---------------------------------------------------------------|-------------------|
| France, South-West, Aquitaine and western Pyrénées | 1993 | *P. attenuata × P. radiata* | In field observations were made. | | Severe tree mortality was observed. French authorities implemented eradication measures and destroyed 127 ha of trees. | Lévy (1996) |
| France, Gironde | 1995 | *P. muricata* | TEF 1 and BT 2 sequencing used for identification, mating type 1 detected. | * | | Ioos et al. (2010), Janoušek et al. (2016) |
| France, Landes | 1995 | *P. attenuata × P. radiata* | TEF 1 and BT 2 sequencing used for identification, mating type 2 detected. | * | | Ioos et al. (2010), Janoušek et al. (2016) |
| France, Pyrénées-Atlantiques | 1995 | *P. radiata* | TEF 1 and BT 2 sequencing used for identification. | * | | Ioos et al. (2010) |
| France, Ariège | 2009 | *P. sylvestris* | Forest surveys were conducted. | | More than 50% of the trees were affected. | Alvère et al. (2010) |
| France, Tarn-et-Garonne | 2009 | *P. nigra var. laricio* | Forest surveys were conducted. | | The trees were moderately affected. | Alvère et al. (2010) |
| France, Pyrénées-Atlantiques | 2012 | *P. radiata* | TEF 1 sequencing used for identification, both mating types were detected. | * | | Janoušek et al. (2016) |
| Germany, Bavaria | 1994 | *P. mugo* | The pathogen was identified based on morphological characteristics. | | | Pehl (1995) |
| Germany, Bavaria | 1994, 2000, 2010, 2011 | *P. mugo* | TEF 1 sequencing used for identification, both mating types were detected. | * | | Janoušek et al. (2016) |
| Germany, Bavaria, Munich Botanical gardens | 2018 | *P. mugo* | Collected by I. Barnes. The identity was confirmed by ITS sequencing. *Dothistroma septosporum* was also present. | * | | I. Barnes, FABI, Pretoria, South Africa, personal communication |
| Guatemala, El Progreso | 1983 | *P. oocarpa* | Morphological identification methods were used. As *L. acicola* was not identified in Central America using molecular identification techniques (van der Nest et al., 2019), this report will need to be verified. | | | Evans (1984) |
| Country, region, locality | Year collected | Host | Identification method and additional notes | Identification verified using molecular methods (*) | Reported severity of infections and applied eradication methods | Report references |
|---------------------------|----------------|------|---------------------------------------------|---------------------------------|--------------------------------------------------|-----------------|
| Honduras                  | 1980–1983      | P. caribaea, P. maximinoi, P. oocarpa, P. tecunumanii| Morphological identification methods were used. As L. acicola was not identified in Central America using molecular identification techniques (van der Nest et al., 2019), this report will need to be verified. | * | | Evans (1984) |
| Ireland, Wexford county   | 2016           | P. mugo, P. sylvestris | ITS sequencing was used for identification purposes. Mating type 1 was detected. | * | | Mullett et al. (2018) |
| Italy, Brescia            | 1997           | P. mugo | Symptoms were noted in the botanical garden and the presence of the pathogen was confirmed with morphological identifications. | | Extensive necrosis and crown defoliation were observed in all 12 of the P. mugo trees present in the botanical garden. | La Porta and Capretti (2000) |
| Italy, Brescia            | 2008           | P. mugo | TEF 1 sequencing used for identification and mating type 1 detected. | * | | Janoušek et al. (2016) |
| Japan, Shimane Prefecture (Honshu)  | 1996       | P. thunbergii, P. densiflora (tested in controlled environment) | The pathogen was morphologically identified. | | P. thunbergii was severely infected. Inoculation trials on this host as well as P. densiflora also revealed that P. densiflora is susceptible although it was not reported in the host’s natural environment. | Suto and Ougi (1998) |
| Japan, Shimane            | 2010           | P. thunbergii | TEF 1 sequencing used for identification, mating type 2 was detected. | * | | Janoušek et al. (2016) |
| Latvia, Salaspils         | 2012           | P. pumila | Morphological identification. Later it was confirmed with PCR-based methods. | * | Eradication measures were taken. | EPPO (2012a) |
| Latvia, Salaspils         | 2016           | P. mugo | Identification was done by ITS sequencing. Mating type 1 was detected. | * | | Mullett et al. (2018) |
Table 1 (Continued)

| Country, region, locality | Year collected | Host          | Identification method and additional notes | Identification verified using molecular methods (*) | Reported severity of infections and applied eradication methods | Report references |
|---------------------------|----------------|---------------|---------------------------------------------|---------------------------------------------------|-----------------------------------------------------------------|-------------------|
| Lithuania, Curonian Spit, Smiltyne Forest District | 2009 | P. mugo | Morphological characteristics as well as ITS sequencing and ITS-RFLP was used to identify the pathogen. This material was again examined by Janoušek et al. (2016) and the identity confirmed with TEF 1. Mating type 1 was detected. | * | A monitoring programme was initiated and infected trees felled and burned. | Markovskaja et al. (2011), Janoušek et al. (2016) |
| Lithuania, Curonian Spit, Smiltyne Forest District and Juodkrante Forest District | 2010 | P. mugo | Morphological characteristics as well as ITS sequencing and ITS-RFLP was used to identify the pathogen. | * | A monitoring programme was initiated and infected trees felled and burned. | Markovskaja et al. (2011) |
| Lithuania, Curonian Spit, near Juodkrante | 2012 | P. mugo, P. sylvestris | Morphological identifications and PCR-based methods. | * | Phytosanitary methods were implemented. | EPPO (2012b) |
| Lithuania, Curonian Spit, Smiltyne Forest District and Juodkrante Forest District | 2014 | P. mugo | Infected needles were collected by S. Markovskaja. Isolations were made by A. van der Nest. A multigene phylogenetic approach was used to determine the identity of the isolates. | * | | van der Nest et al. (2019) |
| Mexico, Puebla | 1983 | P. patula | Morphological identification. | | | Evans (1984) |
| Mexico | 2000 | P. ayacahuite, P. cembroides, P. halepensis | Morphological characteristics were examined. | | High disease severity was reported on P. halepensis. | Marmolejo (2000) |
| Mexico, Nuevo León | 2010, 2011 | P. halepensis | TEF 1 sequencing used for identification, both mating types detected. KJ938447–KJ938449 were later identified as L. variabilis (van der Nest et al., 2019) and the remaining isolates are part of L. acicola lineage 3. | * | | Janoušek et al. (2016) |
| Nicaragua | 1981–1983 | P. caribaea, P. maximinoi, P. oocarpa, P. tecunumanii | Morphological identification methods were used. As L. acicola was not identified in Central America using molecular identification techniques (van der Nest et al., 2019), this report will need to be verified. Both the sexual and asexual state was observed. | | | Evans (1984) |
| Portugal, Minho | 2016 | P. radiata | Identification was done by ITS sequencing. Mating type 1 was detected. | * | | Mullett et al. (2018) |
| Country, region, locality | Year collected | Host | Identification method and additional notes | Identification verified using molecular methods (*) | Reported severity of infections and applied eradication methods | Report references |
|---------------------------|---------------|------|---------------------------------------------|-----------------------------------------------|-------------------------------------------------|-----------------|
| Romania, Vrancea          | 2017          | Pinus sp. | The pathogen was detected during a forest survey in a 30-year-old plantation. | Eradication reported to be under way in the 19-hectare forest. | EPPO (2018) | |
| Russia, Krasnodar region, Sochi | 2016 | *P. mugo, P. thunbergii | Identification was done by ITS sequencing. Mating type 2 was detected. | | | Mullett et al. (2018) |
| Slovenia, Bled            | 2008–2009     | P. mugo, P. sylvestris | Morphological identifications. The identity of isolates on P. mugo were confirmed with TEF 1 sequencing and mating type 2 was detected (Janoušek et al., 2016; Sadiković et al., 2019). | | * | Jurc and Jurc (2010), Janoušek et al. (2016), Sadiković et al. (2019) |
| Slovenia, Čatež           | 2015          | P. mugo | TEF 1 sequencing was used for identification. Mating type 1 was detected. | | | | |
| Slovenia, Ljubljana       | 2008–2009     | P. mugo, P. sylvestris | Morphological identifications. The identity of isolates from P. mugo were confirmed with TEF 1 sequencing by Sadiković et al. (2019). | All affected trees were eradicated. | * | Jurc and Jurc (2010), Sadiković et al. (2019) |
| Slovenia, Ljubljana       | 2013          | P. mugo | TEF 1 sequencing was used for identification. Mating type 1 was detected. | | | Sadiković et al. (2019) |
| Slovenia, Tolmin          | 2016          | P. nigra | TEF 1 sequencing was used for identification. Mating type 1 was detected. | | | Sadiković et al. (2019) |
| Slovenia, Trenta          | 2014–2015     | P. mugo | TEF 1 sequencing was used for identification. Mating type 2 was detected. | | | Sadiković et al. (2019) |
| South Korea, Naju         | 2010–2011     | P. thunbergii | L. acicola symptoms were observed and confirmed with ITS sequencing. TEF 1 sequencing was used for identification by Janoušek et al. (2016) and mating type 2 was detected. | | * | Janoušek et al. (2016), Seo et al. (2012) |
| Spain                     | 1942          | P. radiata | Probably oldest official report of L. acicola in Europe based on morphological identification. | | | Martínez (1942) |
| Spain, Cantabria          | 2012          | P. radiata | TEF 1 sequencing used for identification, mating type 2 was detected. | | | Janoušek et al. (2016) |
| Spain, Spanish Atlantic climate region | 2015 | *P. nigra, P. radiata | Sequenced directly from needles using conventional PCR (Loos et al., 2010). Both mating types were detected. | | | Ortiz de Urbina et al. (2017) |
### Table 1 (Continued)

