Mycobiota Associated with the Vascular Wilt of Poplar

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Abstract: In 2017, a 560-ha area of hybrid poplar plantation in northern Poland showed symptoms of tree decline. The leaves appeared smaller, yellow-brown, and were shed prematurely. Twigs and smaller branches died without distinct cankers. Trunks decayed from the base. The phloem and xylem showed brown necrosis. Ten percent of the trees died 1–2 months after the first appearance of the symptoms. None of these symptoms were typical for known poplar diseases. The trees’ mycobiotia were analysed using Illumina sequencing. A total of 69,467 and 70,218 operational taxonomic units (OTUs) were obtained from the soil and wood. Blastocladiales and Chytridiales occurred only in the soil, with very low frequencies (0.005% and 0.008%). Two taxa of Glomeromycota, with frequencies of 0.001%, occurred in the wood. In the soil and wood, the frequencies of Zygomycota were 3.631% and 0.006%, the frequencies of Ascomycota were 45.299% and 68.697%, and the frequencies of Basidiomycota were 4.119% and 2.076%. At least 400 taxa of fungi were present. The identifiable Zygomycota, Ascomycota, and Basidiomycota were represented by at least 18, 263 and 81 taxa, respectively. Many fungi were common to the soil and wood, but 160 taxa occurred only in soil and 73 occurred only in wood. The root pathogens included species of Oomycota. The vascular and parenchymal pathogens included species of Ascomycota and of Basidiomycota. The initial endophytic character of the fungi is emphasized. Soil, and possibly planting material, may be the sources of the pathogen inoculum, and climate warming is likely to be a predisposing factor. A water deficit may increase the trees’ susceptibility. The epidemiology of poplar vascular wilt reminds grapevine trunk diseases (GTD), including esca, black foot disease and Petri disease.

Keywords: fungi; pathogens; plantation; poplar hybrids; vascular wilt

1. Introduction

Populus is a genus of deciduous trees in the family Salicaceae, native to most of the Northern Hemisphere. They are among the fastest-growing trees, and the most efficient in terms of sustainability. Poplar is significant because of: (i) its rapid production of wood (in Europe, 1 m³ of lumber can be produced on average in 15 years, six times faster than with oak); (ii) its very versatile wood, with an excellent ratio between specific weight and mechanical features, making it suitable for furniture, plywood and the paper industry; (iii) its excellent capacity for purifying the air by capturing CO₂ and storing it in the biomass (1 ha can capture 11 t CO₂/year); (iv) its capacity for purifying water while acting as a green filter, absorbing nitrates and sediments; (v) its potential for biofuel production using the coppicing method; (vi) the possibility for its cultivation on abandoned and degraded land, thus optimizing land use.

Poplar is an important source of wood for pulp and paper products, but mostly paper, for which worldwide production reaches 420 Mt, including 5 Mt in Poland [1]. Its
wood is also suitable for use as a renewable energy source. The development of renewable sources for energy purposes has been substantially supported and promoted by a European Union Directive. Poland is obliged to obtain at least 30% of its energy from renewable sources by 2030 (Directive (EU) 2018/2001). Wood that is suitable for renewable energy includes that derived from trees grown in short- and medium-rotation plantations, often on agricultural land or non-forested areas. Plantations based on varieties of *Acacia* and *Eucalyptus* have been particularly effective in tropical countries with favourable climate and soil conditions for faster growth; *Eucalyptus* has produced 25 m³ of wood per ha annually, compared with 7–8 m³ in the temperate climate zone (1). Plantations of fast-growing trees are now also being established in the temperate zone. The most promising genus in Poland is poplar (*Populus* spp.), with plantations usually in short- (up to 10 years) or medium-rotation (up to 15–25 years) coppice systems [2–4].

Hybrid poplar trees are often the progeny of crosses between cottonwood (*Populus deltoides* W. Bartram ex Marshall) and black poplar (*Populus nigra* L. ‘Italica’). They have the advantages of: (i) rapid growth (1.5–2.5 m per year), (ii) a large range of hardiness zones (3–9), (iii) high productivity resulting from a prolonged vegetation period, and (iv) better resistance to pests and diseases [5].

Poplars are frequently attacked by microorganisms that cause discolorations, necrosis, depressions, deformations (thickening of the trunk and branches, the abnormal proliferation of the underlying phloem, the formation of the corky ridges or woody galls). Stresses predispose trees to infection by phytopathogens. Attacks on the trunk and branches of younger trees often kill the main shoot.

The bark necrosis of poplars can be caused by *Discosporium populeum* (Sacc.) B. Sutton (=*Chondroplea populea* (Sacc.) Kleb. =*Dothichiza populea* Sacc. Sacc. & Briard, anamorph of *Cryptodiaporthe populea* (Sacc.) Butin). Necrosis and cankers are often caused by *Cystospora* spp. (*C. populina* (Pers.) Rabenh. =*C. ambiens* Sacc., teleomorph *Valsa ambiens* (Pers.) Fr., and *C. nivea* Fuckel, teleomorph *V. nivea* (Hoffm.) Fr.). Cankers can be caused by *Entoleuca mammata* (Wahlenb.) Rogers and Ju (=*Hypoxylon mammatum* (Wahl.: Fr.) Karst.). Sooty-bark canker is caused by *Seleroncola pruinosa* (Ellis and Everh.) PärTel and Baral (=*Enocidium pruinosa* (Ell. and Ev.) Torkelsen and Eckblad). Black or target canker can be caused by *Ceratocystis fimbriata* Ellis and Halst. Other agents of necrosis and cankers or wood rots and bark alterations, of which the incidence is more local and/or secondary, include *Boeremia populii* (Gruyter and Scheer) Jayawardena, Jayasiri and Hyde (=*Phoma exigua* var. *populi* Gruyter and Scheer), *Botryodiplodia* populea Zhong, *Diplodia tumefaciens* (Shear) Zalasky (the anamorph of *Keissleriella emergens* (Karst.) Bose), *Fusarium* spp., *Neofusicoccum ribis* (Slippers, Crous and M.J. Wingf.) Crous, Slippers and Phillips (=*Dothiorella gregaria* Sacc., the anamorph of *Botryosphaeria dothidea* (Moug.) Ces. and De Not), *Neonectria ditissima* (Tul. and C. Tul.) Samuels and Rossman (with anamorph *Cylindrocarpon mali* (Allesch.) Wollenw.), *Phomopsis* spp., *Rhytidella moriformis* Zalasky, *Rhytidella baranyai* Funk and Zalasky, and basidiomycetous *Erythricium salmonicolor* (Berk. and Broome) Burds. (=*Corticium salmonicolor* Berk. and Broome). Damage to heartwood can be caused by bacteria (*Erwinia nimipressuralis*). Disease of the leaves are usually caused by *Melampsora medusae* Thüm. (rust), *Venturia tremulae* Aderh. (scab, shoot blight), *Sphaerulina musiva* (Peck) QuaeDvl., Verkle and Crous (=*Septoria musiva* Peck), and *Marssonina* spp. Most infections of woody tissues are initiated by wind-borne ascospores, which are forcibly ejected from perithecia during periods of damp weather. Fungi infect trees through wounds and invade the inner bark and cambium.

In 2017, a 560 ha plantation of hybrid poplar (*P. deltoides × P. nigra*) in northern Poland showed symptoms of tree decline. The leaves of the diseased trees appeared smaller, turned yellow-brown, and were shed prematurely. Twigs and smaller branches died without definite cankers. The bark of the entire trunk was sunken and discolored, often loosened and split. It often fell off, exposing wet wood. The trunks decayed from the base. The phloem showed brown necrosis. Ten percent of the trees died in 1–2 months
(in June) after the first appearance of the symptoms. None of the observed symptoms were typical for known poplar diseases.

The objectives of the study on the structure of the fungal communities present in the rotten wood of poplar trunks and in the soil were to: (i) determine the abundance and diversity of pathogens and other fungi; (ii) identify interactions among fungi that may contribute to the disease progress; (iii) assess associations between the disease and global warming, with consequences for host and pathogen physiology, reproduction, survival, spatial and temporal distribution, resource availability and competition.

2. Materials and Methods
2.1. Site and Sampling

The study was carried out in the Łoża, Czarne District, Człuchów County, Pomeranian Voivodeship, northern Poland (53°41′29″ N 17°04′19″ E), in a 560 ha plantation of 5–6-year-old hybrid poplar (P. deltoides × P. nigra, cultivar AF2, from Italy) showing symptoms of crown decline, trunk-base decay (520 ha) and tree death (40 ha) (Figures 1 and 2). The plantation was so intensively affected that the inclusion of a control (healthy plantation) from the same area with the same conditions of climate and soil was impossible.

![Figure 1. Poplar plantation with diseased trees.](image)

The trees were grown at a density of 425 trees/ha (4 m × 4m spacing), and had a mean diameter of 9–10 cm at breast height. The post-agricultural soil was sandy loam, consisting of sand (60%), silt (20%) and clay (20%), with a low humus level. The former crop was rye (Secale cereale L.). The average temperature is 7.9 °C and the rainfall is 680 mm.

The understorey vegetation included Achillea millefolium L., Agrostis stolonifera L., Artemisia absinthium L., Artemisia vulgaris L., Cichorium intybus L., Elymus repens (L.) Gould, Lamium purpureum L., Lolium perenne L., Papaver rhoeas L., Poa annua L., Poa pratensis L., Poa trivialis L., Polygonum aviculare L., Polypodium vulgare L., Polytrichum commune Hedw., Stellaria media Hist. Pl. Dauphiné, Taraxacum officinale F.H. Wigg., and Trifolium arvense L.

Five wood cores; 10 cm long and 3 cm in diam., each including bark, phloem and xylem, were sampled from the bases of the necrotic trunks of five symptomatic trees, 0 cm and 50 cm above the ground, with a Pressler borer. The core samples were surface-sterilized and ground to sawdust with a cordless SPARKY BUR2 15E drill.
Additionally, five subsamples of soil were taken as cylindrical cores, 10 cm long and 5 cm in diam., from the surroundings of roots of five symptomatic trees. They were placed in sterile glass containers and refrigerated for 48 h.

Figure 2. Necrosis and decay at the base of the trunk of a diseased poplar.

2.2. DNA Extraction, Amplification and Illumina Sequencing

Five samples of sawdust were prepared from five wood cores in the SPEX™ SamplePrep™ Freezer/Mill™ cryogenic mill. The wood’s genomic DNA was extracted from each of five 30 mg heavy sawdust samples using a Plant Genomic DNA Purification Kit (Thermo Scientific, Carlsbad, California, USA). The soil’s genomic DNA was extracted from each 300 mg soil subsample using a Power Soil™ DNA Isolation Kit (MO BIO Laboratories, Carlsbad, CA, USA).

The rDNA was amplified with fungi specific primers ITS1 FI2 (5′-GAACCWGGGARGGATCA-3′) [6] and 5.8S (5′-CGCTGCGTT CTTCATCG-3′) [7].

The PCR reaction mixture consisted of 12.5 μL of 2 × Mix PCR (A & A Biotechnology, Gdansk, Poland), 0.2 μM of each primer, 1.5 μL purified and diluted DNA, and 10.6 μL water. The DNA amplification was performed under the following conditions: denaturation at 94 °C for 5 min followed by 35 cycles of denaturation at 94 °C for 30 s, annealing at 56 °C for 30 s, elongation at 72 °C for 30 s, and a final elongation at 72 °C for 7 min. The visualization of 5-μL amplicons was performed in 1% agarose gel dyed with Midori Green Advance DNA (Genetics). The pooled PCR products were purified using a MinElute PCR Purification Kit (Qiagen, Hilden, Germany). The concentration of PCR products was quantified using a Qubit 2.0 Fluorometer (Life Technologies, Carlsbad, CA, USA), and an equimolar mix of PCR products from each sample was prepared. The amplicons were sequenced using the Illumina system in the Genomic Laboratory, DNA Research Center, Rubież 46, Poznań, Poland.
2.3. Bioinformatics Analysis

A table of Operational Taxonomic Units (OTUs) was prepared by PIPITS, version 1.2.0 [8]. The read-pairs were joined with PEAR, version 0.9.6 [9], filtered with a quality threshold of $q = 30$ by FASTX-toolkit, version 0.0.13 (http://hannonlab.cshl.edu/fastx_toolkit/index.html, accessed on 26-April-2012) converted to the Fasta format, and merged into a single file. The prepared sequences were de-replicated, and subregions of ITS were selected with the use of ITSx, version 1.0.11 [10]. Unique sequences and those shorter than 100 bp were removed. The remaining sequences were clustered with 97% sequence identity. The resulting representative sequences for each cluster were subjected to chimera detection and removal using the UNITE UCHIME reference dataset, version 6.0 (https://unite.ut.ee/index.php (accessed on 26-April-2012)). The input sequences were then mapped onto the representative sequences, and taxonomy was assigned using RDP Classifier, version 2.10.2 [11] against the UNITE fungal ITS reference database, version 11.2 [12]. This process resulted in the creation of a table of OTUs. The sequences were identified by comparison with reference sequences from the National Center for Biotechnology Information (NCBI) database.

