Phytophthora Species on Woody Plants

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The genus *Phytophthora*, with 326 species in 12 phylogenetic clades currently known, includes many economically important pathogens of woody plants. Different *Phytophthora* species often possess a hemibiotrophic or necrotrophic lifestyle, have either a broad or narrow host range, can cause a variety of disease symptoms (root rot, damping-off, bleeding stem cankers, or blight of foliage), and occur in different growing environments (nurseries, urban and agricultural areas, or forests).

Keywords: forest ; pathogens ; oomycetes ; tree diseases ; woody plants

1. Introduction

The genus *Phytophthora*, which includes fungus-like microorganisms, also known as water molds, belongs to the family Peronosporaceae and phylum Oomycota in the Stramenopila kingdom [1][2][3][4]. Initially, the classification of *Phytophthora* species was based on morphological characters (e.g., sporangia, homothallism, and configuration of antheridia), showing the presence of six groups [5]. However, homology and homoplasty among different *Phytophthora* species showed a high plasticity of the morphological features and their often inseparability [6][7][8][9]. Since the 2000s, the number of described *Phytophthora* species increased by over 180 species, which was primarily due to the use of novel molecular techniques, reaching a total of 326 species distributed in 12 phylogenetic clades [10]. Consequently, the taxonomy of the genus *Phytophthora* shifted from the morphology-based methods towards the development of molecular markers for multilocus phylogenies [11][12][13][14][15]. For example, phylogenies of *Phytophthora* species were constructed using an internal transcribed spacer (ITS) region [11], four nuclear and mitochondrial genes [16], or seven nuclear markers [17]. A more recent study advanced the *Phytophthora* phylogeny by including more than 180 species and by creating ancestral phylogeny reconstructions on the sporangial papillation [18]. These studies allow researchers to better understand the evolution of the genus *Phytophthora* and to link molecular phylogenies and individual morphological and physiological traits.

2. Characteristics of *Phytophthora* Species Detected on Woody Plants in Sweden and Other Nordic Countries

Phytophthora* × *alni Clade 7a

Key woody hosts: *Alnus alnobetula*, *A. glutinosa*, *A. cordata*, *A. incana*, *A. rubra*, *A. rubra* subs. *tenufolia*, *Castanea sativa.*

Symptoms: canker, collar rot, and dieback of alders

Aggressiveness: *Phytophthora* disease of alder is now widespread in Europe in the riparian ecosystems where alder commonly grows. In Europe, surveys and modeling show that the risk of infection is higher in warmer, slow-moving waters, and in fine-textured soils, especially clay loams. Although the disease is usually observed along river systems, it has been found in sites far from riverbanks or other water courses, e.g., in orchard shelter belts and in new woodland plantings. This suggests that alder trees were already infected prior to planting [3]. *P.* × *alni* is an aggressive pathogen as, e.g., inoculations of mycelia culture on one-year-old seedlings of *A. glutinosa* and *B. pendula* showed the development of lesions in 89% and 67% of seedlings, respectively [19].

Occurrence: In Sweden, the first report of the *P. alni* complex was from nurseries and alder-planted areas in the southwest in the 1990s [20]. In 2006 and 2010, it was discovered on *A. incana* at the Klarälven river in the city of Karlstad. A comprehensive study on the *Phytophthora alni* complex in Sweden was carried out between 2013 and 2018 to investigate the pathways of introduction and the spread of the two subspecies, *alni* and *uniformis* [21][22]. Both species were associated with *Phytophthora* bleeding cankers on 93% of declining *A. glutinosa* and some *A. incana* trees along the riverbanks, and within sampling plots connected to river swamps or ponds (**Figure 1**a) [21][22]. It was considered that both

P. alni subsp. *alni* and *P. alni* subsp. *uniformis* are invasive species that arrived in Sweden with plant material imported to forest nurseries, and that these species may further spread into natural ecosystems. *P. alni* subsp. *uniformis* was widespread throughout the country, whereas *P. alni* subsp. *alni* was only discovered in the southern and coastal part of Sweden [21][22]. *P. alni* subsp. *alni* is one of the most aggressive *Phytophthora* species [23], however, it is more sensitive to cold winters [24]. It was concluded that southern Sweden could be the northernmost distribution limit of *P.* × *alni*, however, there is a possible risk of its migration northwards due to climate change [22][25]. Due to the poor genetic potential of alder trees to resist *P alni* subsp. *alni*, alder decline is expected to increase in Sweden in the future [26]. In Finland, *P. alni* subsp. *uniformis* (identified as *Phytophthora* cf. *uniformis*) was found, for the first time, to cause dark stem lesions on *A. glutinosa* seedlings in 2015 [19]. In Denmark, *P. alni* subsp. *uniformis* (identified as *Phytophthora uniformis*) was isolated for the first time from symptomatic trees of *A. glutinosa* in 2016 [27].