| Country, region, locality | Year collected | Host | Identification method and additional notes | Identification verified using molecular methods (*) | Reported severity of infections and applied eradication methods | Report references |
|---------------------------|----------------|------|---------------------------------------------|---------------------------------------------------|-----------------------------------------------------------------|-------------------|
| Sweden                    | 2017           | P. mugo ‘Hesse’ | Morphological identification and ITS sequencing. | *                                                   | Single tree in arboretum that was severely affected.             | Cleary et al. (2019) |
| Switzerland, Zollikon     | 1995           | P. mugo, P. uncinata | Morphological identification of the pathogen. |                                                    | Control measures were initiated in accordance with the phytosanitary policy of the EPPO. | Holdeneried and Sieber (1995) |
| Switzerland, Canton St Gallen | 1999      | P. mugo       | TEF 1 sequencing used for identification. | *                                                   |                                                                  | Janoušek et al. (2016) |
| Switzerland, Canton Zug   | 2009           | P. mugo       | Symptoms were observed in the field. Later, TEF 1 sequencing was used to confirm identification (Janoušek et al., 2016). Mating type 1 was detected. | *                                                   |                                                                  | Angst (2011), Janoušek et al. (2016) |
| Switzerland, Zürich       | 2009           | P. mugo       | Symptoms were observed in the field. Later, TEF 1 sequencing was used to confirm identification (Janoušek et al., 2016). Mating type 1 was detected. | *                                                   |                                                                  | Angst (2011), Janoušek et al. (2016) |
| Switzerland, Bern and Zürich | 2017      | P. mugo       | Detection with qPCR and a conventional PCR directly from pine needles. | *                                                   |                                                                  | Schneider et al. (2019) |
| Switzerland, Schwyz       | 2017           | P. sylvestris | Detection with qPCR and a conventional PCR directly from pine needles. | *                                                   |                                                                  | Schneider et al. (2019) |
| USA, Alabama              | 1929           | P. palustris  | Hedgcock reported on collections of the pathogen at the office of Forest Pathology at Washington, D.C. and the Mycological collections of the US Department of Agriculture. |                                                      |                                                                  | Hedgcock (1929) |
| USA, Alabama              | 1944           | P. echinata, P. palustris, P. taeda | Siggers reported Lecanosticta isolates that are in the collections in the Division of Forest Pathology in Louisiana and Maryland, USA. These reports should be verified. |                                                      |                                                                  | Siggers (1944) |
| USA, Alabama              | 1948–1967     | P. palustris  | Symptoms were observed annually on seedlings and the proportion of seedlings affected were recorded. |                                                      | In a 4-year study, 78% or more seedlings were infected yearly with L. acicola. | Boyer (1972) |
| Country, region, locality | Year collected | Host | Identification method and additional notes | Identification verified using molecular methods (*) | Reported severity of infections and applied eradication methods | Report references |
|--------------------------|---------------|------|------------------------------------------|-------------------------------------------------|----------------------------------------------------------|-------------------|
| USA, Arkansas            | 1929          | *P. taeda* | Hedgcock reported on collections of the pathogen at the office of Forest Pathology at Washington, D.C. and the Mycological collections of the US Department of Agriculture. | Identification verified using molecular methods (*) | Hedgcock (1929) | |
| USA, Arkansas            | 1944          | *P. taeda* | Siggers reported *Lecanosticta* isolates that are in the collections in the Division of Forest Pathology in Louisiana and Maryland, USA. These reports should be verified. | | Siggers (1944) | |
| USA, Arkansas            | 1967–1971     | *P. sylvestris* | Symptoms were observed in the field and the proportion of needles affected were noted. In some cases, microscopic examinations of conidia were used for identification. | | Skilling and Nicholls (1974) | |
| USA, Florida             | 1929          | *P. caribaea, P. glabra, P. palustris, P. taeda* | Hedgcock reported on collections of the pathogen at the office of Forest Pathology at Washington, D.C. and the Mycological collections of the US Department of Agriculture. | | Hedgcock (1929) | |
| USA, Florida             | 1944          | *P. attenuata, P. caribaea, P. coulteri, P. jeffreyi, P. glabra, P. halepensis, P. latifolia, P. muricata, P. palustris, P. pinaster, P. pinea, P. ponderosa var. scopulorum, P. radiata, P. thunbergii* | Siggers reported *Lecanosticta* isolates that are in the collections in the Division of Forest Pathology in Louisiana and Maryland, USA. These reports should be verified. | | Siggers (1944) | |
| USA, Georgia             | 1929          | *P. palustris, P. taeda, P. virginiana* | Hedgcock reported on collections of the pathogen at the office of Forest Pathology at Washington, D.C. and the Mycological collections of the US Department of Agriculture. | | Hedgcock (1929) | |
| USA, Georgia             | 1944          | *P. caribaea, P. palustris, P. taeda, P. virginiana* | Siggers reported *Lecanosticta* isolates that are in the collections in the Division of Forest Pathology in Louisiana and Maryland, USA. These reports should be verified. | | Siggers (1944) | |
| Country, region, locality | Year collected | Host | Identification method and additional notes | Identification verified using molecular methods (*) | Reported severity of infections and applied eradication methods | Report references |
|---------------------------|----------------|------|---------------------------------------------|---------------------------------------------------|-----------------------------------------------------------------|-------------------|
| USA, Idaho                | 1929           | *P. ponderosa* | Hedgcock reported on collections of the pathogen at the office of Forest Pathology at Washington, D.C. and the Mycological collections of the US Department of Agriculture. According to Siggers (1944) the identification was based on characteristics that do not fit *Lecanosticta* and therefore this record should be verified. | | | Hedgcock (1929) |
| USA, Iowa                 | 1967–1971      | *P. sylvestris* | Symptoms were observed in the field and the proportion of needles affected were noted. In some cases, microscopic examinations of conidia were used for identification. | | | Skilling and Nicholls (1974) |
| USA, Kansas               | 1929           | *P. nigra var. austriaca* | Hedgcock reported on collections of the pathogen at the office of Forest Pathology at Washington, D.C. and the Mycological collections of the US Department of Agriculture. According to Siggers (1944) the identification was based on characteristics that do not fit *Lecanosticta* and therefore this record should be verified. | | | Hedgcock (1929) |
| USA, Kansas               | 1951           | *P. nigra, P. ponderosa* | Reports in the field and mycological identification. | | | Rogerson (1953) |
| USA, Kansas               | 1967–1971      | *P. sylvestris* | Symptoms were observed in the field and the proportion of needles affected were noted. In some cases, microscopic examinations of conidia were used for identification. | | | Skilling and Nicholls (1974) |
| USA, Kentucky             | 1929           | *P. nigra var. austriaca* | Hedgcock reported on collections of the pathogen at the office of Forest Pathology at Washington, D.C. and the Mycological collections of the US Department of Agriculture. According to Siggers (1944) the identification was based on characteristics that do not fit *Lecanosticta* and therefore this record should be verified. | | | Hedgcock (1929) |
| USA, Kentucky             | 1967–1971      | *P. sylvestris* | Symptoms were observed in the field and the proportion of needles affected were noted. In some cases, microscopic examinations of conidia were used for identification. | | | Skilling and Nicholls (1974) |
### Table 1  (Continued)

| Country, region, locality | Year collected | Host | Identification method and additional notes | Identification verified using molecular methods (*) | Reported severity of infections and applied eradication methods | Report references |
|---------------------------|---------------|------|---------------------------------------------|---------------------------------------------------|-----------------------------------------------------------------|-------------------|
| USA, Louisiana            | 1929          | *P. palustris, Pinus × sondereggeri, P. taeda* | Hedgcock reported on collections of the pathogen at the office of Forest Pathology at Washington, D.C. and the Mycological collections of the US Department of Agriculture. | Hedgcock (1929) |
| USA, Louisiana            | 1929–1930, 1960 | *P. palustris* | Symptoms were observed and the proportion of seedlings affected were recorded at 4–5 years of age and again at 30 years. | Most of the trees were affected. | Wakeley (1970) |
| USA, Louisiana            | 1944          | *P. attenuata, P. caribaea, P. contorta var. latifolia, P. echinata, P. nigra var. laricio, P. palustris, P. pinaster, P. ponderosa var. scopulorum, P. radiata, P. rigida, P. serotina, P. sabiniana, Pinus × sondereggeri, P. taeda* | Siggers reported on Lecanosticta isolates that are in the collections in the Division of Forest Pathology in Louisiana and Maryland, USA. These reports should be verified. | Siggers (1944) |
| USA, Maine                | 2011          | *P. strobus* | Isolates were collected and morphologically identified in a survey. These isolates were later identified with TEF 1 sequencing and both mating types were detected. | * | Munck et al. (2012), Janoušek et al. (2016) |
| USA, Maine                | 2011–2012     | *P. strobus* | Lecanosticta acicola was identified as part of a complex of pathogens that cause white pine needle damage (WPND). Morphological identifications and selected ITS PCR sequencing was performed to confirm the presence of L. acicola. | * | Broders et al. (2015) |
| USA, Michigan             | 2016          | *P. sylvestris* | TEF 1 sequencing used for identification, mating type 2 was detected. | * | Janoušek et al. (2016) |
| USA, Minnesota            | 1967–1971     | *P. sylvestris* | Symptoms were observed in the field and the proportion of needles affected were noted. In some cases, microscopic examinations of conidia were used for identification. | | Skilling and Nicholls (1974) |
| Country, region, locality | Year collected | Host | Identification method and additional notes | Identification verified using molecular methods (*) | Reported severity of infections and applied eradication methods | Report references |
|---------------------------|----------------|------|---------------------------------------------|-------------------------------------------------|-------------------------------------------------|------------------|
| USA, Minnesota and Wisconsin | 1970–1972 | *P. banksiana, P. glauca, P. nigra, P. palustris, P. resinosa, P. strobus, P. sylvestris, Picea glauca | Symptoms were observed in the field and the proportion of needles affected were noted. | | These species were tested for susceptibility in a field trial by planting the hosts underneath heavily infected *P. sylvestris*. Four varieties of *P. sylvestris*, as well as *P. nigra* and *P. resinosa*, were the most susceptible. *P. strobus* was moderately resistant. *P. banksiana* was the most resistant. Less than 1% of *Picea glauca* was infected. | Skilling and Nicholls (1974) |
| USA, Mississippi | 1929 | *P. caribaea, P. palustris, P. taeda* | Hedgcock reported on collections of the pathogen at the office of Forest Pathology at Washington, D.C. and the Mycological collections of the US Department of Agriculture. | | | Hedgcock (1929) |
| USA, Mississippi | 1944 | *P. caribaea, P. palustris, P. pinaster, P. taeda, P. thunbergii* | Siggers reported on *Lecanosticta* isolates that are in the collections in the Division of Forest Pathology in Louisiana and Maryland, USA. These reports should be verified. | | | Siggers (1944) |
| USA, Mississippi | 1952–1953 | *P. palustris* | Microscopic identification. Both the sexual and asexual states were observed. | | | Henry (1954) |
| USA, Mississippi | 1966–1967 | *P. palustris* | Morphological identifications. Both the sexual state and asexual state were observed throughout the year on infected *P. palustris*. | | | Kais (1971) |
| USA, Mississippi | 2012 | *P. palustris, P. taeda* | *TEF 1* sequencing used for identification, both mating types detected. | * | * | *Janoušek et al. (2016)* |
| Country, region, locality | Year collected | Host | Identification method and additional notes | Identification verified using molecular methods (*) | Reported severity of infections and applied eradication methods | Report references |
|--------------------------|---------------|------|---------------------------------------------|-----------------------------------------------|-------------------------------------------------|------------------|
| USA, Missouri            | 1929          | *P. nigra var. austriaca* | Hedgcocck reported on collections of the pathogen at the office of Forest Pathology at Washington, D.C. and the Mycological collections of the US Department of Agriculture. According to Siggers (1944) the identification was based on characteristics that do not fit Lecanosticta and therefore this record should be verified. | Hedgcocck (1929) | | |
| USA, Missouri            | 1947–1949     | *P. ponderosa* | Symptoms were observed in the field and morphological identifications were made. Both the sexual state and asexual state were observed. | | All trees were affected. Excessive needle defoliation and in some cases tree mortality was observed. | Lutrell (1949) |
| USA, Missouri            | 1967–1971     | *P. sylvestris* | Symptoms were observed in the field and the proportion of needles affected were noted. In some cases, microscopic examinations of conidia were used for identification. | | | Skilling and Nicholls (1974) |
| USA, New England         | 2016          | *P. strobus* | Severe needle browning was observed and *L. acicola* was identified as part of a complex of species causing premature defoliation. This is possibly WPND although it was not defined as such. | | | Brazee (2016) |
| USA, New Hampshire       | 2011          | *P. strobus* | Isolates were collected and morphologically identified in a survey. These isolates were later identified with TEF 1 sequencing and mating type 1 was detected. | * | | Munck et al. (2012), Janoušek et al. (2016) |
| USA, New Hampshire       | 2011–2012     | *P. strobus* | *Lecanosticta acicola* was identified as part of a complex of pathogens that cause WPND. Morphological identifications and selected ITS PCR sequencing confirmed the presence of *L. acicola*. | * | It was observed that affected trees were defoliated annually. | Broders et al. (2015) |
| USA, New York            | 1976          | *P. mugo* | *Lecanosticta acicola* was identified with morphological methods and brown spot needle blight symptoms confirmed on trees. Specimens are in the Cornell University Plant Pathology Herbarium. | | | Sinclair and Hudler (1980) |
| Country, region, locality | Year collected | Host | Identification method and additional notes | Identification verified using molecular methods (*) | Reported severity of infections and applied eradication methods | Report references |
|---------------------------|----------------|------|--------------------------------------------|---------------------------------------------------|---------------------------------------------------------------|------------------|
| USA, North Carolina       | 1929           | P. echinata, P. palustris, P. rigida, P. taeda, P. virginiana | Hedgcock reported on collections of the pathogen at the office of Forest Pathology at Washington, D.C. and the Mycological collections of the US Department of Agriculture. | | | Hedgcock (1929) |
| USA, North Carolina       | 1944           | P. palustris, P. rigida, P. strobus, P. taeda, P. virginiana | Siggers reported on Lecanosticta isolates that are in the collections in the Division of Forest Pathology in Louisiana and Maryland, USA. These reports should be verified. | | | Siggers (1944) |
| USA, North Carolina       | 1957, 1958     | P. strobus | Morphological identifications of L. acicola. | | | Boyce (1959) |
| USA, Ohio                 | 1944           | P. contorta var. latifolia, P. coulteri, P. jeffreyi | Siggers reported on Lecanosticta isolates that are in the collections in the Division of Forest Pathology in Louisiana and Maryland, USA. These reports should be verified. | | | Siggers (1944) |
| USA, Oregon               | 1929           | P. attenuata | Hedgcock reported on collections of the pathogen at the office of Forest Pathology at Washington, D.C. and the Mycological collections of the US Department of Agriculture. | | | Hedgcock (1929) |
| USA, Oregon               | 1944           | P. attenuata | Siggers reported on Lecanosticta isolates that are in the collections in the Division of Forest Pathology in Louisiana and Maryland, USA. These reports should be verified. | | | Siggers (1944) |
| USA, Pennsylvania         | 1929           | P. rigida | Hedgcock reported on collections of the pathogen at the office of Forest Pathology at Washington, D.C. and the Mycological collections of the US Department of Agriculture. | | | Hedgcock (1929) |
| USA, Pennsylvania         | 1987–1989      | P. strobus | Morphological identifications were done. | | | Stanosz (1990) |
| USA, South Carolina       | 1876           | P. echinata (P. variabilis) | Morphological description of Cryptosporium acicolum. | | | de Thümen (1878) |
| USA, South Carolina       | 1929           | P. caribaea, P. echinata, P. palustris, P. serotina, P. taeda | Hedgcock reported on collections of the pathogen at the office of Forest Pathology at Washington, D.C. and the Mycological collections of the US Department of Agriculture. | | | Hedgcock (1929) |
| USA, South Carolina       | 1944           | P. caribaea, P. palustris, P. taeda | Siggers reported on Lecanosticta isolates that are in the collections in the Division of Forest Pathology in Louisiana and Maryland, USA. These reports should be verified. | | | Siggers (1944) |
| Country, region, locality | Year collected | Host | Identification method and additional notes | Identification verified using molecular methods (*) | Reported severity of infections and applied eradication methods | Report references |
|---------------------------|----------------|------|--------------------------------------------|-------------------------------------------------|-------------------------------------------------|------------------|
| USA, Tennessee            | 1929           | P. rigida, P. taeda | Hedgcock reported on collections of the pathogen at the office of Forest Pathology at Washington, D.C. and the Mycological collections of the US Department of Agriculture. | | | Hedgcock (1929) |
| USA, Tennessee            | 1944           | P. palustris, P. ponderosa var. scopulorum, P. rigida, P. taeda | Siggers reported on Lecanosticta isolates that are in the collections in the Division of Forest Pathology in Louisiana and Maryland, USA. These reports should be verified. | | | Siggers (1944) |
| USA, Texas                | 1929           | P. palustris, P. taeda | Hedgcock reported on collections of the pathogen at the office of Forest Pathology at Washington, D.C. and the Mycological collections of the US Department of Agriculture. | | | Hedgcock (1929) |
| USA, Texas                | 1929           | P. palustris, P. taeda | Symptoms were observed on trees inside and surrounding the nurseries. | | Low severity recorded. Nursery beds were sprayed with Bordeaux 4-4-50 with good results. | Webster (1930) |
| USA, Texas                | 1944           | P. caribaea, P. palustris, P. pinaster, P. taeda | Siggers reported on Lecanosticta isolates that are in the collections in the Division of Forest Pathology in Louisiana and Maryland, USA. These reports should be verified. | | | Siggers (1944) |
| USA, Vermont              | 2008           | P. mugo, P. resinosa, P. sylvestris, P. strobus | Forest surveys were conducted and the pathogen identified based on symptomology. | | | Gibbs and Sinclair (2008) |
| USA, Vermont              | 2011           | P. strobus | Isolates were collected and morphologically identified in a survey. These isolates were later identified with TEF 1 sequencing and both mating types were detected. | | | Munck et al. (2012), Janoušek et al. (2016) |
| USA, Vermont              | 2011–2012      | P. strobus | Lecanosticta acicola was identified as part of a complex of pathogens that cause WPND. Morphological identifications and selected ITS PCR sequencing confirmed the presence of L. acicola. | * | It was observed that affected trees were defoliated annually. | Broders et al. (2015) |
| USA, Virginia             | 1929           | P. rigida | Hedgcock reported on collections of the pathogen at the office of Forest Pathology at Washington, D.C. and the Mycological collections of the US Department of Agriculture. | | | Hedgcock (1929) |
| Country, region, locality | Year collected | Host | Identification method and additional notes | Identification verified using molecular methods (*) | Reported severity of infections and applied eradication methods | Report references |
|--------------------------|----------------|------|---------------------------------------------|-------------------------------------------------|----------------------------------------------------------|------------------|
| USA, Wisconsin           | 1966–1970      | *P. sylvestris* | A forest survey was conducted and symptoms of *L. acicola* was observed. | * | Approximately 3000 acres in 55 plantations were severely infected. Short leaf French and Spanish *P. sylvestris* were severely affected. Long leaf *P. sylvestris* varieties were reported as resistant. | Prey and Morse (1971) |
| USA, Wisconsin           | 1967–1971      | *P. sylvestris* | Symptoms were observed in the field and the proportion of needles affected were noted. In some cases, microscopic examinations of conidia were used for identification. | * | | Skilling and Nicholls (1974) |
| USA, Wisconsin           | 1970           | *P. resinosa* | Symptoms were observed in the field and morphological identifications were made. | * | After the pathogen was observed in pine stands, an inoculation trial revealed that *P. resinosa* is highly susceptible to *L. acicola*. | Nicholls and Hudler (1972) |
| USA, Wisconsin           | 2010           | *P. sylvestris* | TEF 1 sequencing used for identification, mating type 2 was detected. | * | | Janoušek et al. (2016) |
| *Lecanosticta brevispora* | 2010           | *P. oocarpa* | Multigene phylogenetic analysis. | * | | van der Nest et al. (2019) |
| Guatemala, Alta Verapaz, Santa Cruz Verapaz, near Tactic | 2010           | *P. oocarpa* | Multigene phylogenetic analysis. | * | | van der Nest et al. (2019) |
| Guatemala, Chimaltenango, Tecpán, Finca La Esperanza | 2010           | *P. pseudostrobus* | Multigene phylogenetic analysis. | * | | van der Nest et al. (2019) |
| Guatemala, Lugar, La Soledad, Jalapa site II | 2010           | *P. oocarpa* | Multigene phylogenetic analysis. | * | | van der Nest et al. (2019) |
| Honduras                 | 2010           | *P. oocarpa* | Multigene phylogenetic analysis. | * | | van der Nest et al. (2019) |
| Mexico                   | 2000           | Pinus sp. | Multigene phylogenetic analysis. | * | | Quaedvlieg et al. (2012) |
### Table 1 (Continued)