The abundance of fungi was defined as the average number of OTUs from five subsamples. The frequency of an individual taxon was defined as the percentage (%) of OTUs in the total number of OTUs. The similarity and relationships between the fungal communities from the soil and wood is shown by a heat map.

2.4. Statistical Analyses

The differences in the abundance of microfungi in the soil and wood were analysed with chi-squared tests ($\chi^2$). The diversity between the communities of microfungi was compared with Margalef’s diversity index ($D_{\text{Marg}}$), Shannon’s diversity index ($H$), Simpson’s diversity index ($D$), Shannon’s evenness index ($E$) and Berger–Parker’s index ($d$) [13].

3. Results

Totals of 69,467 and 70,218 OTUs were obtained, respectively, from the soil and wood of the *Populus* hybrid using the Illumina sequencing technique (Table 1, Figure 3). Of these, 44,506 (64%) and 53,592 (76%) were of fungi known from culture, and 24,961 (36%) and 16,628 (24%) were unidentified fungi and other organisms. Fungi from Blastocladiomycota, Chytridiomycota, Glomeromycota, Zygomycota, Ascomycota and Basidiomycota were detected. Blastocladiomycota and Chytridiomycota occurred only in the soil, with very low frequencies of 0.005% and 0.008%. Two taxa of Glomeromycota with a frequency of 0.001% occurred in the wood. The frequencies of Zygomycota in the soil and wood were 3.631% and 0.006%, the frequencies of Ascomycota were 45.299% and 68.697%, and the frequencies of Basidiomycota were 4.119% and 2.076%. The samples were colonized by at least 400 taxa of fungi. Identifiable Zygomycota, Ascomycota, and Basidiomycota were represented by at least 18, 263 and 81 taxa, respectively. Many fungi were common to the soil and wood, but 160 taxa occurred only in the soil, and 73 occurred only in the wood.
| No. | Taxon                                                                 | Chromista   | Order                        | Soil     | Wood    | Trophic Group |
|-----|----------------------------------------------------------------------|-------------|------------------------------|----------|---------|---------------|
| 1   | *Aphanomyces* spp.                                                   | Oomycota    | Saprolegniales               | 0.042    |         | Pathogens     |
| 2   | *Elongisporangium ananandum* (Drechsler) Uzuhashi, Tojo & Kakish     | Oomycota    | Peronosporales               | 0.004    |         | Pathogen      |
|     | *Globisporangium apicalatum* (B. Paul) Uzuhashi, Tojo & Kakish       | Oomycota    | Peronosporales               | 0.101    | 0.001   | Pathogens     |
|     | + *G. heterothalicum* W.A. Campb. & F.F. Hendrix + *G. intermedium* (de Bary) Uzuhashi, Tojo & Kakish + *G. macrosporum* (Vaartaja & Plaats-Nitt) Uzuhashi, Tojo & Kakish + *G. mamillatum* (Meurs) Uzuhashi, Tojo & Kakish + *G. perlopticum* (Takesi hō) Uzuhashi, Tojo & Kakish. + *G. sylvaticum* (W.A. Campb. & F.F. Hendrix) Uzuhashi, Tojo & Kakish. + *G. ultimum* (Trow) Uzuhashi, Tojo & Kakish     |                                          |                                          |          |         |               |
| 4   | *Hyaloperonospora cockleariae* (Gäum.) Göker, Riethm., Voglmayr, Weiss & Oberw     | Oomycota    | Peronosporales               | 0.017    |         | Pathogen      |
| 5   | *Isochrysis intermedia* (Coker & J.V. Harv.) Coker                  | Oomycota    | Saprolegniales               | 0.007    |         | Saprotroph    |
| 6   | *Mycosporangium sp.*                                                 | Oomycota    | Peronosporales               | 0.005    |         | Nematopathogenic |
| 7   | *Pythium conidosporum* Jokl. + *P. oligandrum* Drechsler + *P. pachycaule* Ali-Shtayev + *P. selbii* M.L. Ellis, Broders & Dorrance + *P. vanterpoolii* V. Kouyeas & H. Kouyeas + *P. volatum* Vanterp. & Truscott + *Pythium* sp. | Oomycota    | Peronosporales               | 0.053    | 0.001   | Pathogens     |
| 9   | *Thraustotheca clavata* (de Bary) Humphrey                          | Oomycota    | Saprolegniales               | 0.021    |         | Saprotroph    |

**Fungi**

| Frequency Oomycota | 1.199 | 0.002 |
|-------------------|-------|-------|
| Number of taxa Oomycota | 26 | 2 |

**Blastocladiomycota**

| Frequency Blastocladiomycota | 0.005 |
|-------------------------------|-------|
| Number of taxa Blastocladiomycota | 1 |

**Chytridiomycota**

| Frequency Chytridiomycota | 0.008 |
|---------------------------|-------|
| Number of taxa Chytridiomycota | 2 |

**Glomeromycota**

| Frequency Glomeromycota | 0.001 |
|-------------------------|-------|
| Number of taxa Glomeromycota | 2 |

**Zygomycota**

| Frequency Zygomycota | 3.631 | 0.006 |
|----------------------|-------|-------|
| Number of taxa Zygomycota | 18 | 3 |

**Ascomycota**

| Frequency Ascomycota | 0.004 |
|----------------------|-------|
| Number of taxa Ascomycota | 2 |

### Table 1. Microbiota present in the soil and wood of the diseased poplar.
| No. | Genus and Species | Family | Order | Saprotroph | Mycoparasite | Parasite | Human Pathogen | Animal Pathogen |
|-----|------------------|--------|-------|-------------|--------------|----------|----------------|----------------|
| 7.  | *Amesia nigricolor* (L.M. Ames) X. Wei Wang & Samson | Sordariales | 0.001 |  |  |  |  |  |
| 8.  | *Angustimassarina acerina* Jayasiri, Thambug., R.K. Schumach. & K.D. Hyde + *A. populi* Thambug. & K.D. Hyde | Pleosporales | 0.354 |  |  |  |  |  |
| 9.  | *Arthronymycetes* |  |  |  |  |  |  |  |
| 10. | *Ascobolus* sp. | Pezizales | 0.005 |  |  |  |  |  |
| 11. | *Ascochyta skagayensis* (R. Sprague) Punith. | Pleosporales | 0.001 |  |  |  |  |  |
| 12. | *Ascomyces* |  |  |  |  |  |  |  |
| 13. | *Ascomycota* |  |  |  |  |  |  |  |
| 14. | *Aspergillus conicus* Blochwitz + *A. niger* Tiegh. + *A. penicillioides* Spel. + *A. versicolor* (Vuill.) Tirab. | Eurotiales | 0.008 |  |  |  |  |  |
| 15. | *Atrocalyx lignicola* (Ying Zhang, J. Fourn. & K.D. Hyde) A. Hashim. & Kaz. Tanaka | Pleosporales | 0.009 |  |  |  |  |  |
| 16. | *Aureobasidium melanogenum* (Herm.-Nijh.) Zalar, Gostinčar & Gunde-Cim. + *A. pullulans* (de Bary & Löwenthal) G. Arnaud + *Aureobasidium* sp. | Dothideales | 0.003 |  |  |  |  |  |
| 17. | *Bacillus* sp. | Lecanorales | 0.018 |  |  |  |  |  |
| 18. | *Beauveria bassiana* (Bals.-Criv.) Vuill. + *Beauveria* sp. | Hypocreales | 0.049 |  |  |  |  |  |
| 19. | *Blastobotrys malaysiensis* Kurtzman + *Blastobotrys* sp. | Saccharomycetales | 0.009 |  |  |  |  |  |
| 20. | *Boeremia exigua* (Desm.) Aveskamp, Gruyer & Verkley + *B. nozakiana* (Allesch.) Gruyer & Verkley | Pleosporales | 0.006 |  |  |  |  |  |
| 21. | *Cadophora luteo-olivacea* (J.F.H. Beyma) T.C. Harr. & McNew + *C. spadics* Travadon, D.P. Lawr., Roon-Lath., Gubler, W.F. Wilcox, Rolsh. & K. Baumgartner + *Cadophora* sp. | Helotiales | 0.114 | 1.435 |  |  |  |  |
| 22. | *Candida sake* (Saito & M. Ota) Uden & H.R. Buckley ex S.A. Mey. & Abeer + *C. subrasa* M. Groenew., Sigler & S.E. Richardson + *C. variaeurae* (Cap.) Uden & H.R. Buckley + *Candida* sp. | Saccharomycetales | 0.093 | 0.012 |  |  |  |  |
| 23. | *Capnobotryrella renispora* Sugiy | Capnodiaceae | 0.005 |  |  |  |  |  |
| 24. | *Capnodiaceae* | Capnodiaceae | 0.017 |  |  |  |  |  |
| 25. | *Ceroascus geophilum* Fr. | Myceliaceae | 0.039 |  |  |  |  |  |
| 26. | *Cephalothecaceae* | Sordariales | 0.003 |  |  |  |  |  |
| 27. | *Ceratostomataceae* | Melanosporales | 0.004 |  |  |  |  |  |
| 28. | *Cercophora* sp. | Sordariales | 0.014 |  |  |  |  |  |
| 29. | *Cercosporella beticola* Sacc. | Capnodiaceae | 0.012 |  |  |  |  |  |
| 30. | *Chaetomiaceae* | Sordariales | 0.085 |  |  |  |  |  |
| 31. | *Chaetomium globosum* Kunze + *Ch. piliferum* J. Daniels + *Chaetomium* sp. | Sordariales | 0.062 | 0.002 |  |  |  |  |
| 32. | *Chaetosphaeria vernicularioides* (Sacc. & Roum.) W. Gams & Hol.-Jech. | Chaetosphaeriaceae | 0.005 |  |  |  |  |  |
| 33. | *Chaetothyriales* | Chaetothyriales | 0.104 |  |  |  |  |  |
| 34. | *Chalara micropora* (Corda) S. Hughes + *Chalara* sp. | Helotiales | 0.007 | 0.001 |  |  |  |  |
| 35. | *Chloridium paucisporum* C.J.K. Wang & H.E. Wilcox | Helotiales | 0.001 |  |  |  |  |  |
| 36. | *Chrysosporium pseudomeridarium* Oorschot | Onygenales | 0.004 |  |  |  |  |  |
| 37. | *Cistella albidolata* (Feltgen) Baral | Helotiales | 0.003 |  |  |  |  |  |
| 38. | *Cladosiphophora minutissima* M.L. Davey & Currah + *Cladosiphophora* sp. | Chaetothyriales | 0.002 |  |  |  |  |  |
| 39. | *Cladorrhinum flexuosum* Madrid, Cans, Genè & Guarro | Sordariales | 0.008 |  |  |  |  |  |
| 40. | *Cladosporium alatum* (Fr.) Bensch, U. Braun & Crous + *C. cladosporioides* (Fresen.) G.A. de Vries + *C. colosacas* Sawada | Capnodiaceae | 0.096 | 0.015 |  |  |  |  |
| 41. | *Clonostachys divergens* Schroers + *C. parva* (Schroers) Rossman, L. Lombard & Crous + *C. rosea* (Link) Schroers, Samuels + *Clonostachys* sp. | Hypocreales | 0.187 | 0.033 |  |  |  |  |
| 42. | *Coleophoma cylindrospora* (Desm.) Höhn | Helotiales | 0.010 |  |  |  |  |  |
| 43. | *Collophorina* sp. | Leotiales | 0.001 |  |  |  |  |  |
| No. | Genus and Species | Class | Order | Pathogens | Saprotrophs | Mycoparasite | Endophytes | Coprophilous |
|-----|-------------------|-------|-------|-----------|-------------|--------------|------------|-------------|
| 44. | Coniochaeta sp.   | Coniochaetales | 0.015 | 0.002 | Pathogens, saprotrophs, endophytes, coprophilous, mycoparasite, human pathogens |
| 45. | Cordyceps bassiana Z.Z. Li, C.R. Li, B. Huang & M.Z. Fan + C. bronniaria Shimazu | Hypocreales | 0.047 | Entomopathogenic, mycoparasite |
| 46. | Cosmospora berkeleyana (P. Karst.) Gräfenhan, Seifert & Schroers | Hypocreales | 0.027 | Saprotroph, pathogen, mycoparasite |
| 47. | Crocierea sp. | Helotiales | 0.005 | Saprotrophs |
| 48. | Cucurbitariaceae | Pleosporales | 0.076 | Saprotrophs, pathogens, |
| 49. | Cadoniella indica | Helotiales | 0.002 | Saprotroph |
| 50. | Cytidium cyathoideum (Bull.) Thüm. | Helotiales | 0.006 | Saprotrophs |
| 51. | Cypellocyphora sessilis (de Hoog) Riebövá & Unter | Chaetothyriales | 0.001 | Pathogen |
| 52. | Cytospora davidiana Y.L. Wang & X.Y. Zhang + C. licostoma (Pers.) Sacc. + C. pararubescens Norphanph., Bulgakov, T.C. Wen & K.D. Hyde + Cytospora sp. | Diaporthales | 0.012 | Pathogens |
| 53. | Dactylaria donophilosa Veene & Rijks | Helotiales | 0.016 | Saprotroph |
| 54. | Dactylonectria borealis (A. Cabral, Rego & Crous) L. Lombard & Crous | Hypocreales | 0.008 | Pathogen |
| 55. | Debaryomyces hansenii (Zopf) Lodder & Kreger-van Rij | Saccharomycetales | 0.023 | Pathogen |
| 56. | Dendryphon eurasiaticum Crous & R.K. Schumach. + D. narum (Nees) S. Hughes | Pleosporales | 0.268 | Saprotroph |
| 57. | Dermatocaeae | Helotiales | 0.002 | |
| 58. | Desmazierella acicola Lib. | Poziases | 0.001 | Saprotroph |
| 59. | Diaporth Myrocoelum | Diaporthales | 0.017 | Pathogens, endophytes |
| 60. | Didymella macrostoma (Mont.) Qian Chen & L. C. + D. pedeiace | Pleosporales | 0.039 | Pathogens |
| 61. | Didymosphaeria futilis (Berk. & Broome) Rehm | Pleosporales | 0.005 | Saprotroph |
| 62. | Dissoconium ecuvalyi Crous & Carnegie | Capnodiales | 0.001 | Commensalist, mycoparasite |
| 63. | Dothideomycetes | | | |
| 64. | Emericellopsis glabra (J.F.H. Beyma) Backus & Orpurt + E. minima Stolk | Hypocreales | 0.179 | Endophytes |
| 65. | Endoplasma elongata Tsuneda & M.L. Dave | Incertae sedis | 0.005 | |
| 66. | Epicoccum nigrum Link | Pleosporales | 0.002 | Endophyte, saprotroph, pathogen |
| 67. | Erythothalma cerasi | Eurotiiales | 0.001 | |
| 68. | Eurotheciales | Eurotheciales | 0.002 | Saprotrophs, human pathogens |
| 69. | Exophiala capsiphilus Crous + E. equina (Pollacci) de Hoog, V.A. Vicente, Najafz., Harrak, Badali & Seyedm. + E. opportunitas de Hoog, V.A. Vicente, Najafz., Harrak, Badali & Seyedm. + Exophiala sp. | Chaetothyriales | 0.129 | Saprotrophs, human pathogens |
| 70. | Fusarium oxysporum (Fr.) Sacc. + F. equiseti (Corda) Sacc. + F. fujikuroi Nirenberg + F. oxysporum Schldl. + F. petrieliae L. Lombard + F. redolens Wollenw. + F. solani (Mart.) Sacc. + F. torulosum (Berk. & M.A. Curtis) Gruyer & J.H.M. Schneid. + Fusarium sp. + Neocosmospora solani (Mart.) L. Lombard & Crous | Hypocreales | 0.890 | Pathogens |
| 71. | Fusinia aquacutum (Radl. & Raben.) Gräfenhan, Seifert & Schroers + F. merismsoides (Corda) Gräfenhan, Seifert & Schroers | Hypocreales | 0.096 | Pathogens |
| 72. | Gibelulopsis nigrescens (Pethybr.) Zare, W. Gams & Summerb | Glomerellales | 0.009 | Saprotroph |
| 73. | Glomaxia murrorum var. furina (Marchal) S. Hughes | Hypocreales | 0.023 | Saprotroph |
| No. | Genus | Species | Orders | Ranges | Comments |
|-----|-------|---------|--------|--------|----------|
| 74. | Graphium basitruncatum | (Matsush.) Seifert & G.Okada + G. penicillioides Corda | Microascales | 0.007 | 2.451 | Saprotrophs, plant and human pathogens |
| 75. | Gaphostroma platystemum | (Schwein.) Piroz. | Xylariales | 0.004 | | Saprotroph |
| 76. | Halenospora varia | (Anastasiou) E.B.G. Jones + Halenospora sp. | Helotiales | 0.443 | | Saprotrophs, aquatic |
| 77. | Halokirschsteiniothelia maritima | (Linder) Boonmee & K.D. Hyde | Myxillidales | 0.023 | | Saprotroph |
| 78. | Halosphaeria quadri-remis | (Höhnl.) Kohlm | Microascales | 0.007 | | Saprotroph |
| 79. | Halosphaeriaceae | | Microascales | 0.008 | | |
| 80. | Harzia acronionides | (Harz) Costantin + H. sphaerospora | Melanosporales | 0.028 | | Saprotrophs |
| 81. | Helicodendron lutoalbum | Glen Bott + H. westerdijkiae Beverw | Helotiales | 0.009 | | Saprotrophs |
| 82. | Helicosporium sp. | | Tubeufiales | 0.006 | | Saprotrophs |
| 83. | Heliotiaceae | | Helotiales | 0.005 | | |
| 84. | Heliotiales | | Helotiales | 3.087 | 4.565 | |
| 85. | Hemibeltrania sp. | | | | | Pathogen |
| 86. | Herpotrichia pinetorum | (Fuckel) G. Winter + Herpotrichia sp. | Pleosporales | 0.183 | 0.002 | Pathogens |
| 87. | Herpotrichiellaceae | | | | 0.004 | |
| 88. | Hyalodendriella betulae | Crous | Helotiales | 0.012 | 0.001 | Saprotroph, pathogen |
| 89. | Hyalopectiza sp. | | Helotiales | 0.014 | | Saprotroph |
| 90. | Hyaloscypha bicolor | (Hambl. & Sigler) Vohnik, Fehrér & Réblová | Helotiales | 0.012 | | Endophyte, saprotroph |
| 91. | Hyaloscyphaceae | | Helotiales | 0.003 | 0.040 | |
| 92. | Hymenoscyphus caudatus | (F. Karst.) Dennis + H. imberbis | Helotiales | 0.007 | 0.017 | Pathogens, saprotrophs |
| 93. | Hypocreales | | Helotiales | 2.979 | | |
| 94. | Hypoxylon fragiforme | (Pers.) J. Kickx f. | | | | |
| 95. | Hymenosticta crassa | (Wollenw.) A. Cabral & Crous + I. cyclaminicola A. Cabral + Crous + I. destruens (Zinssm.) Rossman, L. Lombard & Crous + I. europeas A. Cabral, Rego & Crous + I. mors-pacinas (A.A. Hildebr.) A. Cabral & Crous + I. robusta (A.A. Hildebr.) A. Cabral & Crous + Ilynotectria sp. + Cylindrocarpon sp. | Hypocreales | 2.031 | 6.710 | Saprotrophs, pathogens |
| 96. | Infulichalara microchona | (W. Gams) Réblová & W. Gams + I. minuta Koukol | Helotiales | 0.014 | 0.001 | Saprotrophs, pathogens, mycoparasitic |
| 97. | Juttae taediosa | (Sacc.) Réblová & Jaklitsch | Calosphaeriales | 0.005 | | Endophyte |
| 98. | Juxtapithema eurypha Sacc. | | Pleosporales | 0.001 | | Pathogen |
| 99. | Knufia cryptophila (L.J. Hutchison & Unter.) + K. peltigerae (Fuckel) Réblová & Unter | Incertae sedis | | 0.006 | 0.015 | Pathogens, lichenicolous |
| 100. | Lambertella tubulosa | Abdullah & J. Webster | Helotiales | 1.445 | | Saprotroph |
| 101. | Lasiosphaeriaceae | | Sordariales | 0.095 | 0.005 | |
| 102. | Lecania cyrtella | (Ach.) Th. Fr. + L. nagelii (Hepp) Diederich & van den Boom | Lecanorales | 0.001 | 0.034 | Lichenicolous |
| 103. | Lecanorales | | Lecanorales | 0.001 | | |
| 104. | Lecanorales | | Lecanorales | 0.001 | | |
| 105. | Lecanorales | | Lecanorales | 0.002 | | |
| 106. | Leotiomycetes | | Leotiomycetes | 0.003 | 0.876 | |
| 107. | Leptaria caesiella | R.C. Harris | Lecanorales | 0.002 | | Lichenicolous |
| 108. | Leptodontidium sp. | | Helotiales | 0.011 | 0.254 | Endophyte, mycorrhizal |
| 109. | Leptosphaeriaceae | | | | 0.023 | |
| 110. | Leptosphaerulina australis | McAlpine | Pleosporales | 0.014 | | Endophyte |
| 111. | Lophiodermum corticola | (Fuckel) E.C.Y. Liew, Aproot & K.D. Hyde + Lophiodermum sp. | Pleosporales | 0.788 | | Pathogens |
| 112. | Lophodermum pinastri (Schrad.) Chevall. + L. seditiosum | Minter, Staley & Millar + Lophodermium sp. | Rhytismatales | 0.107 | 0.003 | Pathogens |
| 113. | Lophotrichus sp. | | Microascales | 0.017 | | Pathogen |
| No. | Genus and Species | Class | Order | Genus | Family | Saprotroph, coprophilous, endophytic, mycoparasitic, pathogenic |
|-----|------------------|-------|-------|-------|--------|---------------------------------------------------------------|
| 114 | Macroconia sphaerias (Fuckel) Gräfenhan & Schroers | Hypocreales | 0.013 | Hypocreales | Saprotroph, mycoparasitic |
| 152 | Magnatothecospora fuscospora (Linder) R.F. Castañeda, Hern.-Restr. & Gené | Incertae sedis | 0.269 | | Saprotroph |
| 166 | Massarina sp. | Pleosporales | 0.002 | | Saprotroph |