| Country, region, locality | Year collected | Host | Identification method and additional notes | Identification verified using molecular methods (*) | Reported severity of infections and applied eradication methods | Report references |
|---------------------------|---------------|------|-------------------------------------------|--------------------------------------------|-------------------------------------------------|------------------|
| *Lecanosticta gloeospora* |               |      |                                           |                                            |                                                 |                  |
| Mexico, Nuevo León, Iturbi-de-Galeana | 1983 | *P. pseudostrobus* | Morphological identification. The type was later sequenced using multiple genes (van der Nest et al., 2019). | * | Evans (1984), Marmolejo (2000), van der Nest et al. (2019) |
| *Lecanosticta guatemalensis* |               |      |                                           |                                            |                                                 |                  |
| Guatemala, Baja Verapaz | 1983 | *P. oocarpa* | The type culture was previously identified as *L. acicola* based on morphological characteristics (Evans, 1984). Multigene phylogenetic analysis revealed it as a new species, *L. guatemalensis*. | * | Quaedvlieg et al. (2012), van der Nest et al. (2019) |
| Guatemala, Alta Verapaz, Santa Cruz Verapaz, near Tactic | 2010 | *P. oocarpa* | Multigene phylogenetic analysis. | * | Very low. | van der Nest et al. (2019) |
| Guatemala, Chiquimula | 2011 | *P. oocarpa* | Multigene phylogenetic analysis. | * | Very low. | van der Nest et al. (2019) |
| Guatemala, Jalapa, Finca Forestal Soledad | 2012 | *P. oocarpa* | Multigene phylogenetic analysis. | * | Very low. | van der Nest et al. (2019) |
| Guatemala, Coban, San Juan Chamalco | 2012 | *P. oocarpa* | Multigene phylogenetic analysis. | * | Very low. | van der Nest et al. (2019) |
| Nicaragua | 1982 | *P. tecunumanii* | This isolate was previously identified as *L. acicola* based on morphological characteristics (Evans, 1984). Multigene phylogenetic analysis revealed it to be *L. guatemalensis*. | * | van der Nest et al. (2019) |
| Nicaragua, Matagalpa | 2010 | *P. oocarpa* | Multigene phylogenetic analysis. | * | Very low. | van der Nest et al. (2019) |
| Honduras, Yoro | 1981 | *P. caribaea, P. oocarpa* | These isolates were previously identified as *L. acicola* based on morphological characteristics (Evans, 1984). Multigene phylogenetic analysis revealed it to be *L. guatemalensis*. | * | van der Nest et al. (2019) |
| *Lecanosticta jani* |               |      |                                           |                                            |                                                 |                  |
| Guatemala, Alta Verapaz, Santa Cruz Verapaz, near Tactic | 2010 | *P. oocarpa* | Multigene phylogenetic analysis. | * | Very low. | van der Nest et al. (2019) |
| Guatemala, Chiquimula | 2010 | *P. oocarpa* | Multigene phylogenetic analysis. | * | Very low. | van der Nest et al. (2019) |
| Guatemala, Jalapa, Finca Forestal Soledad | 2012 | *P. maximinoi* | Multigene phylogenetic analysis. | * | Very low. | van der Nest et al. (2019) |
| Guatemala, Jalapa, Finca La Soledad, Mataquescuinlta | 2012 | *P. tecunumanii* | Multigene phylogenetic analysis. | * | Very low. | van der Nest et al. (2019) |
Central America based on morphological characteristics (Evans, 1984), it is now recognized as a Northern Hemisphere pathogen for which phylogenetic analyses of the translation elongation factor 1-α gene (TEF 1) sequences have revealed three distinct lineages (van der Nest et al., 2019). One of these lineages includes isolates from Canada, the northern parts of the USA (Maine, Michigan, New Hampshire, Vermont and Wisconsin) and Central and Northern Europe (Austria, Croatia, Czech Republic, Estonia, Germany, Italy, Lithuania, Slovenia, Switzerland) (van der Nest et al., 2019). A second lineage includes isolates from China, Colombia, France, Japan, Spain, South Korea and the southern part of the USA (Mississippi) (van der Nest et al., 2019). A third lineage includes isolates only from Mexico (van der Nest et al., 2019).

The eight other species described in Lecanosticta during the course of the past 35 years are present only in Mesoamerica (Tables 1 and 2) (Evans, 1984; Marmolejo, 2000; Quaedvlieg et al., 2012; van der Nest et al., 2019). Evans (1984) recognized

| Country, region, locality | Year collected | Host | Identification method and additional notes | Identification verified using molecular methods (*) | Reported severity of infections and applied eradication methods | Report references |
|---------------------------|----------------|------|------------------------------------------|------------------------------------------------|------------------------------------------------|-------------------|
| Nicaragua, Matagalpa      | 2010           | P. oocarpa | Multigene phylogenetic analysis. | * | Very low. | van der Nest et al. (2019) |
| Lecanosticta pharomachri |                |      |                                          |                                                |                                                    |                   |
| Guatemala, Baja Verapaz, San Jerónimo, Salamá | 2012 | P. tecunumanii | Multigene phylogenetic analysis. | * | Very low. | van der Nest et al. (2019) |
| Guatemala, Jalapa, Finca La Soledad, Mataquescuintla | 2010–2012 | P. oocarpa | Multigene phylogenetic analysis. | * | Very low. | van der Nest et al. (2019) |
| Honduras                  | 2010           | P. oocarpa | Multigene phylogenetic analysis. | * | Very low. | van der Nest et al. (2019) |
| Lecanosticta tecunumanii |                |      |                                          |                                                |                                                    |                   |
| Guatemala, Baja Verapaz, San Jerónimo, Salamá | 2012 | P. tecunumanii | Multigene phylogenetic analysis. | * | Very low. | van der Nest et al. (2019) |
| Guatemala, Alta Verapaz, Santa Cruz Verapaz, near Tactic | 2010 | P. oocarpa | Multigene phylogenetic analysis. Both mating types were present (Janoušek et al., 2016). | * | Very low. | van der Nest et al. (2019) |
| Guatemala, Jalapa, Finca Forestal Soledad | 2012 | P. maximinoi | Multigene phylogenetic analysis. | * | Very low. | van der Nest et al. (2019) |
| Honduras, Santa Barbara, Lago de Yojoa | 1984 | P. caribaea | This isolate was previously identified as L. acicola in a morphological study by Evans (1984). A multigene phylogenetic analysis indicated that this is a new species, L. tecunumanii. | * | Very low. | Evans (1984), van der Nest et al. (2019) |
| Mexico                    | 2000           | Pinus sp. | Multigene phylogenetic analysis. | * | van der Nest et al. (2019) |
| Mexico                    | 2010           | P. arizonica var. stormiae, P. halepensis | Multigene phylogenetic analysis. The isolates were previously identified as L. acicola (Janoušek et al., 2016) and both mating types were detected. | * | van der Nest et al. (2019) |
Table 2  A summarized history of the taxonomy and nomenclature of the genus *Lecanosticta*.

| Year | Species epithet | Reference | Sexual state reported | Country, location | Host | Description | Notes |
|------|----------------|-----------|-----------------------|------------------|------|-------------|-------|
| 1878 | Cryptosporium acicolum Thüm | de Thümen (1878) | Asexual | USA, South Carolina, Aiken | Pinus echinata (P. variabilis) |  |
| 1884 | Septoria acicola (Thüm) Sacc | Saccardo (1884) | Asexual | USA, Carolina, Aiken | P. variabilis | Saccardo moved C. acicolum to Septoria due to the characteristic septate conidia. |
| 1922 | Lecanosticta pini | Sydow and Petrak (1922) | Asexual | USA, Arkansas and Oregon | P. taeda and P. palustris in Arkansas and P. attenuata in Oregon | The genus *Lecanosticta* was erected to accommodate *L. pini*, a fungus with erumpent stromata and pigmented conidia. |
| 1924 | Lecanosticta acicola | Sydow and Petrak (1924) | Asexual | USA | – | The authors recognized that *L. pini* was *C. acicolum*. The genus was retained and the name *L. acicola* was proposed as the valid name. |
| 1926 | Oligostroma acicola | Dearness (1926, 1928) | Sexual | USA, Florida, Silver Springs | P. palustris | The sexual state of *L. acicola* was isolated from old pine needles from which the asexual state was previously isolated. In 1928, it was proposed that the asexual state *Septoria acicola* fits better in the genus *Cryptosporium* and that *Oligostroma acicola* could be *Cryptosporium acicolum*’s sexual state (Dearness, 1928). |
| 1939 | Schirria acicola | Siggers (1939) | Sexual | USA, Arkansas, Florida, Georgia, Louisiana, North Carolina, Texas | P. palustris, P. taeda, P. thunbergii | Ascospores as well as conidia were plated onto media and morphologically examined to come to the conclusion that the sexual and asexual state are connected. *Oligostroma acicola* was changed to *Schirria acicola* as erumpent acervuli were observed, characteristic of *Schirria*. |

*P. variabilis* is a synonym of *P. echinata*. In Wolf and Barbour (1941), it was mentioned that it was in fact on *P. caribaea* and that the host was previously incorrectly identified.
Table 2 (Continued)

| Year  | Species epithet         | Reference                          | Sexual state reported | Country, location          | Host     | Description                                                                 | Notes                                                                 |
|-------|-------------------------|------------------------------------|-----------------------|---------------------------|----------|-----------------------------------------------------------------------------|------------------------------------------------------------------------|
| 1941  | *Systremma acicola*     | Wolf and Barbour (1941)            | Sexual                | USA                       | Pinus spp. | It was recognized that the pathogen was better suited in the Dothideaceae and therefore the fungus was moved to the genus *Systremma* and all the above names for the sexual state synonymized with *S. acicola*. |                                                                        |
| 1967  | *Dothistroma acicola*   | Shishkina and Tsanava (1967)       | Asexual               | –                         | –        | The name *D. acicola* was incorrectly assigned to both *D. pini* and *L. acicola*. The name was not used in subsequent literature. | Due to similarities between symptoms caused by *Dothistroma* and *Lecanosticta* the asexual states of *D. pini* (presently *D. septosporum*) and *L. acicola* were synonymized and renamed as *D. acicola* and furthermore associated with the sexual state *Systremma acicola*. |
| 1972  | *Mycosphaerella dearnessii* | Barr (1972)                        | Sexual                | USA                       | –        | *Systremma acicola* was synonymized with *Mycosphaerella dearnessii*. *Mycosphaerella dearnessii* was assigned as the type for *Mycosphaerella* subgenus *Mycosphaerella* section *Caterva*. | MycoBank accession number: 318138.                                      |
| 1996  | *Eruptio acicola*       | Barr (1996)                        | Sexual                | –                         | –        | According to Barr (1996), *Mycosphaerella dearnessii* did not fit the description of *Mycosphaerella* and the new genus *Eruptio* M.E. Barr was erected to accommodate *Eruptio acicola* and *Eruptio pini* (sexual state of *Dothistroma septosporum*). | The validity of the genus *Eruptio* was questioned as *Lecanosticta acicola* phylogenetically clusters with other *Mycosphaerella* anamorphs (Crous et al. 2001). *Eruptio* is not widely used in literature. |
| 2012  | *Lecanosticta acicola*  | Quaedvlieg et al. (2012)           | Both                  | Europe and North America  | Pinus spp. | As it was recognized that the genus *Mycosphaerella* should only be used with the anamorphic genus *Ramularia* (Crous et al., 2007; Crous, 2009), *Lecanosticta acicola* was selected as the valid name and type of the genus under the one fungus = one name rule. An epitype was designated for *L. acicola* in this study (Quaedvlieg et al., 2012). | MycoBank accession number: 255702 Epitype CBS H-21113, Ex-epitype CBS 133791. |
| Year | Species epithet          | Reference            | Sexual state reported | Country, location | Host             | Description                                                                 | Notes                                                                                                                                                                                                 |
|------|-------------------------|----------------------|-----------------------|-------------------|------------------|-----------------------------------------------------------------------------|-------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| 1984 | Lecanosticta cinerea     | Evans (1984);        | Asexual               | Honduras          | Pinus sp.        | The species name was proposed as the correct name for *Gloeocoryneum cinereum*. | This name is not validly published (Marmolejo, 2000) as no basionym was established. The new combination *Leptomelanconium pinicola* was proposed because it had previously been established that *Gloeocoryneum cinereum* is a synonym of *Stilbospora pinicola* and that the genera *Gloeocoryneum* and *Leptomelanconium* have the same characteristics (Marmolejo, 2000). |
| 1984 | Lecanosticta gloeospora  | Evans (1984)         | Asexual               | Mexico, Iturbide-Galeana, Nuevo León | *P. pseudostrobus* | The second valid species in the genus to be described based on morphological characteristics. MycoBank accession number: 106975 Holotype IMI 283812 Ex-type IMI 283812. | No type was assigned but Quaedvlieg et al. (2012) epitypified the species in 2012.                                                                                                                     |
| 2000 | Lecanosticta longispora  | Marmolejo (2000)     | Asexual               | Mexico, Nuevo León | *P. culminicola*  | The third species described in the genus based on morphological characteristics. | MycoBank accession number: 466255 Epitype CBS H-21111, Ex-epitype CBS 133602.                                                                                                                      |
| 2012 | Lecanosticta longispora  | Quaedvlieg et al. (2012) | Asexual               | Mexico, Nuevo León | *P. culminicola*  | The first phylogenetic study to include this species. An epitype *L. longispora* was designated here. MycoBank accession number: 801940 Holotype CBS H-21110, Ex-type CBS 133601. | MycoBank accession number: 801941 Holotype CBS H-21110, Ex-type CBS 133601.                                                                                                                      |
| 2012 | Lecanosticta brevispora  | Quaedvlieg et al. (2012) | Asexual               | Mexico            | *Pinus sp.*      | This isolate is the fourth species described in the genus based on phylogenetic inference and morphology. MycoBank accession number: 801941 Holotype CBS H-21108, Ex-type IMI 281598. | MycoBank accession number: 801940 Holotype CBS H-21110, Ex-type CBS 133601.                                                                                                                      |
| 2012 | Lecanosticta guatemalensis | Quaedvlieg et al. (2012) | Asexual               | Guatemala         | *P. oocarpa*     | The ex-type of *L. guatemalensis* (IMI281598) was initially described as *L. acicola* based on morphological characteristics (Evans, 1984). The isolate was phylogenetically delineated as a new species in 2012 and subsequently described (Quaedvlieg et al., 2012). | MycoBank accession number: 826875 Holotype PREM 62185, Ex-type CBS 144456.                                                                                                                      |
| 2018 | Lecanosticta janii       | van der Nest et al. (2019) | Asexual               | Guatemala, Nicaragua | *P. maximinoi, P. oocarpa, P. tecunumanii* | New species described based on phylogenetic and morphological data. | MycoBank accession number: 826875 Holotype PREM 62185, Ex-type CBS 144456.                                                                                                                      |
considerable morphological variation amongst his collections of *L. acicola*. In that study, he described a second species, *L. gloeospora* from *Pinus pseudostrobus* in Mexico, and the fungus remains known only from Mexico on this host (Evans, 1984; Marmolejo, 2000). The novelty of this species was recently validated using DNA sequence data (van der Nest et al., 2019).

*Lecanosticta longispora* was first described based on morphological features from *P. culminicola* in Nuevo León, Mexico (Marmolejo, 2000). This species was characterized in a phylogenetic study by Quaedvlieg et al. (2012), and was distinguished from *L. acicola* based on differences in the TEF 1 and β-tubulin 2 (BT 2) gene sequences. That study was the first to delineate species of *Lecanosticta* based on phylogenetic inference (Quaedvlieg et al., 2012). These authors included several samples from Central America that had previously been identified as *L. acicola*, as well as the collection used by Marmolejo (2000) to typify *L. longispora*. In their phylogenetic analyses (Quaedvlieg et al., 2012), *L. acicola* was not identified from Central America but two new species, *L. brevispora* and *L. guatemalensis*, were described (Tables 1 and 2).

Evans (1984) observed that ecotypes or morphotypes exist amongst isolates of *L. acicola* in Central America, depending on the altitude and hosts from which the isolations were made. He therefore hypothesized that Central America could be the centre of origin of *Lecanosticta*. This was later supported by analysis of TEF 1 sequence data that revealed high genetic diversity in this geographical region (Janoušek et al., 2016). An extensive collection of isolates from Central America was recently studied using a phylogenetic approach (van der Nest et al., 2019). Interestingly, *L. acicola* was not identified amongst isolates from Guatemala, Nicaragua or Honduras. Furthermore, the isolates considered to be *L. acicola* by Evans (1984) were sequenced and identified as *L. guatemalensis* and a new species, *L. variabilis* (van der Nest et al., 2019, Table 1). *Lecanosticta brevispora* was identified in Guatemala and Honduras on *P. oocarpa* and *P. pseudostrobus* (Table 1), expanding the host range and distribution for that species. Likewise, *L. guatemalensis* was also identified in Guatemala, Honduras and Nicaragua on *P. caribaea*, *P. oocarpa* and *P. pseudostrobus* (Table 1). The study of van der Nest et al. (2019) introduced four new species, including *Lecanosticta jani* from Guatemala and Nicaragua, *L. pharomachri* from Guatemala and Honduras, *L. tecunumanii* from Guatemala and *L. variabilis* from Mexico, Guatemala and Honduras (van der Nest et al., 2019). Although Central America could not be confirmed as a centre of origin of *L. acicola*, the diversity of species recognized by van der Nest et al. (2019) suggests strongly that Mesoamerica is a centre of diversity for *Lecanosticta*.

With only one exception, which is probably a taxonomic incongruity, *Lecanosticta* species are all associated with *Pinus* species. Petrak (1954) described *Phragmogloeum gauae* on *Callistemon sieberi* in Australia (Petrak, 1954), von Arx (1983) attempted to reduce various species with overlapping characteristics to fewer genera and found that *Phragmogloeum* had the same morphological...
characteristics as Lecanosticta. He proposed the new combination Lecanosticta gaubae. After the genus Eruptio was erected to accommodate Lecanosticta acicola and Dothistroma septosporum (Barr, 1996), Lecanosticta gaubae was transferred to that new genus (Crous, 1999). The genus Eruptio was further evaluated and it was found that L. acicola and D. septosporum were not congeneric (Crous, 2009). Consequently, Lecanosticta was selected as the correct name for Eruptio acicola following the one fungus one name convention (Crous et al., 2009; Hawksworth et al., 2011). Because Eruptio gaubae is morphologically similar to Lecanosticta, phylogenetic analyses are required to resolve this taxonomic confusion.

Lecanosticta acicola is the only species in the genus known to be a significant pathogen. This is particularly important because it is spreading rapidly in Europe and the northeastern parts of North America. Therefore, all data collected over time regarding Lecanosticta pertain to the organism that was assigned the name L. acicola, and the remainder of the review will focus on this species. However, it is relevant to recognize that other species of Lecanosticta cause symptoms similar to those of L. acicola and that they have the potential to emerge as pine pathogens if they were accidentally moved to new environments. They would then be recognized as members of a complex of BSNB pathogens.