| 178 | Megacapitula villosa J.L. Chen & Tzean | Incertae sedis | 0.001 | | Saprotroph |
| 180 | Melanospora kussanoviciana (Beliakova) Czerepan | Melanosporales | 0.009 | | Saprotroph, mycoparasitic |
| 190 | Metarhizium marquandii (Massee) Kepler, S.A. Rehner & Humber | Hypocreales | 0.495 | | Endophyte |
| 929 | Meyeroyzna guillermondii (Wick.) Kurtzman & M. Suzuki | Saccharomycetales | 0.003 | | Coprophilous, human pathogen |
| 121 | Micarea adnata Coppins | Lecanorales | 0.006 | | Lichenicolous |
| 123 | Microsaccaceae | Microascales | 0.002 | | |
| 127 | Microlochium sp. | Amphisphaeriales | 0.063 | | Pathogen |
| 134 | Microtheicum fusicola (E.C. Hansen) Y. Marin, Stichigl, Guarro & Cano | Melanosporales | 0.012 | | Saprotrophs |
| 136 | Minutisphaera parafimbriatisspora Raja, Oberlies, Shearer & A.N. Mill | Minutisphaeraceae | 0.017 | | Saprotroph, aquatic |
| 138 | Mollisia sp. | Helotiales | 0.021 | | Saprotroph |
| 139 | Monographella nivealis (Schaffnit) E. Müll | Amphisphaeriales | 0.004 | | Pathogen |
| 141 | Montagnulaceae | Pleosporales | 0.005 | | Saprotrophs, endophytes, pathogens |
| 142 | Mycofalcella calcarata Marvanová, Om-Kalth. & J. Webster | Helotiales | 0.002 | | Saprotroph, aquatic |
| 143 | Mycosphaerella tassiana (De Not.) Johanson | Capnodiales | 0.008 | | Pathogen, saprotroph |
| 145 | Myrmecridium schulzeri (Sacc.) Arzanlou, W. Gams & Crous | Myrmecridiales | 0.010 | | |
| 148 | Naevola perexigua (Koberge ex Desm.) K. Holm & L. Holm | Helotiales | 0.001 | | Saprotroph |
| 150 | Nakazawaea anatomiae (Zwillenh.) Kurtzman & Robnett + N. populi (Hagler, Mend.-Hagler & Phaff) Kurtzman & Robnett | Saccharomycetales | 0.016 | | Saprotrophs |
| 152 | Nectria sp. | Hypocreales | 0.032 | | Pathogens, saprotrophs |
| 154 | Nectriaceae | Hypocreales | 0.432 | | |
| 156 | Neoschochyna exitialis (Morini) Qian Chen & L. Cai | Pleosporales | 0.012 | | Pathogen |
| 158 | Neobulgaria pannophila Roll-Hansen & H. Roll-Hansen + N. pura (Pers.) Petr. + Neobulgaria sp. | Helotiales | 0.684 | | Saprotrophs |
| 160 | Neocatenuulospora germanicum (Crous & U. Braun) Quaedvliet & Crouss | Capnodiales | 0.001 | | Pathogen |
| 162 | Neocucurbitaria cava (Schulzer) Gruyter, Aveskamp & Verkley | Pleosporales | 0.002 | | Saprotroph |
| 164 | Neofabreae perennis Kiernholz | Helotiales | 0.009 | | Pathogen |
| 166 | Neoleptosphaeria rubefaciens (Togliani) Gruyter, Aveskamp & Verkley | Pleosporales | 0.003 | | Pathogen |
| 168 | Neonecrotica candida (Ehrenb.) Rossman, L. Lombard & Crous + Neocinectria sp. | Hypocreales | 0.560 | | Pathogen |
| 170 | Neopyrenochaeta acicola (Mouëg. & Lév.) Valenz.-Lopez, Crous, Stichigl, Guarro & Cano + N. inflorescentiae (Crous, Marin. & M.J. Wingl.) Valenz.-Lopez, Crous, Stichigl, Guarro & Cano | Pleosporales | 0.014 | | Pathogens, saprotrophs |
| 172 | Neosetophilina clemtidis Wijayaw., Camporesi & K.D. Hyde | Pleosporales | 0.046 | | Saprotroph |
| 174 | Neurospora terricola Goch. & Backus | Sordariales | 0.004 | | Saprotroph |
| 180 | Nesiella muscida (W. Gams) W. Gams & Stielow | Hypocreales | 0.004 | | Saprotroph |
| 182 | Nigrograna mycophila Jaklitsch, Friebes & Voglmayr | Pleosporales | 0.007 | | Saprotroph, mycoparasitic |
| 184 | Nigrospora oryzae (Berk. & Broome) Petch | Incertae sedis | 0.535 | | Saprotroph, pathogen |
| 186 | Ochrocladosporium elatum (Harz) Crous & U. Braun | Pleosporales | 0.022 | | Endophyte |
| 188 | Oedoccephalum nauroense Ts. Watan | Pezizales | 0.049 | | Saprotroph |
| 190 | Onygenales | Onygenales | 0.005 | | |
| 152. | Ophiostomataceae | Ophiostomatales | 0.790 | Pathogens |
| 153. | Orbilia auricolor (A. Bloxam) Sac. | Orbiliales | 0.026 | Saprotrophs, pathogens |
| 154. | Orbiliae | Orbiliales | 0.006 | |
| 155. | Pachyramichloridium pisii (de Hoog & Rahman) C. Nakash., Videira & Crous | Cynodiales | 0.017 | Pathogen |
| 156. | Papulaspora pisicola J.F.H. Beyma | Incertae sedis | 0.019 | Saprotrophs |
| 157. | Paraphoma chrysanthemicola (Hollós) Gruyter, Aveskamp & Verkley + P. radicina (McAlpine) Morgan-Jones & J.F. White + Paraphoma sp. | Pleosporales | 4.852 | Saprotrophs, pathogens |
| 158. | Penicillium citrinum (Dierckx + P. citrosulfuratum Biourge + P. georgenae S.W. Peterson & B.W. Horn + P. glandicola (Oudem.) Seifert & Samson + P. halotolerans Frisvad, Houbraken & Samson + P. lapisosum Raper & Fennell + P. nothofagi Houbraken, Frisvad & Samson + P. raphiae Houbraken, Frisvad & Samson + P. roseomaculatum Biourge + P. sacculum E. Dale + P. unicum Tzean, J.L. Chen & Shiu + P. virgatum Nirenberg & Kwaśn + Pencillium sp. + Talaromyces luteus C.R. Benj. | Eurotiales | 0.295 | 0.001 | Saprotrophs |
| 159. | Penicillium sp. | Pleosporales | 0.012 | Endophyte |
| 160. | Petriella sordida (Zakal) G.L. Barron & J.C. Gilman | Microascales | 0.001 | Coprophilous |
| 161. | Phacidium lacerum Fr. + Phacidium sp. | Phacidiales | 0.027 | Saprotrophs |
| 162. | Phaeosclereosporium cinereum Graz. & Moham. | Togniniales | 0.044 | Pathogens |
| 163. | Phaeosclereosporium constrictum Croux & R.K. Schumach. + P. sparsa B. Sutton | Xylariales | 0.347 | Saprotrophs, coprophilous |
| 164. | Phaeosclereosporium sp. | Phaeosclereosporiales | 0.001 | |
| 165. | Phaeosclereosporium sp. | Phaeosclereosporiales | 0.007 | |
| 166. | Phaeosclereosporium sp. | Phaeosclereosporiales | 0.013 | |
| 167. | Phaeosclereosporium sp. | Pleosporales | 0.032 | Pathogens, saprotrophs |
| 168. | Phialocephala sp. | Helotiales | 0.004 | Saprotrophs |
| 169. | Phialocephala sp. | Chaetothyriales | 10.291 | Saprotrophs, pathogens |
| 170. | Phoma boeremae Gruyter + Phoma sp. | Pleosporales | 0.010 | 0.007 | Saprotrophs, pathogens |
| 171. | Phomopsis phaseoli (Derm.) Sac. + P. velata (Sacc.) Traverso + Phomopsis sp. | Diaporthales | 1.186 | Pathogens, saprotrophs, endophytes |
| 172. | Physcia tenella (Scop.) DC. | Caliciales | 0.001 | Lichenicolous |
| 173. | Pilophorus straminificus Nyl. ex Cromb | Lecanorales | 0.001 | Lichenicolous |
| 174. | Plagiosoma jonesii Senan. & K.D. Hyde | Diaporthales | 0.031 | Saprotroph, endophyte |
| 175. | Plectsphalerella cucumerina (Linfd.) W. Gams + P. niemeyeri Croux, Lombard | Glomerellales | 0.140 | 0.014 | Pathogens |
| 176. | Pleosporaceae | Pleosporales | 0.003 | |
| 177. | Pleosporales | Pleosporales | 0.161 | 0.504 | |
| 178. | Plethaxia aurantia (Corda) Henn.-Resstr., R.F. Cañada & Gené | Pleosporales | 0.307 | 0.013 | Saprotroph, aquatic |
| 179. | Pleurophoma bassiana Crous, Krawczyński & H.-G. Wagner + Pleurophoma sp. | Xylariales | 0.016 | 0.005 | Saprotroph |
| 180. | Podospora appendiculata (Auerw. ex Niessl) Niessl + P. bulbillosa (W. Gams & Mouch.) X. Wei Wang & Houbraken. + P. lopinorina (Cain) Cain + Podospora sp. | Sordariales | 0.074 | Saprotroph, coprophilous |
| 181. | Prussia flanaganii Boylan + P. typharum (Sacc.) Cain | Pleosporales | 0.058 | |
| 182. | Pseudotreutrium hygrophilum (Sogonov, W. Gams, Summer & Schroers) Minnis & D.L. Lindner + P. ovale Stolk + P. zonatum J.F.H. Beyma | Thelebolales | 0.804 | Saprotrophs, human pathogens |
| 183. | Pseudocercospora angolensis (T. Carvalho & O. Mendes) Croux & U. Braun | Mycosphaerellales | 0.004 | Pathogen |
| 184. | Pseudocercospora pannorum (Link) Minnis & D.L. Lindner + P. | Thelebolales | 0.068 | Saprotrophs |
| No. | Species/Subspecies | Genus | Family | Order | Class | Subclass | Phylum | Kingdom | Pathogens | Saprotrophs | Endophytes | Coprophilous | Mycoparasitic | Aquatic | Saprotrophs, Endophytes | Saprotrophs, Pathogen, Acquatic | Saprotrophs, Pathogens | Saprotrophs, Pathogens, Endophytes | Saprotrophs, Pathogens, Mycoparasitic | Saprotrophs, Pathogens, Mycoparasitic | Saprotrophs, Pathogens, Mycoparasitic | Saprotrophs, Pathogens, Mycoparasitic | Saprotrophs, Pathogens, Mycoparasitic | Saprotrophs, Pathogens, Mycoparasitic |
|-----|-------------------|-------|--------|-------|-------|----------|--------|---------|-----------|-------------|-------------|-------------|-------------|-------------|-----------|---------------------|----------------------|---------------------|----------------------|---------------------|---------------------|---------------------|---------------------|---------------------|---------------------|
| 185 | Pyrenochaetopsis leptospora (Sacc. & Briard) Gruyter, Aveskamp & Verkley + P. microspora (Gruyter & Boerema) Gruyter, Aveskamp & Verkley | Pyrenochaetopsis | Pleosporales | 0.007 | 0.001 | Saprotrophs, Pathogens, Endophytes |
| 186 | Pyrenomataceae | Pezizales | 0.081 | | | |
| 187 | Saccharomyces cerevisiae (Desm.) Meyen | Saccharomycetales | 0.001 | | | Saprotroph |
| 188 | Schizothecium glutinans (Cain) N. Lundq | Sordariales | 0.015 | | | Saprotroph, Coprophilous |
| 189 | Sceletosporium constrictum E.V. Abbott + S. umbrinum (Ach.) Arnold | Incertae sedis | 0.016 | 0.002 | Saprotrophs, Endophytes |
| 190 | Sclerotinia scitellata (L.) Lambotte | Pezizales | 0.005 | | | Saprotroph |
| 191 | Scytalidium lignicola Pesante + S. multisepatum Hol.-Jech | Helotiales | 0.055 | 0.001 | Saprotrophs, Pathogens, Mycoparasitic |
| 192 | Sordariales | 0.008 | | | |
| 193 | Sordariomycetes | 0.211 | 0.003 | | | |
| 194 | Sphaeropsis sapinea (Fr.) Dyko & B. Sutton | Botryosphaeriales | 0.003 | | | Pathogen |
| 195 | Sporormiaceae | Pleosporales | 0.003 | | | |
| 196 | Sporothrix dentifunda Aghayeva & M.J. Wingf. + S. stenoceras (Robak) Z.W. de Beer, T.A. Duong & M.J. Wingf. + S. narsissi (Limb) Z.W. de Beer, T.A. Duong & M.J. Wingf | Ophiostomatales | 0.161 | 0.001 | Pathogens, Saprotrophs |
| 197 | Stemphylium herbarum E.G. Simmons + S. majusculum E.G. Simmons + S. vesicarium (Wallr.) E.G. Simmons | Pleosporales | 0.027 | | | Pathogens |
| 198 | Subramaniula fascipila X. Wei Wang & Samson | Sordariales | 0.014 | | | Saprotroph |
| 199 | Sydowiopsis polyoma (Bref. & Tavel) E. Müll | Dothideales | 0.004 | 1.028 | Pathogens, Endophyte, Saprotroph |
| 200 | Tetracadium furcatum Descals + T. setigerum (Grove) Ingold + Tetracadium sp. | Helotiales | 1.171 | 0.862 | Saprotrophs |
| 201 | Theloneuria blackeriella + T. olida (Wollenw.) Wollenw. + T. nodosa Salgado & P. Chavero | Hypocreales | 0.012 | 0.006 | Pathogens |
| 202 | Tricharina sp. | Pezizales | 1.55 | | Saprotrophs |
| 203 | Trichocladium asperum Harz + T. griseum (Traen) X. Wei Wang & Houbraken | Sordariales | 0.593 | | Saprotrophs |
| 204 | Trichoderma aeruginose Jaklitsch + T. hamatum (Bonord.) Bainier + T. koningiopodis Samuels, Carm. Suarez & H.C. Evans + T. martiae Samuels + T. nookonii Samuels & Soberanis + T. piliferum J. Webster & Rifai + T. Polysporum (Link) Rifai + T. pulvescens Bissett + T. stibiophyzi I Samuels & Schroers + T. viziride Pers. + Trichoderma sp. | Hypocreales | 19.464 | 0.001 | Saprotrophs |
| 205 | Trichoderma splendens Ingold | Helotiales | 0.040 | 0.057 | Saprotroph, Aquatic |
| 206 | Truncatella angustata (Pers.) S. Hughes + T. restionacearum S.J. Lee & Crous | Amphylales | 0.003 | 0.001 | Pathogens |
| 207 | Valsa malicola Z. Urb. + V. sordida Sacc. + V. leucostoma (Pers.) Fr. | Diaporthales | 0.012 | 0.214 | Pathogens |
| 208 | Valsaeeae | Diaporthales | 0.003 | | |
| 209 | Venturia hystrioides (Dugan, R.G. Roberts & Hanlin) Crous & U. Braun | Venturiales | 0.018 | | Pathogen |
| 210 | Venturiales | 0.001 | | | |
| 211 | Xanthoparmelia subalpinaeizes (Hale) G. Amo, A. Crespo, Elix & Lumbsch | Lecanorales | 0.005 | | Lichenicolous |
| 212 | Xenocallarum sp. | Helotiales | 0.033 | | Saprotroph |
| 213 | Xenopolluxalum pilosum Crous + X. polypodium sp. | Helotiales | 0.001 | 0.001 | Saprotrophs |
| 214 | Xeromplastaria arxii Videira, Crous & U. Braun | Capnodiales | 0.001 | | Pathogen |
| 215 | Xylariales | Xylariales | 0.061 | | |
| Number | Species Description | Class | Frequency | Morphological Description |
|--------|---------------------|-------|-----------|---------------------------|
| 219.   | *Yamadazyma mexicana* (M. Miranda, Holzschu, Phaff & Starmer) Billon-Grand | Saccharomycetales | 0.039 | Saprotroph |
| 220.   | *Yarrowia lipolytica* (Wick., Kurtzman & Herman) Van der Walt & Arx | Saccharomycetales | 0.001 | Saprotroph |
| 221.   | *Zalerion* sp. | Lulworthiales | 0.001 | Saprotroph, aquatic |
| 222.   | *Zopfia marina* Furuya & Udagawa + *Z. pilifera* Udagawa & Furuya | Sordariales | 0.027 | Saprotrophs, aquatic |

**Frequency of Ascomycota**: 45.299 68.697

**Number of taxa Ascomycota**: 263 178

**Basidiomycota**

1. *Acisporium* sp. | Pucciniales | 0.034 | Pathogen |
2. *Amitella* sp. | Pucciniales | 0.054 | Pathogen |
3. *Amanita* sp. | Pucciniales | 0.008 | Pathogen |
4. *Amanita* sp. | Pucciniales | 0.001 | Pathogen |
5. *Apiotrichum dulcitum* (Berkhout) Yurkov & Boekhout + *A. gracile* (Weigmann & A. Wolff) Yurkov & Boekhout | Trichosporonales | 0.047 | Saprotrophs |
6. *Armillaria mellea* (Vahl) P. Kumm | Agaricales | 0.025 | Pathogen |
7. *Athelia acrospora* Jülich | Atheliaceae | 0.001 | Saprotroph |
8. *Athelia* sp. | Atheliaceae | 0.023 | Saprotroph |
9. *Aurantia* sp. | Polyporales | 0.002 | Saprotroph, pathogen |
10. *Bjerkandera adusta* (Wild.) P. Karst | Polyporales | 0.002 | Saprotroph, pathogen |
11. *Bucklezyupa aurantiaca* (Saito) Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout | Bucklezyupa | 0.048 | Saprotroph |
12. *Bullera crocata* Butz & Hugliar | Tremellales | 0.008 | Saprotroph |
13. *Bulleromyces albicans* Boekhout & A. Forseea | Tremellales | 0.001 | Saprotroph |
14. *Burgau anemona* (Hotson) Goid | Canthareliales | 0.009 | Saprotroph |
15. *Camarophyllus* sp. | Agaricostilbales | 0.001 | Mycorrhizal |
16. *Cantharellus* sp. | Canthareliales | 0.002 | Saprotroph |
17. *Cantharellus* sp. | Canthareliales | 0.001 | Mycorrhizal |
18. *Chondrostereum purpureum* (Pers.) Pouzar | Agaricales | 0.018 | Pathogen, saprotroph |
19. *Coprinellus disseminatus* (Pers.) J.E. Lange | Agaricales | 0.230 | Saprotroph |
20. *Cryptococcus tephrinis* Vishniac + *Cryptococcus* sp. | Tremellales | 0.220 | Saprotrophs, endophytes |
21. *Curvibasidium pallidicoralinum* Golubev, Fell & N.W. Golubev | Incertae sedis | 0.001 | Mycocinogenic |
22. *Cystobasidium pinicola* (F. Bai, L.D. Guo & J.H. Zhao) Yurkov, Kachalkin, H.M. Daniel, M. Groenew., Libkind, V. de Garcia, Zalar, Gouliam., Boekhout & Begerow + *C. pseudopurpuratum* A.M. Yurkov, Kachalkin, H.M. Daniel, M. Groenew., Libkind, V. de Garcia, Zalar, Gouliamova, Boekhout & Begerow | Cystobasidiales | 0.002 | Saprotrophs, mycoparasitic |
23. *Cystobasidium persoonii* | Cystobasidiales | 0.004 | Saprotrophs, aquatic |
24. *Cystofilobasidium* inomotii (Fell, I.L. Hunter & Tallman) Hamam., Sugiy. & Koma | Cystofilobasidiales | 0.012 | Saprotrophs, aquatic |
25. *Daedaleopsis confragosa* (Bolton) J. Schröd | Polyporales | 0.001 | Saprotroph |
26. *Efiobasidium sp.* | Sebacinales | 0.020 | Mycorrhizal |
27. *Entyloma gaillardii* Vánky & *E. polyporum* (Peck) Farl. | Entomatales | 0.044 | Pathogens |
28. *Erythrobasidium* sp. | Erythrobasidiales | 0.001 | Saprotroph |
29. *Erythrobasidium* baequae (Y. Yamada & Komag.) Hamam., Sugiy. & Komag. | Erythrobasidiales | 0.008 | Saprotroph |
30. *Erythrobasidium* sp. | Auriculariales | 0.001 | Saprotroph |
31. *Exobasidium arescens* Nannf. + *Exobasidium* sp. | Exobasidiales | 0.001 | Pathogen |
32. *Exobasidium* sp. | Exobasidiales | 0.001 | Pathogen |
33. *Fellonula* sp. | Tremellales | 0.001 | Saprotroph |
34. *Fellozyma inositophila* (Nakase & M. Suzuki) Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout | Incertae sedis | 0.007 | Saprotroph |
35. *Fibulobasidium inopinicum* Bandoni | Tremellales | 0.004 | Saprotroph |
36. *Filobasidium wieieringae* (A. Forseea, Scozzetti & Fell) Xin Zhan Liu, F.Y. Bai, M. Groenew. & Boekhout | Filobasidiales | 0.008 | Saprotroph |
| No. | Taxon Name                                      | Class              | Mycelial Type                  | Notes                  |
|-----|------------------------------------------------|--------------------|-------------------------------|------------------------|
| 39. | *Fomitopsis pinicola* (Sw.) P. Karst          | Polyporales        | Saprotroph                    | Pathogen, mycoparasitic |
| 40. | *Geotrichopsis mycopharica* Tzcan & Estey    | Incertae sedis     | Saprotroph                    | Mycoparasitic          |
| 41. | *Gymnopus androsaceus* (L.) Della Magg. & Trassin | Agaricales       | Saprotroph                    | Mycoparasitic          |
| 42. | *Hannaella zae* (O. Molnár & Prillinger) F.Y. Bai & Q.M. Wang | Tremellales | Saprotroph                    | Endophyte              |
| 43. | *Helotoma mesophaeum* (Pers.) Quel            | Agaricales         | Saprotroph                    | Mycorrhizal            |
| 44. | *Hydnaceae*                                   | Cantharellales     | Saprotroph                    |                        |
| 45. | *Hygrophoraceae*                              | Agaricales         | Saprotroph                    |                        |
| 46. | *Hymenogaster arenarius* Tul. & C. Tul.       | Agaricales         | Saprotroph                    | Ectomycorrhizal        |
| 47. | *Hypodenderia pallida* (Bres.) J. Erikss     | Hymenocheetales    | Saprotroph                    |                        |
| 48. | *Hypochlactia undulata* (Bourdot) J. Erikss  | Polyporales        | Saprotroph                    |                        |
| 49. | *Inocybe curvipes* P. Karst                  | Agaricales         | Saprotroph                    | Ectomycorrhizal        |
| 50. | *Irsenonila perplexans* Derx                 | Cystofilobasidiales | Saprotroph                    | Pathogen              |
| 51. | *Kockovaella machilophila* Cañ.-Gib., M. Takash., Sugita & Nakase | Tremellales | Saprotroph                    |                        |
| 52. | *Kondoia yuccicola* (Nakase & M. Suzuki) Q.M. Wang, M. Groenew., F.Y. Bai & Boekhout | Agaricostibiales | Saprotroph                    |                        |
| 53. | *Kvoniella neuropsychiae* K. Sylvester, Q.M. Wang & Hittinger + *K. pini* (Golubev & I. Pfeiff.) Xin Zhan Liu, F.Y. Bai, M. Groenew. & Boekhout | Tremellales | Saprotroph                    | Entomopathogenic        |
| 54. | *Laccaria* sp.                                | Agaricales         | Saprotroph                    | Ectomycorrhizal        |
| 55. | *Lachnellia albiovlosencs* (Alb. & Schwein.) Fr. | Agaricales         | Saprotroph                    |                        |
| 56. | *Leptosporonemes galzini* (Bourdot) Jülich | Atheliales        | Saprotroph                    |                        |
| 57. | *Leucosporidiales*                            | Leucosporidiales   | Saprotroph                    |                        |
| 58. | *Malassezia globosa* Midgley, E. Guelho & J. Guillot + *M. restricta* E. Guelho, J. Guillot & Midgley + | Malasseziales | Saprotroph                    | Human pathogens        |
| 59. | *Marasmius coharenens* (Pers.) Cooke & Quel | Agaricales         | Saprotroph                    |                        |
| 60. | *Microbotrymycetes*                           | Agaricales         | Saprotroph                    |                        |
| 61. | *Minimelusa polypora* (Hotson) Weresub & P.M. LeClair | Cantharellales | Saprotroph                    | Mycosphaeridic         |
| 62. | *Mrakia frigida* (Fell, Statzell, I.L. Hunter & Phaff) Y. Yamada & Komag. + *Mrakia* sp. | Cystofilobasidiales | Saprotroph                    |                        |
| 63. | *Mycesa aurantiomarginata* (Fr.) Quel. + *M. galariculata* (Scop.) Gray | Agaricales         | Saprotroph                    |                        |
| 64. | *Naganishia cornalis* (Passoth, A.-C. Andersson, Olstorpe, Theelen, Boekhout & Schnûrer) Xin Zhan Liu, F.Y. Bai, M. Groenew. & Boekhout + *N. diffusus* (Zach) Xin Zhan Liu, F.Y. Bai, M. Groenew. & Boekhout | Tremellales | Saprotroph                    |                        |
| 65. | *Oberwinklerzyma silvestris* Golubev & Scorzzetti ex Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout | Incertae sedis | Saprotroph                    |                        |
| 66. | *Oliveonia* sp.                               | Auriculaires       | Saprotroph                    |                        |
| 67. | *Piniophora* sp.                              | Russulales         | Saprotroph                    | Pathogen, saprotroph   |
| 68. | *Phaolomella frondosa* (Fr.) Spirit & V. Malysheva + *P. roseolecta* (Lloyd) V. Malysheva | Tremellales | Saprotroph                    | Mycoparasites          |
| 69. | *Phleomurus speira* (Fr.) Redhead             | Agaricales         | Saprotroph                    | Aquatic, saprotroph    |
| 70. | *Piskarozyma* sp.                             | Filobasidiales     | Saprotroph                    |                        |
| 71. | *Psathyrella squamosa* (P. Karst.) A.H. Sm.   | Agaricales         | Saprotroph                    |                        |
| 72. | *Rhodotorus glutinis* (Fesen.) F.C. Harrison + *Rhodotorus* sp. | Sporidiobolales | Saprotroph                    | Sporotrophs            |
| 73. | *Saitozyma podzolica* (Babeva & Reshetova) Xin Zhan Liu, F.Y. Bai, M. Groenew. & Boekhout | Tremellales | Saprotroph                    |                        |
| 74. | *Sakaguchia lamellibrachiae* (Nagah., Hamam., Nakase & Horikoshi) Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout | Sakaguchiales | Saprotroph                    |                        |
| 75. | *Sebacinales*                                  | Sebacinales        | Saprotroph                    | Endophyte, mycorrhizal |
| 76. | *Serenidina vermisfera* Oberw.                | Sebacinales        | Saprotroph                    |                        |
| 77. | *Serpula himantioides* (Fr.) P. Karst         | Boletales          | Saprotroph                    | Pathogen               |
| 78. | *Sirotrema translucens* (H.D. Gordon) Bandoni | Tremellales | Saprotroph                    |                        |
| 79. | *Sirotremastrum* sp.                          | Tremioporasales    | Saprotroph                    |                        |
| 80. | *Slofia pilati* (F.H. Jacob, Faure-Reayn. & Berton) Q.M. Wang, | Incertae sedis | Saprotroph                    |                        |
| Plant Name                                                                 | Authors                                                                 | Kingdom                | Filobasidiales Frequency | Saprotrophs Frequency | Basidiomycota Frequency | Oomycota Frequency | Culturable fungi Frequency | Non-culturable fungi Frequency | Other Kingdoms Frequency | No sequence in NCBI database Frequency |
|---------------------------------------------------------------------------|-------------------------------------------------------------------------|------------------------|--------------------------|------------------------|-------------------------|----------------------|-----------------------------|---------------------------------|-------------------------------|--------------------------------------|
| Soricocyzyga fuscescens (Golubev) Yurkov + S. phenolica (Å.)              | Yurkov + S. terre (Di Menna) A.M. Yurkov + S. terricola (T.A. Pedersen) Yurkov | Saprotrophs            | 2.451                    | 0.004                  | 4.119                   | 2.076                | 53.062                       | 17.435                          | 11.728                         | 0.055                                |
| Sporobolomyces roseus Kluyver & C.B. Nielsen + Sporobolomyces sp.        | F.Y. Bai, M. Groenew. & Boekhout                                        | Saprotrophs            | 0.008                    | 0.001                  | 81                      | 59                   | 474                         | 208                             | 15                             | 0.055                                |
| Symmetrospora coprosnae (Hamam. & Nakase) Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout | Incertae sedis                                                          | Saprotrophs            | 0.005                    | 0.001                  | 82                      | 82                   | 81                          | 59                             | 15                             | 0.055                                |
| Tausonia pullulans (Lindner) Xin Zhan Liu, F.Y. Bai, J.Z. Groenew. & Boekhout | Cystofilobasidiales                                                     | Saprotrophs            | 0.094                    | 0.012                  | 83                      | 83                   | 82                          | 82                             | 15                             | 0.055                                |
| Thelephoraceae                                                            | Thelephorales                                                            | Pathogens              | 0.014                    | 0.001                  | 84                      | 84                   | 83                          | 83                             | 15                             | 0.055                                |
| Tremella incarnata Lasch                                                  | Agaricales                                                              | Pathogen               | 0.004                    | 0.001                  | 85                      | 85                   | 84                          | 84                             | 15                             | 0.055                                |
| Tricholomataceae                                                          | Agaricales                                                              | Saprotrophs            | 0.003                    | 0.001                  | 86                      | 86                   | 85                          | 85                             | 15                             | 0.055                                |
| Trichosporon stelae Sugita, Takushima & Kikuchi                           | Trichosporonales                                                        | Human pathogen         | 0.003                    | 0.001                  | 87                      | 87                   | 86                          | 86                             | 15                             | 0.055                                |
| Tulasnelliaceae                                                           | Cantharellales                                                          | Ectomycorrhizal        | 0.006                    | 0.001                  | 88                      | 88                   | 87                          | 87                             | 15                             | 0.055                                |
| Tephiula incarnata Lasch                                                  | Agaricales                                                              | Pathogen               | 0.004                    | 0.001                  | 89                      | 89                   | 88                          | 88                             | 15                             | 0.055                                |
| Pappia fissilis (Berk. & M.A. Curtis) Zmitr                               | Polyporales                                                             | Saprotrophs            | 0.004                    | 0.001                  | 90                      | 90                   | 89                          | 89                             | 15                             | 0.055                                |
| Vishniacozyma carinacens (Verona & Luchetti) Xin Zhan Liu, F.Y. Bai, M. Groenew. & Boekhout | Tremellales                                                             | Pathogens, saprotrophs | 0.007                    | 0.005                  | 91                      | 91                   | 90                          | 90                             | 15                             | 0.055                                |