Fig. 2 Symptoms of Lecanosticta acicola. (A) Pinus mugo in Austria displaying symptoms of both brown spot needle blight (BSNB) and Dothistroma needle blight (DNB) on the same branches. (B) Both the characteristic brown spots associated with BSNB (black arrow) and the red banding associated with DNB (white arrow) can be observed. (C)–(E) Symptoms of BSNB vary from only brown spots as observed on P. mugo (C) to distinct brown bands as observed on P. radiata (D) to irregular mosaic spots as observed on P. palustris (E). (F) Lecanosticta acicola conidiogenous cells giving rise to conidia on malt extract agar. (G) Lecanosticta acicola septate conidia with verruculose surfaces and truncate bases.
SYMPTOMS OF BROWN SPOT NEEDLE BLIGHT

Symptoms of infection can vary depending on the host species affected. Typically, a small and yellow, sometimes light grey-green or reddish brown, irregular circular spot, with defined margins, appears at the point of infection (Hedgcock, 1929) (Fig. 2C–E). These spots soon become brown as the infections mature and they are often surrounded by a yellow halo (Skilling and Nicholls, 1974). In severe cases, infections can occur on several parts of a needle, leading to more rapid necrosis (Fig. 2E). The characteristic brown spots are the first conspicuous symptoms on the pine needles and this has led to the common name 'brown spot needle blight' proposed by Siggers (1932). These brown spots can also appear or reddish brown, irregular circular spot, with defined margins, appearing at the point of infection (Hedgcock, 1929) (Fig. 2C–E). These spots soon become brown as the infections mature and they are often surrounded by a yellow halo (Skilling and Nicholls, 1974). In severe cases, infections can occur on several parts of a needle, leading to more rapid necrosis (Fig. 2E). The characteristic brown spots are the first conspicuous symptoms on the pine needles and this has led to the common name 'brown spot needle blight' proposed by Siggers (1932). These brown spots can also appear or reddish brown, irregular circular spot, with defined margins, appearing at the point of infection (Hedgcock, 1929) (Fig. 2C–E). These spots soon become brown as the infections mature and they are often surrounded by a yellow halo (Skilling and Nicholls, 1974). In severe cases, infections can occur on several parts of a needle, leading to more rapid necrosis (Fig. 2E). The characteristic brown spots are the first conspicuous symptoms on the pine needles and this has led to the common name 'brown spot needle blight' proposed by Siggers (1932). These brown spots can also appear

An asymptomatic phase in which L. acicola establishes within needles can last several days (Setliff and Patton, 1974) to 3 months (Skilling and Nicholls, 1974). This is dependent on the strain of the pathogen (Kais, 1972) and length of the wet season. This delay in symptom development could lead to the accidental movement of infected plants to new areas.

The symptoms of BSNB (Fig. 2) can easily be confused with those of DNB, which is caused by Dothistroma septosporum and D. pini (Barnes et al., 2004, 2016). On some host species, symptoms of DNB are similar to those of BSNB (Fig. 2B) but rather than the characteristic brown discoloration and spots, a distinct red band forms around the point of infection in the case of DNB (Pehl and Cech, 2008). However, in some cases the characteristic red banding pattern associated with DNB is not formed or alternatively the red bands are sufficiently dark to give a false impression of brown spots. This can easily lead to incorrect pathogen diagnoses (Barnes et al., 2016; Petrak, 1961).

LIFE CYCLE

Lecanosticta acicola can occur in either its asexual or sexual state (Fig. 1) (Siggers, 1939). The pathogen overwinters in acervuli (asexual) (Fig. 1Aa) or ascosporas (sexual) (Fig. 1Ba) in the dead tissue of either dead or living pine needles. It can also overwinter as vegetative mycelium in the infected needles that remain attached to the host (Siggers, 1944). Conidia are released in gelatinous masses (Fig. 1Ab) or ascosporas are released from asci in ascosporas (Fig. 1Bb) on the needles when the light, temperature and humidity are favourable (Kais, 1975; Tainter and Baker, 1996).

Conidia begin to germinate on the needle surfaces by developing one to four germ tubes, depending on the number of cells in the conidia (Setliff and Patton, 1974). It is uncertain whether the germ tubes are attracted to the stomata, or whether they grow randomly over the needle surface (Patton and Spear, 1978; Setliff and Patton, 1974). Light plays an indirect, but essential role in the infection process as it stimulates the opening of stomata, allowing the germ tube to penetrate the needle (Fig. 1c) (Kais, 1975). Infections can also occur through wounds (Kais, 1978). Once a germ tube enters the stomatal antechamber, it increases in diameter and becomes thick-walled and melanized (Patton and Spear, 1978). Appressoria, such as those found in Dothistroma (Gadgil, 1967), have never been seen (Patton and Spear, 1978).

Once the mesophyll tissue has been invaded by L. acicola mycelium, conidiomata begin to form. These begin to integrate with the needle tissue and increase in size until they are visible to the naked eye (Wolf and Barbour, 1941). The conidiophores produce conidia towards the leaf exterior (Evans, 1984), which exerts pressure on the needle epidermis. This causes the epidermis to rupture, leaving a flap that partly covers the conidiomata (Wolf and Barbour, 1941). The conidia are released from the conidiomata during wet weather and the disease cycle is repeated.

In the case of the sexual state, asci are formed within the ascosporas on necrotic distal parts of living needles or on dead needles (Henry, 1954; Jewell, 1983). Ascospores are released from asci and dispersed through wind and rain. Ascii and ascospores develop more rarely than conidia and have been reported only from Nicaragua, Honduras, Colombia and the southern parts of the USA (Table 1) (Evans, 1984; Henry, 1954; Kais, 1971; Luttrell, 1949; Siggers, 1944). The reports from Nicaragua and Honduras probably represent species other than L. acicola.

TOXIN PRODUCTION

Many plant pathogenic fungi have adapted to produce toxic secondary metabolites in their plant hosts and these could influence colonization and sporulation, as has been seen in D. septosporum (Kabir et al., 2015). Lecanosticta acicola is known to produce the toxic compounds LA-I and LA-II, which are heat-resistant and non-host specific phytotoxins (Yang et al., 2002, 2005). The two...
compounds interact with the host independently and do not promote or inhibit the interaction of one another (Yang et al., 2002). Different Pinus species have different reactions to LA-I and LA-II. When rooted cuttings of P. thunbergii were exposed to the toxin, they showed little sensitivity to it. In contrast, when P. elliottii and P. taeda, both highly susceptible to BSNB infection, were exposed to the toxin, the results showed high sensitivity to LA-I (Ye and Qi, 1999). It seems likely that these toxins are involved in the destruction of mesophyll tissue of the pine needles at the point of infection (Jewell, 1983).

**BIOLOGY AND DISSEMINATION**

Conidia and ascospores are released throughout the year at temperatures ranging from –5.5 to 28 °C (Kais, 1971; Siggers, 1944; Wyka et al., 2018). However, warm and wet weather is particularly conducive for the development of BSNB, irrespective of whether infection takes place by sexual or asexual spores. The conidia do not germinate below 5 °C, although most survive this temperature and commence germination once the temperature increases (Siggers, 1944). At the other extreme, tolerance to high temperature was found to vary depending on the strain of Lecanosticta involved. It was shown that conidia of isolates from the northern parts of the USA could not germinate at 32 °C, whereas cultures isolated from the southern parts of the USA, as well as China, had a germination success of 80% at the same temperature (Huang et al., 1995). This physiological distinction is reflected in population genetic studies which define two lineages of the pathogen in the USA (Janoušek et al., 2016). The success of the pathogen may therefore be a result of isolates in each lineage adapting to local temperature conditions.

The maximum temperature for the germination of L. acicola conidia is 35 °C (Siggers, 1944). It was also found that high humidity pre- and post-infection is required for high levels of infection (Kais, 1975). The optimal temperature for infection to occur is 30 °C during the day and 21 °C at night, and Kais (1975) showed that these temperatures gave positive results in inoculation trials.

Conidia are dispersed predominantly by rain splash to adjacent trees, and they contribute significantly to rapid disease build-up in pine stands (Tainter and Baker, 1996). High levels of conidial dispersal were recorded during the rainy season in the USA, especially between late spring and summer, as well as when there were rain spells after a long period of dryness (Kais, 1971). In other reports, conidial production and dispersal were recorded throughout the year (Siggers, 1944). Dispersal was not influenced by the temperature range but conidial release was connected to rainfall patterns. In Wisconsin, two peaks of conidial release were recorded, with the first peak in early summer when young pine needles are present and the second in late summer (Skilling and Nicholls, 1974), which was similar to that found in the northeastern USA (Wyka et al. 2018). In Japan, it was found that conidia were produced by the pathogen from early spring to autumn with peak dispersal in mid-summer. However, for a second year of infection, the dispersal was most abundant from late summer to mid-autumn the following year (Suto, 2002). A study in Fujian province (China) showed that the greatest number of conidia were detected between early spring and mid-summer and again in late summer to late autumn in Pinus elliottii plantations (Li et al., 1987). It consequently appears that conidial dispersal varies depending on the rainfall season in any particular geographical region.

Spore traps in several studies failed to capture ascospores (Kais, 1971; Siggers, 1939; Wyka et al., 2018). It was found, however, that conidia could be dispersed to a distance of up to 60 m (Wyka et al. 2018). A recent investigation of the dispersal of Dothistroma, where the mechanisms of conidial and ascospore dispersal are similar to those in L. acicola, showed that conidia could be naturally disseminated over more than 1 km (Mullett et al., 2016). The assumed distance of dispersal in L. acicola may, consequently, be similar.

The ascospores of L. acicola are forcibly expelled into the air (Wolf and Barbour, 1941) and dispersed by wind currents (Kais, 1971) or rain splash driven by wind (Siggers, 1939). Ascospores can also be released during periods of fog, rain and dew (Tainter and Baker, 1996). Ascospores were recorded in the USA mainly during periods when temperatures were above 15 °C and are found in late summer to autumn. Small numbers of ascospores were detected when temperatures were below 10 °C (Kais 1971).

The main component that facilitates spread of conidia and ascospores is moisture, but other factors may also aid in their dispersal. Insect dissemination was suggested as a mechanism of conidial spread when two Lepidopteran wing scales were found to have conidia attached to them (Skilling and Nicholls, 1974). Given the biology of L. acicola, it seems unlikely that insects are involved in its dissemination. It has also been suggested that animals grazing in forests might aid in dissemination of the conidia when spores stick to their coats or hooves (Skilling and Nicholls, 1974; Tainter and Baker, 1996). Again, this mode of dissemination seems unlikely to be particularly important.

Anthropogenic movement of infected plant material has contributed to the dissemination of many tree pathogens (Wingfield et al., 2015). This has been clearly demonstrated for Dothistroma septosporum (Barnes et al., 2014), which has a biology very similar to that of L. acicola. A study that used microsatellite markers has demonstrated that two separate lineages of L. acicola have most likely been introduced into Europe from North America (Janoušek et al., 2016). Long distance dispersal of L. acicola is, therefore, likely to be the result of anthropogenic movement of infected plant material. This would not include seed transmission as L. acicola conidia cannot survive on a pine seed’s surface.
longer than 30 to 34 days and it is thus not considered seed-borne (Jianren and Chuandao, 1988).

**DISEASE MANAGEMENT**

Several measures have been suggested to prevent BSNB during plantation establishment. The most effective is to plant disease-free seedlings of superior quality (Cordell et al., 1990; Skilling and Nicholls, 1974). It is also advisable to avoid establishing new plantations alongside old, infected pines that could potentially serve as reservoirs of inoculum (Taintier and Baker, 1996). For natural pine stands, the application of thinning treatments was investigated as a silvicultural practice against pine needle diseases (McIntire et al., 2018). This practice, conducted on native stands of *P. strobus* in the USA, showed promise in reducing the fungal load of *L. acicola*, resulting in reduced severity of the disease over time in stands already infected with the pathogen (McIntire et al., 2018). This practice is recommended as a preventative measure in stands that are at risk of infection by *L. acicola* and other pine needle pathogens (McIntire et al., 2018).

Pruning of infected pines can contribute to the spread of BSNB if it is conducted during rainy or wet periods. This is because conidia are exuded during these conditions and can attach to the pruning shears, providing a means of spread from infected to healthy trees (Skilling and Nicholls, 1974). Cutting blades should be cleaned during pruning and clipped needles and shoots should be removed (Kais, 1978). In the case of infection on *Pinus palustris*, which begins growth as a grass stage, stimulation of growth during the first 3 years of growth reduces the levels of infection (Taintier and Baker, 1996). Because this treatment is economical, effective and environmentally safe, it is widely used in the southeastern USA (Cordell et al., 1990), where BSNB occurs on *P. palustris*.

Breeding for resistance to *L. acicola* has been successfully used to reduce the impact of the disease on *P. palustris* in Alabama. The source population of these trees found in southwestern Alabama was used in breeding programmes (Snyder and Derr, 1972) where seed was made available to the public (Phelps et al., 1978). Since 1982, resistant phenotypes of *P. elliottii* have also been selected for in plantations affected by BSNB in the Fujian province in China. Over time, and using artificial inoculations, resistant clones were selected and resistant seed orchards were established (Ye and Wu, 2011).

Fungicide treatment can protect pine seedlings from infection by *L. acicola*. For example, when *P. palustris* was sprayed with fungicide, the seedlings displayed increased diameter growth in a single growing season, compared to untreated plants (Siggers, 1932). Seedlings, seed orchard trees and Christmas tree plantations have been protected by Bordeaux mixture of copper sulphate and lime, which inhibits conidial germination, by a benomyl root treatment or by ferbam (Fermate®). Chlorothalonil, a broad-spectrum organochlorine pesticide (products include Bravo®, Dacon® and Maneb®), has also been applied to provide efficient control against BSNB. Chlorothalonil is also very effective against *Lophodermium* needle cast, which could be advantageous when both pathogens are present (Cordell et al., 1990; Kais et al., 1986; Skilling and Nicholls, 1974). Practical details and recommendations concerning fungicide treatment can be found in Skilling and Nicholls (1974). However, the use of chemicals is not considered a desirable solution for disease control due to negative environmental factors and many of these treatments are no longer available.

Controlled burning in pine forests can eliminate competing vegetation and reduce the impact of needle pathogens, especially in *P. palustris* where a grass stage is relevant (Barnett, 1999; Chapman, 1932). This pine species is completely adapted to survive fires as it concentrates all its energy into root development during the first 5 years of growth (Chapman, 1932). Siggers (1934) showed that a single controlled fire can significantly decrease BSNB in *P. palustris* until the next season and that during the initial growth stage, before seedlings begin to increase in height, a winter burn every 3 years is the most beneficial for disease control. The efficacy of controlled burns differs depending on the *Pinus* spp. involved and on the ability to tolerate fire damage.

In countries and regions where *L. acicola* is a quarantine organism, it is suggested that complete eradication of diseased trees or pine stands should be performed once the disease is detected (Pehl and Cech, 2008). This is achieved by felling and burning of infected trees and litter found under infected trees (Sosnowski et al., 2009). In Lithuania, for instance, after positive identification of the pathogen in the Curonian Spit in 2009 and 2010, effective eradication measures were implemented (Markovskaja et al., 2011). Due to this rapid action, the disease has remained under control in that country and is under constant monitoring by the state plant service of the Ministry of Agriculture of Lithuania (https://gd.eppo.int/taxon/SCIRAC/distribution/LT). Eradication efforts are, however, not always effective, and the best preventative method is to limit the movement of plant material across borders and between regions. As new knowledge is emerging regarding different genetic entities of the pathogen, including strains of different mating types (Sadiković et al., 2019), the importance of avoiding new introductions is becoming increasingly obvious.

**HOST RANGE, HOST SUSCEPTIBILITY AND GEOGRAPHIC DISTRIBUTION**

In an effort to consolidate 140 years of literature with regards to the geographical distribution and host range of *L. acicola*, a detailed list of these data has been compiled (Table 1). This shows that the pathogen has been reported in 31 countries and on 53
pine species and pine hybrids. The majority of the host records on native and non-native trees are from the Americas, followed by Europe. The pathogen has not been found in Africa, Australia or New Zealand and in South America it is known only in Colombia. Of the 69 reports of the pathogen (Table 1), 31 were made in the last decade (2009–2019). This suggests that incidences of the pathogen are most likely increasing.

In North America, the first report of *L. acicola* was in 1876 on native *Pinus echinata* as *Cryptosporium aciculum* (de Thümen, 1878). Since then, the pathogen has been reported in the USA on several susceptible species, including non-native *P. caribaea* and *P. pinea*, and native *P. elliottii*, *P. echinata*, *P. glabra*, *P. ponderosa*, *P. rigida*, *P. taeda* and *P. virginiana* (Hedgcock, 1929; Siggers, 1944; Sinclair and Lyon, 2005; Webster, 1930) as well as on regionally planted exotic species such as *P. attenuata*, *P. coulteri*, *P. muricata* and *P. sabini ana* (Siggers, 1944). *Pinus palustris* seedlings are the most severely affected, largely due to the grass stage associated with early growth and where BSNB can cause complete defoliation (Siggers, 1934). Here it can result in mortality reaching 50% and higher in the southeastern USA (Cordell et al., 1990). New reports of *L. acicola* causing damage on *P. strobus* have emerged since 2005 in the northeastern USA and Canada and these have been attributed to changes in precipitation and climate in the regions (Broders et al., 2015; Wyka et al., 2017, 2018). *Lecanosticta acicola* is also recognized as a component of a complex of pathogens that cause white pine needle damage (WPND) in this region (Broders et al., 2015). Additionally, the pathogen has been reported on *P. banksiana* and *P. contorta* var. *latifolia* in Canada (Laut et al., 1966).

*Lecanosticta acicola* has been reported from 17 European countries (for a complete list of records see Table 1). The pathogen was first recorded in northern Spain in 1942 (Martinez, 1942), where it still occurs on *P. radiata* (Ortíz de Urbina et al., 2017). In southwest Europe, *L. acicola* has caused severe defoliation of *P. radiata* × *P. attenuata*, leading to the felling of 100 ha in the 1990s (Lévy, 1996). *Lecanosticta acicola* is spreading through the valleys in the Alps in Switzerland (Holdenrieder and Sieber, 1995), Austria (Cech, 1997; Hintsteiner et al., 2012), Italy (La Porta and Capretti, 2000) and Slovenia (Jurc and Jurc, 2010; Sadiković et al., 2019), which can be attributed to high humidity in deep valleys or the proximity of lakes. In Europe, *L. acicola* often infects *P. mugo*, a susceptible species on which it has recently caused severe outbreaks in Austria (https://gd.eppo.int/reporting/article-5139). It also infects other pine species such as *P. sylvestris* and *P. nigra*. The pathogen has been recorded in several peat bog sites in southern Bavaria (Germany) and southern Bohemia (Czech Republic). These locations are naturally humid throughout the year and the susceptible pine species *P. mugo* and/or *P. uncinata* subsp. *uliginosa* can be heavily infected, leading to considerable mortality. Similarly, *L. acicola* was recorded in the Baltic states (Drenkan and Hanso, 2009) and, most recently, also in Sweden (Cleary et al., 2019). These records usually come from stands close to the sea or, very frequently, from botanical gardens or urban areas.

Other pine species such as *Pinus × rhaetica* and *P. ponderosa* have also been affected by *L. acicola* (Adamson et al., 2015, 2018). *Lecanosticta acicola* has been present in Croatia on *P. halepensis* for more than 40 years (Milatović, 1976; Sadiković et al., 2019). Interestingly, the pathogen was identified only at a single site in Ireland despite large-scale screening throughout the British Isles (Mullett et al., 2018). From all these records, it is reasonable to conclude that *L. acicola* is spreading in Europe in native and non-native pine species, in plantations and natural forests, and associated with different climatic conditions.

In Asia, BSNB has been reported in China in plantations of non-native *P. thunbergii*, *P. elliottii* and *P. taeda* where the trees were severely damaged by the pathogen (Huang et al., 1995), and on *P. caribaea*, *P. palustris*, *P. clausa* and *P. echinata* that were reported to be susceptible to infection (Li et al., 1986). It was suggested that native pines such as *P. taiwanensis*, *P. fenzelian a* and *P. massoniana* were highly resistant to infection (Huang et al., 1995; Li et al., 1986). BSNB has been reported on native *P. thunbergii* in Japan (Suto and Ougi, 1998) as well as on native *P. thunbergii* in South Korea but the disease was not severe (Seo et al., 2012).

Although some species of *Pinus* seem to not be susceptible to infection by *L. acicola*, the pathogen has the potential to overcome host resistance in a favourable environment and expand its host range, as is suggested for *D. septosporum* and *D. pini* (Drenkan et al., 2016). For example, *L. acicola* is rarely reported on native *P. sylvestris* in Europe. Considering the importance of *P. sylvestris* in Europe, it will be important to monitor the presence of the pathogen on this host. Only single incidences of *L. acicola* have been reported on *P. sylvestris* in Austria (Cech and Krehan, 2008), Slovenia (Jurc and Jurc, 2010) and most recently in Estonia (Adamson et al., 2018) and Ireland (Mullett et al., 2018). In contrast, *L. acicola* is an important pathogen of *P. sylvestris* grown as part of the Christmas tree industry since the 1960s in the USA (Skilling and Nicholls, 1974). This implies that under favourable conditions this host could be infected by the pathogen. Investigations on the impact of DNB on *P. sylvestris* revealed that there is high intraspecific variability of *P. sylvestris* in Europe and that susceptibility of the host to the pathogen varies between individuals (Perry et al., 2016a,b) and this could also influence the potential importance of *L. acicola*. Unusually high humidity associated with climate change could increase pathogen pressure on *P. sylvestris* (Perry et al., 2016a) and the single incidences in Europe should carefully be monitored. Caution must also be taken when planting susceptible exotic hosts alongside native forests, as this could influence the vulnerability of native forests (Piotrowska et al., 2018).
Of the 69 reports of *L. acicola*, only 22 used DNA sequence comparisons for species verification. This is of concern as there might be an over- or underestimation of hosts affected by BSNB globally. In Central America, for example, *L. acicola* was reported based on identifications using morphological characters. Because the pathogen has not yet been confirmed as occurring in this region using DNA sequences (Quaedvlieg et al., 2012; van der Nest et al., 2019), those reports could be erroneous and may represent different species which could possibly cause new outbreaks if not contained in their native environment.

Molecular markers used for species identification

Three molecular methods are currently being used to accurately identify *L. acicola*. These include sequencing of various gene regions, an ITS-RFLP method and a conventional PCR that uses species-specific primers. The most common of these approaches is comparison of DNA sequences for the ITS gene region (Adamson et al., 2015, 2018; Cleary et al., 2019; Markovskaja et al., 2011; Mullett et al., 2018). However, the TEF 1 (Fig. 3) and BT 2 gene regions have been recommended to distinguish between species of the Mycosphaerellaceae (Quaedvlieg et al., 2012). In order to accurately distinguish between different species of *Lecanosticta*, van der Nest et al. (2019) used a multi-gene phylogenetic approach using sequences for the ITS, TEF 1, BT 1, MS204 and RPB 2 gene regions. The outcome was the discovery of four new species, with the ITS and TEF 1 proving to be the gene regions showing the best amplification success across all species. Pehl et al. (2004) developed an ITS-RFLP method to distinguish between *L. acicola*, *D. septosporum* and ten other plant pathogens. However, whether this method remains valid after the recognition of various new species (van der Nest et al., 2019) will need to be established.

Another rapid method allowing for the identification of *L. acicola*, *D. septosporum* and *D. pini* is a conventional PCR that uses species-specific primers (loos et al., 2010). These were developed to partially amplify the TEF 1 gene for *L. acicola* and *D. pini*, and partially amplify the BT 2 gene region in *D. septosporum* (loos et al., 2010). Importantly, this method can be used to identify the pathogens directly from infected needles (Adamson et al., 2015; Ortiz de Urbina et al., 2017; Schneider et al., 2019) and is now widely used for preliminary identification of *L. acicola* (Adamson et al., 2018; Sadiković et al., 2019). A multiplex qPCR was also recently developed to detect *L. acicola* as well as *Dothistroma* species from needles simultaneously using probe-labelled primers developed by loos et al. (2010) and Schneider et al. (2019), which could become more widely used once that technology is more easily available.

Population genetic studies

Knowledge regarding the population structure and diversity of pathogens such as *L. acicola* allow for an understanding of migration patterns as well various aspects of their invasion biology. Eleven polymorphic microsatellite markers and mating type primers have been developed for this purpose (Janoušek et al., 2014). The first population genetic study using these markers revealed that two lineages of *L. acicola* were introduced into Europe, possibly on two separate occasions (Janoušek et al., 2016). These results are similar to an earlier study where RAPD analysis of *L. acicola*, collected in the northern and southern parts of the USA and China, showed that the Chinese population originated from the southern USA and that the collection from the northern USA was unique (Huang et al., 1995). A second population genetic study compared populations from Croatia and Slovenia and revealed four distinct populations with possible introductions from other sources within the two countries (Sadiković et al., 2019). Currently available knowledge suggests a Northern American centre of origin for this pathogen (Huang et al., 1995; Janoušek et al., 2016; van der Nest et al., 2019) but further sampling and analyses are required to support this hypothesis. In the population genetic study of Janoušek et al. (2016), the microsatellite markers amplified poorly for the *L. acicola* isolates from Mexico and Central America. A later study (van der Nest et al., 2019) showed that these isolates were *L. variabilis*, a new and recently described species.