**Margalef’s diversity index—DMg**  
**Shannon’s diversity index—H**  
**Simpson’s diversity index—D**  
**Shannon’s evenness index—E**  
**Berger-Parker’s dominance index—d**

Percentage of variation. Pathogens are in bold. * Indicates a statistically significant difference according to a χ²-test, p < 0.001.
Saprotrophs were the most abundant (Figure 4). In the soil, their frequency exceeded 80%. In the soil, the most common (with frequency > 0.1%) were species of Mortierella (Zygomycota), Alatospora, Clonostachys, Dendryphion, Emericelopsis, Exophiala, Halenospora, Lambertella, Leptodontidium, Magnohelicospora, Metarhizium, Neobulgaria, Nigrospora, Penicillum, Petriella, Pleotrichocladium, Pseudeurotium, Tetracladium, Tricharina and Trichoderma (Ascomycota), Coprinellus, Cryptococcus, Fibulobasidium, Phaeotremella and Solicoccozyma (Basidiomycota).
Figure 4. Frequency of the fungi in specific trophic groups.

Individual taxa of obligate or facultative phytopathogens were more or less frequent.

The root pathogens included species of *Aphanomyces, Globisporangium, Phytophthora* and *Pythium* (Oomycota: 1.17%), and *Trunctella* (Ascomycota: 0.003% in the soil, 0.001% in the wood).

Vascular pathogens included species of *Cadophora, Dactylonectria, Debaryomyces, Fusarium, Fusicola, Graphium, Hymenoscyphus, Ilyonectria, Microdochium, Neonectria*, *Ophiostomataceae, Phaeoacremonium, Phaeomoniella, Phialophora, Sporothrix, Thelonectria* and *Verticillium* (Ascomycota: 4.783% in soil, 21.831% in the wood).

The parenchymal pathogens included species of *Alternaria, Boeremia, Cladosporium, Coniochaeta, Cosmospora, Cytospora, Diaporthe, Didymella, Epicoccum, Herpotrichia, Hypoxylon, Lophiostoma, Mycosphaerella, Neascchohyta, Neocatenulostroma, Neofabraea, Neoleptosphaeria, Neopyrenochaeta, Paraphoma, Phacoisaria, Phaeosphaeria, Phaeosphaeriopsis, Phoma, Phomopsis, Plectosphaerella, Pseudocercospora, Pyrenochaeta, Pyrenochaetopsis, Scytalidium, Sphaeropsis, Stemphylium, Sydowia, Valsa, Volutella and Xenoramularia* (Ascomycota: 1.647% in the soil, 11.645% in the wood), and *Armillaria, Aurantiporus, Chondrostereum, Fomitopsis, Peniophora* and *Serpula* (Basidiomycota: 0.026% in the soil, 0.618% in the wood).

The soft-rot fungi included species of *Alatospora, Alternaria, Cadophora, Chaetomium, Cladosporium, Clonostachys, Exophiala, Halenospora, Leptodontium, Neosetophoma, Orbilia, Phialophora, Plagiostoma, Sydowia* and *Tricladium* (Ascomycota: 0.821% in the soil, 13.757% in the wood).

The wood-decay Basidiomycota included the white rot fungi *Armillaria mellea, Aurantiporus fissilis, Bjerkandera adusta, Chondrostereum purpureum, Hyphodontia pallidula*. 
and *Peniophora*, and the brown rot fungus *Fomitopsis piniola*. They occurred with frequencies of 0.028% in the soil and 0.62% in the wood.

The mycorrhiza-forming fungi present in the soil and wood included 12 taxa: arbuscular *Entrophospora* (Glomeromycota: 0.001% in the wood); ectomycorrhizal *Cenococcum geophilum* (Ascomycota: 0.039% in the soil), *Hymenogaster arenarius*, *Inocybe curvipes*, *Laccaria* sp., *Serendipita vermisfera* and *Tomentella* (Basidiomycota: 0.048% in the soil, 0.019% in the wood); ectendomycorrhizal *Cladophialophora* spp., *Fellomyces* spp., *Fibulobasidium* spp., *Filobasidium* spp., *Geotrichopsis* sp., *Knufia* spp., *Kwoniella* spp., *Laccaria* sp., *Ledermucor* spp., *Lophotrichus* ssp., *Mycophila* spp., *Nakazawaea* spp., *Saccharomyces cerevisiae*, *Yamadazyma mexicana*, *Yarrowia lipolytica* and *Xanthoparmelia subchalybaeans* (Ascomycota: 0.296% in the soil, 13.072% in the wood); *Aiptotrichum dulcitum*, *Bensingtonia* ssp., *Buckleyzyma aurantiaca*, *Bullera croce*, *Bulleromyces albus*, *Cryptococcus* spp., *Curvibasidium pallidicorallinum*, *Cystobasidium* spp., *Erythrobasidium hasegawanum*, *Fellomyces* spp., *Fellozyma inositolaphila*, *Fibulobasidium inconspicuum*, *Filobasidium wieringae*, *Hannaella zaee*, *Itersonia perplexans*, *Kockovaella machilophila*, *Kondoayuccicola*, *Kwoniiella newnhampshireensis*, *Malassezia* spp., *Mtrakia frigida*, *Naqanishia cerealis*, *Phaeotremella* spp., *Piskurozyma* sp., *Rhodotorula* spp., *Saitozyma podzolica*, *Sakaguchia lamellibrachiae*, *Sirotrema translucens*, *Slooffia pilatii*, *Solicoccozyma* spp., *Sporobolomyces* spp., *Symmetrospora coprosmae*, *Tausonia pullulans*, *Tremella encephala*, *Trichosporon oatei* and *Vishniacozyma barnesica* (Basidiomycota: 3.061% in the soil, 1.017% in the wood).

The lichenicolous fungi present in the soil and wood included eight taxa: *Bacidina* sp., *Knufia peltigerae*, *Lecaria cyrtella*, *Lepraria caesia*, *Mycarea agrata*, *Physcia tenella*, *Pilophorus strumaticus* and *Xanthoparmelia subchalybaeans* (Ascomycota: 0.02% in the soil, 0.068% in the wood).

The coprophilous fungi present in the soil and wood included 10 taxa: *Ascobolus* sp., *Cercophora* sp., *Coniochaeta* sp., *Lophotrichus* sp., *Meyeroyzma guilliermondii*, *Petriella sordida*, *Phacoisaria*, *Podospora appendiculata* (forest specific), *Preussia* spp. and *Schizotheccium glutinans* (Ascomycota: 0.548% in the soil, 0.002% in the wood). The entomopathogenic fungi present in the soil and wood included three taxa: *Beauveria bassiana* and *Cordyceps* spp. (Ascomycota: 0.096% in the soil, 0.023% in the wood), and *Kwoniiella* spp. (Basidiomycota: 0.016% in the soil, 0.003% in the wood).

The nematocarcinogenic fungi included one species, *Myzocyttopus* sp. (Oomycota: 0.005% in the soil).

The mycorrhizal fungi present in the soil and wood included 18 taxa: *Syncephalis* sp. (*Zygomyca*: 0.107% in the soil), *Angustimassarina* spp., *Cladosporium* spp., *Clonostachys* spp., *Coniochaeta* sp., *Cordyceps* spp., *Cosmospora* sp., *Dissoconium eucalypti*, *Infundibulencera microchona*, *Macroconia spheraeae*, *Melanospora kurssanoviana*, *Nigrograna mycophila* and *Scytalidium lignicola* (Ascomycota: 1.063% in the soil, 0.056% in the wood), *Cystobasidium* spp., *Geotrichopsis mycopharatica*, *Gymnopus androsaceus*, *Minimedusa polyspora* and *Phaeotremella frondosa* (Basidiomycota: 0.16% in the soil, 0.139% in the wood).

The animal and human pathogens included *Coniochaeta*, *Exophila*, *Graphium* spp., *Lophotrichus* sp., *Meyeroyzma guilliermondii* and *Pseudoptotium ovale* (Ascomycota: 0.975% in the soil, 2.504% in the wood), and *Malassezia* spp. (Basidiomycota: 0.16% in the soil, 0.001% in the wood).

The aquatic fungi present in the soil and wood included 11 taxa: *Aureobasidium melanogenum*, *Halospora* spp., *Lemonniera terrestris*, *Minutisphaera parafimbriatispora*, *Mycocelula calcarea*, *Pleurotrichodium opacum*, *Trichladium splendens*, *Zalerion* spp. and *Zopfiella* spp. (Ascomycota: 0.041% in the soil, 0.527% in the wood), *Cystofilobasidium* spp. and *Phloeomana speirea* (Basidiomycota: 0.012% in the soil, 0.025% in the wood).
The rock-inhabiting fungi included one taxon, *Capnobotryella renispora* (Ascomycota: 0.005% in the soil).

The individual fungi often belonged to more than one trophic group. Margalef's index ($D_{mb}$), Shannon's diversity index ($H$) and Simpson's diversity index ($D$) indicated greater diversity in the soil than in the wood. Shannon's evenness index ($E$) showed more evenness in the soil and, conversely, Berger-Parker's dominance index ($d$) showed more dominance of individual taxa in the wood.

4. Discussion

4.1. Disease Characteristics

The vascular wilt of hybrid poplar appeared locally in Poland in 2017. The symptoms appeared suddenly in 5-6-year-old trees, and the disease developed very quickly, in less than 2 months. The activity of the pathogens, either already known or previously unrecognized, apparently circumvented any resistance in the host and led to the failure of the plantations. The disease was asymptomatic in its initial stage. Diagnosis at the final stage was not possible because of either: (i) the immaturity of the pathogen, or (ii) the absence of the distinctive morphological elements essential for the identification of causal fungi. Poplar diseases have a serious economic impact on wood production worldwide, and so the development of effective management strategies depends on the clear identification of the pathogens involved. The affected tissues were therefore analyzed by DNA sequencing.

The symptomatology of poplar wilt can be compared with that of some grapevine diseases, notably grapevine trunk diseases (GTD), including the esca and black foot diseases, and Petri disease [14,15]. Grapevine trunk disease symptoms include the sectorial and/or central necrosis of the trunk wood, brown streaking of the wood, cankers, and the discoloration and wilting of the foliage, which can occur suddenly [15,16]. Petri disease is a vascular disease associated with the decline and dieback of young grapevines. Typical black foot disease symptoms include stunted growth, reduced vigour, retarded or absent sprouting, sparse and chlorotic foliage with necrotic margins, wilting, dieback and death. Characteristic sunken necrotic root lesions with a reduction in root biomass and root hairs may also occur.

Grapevine trunk disease is caused by fungi in the Botryosphaeriaceae [17,18], *Phomopsis viticola* [17,19], *Euypa lata* [20] and *Truncatella* [21]. Petri disease and esca are caused by six species of Cadophora, including *C. luteo-olivacea*, 29 species of *Phaeoacremonium* (particularly *P. cinereum*), *Phaeonomiella chlamydospora* (Gams, Crous, Wingf. and Mugnai) Crous and Gams, *Pleurostoma richardiae* (Nannf.) Rěblová and Jaklitsch (=*Phialophora richardiae* (Nannf.) Conant), and basidiomycetous *Fomitiporia mediterranea* (Fisch.) and *Stereum hirsutum* (Willd.) Pers. [15,22–25]. Black foot disease is caused by species of *Campylacarpon*, *Cylindrocladiella*, *Dactylonectria*, *Ilyonectria*, *Neonecricia* and *Thelonecricia* [26]. The fungal species associated with grapevine diseases, mentioned above, have also been reported from a broad range of woody and herbaceous host plants [23,27–30]. In Italy, *Cadophora, Coniochaeta* (in its *Lecythophora* anamorphic stage) and *Phaeoacremonium* have been isolated from the wood of kiwifruit plants suffering from elephantiasis, which had trunk necrosis, hypertrophy and longitudinal bark cracks [31].