The study by Janoušek et al. (2014) showed that *L. acicola* is heterothallic and that two individuals, one with a MAT1-1-1 idiomorph and the other with a MAT1-2 idiomorph, are needed for sexual reproduction to occur. Consequently, to understand whether sexual recombination might occur in a region, it is important to have a knowledge of the mating type idiomorph distribution. Mating type primers that amplify the MAT1-1-1 and MAT1-2 idiomorphs and that tested positive for *Dothistroma* species as well as *L. acicola*, *L. guatemalensis* and *L. gloeosporia* have been developed (Janoušek et al., 2014). It is, however, not yet known whether these markers will amplify these gene regions for the other, newly described *Lecanosticta* species.

Janoušek et al. (2016) considered the global *L. acicola* population and showed that the ratio of mating type idiomorphs in Mississippi, Austria, France and Germany reflected sexual recombination in these regions/countries. In contrast, only asexual reproduction occurs in the Czech Republic and northern parts of America. Using the mating type markers of Janoušek et al. (2014), the distribution of MAT1 and MAT2 isolates was detected in studies with isolates from Croatia (Sadiković et al., 2019), Estonia (Adamson et al., 2015, 2018), Ireland, Portugal, Russia (Mullett et al., 2018) and Slovenia (Janoušek et al., 2016) but further sampling and analyses are required to support this hypothesis.
et al., 2018) as well as Spain (Ortíz de Urbina et al., 2017). In Spain, both mating types were detected whereas only single mating types were detected in all other areas studied. However, in Estonia it was suggested that a second introduction of the pathogen occurred since only MAT1 was initially present but that later both mating types were detected in the same region (Adamson et al., 2015). In populations with equal ratios of mating types or with both mating types present, sexual reproduction could occur, possibly giving rise to more virulent strains. This emphasizes a need to exercise caution and thus to prevent introduction of new strains into regions where the pathogen is already present.

**Future prospects in the age of genomics**

Canada’s Michael Smith Genome Sciences Centre has recently released a full genome for a *L. acicola* isolate from France (https://www.ncbi.nlm.nih.gov/assembly/GCA_000504345.2/#/def). This genome has not yet been annotated but provides a valuable resource for future studies. Many other genomes of Dothidiomycetes, which have been sequenced and annotated, are available for comparative purposes (de Wit et al., 2012; Ohm et al., 2012). Annotation of putative genes of the *L. acicola* genome, utilizing knowledge of these other genomes, will provide insights into questions regarding many aspects of the biology of *L. acicola*. Opportunities also now arise to sequence the genomes of other *Lecanosticta* spp. and to compare these in order to better understand their relative importance. It will also be possible to follow the *Dothistroma* example where a transcriptomic study considered which genes are expressed during various stages in the infection of *P. radiata* (Bradshaw et al., 2016) and genome sequencing of global representatives of *D. septosporum* revealed that gene copy numbers could play a role in dothistromin production by the pathogen (Bradshaw et al., 2019).

**CONCLUSIONS**

*Lecanosticta acicola* has been known in the southern USA for many decades. Consequently, its life cycle, mode of infection, host susceptibility and strategies to prevent infection, particularly on *P. palustris*, have been extensively studied in that region. Yet there is evidence to show that the pathogen, which now has an extensive host range, is spreading rapidly northwards. The reasons for this host range and geographical expansion require further study. Contemporary knowledge has also shown that there have been two introductions of *L. acicola* into Europe. Consequently, BSNB is becoming a disease of great concern in Europe, where it is increasingly being discovered on both non-native and native *Pinus* spp. There are many relevant hypotheses to explain the growing importance of BSNB and these include the effects of climate change, emergence of more aggressive strains of the pathogen and anthropogenic processes leading to new introductions. There is clearly a need for increased attention to and studies of *L. acicola*, particularly in Europe.

Recent studies have shown that there are eight species of *Lecanosticta* in addition to *L. acicola*. All of these other species appear to have a Mesoamerican origin. Much of the literature pertaining to *L. acicola* needs to be reconsidered given the fact that a single name has been widely used to refer to what we now know represents numerous cryptic species. *Lecanosticta acicola* identified based on DNA sequence comparisons has not been found in Central America, suggesting a North American centre of origin. Of the 69 reports of *L. acicola*, only 25 from 12 countries have been confirmed using DNA sequence-based tools (Table 1). Many reports of the pathogen could thus be erroneous and there is an urgent need to resolve this important question.

All the available knowledge regarding BSNB relates to studies on *L. acicola* and these are predominantly from the USA. Nothing is known regarding the relative importance of the remaining eight species of *Lecanosticta*. At least some of these are most likely also important pathogens and their relative threat to global forests and forestry needs to be assessed. A concerted effort must be made to prevent their accidental introduction into new regions of the world and as part of this process DNA sequence-based techniques need to be routinely applied to allow for meaningful identification.

The development of new tools to study *Lecanosticta* spp. and BSNB provides many exciting opportunities to enhance our knowledge of this important group of pathogens. The population structure and diversity of *L. acicola* can now be easily studied in the USA as well as where new invasions occur in Europe, and at levels that were previously not possible. For example, application of the available microsatellite markers will enable a more comprehensive understanding of the pathogen as well as determination of its centre of origin.

Genome sequencing is rapidly becoming cheaper and more readily available, and an isolate of *L. acicola* is already available in the public domain for study. We envisage that all the species of *Lecanosticta* will be sequenced in the relatively near future and many isolates of some species will likely also be studied at this level. These studies, and others relating to the ‘omics’ level, will surely have a substantial impact on our understanding of a group of pathogens that is growing in importance and relevance. Overall, BSNB (including all species of *Lecanosticta*) has the potential to become a pine needle disease of global importance if proper preventative measures for the spread of the causal pathogens are not implemented.

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**REFERENCES**

Adamson, K., Drenkhan, R. and Hanso, M. (2015) Invasive brown spot needle blight caused by Lecanosticta acicola in Estonia. Scand. J. Forest Res. 30, 587–593.

Adamson, K., Laas, M., Drenkhan, R. and Hanso, M. (2018) Quarantine pathogen Lecanosticta acicola, observed at its jump from an exotic host to the native Scots pine in Estonia. Bait. For. 24, 36–41.

Alvère, M., Aumonier, T. and Kersaudy, E. (2010) Bilan sylvosanitaire 2009–2009, ed), pp. 1–7. Direction régionale de l’agriculture et de la forêt d’Aquitaine, République Française.

Anstg, A. (2011) Braune Föhren in Gärten und Parks. Wald Holz, 92, 41–42.

Anonymous (1972) Brown spot resistance in natural stands of longleaf pine. Sustain. Forest Rep.

Barnes, I., van der Nest, A., Mullett, M.S., Crous, P.W., Drenkhan, R., Bose, S.K., Jagodzinski, P., Cordon, J., Batt, B. and Boyce, J.S. (2016) Population structure and diversity of an invasive pine needle pathogen reflects anthropogenic activity. Ecol. Evol. 4, 3642–3661.

Barnes, I., Wingfield, B.D. and Wingfield, M.J. (2004) Multigene phylogenies reveal that red band needle blight of Pinus is caused by two distinct species of Dothistroma, D. septosporum and D. pini. Stud. Mycol. 50, 551–565.

Barnes, I., Wingfield, M.J., Carbone, I., Kirisits, T. and Wingfield, B.D. (2014) Population structure and diversification of an invasive pine needle pathogen reflects anthropogenic activity. Ecol. Evol. 4, 3642–3661.

Barnes, I., van der Nest, A., Mullett, M.S., Crous, P.W., Drenkhan, R., Musolin, D.L. and Wingfield, M.J. (2016) Neotypification of Dothistroma septosporum and epitypification of D. pini, causal agents of Dothistroma needle blight of pine. Forest Pathol. 46, 388–407.

Barnett, J.P. (1999) Longleaf pine ecosystem restoration: the role of fire. J. Sustain. Forest. 9, 89–96.

Barr, M.E. (1972) Preliminary studies on the Dothideales in temperate North America. Contributions from the University of Michigan Herbarium, 9, 523–638.

Barr, M.E. (1996) Planistromellaeae, a new family in the Dothideales. Mycotaxon, 60, 433–442.

Boyce, J.S. (1959) Brown spot needle blight on eastern white pine. Plant Dis. Rep. 43, 420.

Boyer, W.D. (1972) Brown-spot resistance in natural stands of longleaf pine seedlings. US Department of Agriculture Forest Service Research Paper, 50–142, 1–4.

Bradshaw, R.E., Guo, Y., Sim, A.D., Kabir, M.S., Chetrii, P., Ozturk, I.K., Hunziker, L., Gmelin, R.J. and Cox, M.F., M.P. (2016) Genome-wide gene expression dynamics of the fungal pathogen Dothistroma septosporum throughout its infection cycle of the gymnosperm host Pinus radiata. Mol. Plant Pathol. 17, 210–224.

Bradshaw, R.E., Sim, A.D., Chettri, P., Dupont, P.-Y., Guo, Y., Hunziker, L., McDougall, R.L., van der Nest, A., Fourie, A., Wheeler, D., Cox, M.P. and Barnes, I. (2019) Global population genomics of the pathogen Dothistroma septosporum suggest that chromosome duplications influence virulence factor levels. Mol. Plant Pathol. 20, 784–799.

Brandtstetter, M. and Cech, T.L. (1999) Neue Nadelkrankheiten an Kiefer. Österreichische Forstzeitung, 99, 35–36.

Brandtstetter, M. and Cech, T. (2003) Lecanosticta – Kiefernmadelbräune (Mycosphaerella dearnessii Barr) in Niederösterreich. Centralblatt für das gesamte forstwesen, 120, 163–176.

Brazeé, N.J. (2016) Dramatic needle browning and canopy dieback of eastern white pine (Pinus strobus) in southern New England. (UMass Extension, Amherst, University of Massachusetts, ed), pp. 1–5. Massachusetts: United States Department of Agriculture.

Broders, K., Munck, I.A., Wyka, S.A., Iriarte, G. and Beaudoin, E. (2015) Characterization of fungal pathogens associated with white pine needle damage (WPND) in northeastern North America. Forests, 6, 4088–4104.

Cech, T.L. (1997) Brown spot disease in Austria – the beginning of an epidemic. Forstschutz Aktuell, 19, 17.

Cech, T.L. and Krehan, H. (2008) Lecanosticta-Krankheit der Kiefer erstmals im Wald nachgewiesen. Forstschutz Aktuell, 45, 4–5.

Chapman, H.H. (1926) Factors determining natural reproduction of longleaf pine on cut-over lands in LaSalle Parish, Louisiana. Yale School of Forestry Bulletin, 16, 1–44.

Chapman, H.H. (1926) Is the longleaf type a climax? Ecology, 13, 328–334.

Cleary, M., Laas, M., Oskay, F. and Drenkhan, R. (2019) First report of Lecanosticta acicola on non-native Pinus mugo in southern Sweden. Forest Pathol. 49, e12507.

Cordell, C.E., Anderson, R.L. and Kais, A.G. (1990) Brown-Spot needle blight. In: Southwide Forest Disease Workshop, (Boone, A.J., Anderson, R.L., Fenn, P., Powers, H.R. and Stambaugh, W.J., eds.) pp. 18–19. Charleston, South Carolina: South Carolina Forestry Commission, Insect and Disease Section, Columbia, South Carolina.

Crous, P.W. (1999) Species of Mycosphaerella and related anamorphs occurring on Myrtacea (excluding Eucalyptus). Mycol. Res. 103, 607–621.

Crous, P.W. (2009) Taxonomy and phylogeny of the genus Mycosphaerella and its anamorphs. Fungal Divers. 38, 1–24.

Crous, P.W., Braun, U. and Groenewald, J.Z. (2007) Mycosphaerella is polyphyletic. Stud. Mycol., 58, 1–32.

Crous, P.W., Kang, J. and Braun, U. (2001) A phylogenetic redescription of Dothistroma septosporum in Mycosphaerella based on ITS rDNA sequence and morphology. Mycologia, 93, 1081–1101.

Crous, P.W., Summerrell, B.A., Carnegie, A.J., Wingfield, M.J., Hunter, G.C., Burgess, T.I., Andjic, V., Barber, P.A. and Groenewald, J.Z. (2009) Unravelling Mycosphaerella: Do you believe in genera? Persoonia, 29, 93–118.

Dearness, J. (1926) New and noteworthy fungi: IV. Mycologia, 18, 236–255.

Dearness, J. (1928) New and noteworthy fungi V. Mycologia, 20, 235–246.

Drenkhan, R. and Hanso, M. (2009) Recent invasion of foliage fungi of pines (Pinus spp.) to the Northern Baltics. Forestry Studies, 51, 49–64.