4.2. Pathogens in Diseased Poplar Trunk

According to EN 350:2016, poplar wood is non-durable, and some studies have shown that it is highly susceptible to wood-rotting fungi [32,33].

The dominant taxonomic group of poplar-associated fungi was Ascomycota. Those fungi are often cosmopolitan species known from the above- and below-ground parts of *Populus* species. Many species found in the wood of diseased trees are, however, known from diseased grapevine: Botryosphaeriaceae, *C. luteo-olivacea*, *Dactylonectria* spp., *Ilyonecricia* spp., *Neonecricia* spp., *P. cinereum*, *Phaeonomiella* spp., *Phialophora* spp., *Phomopsis*
spp., Thelonectria spp. and Truncatella spp. Other vascular and parenchymal fungi, frequently necrotrophic species, were also found: Angustimassarina, Aureobasidium, Boeremia, Chaetomium, Chaetosphaeria, Cyathicula, Cudoniella, Dendryphion, Didymella, Fusarium, Graphium, Helicodendron, Helicosporium, Hymenoscyphus, Hypoxylon, Knufia, Leptodontidium, Leptosphaeria, Lophiostoma, Massarina, Megacapitula, Mollisia, Neocatenulostroma, Neoleptosphaeria, Neosetophoma, Niesslia, Ophiostomataceae (with its anamorphs), Phoma, Plagiostoma, Pleurophoma, Podospora, Pyrenochaeta, Scutellinia, Scythalidium, Sporothrix, Tricharina, Xenopolyscytalum, Verticillium, and basidiomycetous Burgoa. These fungi were also often in the surrounding soil. Some of them seem likely to have contributed to the disease-causing species complex. The fungi associated with the diseased poplars, and which had been found previously in the wood of poplar or other deciduous trees, included: Angustimassarina on the wood of grapevine and poplar [34], Chaetosphaeria on the necrotic wood of Prunus [35], Graphium penicillioides in a wood core of Populus nigra in the Czech Republic 200 years ago [36], Graphostroma platystomum on the bark of oak [37], Helicodendron lutealbum on poplar roots [38], Helicosporium on a wilted chestnut tree [39], and Hymenoscyphus caudatus on the rotten leaves of Populus nigra [40]. The last species is related to Hymenoscyphus fraxineus (T. Kowalski) Baral, Queloz and Hosoya, which causes a very destructive wilt disease of ash, ash dieback - with similar trunk symptoms to those observed in the hybrid poplar [41,42]. Infundichalara microchona occurred in conifers [43,44]; Knufia in black galls on the stems and branches of Populus tremuloides Michx. in Canada [45]; Leptodontidium on the roots of healthy Populus deltoides [46]; Lophiostoma corticola on the above-ground organs of dying oaks in Poland [47]; Megacapitula on fallen, decaying petioles of broad-leaves trees [48]. Mollisia occurred on decaying plant tissues throughout the Northern Hemisphere; Neocatenulostroma germanicum in oak-wood debris [49]; Neoleptosphaeria rubefaciens on the wood, bark and fruits of herbaceous or woody plants in terrestrial habitats [50–52]. Neosetophoma clematidis occurred on the branches of Clematis vitalba L. [53] and Niesslia mucida on the bark of diverse plants, especially conifers [54]. Ophiostomataceae have been associated with wounds on hardwood trees in Poland [55]. Phaeoacremonium species occurred on European olive, quince and willow [27]; Phialocephala on rotten deciduous wood [56]; Phoma on the decaying wood of oak and pine [57]; Plagiostoma in the stems, twigs, and branches of woody and herbaceous plants from a wide range of plants in temperate regions of the Northern Hemisphere [58,59]. Pleurophoma ossicola occurred in Scots pine [60], and Pyrenochaeta occurred in oak [57]. Scythalidium lignicola causes diseases in Citrus and Manihot [58,61,62]. Sporothrix occurred in eucalyptus, pine and rosebush [63], and Xenopolyscytalum pinea in pine stumps [64].

Basidiomycetous Burgoa anomala was found in pine wood and litter [65].

Some of the fungi are, surprisingly, often common on wood in water, including sea-waters. This group includes Didymosphaeria guttata, Halenospora varia, Halosphaeria quadriennis, Paraphoma radicina, Trichocladium and basidiomycetous Cystobasidium [66–72]. Fusarium spp. were not abundant in the poplar wood, but occurred frequently in the soil. Various Fusarium spp. have been reported in Poland as causing swellings, necrosis, bark-fray, reddish-purple discoloration, and ultimately the characteristic cankers in poplar [73]. Fusarium avenaceum is perhaps the most important species, first reported in the 1950s on Euramerician poplar clones in France. Since then it has spread in Europe, from central and eastern areas with a continental climate to sub-mediterranean areas, and recently to Portugal, with its oceanic climate. Neocosmospora solani (=Fusarium solani (Mart.) Sacc. (found mostly on Algeiros and Tacamahaca poplars and intersectional hybrids) seemed to be confined to North America until it was reported in Poland [74]. Species with sporadic occurrence and of limited importance include F. lateritium Nees, observed in France and in the USA on Populus trichocarpa Torr. and A. Gray, and F. sporotrichoides Sherb., observed in eastern Europe and central Italy on Populus × euramericana. Fusarium spp., constituting a threat to young trees. Colonized trunks are susceptible to breakage, and to attacks by other bark parasites which are also active during a plantation’s early
years. The symptoms are not immediately visible, and mostly take the form of the disorganization of the cortical tissues in part of the trunk.

Fungi which are more frequent and perhaps more significant than *Fusarium* spp. in diseased poplar wood include *Cytopsora*, *Diaporthe* (with its *Phomopsis* anamorph), *Graphium*, *Hydnocercia*, *Paraphoma*, *Phaeoisaria* and *Phialophora*.

*Cytopsora* species are cosmopolitan, facultative parasites, and appear in tree stands subjected to some form or stress, with poor agronomic management or infected by other pathogens. Infection occurs in late autumn or winter, when the host is dormant, usually behaving as a distinctly secondary parasite. The initial symptoms include brown-blackish discolorations, necrosis, depressions in the bark and underlying wood, callus production and withering. Older, sturdier tissues may develop resistance to further invasion. The disease then appears as small brown depressions bounded by distinct calluses. In the advanced stage, the bark tissues may peel away to reveal underlying stained wood [75]. *Cytopsora ambiens*, *C. chrysosperma* and *C. nivea* (Hoffm.) Sacc., which are usually present on/in poplar wood worldwide, with their highest incidence in central and southern Italy, eastern Europe, the Near East, northern India, southern Africa (mainly in plantations) and the west-central USA (especially in Colorado), were not detected in the diseased hybrid poplars.

Species of *Diaporthe* and its *Phomopsis* anamorph comprise a phytopathologically important group, with diverse host associations and worldwide distribution. They cause leaf spots, blights, decay, wilt, root rots, dieback and cankers. *Phomopsis* pathogens are hemibiotrophs, i.e., first latent endophytes requiring living plants as a nutrient source, then sometimes becoming necrotrophic in the latent phase of colonization, or saprotrophic, their nutrients provided by tissue they have killed [76,77]. They occur in both temperate and tropical regions, and are especially common in the sapwood of angiosperms [78–92]. Endophytic and saprotrophic strains of *Phomopsis* produce similar degrading enzymes, supporting the thesis that endophytes become saprotrophs at the plant’s senescence [87,93]. *Graphium basistruncatum* has been reported from the gallery of the ambrosia beetle in poplar in South America [94]. *Graphium penicillioides* has been detected in the fully functional, wet sapwood of poplars [36]. Although the teleomorph of *G. penicillioides* is unknown, the genus is believed to have ophiostomatoid affinities [95–97].

*Paraphoma* is root-associated on *Populus*, although *P. chrysanthemicola* has so far been reported only from *Juniperus, Malus* and herbaceous plants [97,98]. The fungus can infect the leaves of certain plant species and provoke disease [99]. On poplar, it caused foliar blight [100]. The fungus can also live benignly in asymptomatic plant tissues, and has been detected or isolated from the roots of healthy plants [101].

*Phaeoisaria loranthacearum* has so far been reported from twigs of *Loranthus europaeus* in Germany [102].

*Phialophora* species, found very abundantly, may include *P. richardiae*, a serious pathogen implicated in the Petri disease of grapevine. The significance of other *Phialophora* spp. potentially occurring in the diseased poplar wood should also be emphasized. They are mostly saprotrophic and common in soil and wood, in which they cause soft rot. Growth at the hyphal tip and the secretion of lignolytic enzymes (pectinase, amylase, xylanase, cellulase and mannanase) causes widened cavities in sapwood and the degradation of the wood [103,104]. They can also cause cavities in the wood and plants via an erosion-type attack [105]. The degradation of *Populus tremuloides* wood has been known to affect sales of commercial aspen timber. The blue staining of wood by *Phialophora* has also been reported [106]. The fungus is psychrotolerant (able to grow at a low temperature).

Many of the taxa recorded, especially in the soil, may not be poplar-specific. They would originate from nearby vegetation, litter and decaying organic matter. Ascomycetous *Boeremia* spp., *Desmazerella acicola*, *Dissocionium eucalypti*, *Entyloma gaillardianum*, *Lambertella tubulosa*, *Leptosphaerulina australis*, *Microdochium* sp.,
Monographella nivalis, Neosetophoma clematidis, Periconia sp., Phacidium spp., Phaeosphaeria sp., Phaeospheriaeopsis sp., Phialocephala sp., Pyrenochaetopsis spp., Schizothecium glutinans, Xenochalara sp., Xenopolyscytalum spp., Xenorandumaria arxii, and basidiomycetous Aecidium sp., Entyloma spp. and Itersonilia perplexans possibly spread from weeds, grass roots, leaf litter and woody debris [107–121]. Neocatenulaostroma germanicum, recently found in Europe, seems to spread from pine needles or oak wood debris [49,122].

The cosmopolitan Cenococcum geophilum, one of the most frequently encountered ectomycorrhizal fungi in nature, is well recognized for its extremely wide host and habitat range [123].

Fungi of the genera Alternaria, Epicoccum, Fusarium, Cladosporium, Penicillium and Trichoderma are highly robust and ubiquitous, with an almost global distribution, occurring in the Americas, Asia, and Europe [103]. Their spores have been found in a variety of habitats, predominantly in soil of various types and in sand, often in extreme conditions. Epicoccum can grow on leaves submerged in water, even at 0 °C; hyphal growth can resume within an hour of exposure to water [104,124].

Some fungi were recorded for the first time on wood, or have been found rarely on wood. Ascomycetous Neocatenulaostroma germanicum is known from pine needles, and is known to cause needle blight on Pinus mugho Turra, P. nigra Arn. ssp. pallassiana and P. sylvestris L. in Lithuania, Poland and Ukraine [44,122], but has also occurred in the soil in Poland [125]. Sydowiella polypora is so far known from the foliage of Abies spp., Pinus spp. and Pseudotsuga menziesii (Mirb.), and litter [126]. Research suggests that some of these hosts can be primary inoculum sources when located near poplar plantations [127].

Some more- or less-frequent colonizers are untypical and dubious. Acaulium retardatum has so far been recorded from rice-field soil [128], Acrornium crateriforme from trap-liquid of pitcher plant Nepenthes khasiana Hook f. A.L.P.P. de Candolle, Prodr. in India [129], Alatospora has been recorded from aquatic habitats [130], Amnesia nigricolor has been recorded from an indoor habitat in India [131], Cercospora beticola from sugar beet leaves, Desmozierella acicola from pine needle litter [132,133], Dissoconium eucalypti from Eucalyptus leaf [134], Halokirschsteiniothelium maritima from decaying wood in Thailand [135], Nigrospora oryzae from tropical plants [136], Pleurophoma ossicola from bone [102], Pseudocercospora angolensis from leaf spot on Citrus in Africa [137], Sakaguchia lamellibrachiae (Nagah., Hamam., Nakase and Horikoshi) Wang, Bai, Groenew. and Boekhout from a deep-sea tubeworm in Japan [138], and the basidiomycetous yeast Erythrobasidium hasegawianum has been recorded from old beer yeast culture in USA [139].

Some can occur at the extreme of their host ranges. Graphium basitruncatum has been isolated from wood and soil, even in the Solomon Islands and Japan, and from a leukemic patient [140,141]. Scytalidium lignicola and Sporothrix are recognized as saprotrophic opportunists of which the lifestyle can change from plant to human or animal pathogenicity.

Oomycota with eight species of Globisporangium, two species of Phytophthora and eight species of Pythium were mostly in the soil, and were not very common. Their contribution to the development of the disease cannot be excluded. All of them are plant pathogens, which cause root rot and damping off in a multitude of species. Phytophthora plurivora Jung and Burgess, followed by P. pini Leonian., P. polonica Belbahri, E. Moralejo, Calmin and Oszako, P. lacustris Brasier, Cacciola, Nechw., Jung and Bakonyi, P. cactorum (Lebert and Cohn) Schrüt, and P. gonapodyides (Petersen) Buisman. were common in three declining and three healthy poplar plantations in Serbia [142].

4.3. Yeasts in Diseased Poplar Trunks

Yeasts are now identified and classified almost exclusively by DNA sequence analysis, which has resulted in the discovery of many new species and taxonomic revisions.
Filamentous fungi have a key role in the decomposition of plant material because of their ability to produce a wide range of extracellular enzymes that efficiently attack the recalcitrant lignocellulose matrix. However, the presence of yeasts during the different stages of wood breakdown highlights the ecological role of these microorganisms. Yeasts have been found to produce enzymes acting on cellulose, hemicelluloses and pectin [143]. They can therefore degrade plant material. They can also be transient fungi, using products released during decomposition by other organisms. Many yeast species found in live or decaying plant parts are associated with insects that also use these habitats as feeding or breeding sites.

The general opinion is that the most abundant yeast taxa associated with decayed wood are basidiomycetous (Agaricomycotina) and xylose-assimilating species. The present data do not support this thesis. Some ascomycetous yeasts were particularly abundant in the wood, where basidiomycetous yeasts were much less frequent.

Ascomycetous *Aureobasidium pullulans* and *Candida* spp., and basidiomycetous species of *Apiotrichum*, *Cystofilobasidium*, *Naganishia*, *Saitozyma*, *Solicoccozyma*, *Tausonia*, *Tremella*, *Trichosporon* and *Vishniacozyma* are frequently found in decaying plant material [143]. However, variations in their abundance and diversity reflect the environment, and also correlate with the natural abundance and distribution of basidiomycetous fungi in the study areas [144]. *Apiotrichum*, for example, was reported as being abundant in wood decayed by *Armillaria*. The abundance of ascomycetous yeasts in the wood resulted from the high frequency of *Nakazawaiella* spp., especially *N. populi*, which was previously found in exudates of *Populus* species [145].

### 4.4. Mycorrhiza-Forming Fungi

Mycorrhiza-forming fungi were rare, especially in the soil. Basidiomycetous species occurred, surprisingly, more often in the wood, probably as: (i) facultative biotrophic encounters that either formed mycorrhizal structures or colonized the tissues as endophytes (i.e., grew within living plant tissues, without apparent infection, but not forming true mycorrhizae or causing any disease symptoms), or (ii) saprotrophs. Transition from saprotrophy to mycorrhizal status is common in fungal development [146], and other unexpected trophic conversions within the mycobiota may be possible.

### 4.5. The Endophytic State/Habit/Lifestyle of Fungi

As with grapevine diseases, it is assumed that the causal fungi are endophytic, living for a time asymptomatically in the plant. Then, at some point, in association with plant stress, they modify their behaviour and become pathogenic, which leads to the expression of disease symptoms [147]. As endophytes, they would often have key positive roles in plant function and fitness [148,149]. As parasites, they are cryptic, often opportunistic pathogens, which in special conditions induce disease [150]. Their virulence may be dictated by multi-partner interactions and environmental conditions. The most favoured conditions include: (i) the presence of very vigorous plants with succulent tissues; (ii) prolonged periods of damp and wet weather; (iii) free-standing water on the leaves; (iv) injuries such as pruning and leaf wounds; (v) the presence of senescent tissues, especially older, lower leaves; (vi) frost damage; and (vii) excessive crowding. Tissues are invaded by enzyme action, and roots and stems are gradually enveloped until the vessels are eventually reached, and wilting and desiccation occur. Different lifestyles and functions may occur depending on the situation. *Phoma* may at first be a plant-growth-promoting fungus [151]. The lifestyles of *Phaeoisaria* and *Pyrenochaetopsis* depend on secreted peptidases [121,152]. *Plectosphaerella* (mostly *P. populi*) damages poplar stems [102,152], but simultaneously induces the formation of antifungal phenolic metabolites that protect poplar against foliar pathogens [153]. Some, such as *Pyrenochaeta*, are weak pathogens [154], but their adaptability to different climates allows them to infect many hosts and to survive in a broad range of pH, temperature and aeration conditions and soil types. Fungi such as *Ilyonectria* may survive
in the roots of apparently healthy (asymptomatic) poplars, where they may suppress other fungal root pathogens and help maintain tree health [27,30]. These examples show that caution is necessary in classifying fungi according to function. There is no indication that other species, uncommon on Populus or so far not detected, might be pathogenic.

4.6. Interactions among Fungi

*Trichoderma* spp. occurred at a high natural frequency in the plantation soil. They are well known for their antagonistic activity, hyperparasitism and ability to induce defensive systems in plants to other microorganisms (specifically soil microorganisms). They are used in the biological control of several pathogens. *Trichoderma harzianum* Rifai and *T. atroviride* Karst. have shown promise in controlling Botryosphaeria dieback and esca disease in vineyards and other common trunk diseases [155]. *Trichoderma* significantly improved grapevine root growth and decreased the incidence of fungi involved in diseases when tested *in vitro* or in nurseries [24,156]. Grapevine defence systems have also been induced by Oomycota. The necrosis of root systems of vine cuttings was reduced by 50% after colonization by *Pythium oligandrum* [157–159]. Other biological control agents (*Aureobasidium pullulans, Cladosporium herbarum, Fusarium lateritium* and *Rhodotorula rubra*) have been reported to be effective against grapevine trunk disease pathogens, alone or in combination with fungicides, although some were tested only *in vitro* or in nurseries [160]. Arbuscular mycorrhizal fungi have been shown to increase the tolerance of grapevine rootstocks to *Ilonectria* spp. [161]; *Glomus intraradices* was the most effective [162]. *Aureobasidium pullulans, P. oligandrum, Trichoderma* spp. and two species of Glomeromycota, present in the poplar plantation soil, may naturally decrease the incidence of pathogens involved in disease. *Mortierella elongata*, also detected, has been found to manipulate poplar defenses while promoting plant growth [30]. This response was particularly beneficial because it was independent of cultivars.

4.7. Soil and Planting Material as the Source of the Inoculum

The soil origin was shown to be a significant factor affecting the composition of the fungal communities and networks in *Populus* [149,163]. The soil was here shown to be a natural source of many vascular and parenchymal pathogens found in the affected hybrid poplars, i.e., species of ascomycetous *Alternaria, Cadophora, Cladosporium, Fusarium, Ilonectria, Nectria, Neocentra, Neopyrenochna Ophiostomataceae, Phoma, Pyrenochaeta, Sporothrix, Thelonecpta and Verticillium*, and of basidiomycetous *Armillaria* and *Entyloma*. Their presence in the soil has been associated with their occurrence on plant debris and plant roots [164]. Soil was also the main source of pathogenic Oomycota (*Aphanomyces, Elongisporangium, Globisporangium, Phytophthora* and *Pythium*), which can, generally, cause extensive and devastating root rot. The destruction of roots can lead to minor or severe wilting caused by impeded root functioning or further biotrophic infections that can become necrotrophic in response to infection pressure or environmental stress. Oomycota tend to be very generalistic and non-specific, with a wide range of susceptible host roots, including poplar [142]. The wilt results from root degradation by Oomycota and a lack of oxygen, followed by disrupted water transport. A moist habitat and low pH in forest soils favour the growth, propagation, and dispersal of Oomycota spores. At optimal temperatures (28–30 °C), some species of *Globisporangium* grow very fast, i.e., 2.7 cm in 24-h.

Fungi such as *Collophorina, Hyalodendriella* and *Hyaloscypha bicolor*, which occurred sporadically in the soil, whilst being biotrophic parasites, may contribute to the final wilt [165,166].

The planting material may, however, already have been infected, either systemically from infected mother poplars or by contamination during the propagation process.
4.8. Colonization

As in grapevine disease, poplar wilt may be a complex disease in which symptoms result from the concomitant action of several factors.

The initial stage of the disease seems to be accomplished by highly specialized vascular fungi in the plant’s phloem. Their presence in the soil suggests that the infection can be soil-borne. Hyphae from established mycelia, and germ tubes developing from spores, perceive signals from root exudates. The hyphae secrete cell-wall-degrading enzymes and enter roots through wounds, at branching points, or directly through root tips. The mycelium spreads between root cortex cells to reach phloem and xylem vessels, from which the fungus travels as conidia in the sap stream, mostly upwards. The phloem and xylem become obstructed by mycelium and spores, and by plant-produced gels, gums and tyloses. Water transport to the leaves fails, and the plant wilts and dies. The fungus then invades all of the plant tissues and obtains nutrition by decomposing them. The response to the degradation of hemicellulose or lignin by the pathogen is usually the accumulation of tylose, polysaccharides and phenolic compounds (gummosis), tannins and phytoalexins. It is likely that at least a part of the external and internal symptoms are caused by phytotoxic fungal metabolites produced in decayed wood, or by the oxidation of some host-response substances. Some chemicals produced in grapevine in response to fungal infection are toxic, notably α-glucans and two naphthalenone pentaketides, scytalone and isosclerone [22]. A similar situation may be expected in poplar.

The final stage of the disease is apparently accomplished by parenchymal fungi. The spores released from reproductive structures produced in dead wood in the presence of water are dispersed by wind, potentially infecting fresh new wounds. Among the parenchymal fungi, bracket fungi (Polyporales, Basidiomycota) were, surprisingly, found only sporadically; they usually dominate communities of wood-rotting organisms. In grapevine, the phytoalexin resveratrol showed a direct antifungal effect, inhibiting the in vitro growth of two bracket species, Fomitiporia mediterranea and Stereum hirsutum. It is possible that the accumulation of certain compounds produced by poplar suppresses the colonization of wood by bracket fungi.

4.9. Effects of Climate

Up to 133 fungal species of 34 genera have so far been associated with grapevine trunk diseases worldwide [127]. The incidence of particular taxa differs between regions. All known grapevine trunk pathogens have been encountered in all grape-cultivation regions, mainly between latitudes of 30° to 50°, where annual mean temperatures are generally 10–20 °C [127,167]. There are conflicting reports on the effects of temperature and water stress on the incidence of grapevine trunk disease [127]. Therefore, it is not possible to assume a straightforward relationship between poplar disease and climatic conditions, particularly concerning water stress. Water stress is likely, however, to increase susceptibility. In recent years, precipitation in central Europe has often been characterized by extreme events (fog, hailstorms, thunderhails, heat waves, heavy rains, floods, winds), followed by drought. Increased humidity favours disease development. Infection by ascospores or conidia released from perithecia or pycnidia embedded in the bark or wood will be promoted by high humidity, often associated with higher temperatures; such conditions encourage the release and spread of spores, and favour spore germination [168–171]. The inoculum potential is consequently increased.

An extremely hot and dry summer (particularly August and September) occurred across Poland in 2015. The climate projections for Poland and central Europe predict further warming and the continuation of the changes already observed, including decreased precipitation and drought, especially in summer [172]. Such conditions may be expected to affect the health of poplar and other trees.
4.10. Control and Mitigation

Fungicides such as sodium arsenite or 8-hydroxyquinoline, used against esca and with the potential to control the wilt of poplar, are banned in Europe. No other highly effective treatments are available. Other chemical products and biological stimulators used in vineyards are not curative, and so only preventive methods are available in poplar plantations. Infections in grapevine from propagating materials can increase from 40% before cuttings are taken up to 70% after nursery processing [172]. Detection prior to planting is therefore critical to assure the longevity of newly established plantations [173]. A healthy poplar at planting is fundamental to the establishment and sustainability of a plantation. Good hygiene and wound protection are of the utmost importance. The disinfection of propagating materials with fungicides or hot water treatment (50 °C for 30 min), applied correctly to avoid plant stress and death, is advisable. Where soil constitutes the main source of the inoculum, disease management practices based on soil disinfection and amendments, plant-based resistance to infection, and prophylactic cultural practices should be applied. Infected plant parts and infected dead wood on the soil should be removed, pruning wounds should be chemically protected, and the elimination of plant-stress factors should be taken into account.

5. Conclusions

1. *Populus* hybrids may be subjected to various, thus far unidentified pathogenic agents.
2. New diseases may be asymptomatic, at least in the initial phase.
3. The indigenous microbiota can be involved in the development of the disease, but can also have an important role in limiting or preventing the development of pathogens.
4. The development of new diseases is related to climate change. It can lead to the near-total disappearance of some diseases, the sudden emergence of a new pathogens, or to the fungi already present becoming pathogenic.
5. Poplar wilt symptoms may be a consequence of various factors, the most important being climate and its effects on fungal development and the host–pathogen relationship.
6. Fungal diseases can spread from the soil or from introduced plant material, with the latter potentially introducing them into new areas.

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