Drenkhan, R., Tomšová-Haataja, V., Fraser, S., Bradshaw, R.E., Vahalik, P., Mullett, M.S., Martin-Garcia, J., Bulman, L.S., Wingfield, M.J., Kirisits, T., Cech, T.L., Schmitz, S., Baden, R., Tubbby, K., Brown, A., Georgieva, M., Woods, A., Ahumada, R., Jankovský, L., Thomsen, I.M., Adamson, K., Marçais, B., Vuorinen, M., Tsopelas, P., Koltay, A., Halasz, A., La Porta, N., Anselmi, N., Kiesere, R., Markovskaja, S., Kačergius, A., Papazova-Anakieva, I., Risteski, M., Sotirovski, K., Lazarević, J., Solheim, H., Boroii, P., Bragača, H., Chira, D., Musolin, D.L., Selikhovkin, A.V., Bulgakov, T.S., Keća, N., Karadžić, D., Galovic, V., Pap, P., Markovic, M., Poljakovic Pajnik, L., Vasic, V., Ondrušková, E., Piskur, B., Sadiković, D., Diez, J.J., Solla, A., Millberg, H., Stenlid, J., Angst, A., Queloz, V., Leitjárví, A., Dogmus-Lehtijärvi, H.T., Oskay, F., Davydenko, K., Meshkova, V., Craig, D., Woodward, S. and Barnes, I. (2016) Global geographic distribution and host range of Dothistroma species: a comprehensive review. Forest Pathol. 46, 408–442.

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López Castilla, R.A., Duarte Casanova, A., Guerra Rivero, C., Cruz Escoto, H. and Triguero Issasi, N. (2002) Forest Nursery pest management in Cuba. In: National Proceedings: Forest and Conservation Nursery Associations – 1999, 2000, 2001. (Dumroese, R.K., Riley, L.E., Landis, T.D., technical coordinators, eds), pp. 213–218. Ogden, UT: USDA Forest Service, Rocky Mountain Research Station.

Luttrel, E.S. (1949) Schirhia acicola, Phaeo cryptocpus pinastri, and Lophodermium pinastri associated with the decline of ponderosa pine in Missouri. Plant Dis. Rep. 33, 397–401.

Markovskaja, S., Kacergius, A. and Treigiene, A. (2011) Occurrence of new alien pathogenic fungus Mycosphaerella dearnessii in Lithuania. Bot. Lith. 17, 29–37.

Marmolejo, J.G. (2000) The genus Lecanosticta from Nuevo Leon, Mexico. Mycologia, 76, 393–397.

Martínez, J.B. (1942) The mycoses of Pinus insignis in Guipúzcoa. Publ. Inst. for. Invest. Exp. 13, 1–72.

McIntire, C.D., Munk, I.A., Ducey, M.J. and Asbjørnsen, H. (2018) Thinning treatments reduce severity of foliar pathogens in eastern white pine. Forest Ecol. Manag. 423, 106–113.

Miliatovíc, I. (1976) Needle cast of pines caused by fungi Schirhia pini Funk et Parker and Schirhia acicola (Dearn.) Siggers in Yugoslavia. Poljoprivredna Znanstvena Smotra – Agriculturae Conspectus Scientificus, 39, 511–513.

Mullett, M., Tabby, K., Webber, J. and Brown, A. (2016) A reconsideration of natural dispersal distances of the pine pathogen Dothistroma septosporum. Plant Pathol. 65, 1462–1472.

Mullett, M., Adamson, K., Bragança, H., Bulgakov, T., Georgieva, M., Henriques, J., Júrísso, L., Laas, M. and Drenkhan, R. (2018) New country and regional records of the pine needle blight pathogens Lecanosticta acicola, Dothistroma septosporum and Dothistroma pini. Forest Pathol. 48, e12440.

Munk, I.A., Ostrofsky, W. and Burns, B. (2012) Pest Alert: Eastern white pine needle damage. NA-PR-01-11. In: USDA Forest Service, Northeastern Area State and Private Forestry. Newtown, PA, USA.

van der Nest, A., Wingfield, M.J., Ortiz, P.C. and Barnes, I. (2019) The mycoses of Pinus insignis in Guipúzcoa. Publ. Inst. for. Invest. Exp. 33, 397–401.

Mullett, M., Adamson, K., Bragança, H., Bulgakov, T., Georgieva, M., Henriques, J., Júrísso, L., Laas, M. and Drenkhan, R. (2018) New country and regional records of the pine needle blight pathogens Lecanosticta acicola, Dothistroma septosporum and Dothistroma pini. Forest Pathol. 48, e12440.

Pehr, L., and Cech, T. (2008) Mycosphaerella dearnessii and Mycosphaerella pini. Eur. Med. Plant Protec. Org. Bull. 38, 349–362.

Pehr, L., Burgermeister, W. and Wulf, A. (2004) Mycosphaerella-Nadelpilze der Kiefer – Identifikation durch ITS-RFLP-Muster. Nachrichtenbl. Deut. Pflanzenschutz, 56, 239–244.

Perry, A., Brown, A.V., Cavers, S., Cottrell, J.E. and Ennos, R.A. (2016a) Has Scots pine (Pinus sylvestris) coevolved with Dothistroma septosporum in Scotland? Evidence for spatial heterogeneity in the susceptibility of native provenances. Evol. Appl., 9, 982–993.

Perry, A., Wachowiak, W., Brown, A.V., Ennos, R.A., Cottrell, J.E. and Cavers, S. (2016b) Substantial heritable variation for susceptibility to Dothistroma septosporum within populations of native British Scots pine (Pinus sylvestris). Plant Pathol., 65, 987–996.

Petrak, V.F. (1954) Phragmogloeum n. gen. eine neue Gattung der Sphaeropsidien. Sydowia, 8, 158–161.

Petrak, F. (1961) Die Lecanosticta Krankheit der Fohren in Osterreich. Sydowia, 15, 252–256.

Phelps, W.R., Kais, A.G. and Nicholls, T.H. (1978) Brown-spot needle blight of pines. US Department of Agriculture Forest Service, pp. 1–6.

Piotrowska, M.J., Riddell, C., Hoebe, P.N. and Ennos, R.A. (2018) Planting exotic relatives has increased the threat posed by Dothistroma septosporum to the Caledonian pine populations of Scotland. Evol. Appl., 11, 350–363.

La Porta, N. and Capretti, P. (2000) Mycosphaerella dearnessii, a needle-cast pathogen on mountain pine (Pinus mugo) in Italy. Disease Notes, 84, 922.

Prey, A.J. and Morse, F.S. (1971) Brown-spot needle blight of scotch pine christmas trees in Wisconsin. Plant Dis. Rep. 55, 648–649.

Quaedvlieg, W., Groenewald, J.Z., Yáñez-Morales, M.D.J. and Crous, P.W. (2012) DNA barcoding of Mycosphaerella species of quarantine importance to Europe. Persoonia, 29, 101–115.

Roigros, C.T. (1953) Kansas mycological notes: 1951. Trans. Kans. Acad. Sci. 8, 53–57.

Saccardo, P.A. (1884) Sylloge Fungorum. Patavii, Italy, 5, 307.

Sadiković, D., Piškur, B., Barnes, I., Hauptman, T., Diminić, D., Wingfield, M.J. and Jurc, D. (2019) Genetic diversity of the pine pathogen Lecanosticta acicola in Slovenia and Croatia. Plant Pathol. 68, 1120–1131.

Schneider, S., Jung, E., Quezol, V., Meyer, J.B. and Rigling, D. (2019) Detection of pine needle diseases caused by Dothistroma septosporum, Dothistroma pini and Lecanosticta acicola using different methodologies. Forest Pathol. 49, e12495.

Seo, S.T., Park, M.J., Park, J.H. and Shin, H.D. (2012) First report of brown spot needle blight on Pinus thunbergii caused by Lecanosticta acicola in Korea. Disease Notes, 96, 914.

Setliff, E.C. and Patton, R.F. (1976) Germination behaviour of Schirhia acicola conidia on pine needles. Phytopathology, 64, 1462–1464.

Shishkina, A.K. and Tsnava, N.I. (1967) Systema acicola (Dearn.) Wolf et Barbour: the perfect stage of Dothistroma acicola (Thüm.). A. Schischk. et N. Tsn. Novosti Sist. Nizsh. Rast. 278–277.

Siggers, P.V. (1932) The brown-spot needle blight of longleaf pine seedlings. J. Forest. 30, 579–593.

Siggers, P.V. (1934) Observations on the influence of fire on the brown-spot needle blight of longleaf pine seedlings. J. Forest. 32, 556–562.

Siggers, P.V. (1939) Phytopathological note. Phytopathology, 29, 1076–1077.

Siggers, P.V. (1944) The brown spot needle blight of pine seedlings. US Department of Agriculture, Washington, D.C. Technical Bulletin, 870, 1–36.

Sinclair, W.A. and Hudler, G.W. (1980) Tree and shrub pathogens new or noteworthy in New York state. Plant Dis. 64, 590–592.

Sinclair, W.A. and Lyon, H.H. (2005) Mycosphaerella diseases. In: Diseases of Trees and Shrubs. Ithaca and London: Cornell University Press.
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Skilling, D.D. and Nicholls, T.H. (1974) Brown spot needle disease – biology and control in Scotch pine plantations. US Department of Agriculture. Forest Service Research Paper, NC-109, 1–19.

Snyder, E.B. and Derr, H.J. (1972) Breeding Longleaf pines for resistance to brown spot needle blight. Phytopathology, 62, 325–329.

Sosnowski, M.R., Fletcher, J.D., Daly, A.M., Rodoni, B.C. and Viljanen-Rollinson, S.I.H. (2009) Techniques for the treatment, removal and disposal of host material during programmes for plant pathogen eradication. Plant Pathol. 58, 621–635.

Stanosz, G. (1990) Premature needle drop and symptoms associated with brown spot needle blight on Pinus strobus in Northcentral Pennsylvania. In: The American Phytopathological Society, Northeastern Division Annual Meeting, pp. 124. Phytopathology.

Suto, Y. (2002) Seasonal development of symptoms and conidial production and dispersal of Lecanosticta acicola in Pinus thunbergii. Appl. For. Sci. 11, 17–22.

Suto, Y. and Ougi, D. (1998) Lecanosticta acicola, causal fungus of brown spot needle blight in Pinus thunbergii, new to Japan. Mycoscience, 39, 319–325.

Sydow, H. and Petrak, F. (1922) Ein beitrag zur kenntnis der Pilzflora Nordamerikas, insbesondere der nordwestlichen Staaten. Annales Mycologici, 20, 178–218.

Sydow, H. and Petrak, F. (1924) Zweiter Beitrag zur Kenntnis der Pilzflora Nordamerikas, insbesondere der nordwestlichen Staaten. Annales Mycologici, 22, 387–409.

Tainter, F.H. and Baker, F.A. (1996) Brown spot. In: Principles of Forest Pathology, pp. 467–492. New York, USA: John Wiley.

de Thümen, F. (1878) Fungorum americanorum triginta species novae. Flora, 61, 177–184.

de Wit, P.J., Van Der Burgt, A., Ökmen, B., Stergiopoulos, I., Abd-Elsalam, K.A., Aerts, A.L., Bahkali, A.H., Beenen, H.G., Chettiri, P. and Cox, M.P. (2012) The genomes of the fungal plant pathogens Cladosporium fulvum and Dothistroma septosporum reveal adaptation to different hosts and lifestyles but also signatures of common ancestry. PLoS Genet. 8, e1003088.

Thyr, B.D. and Shaw, C.G. (1964) Identity of the fungus causing red band disease on pines. Mycologia, 56, 103–109.

Wakeley, P.C. (1970) Thirty-year effects of uncontrolled brown spot on planted longleaf pine. Forest Sci. 16, 197–202.

Webster, C.B. (1930) Comments on “Brown-Spot” disease of pine needles in Texas. J. Forest. 30, 763–778.

Wingfield, M.J., Brockerhoff, E.G., Wingfield, B.D. and Slippers, B. (2015) Planted forest health: the need for a global strategy. Science, 349, 832–836.

Wolf, F.A. and Barbour, W.J. (1941) Brown-spot needle disease of pines. Phytopathology, 31, 61–73.

Wu, X. and Qi, G. (1999) Studies on the biological specialization of the toxin producing by brown spot needle blight fungus (Lecanosticta acicola). Sci. Silvae Sin. 38, 84–88.

Ye, J. and Qi, G. (2011) Resistance in nature systems to brown-spot needle blight of pine in China. In: Fourth international workshop on the genetics of host–parasite interactions in forestry, pp. 107. Eugene, Oregon, USA: US Department of Agriculture.