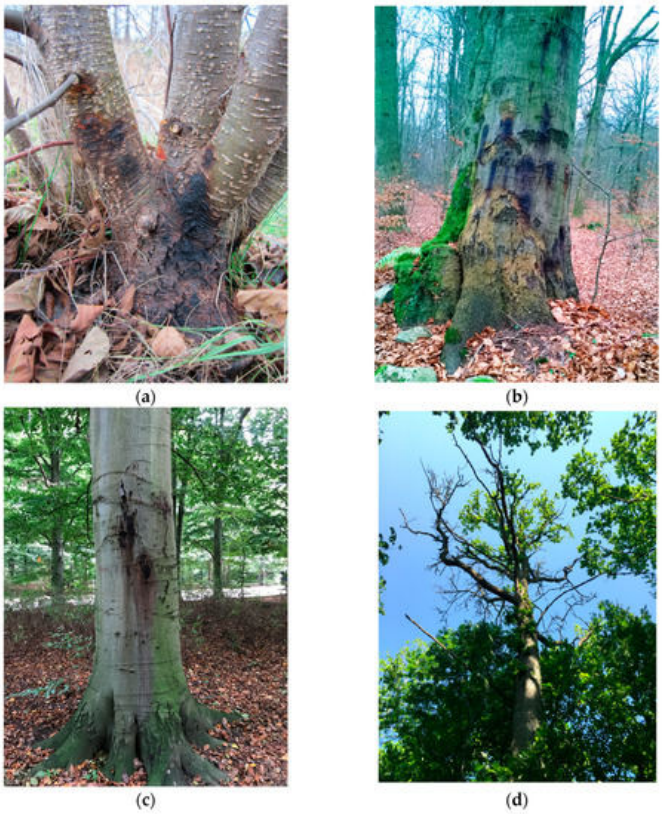

Figure 1. *Phytophthora* infected trees in Sweden: (**a**) *Phytophthora alni* lesions at the stem base of *Alnus glutinosa* (photo by Miguel Angel Redondo; retrieved from https://internt.slu.se/en/news-originals/2020/2/alders-lack-resistance-against-aggressive-type-of-pathogen/; accessed on 21 March 2023); (**b**) infected *Fagus sylvatica* with characteristic “bleeding” lesions on the stem in Kullaberg nature reserve (photo by Michelle Cleary); (**c**) infected *Fagus sylvatica* with “bleeding” lesions on the stem caused by *P. plurivora* and *P. gonapodyides* in Pildamms Park, Malmö city (photo by Mimmi Blomquist); (**d**) extensive crown dieback of *Quesrcus robur* in Visingrö oak forest caused by *P. plurivora* root rot infection (photo by Michelle Cleary).

Phytophthora cactorum Clade 1a

Key woody hosts: *Abies* sp., *Acer* sp., *Aesculus hippocastanum*, *Fagus sylvatica*, *Juglans regia*, *Fraxinus excelsior*, *Malus domestica*, *Populus alba*, *Quercus* sp., *Rhododendron* sp. (however, in total, at least 154 genera of vascular plants in 54 families are affected).

Symptoms: root, collar, and crown rot on many species; brown-reddish stem lesions; slow decline or rapid dieback, depending on age and location of infections; root rot of nursery plants. For example, on woody plants, such as *Malus domestica*, *P. cactorum* is causing crown and root rot; on *Betula* spp., it causes stem lesions; and on rhododendron, it causes root rot and dieback symptoms [28].

Aggressiveness: *P. cactorum* is unequivocally a serious pathogen of a wide range of plant species. Despite its broad geographic distribution and host range, *P. cactorum* has similar symptomatology with other species of *Phytophthora.* Therefore, it is difficult to ascribe specific damage to *P. cactorum* and evaluate the extent of its damage to forest trees. There are several reports of noticeable “outbreaks” on *Fagus* and *Betula* [29], however, it appears that there is a considerable host specificity among strains of this pathogen. Swedish isolates of *P. cactorum* together with *P. cambivora* and *P. plurivora* were used for inoculation of common conifer and broadleaf tree species in Sweden (*Pinus sylvestris*,

Picea abies, *Larix* × *eurolepis*, *Betula pendula*, *Quercus robur*, *Fagus sylvatica*, *Populus trichocarpa*, and *Tilia cordata*) to determine their relative susceptibility to root pathogens [30]. All the tested *Phytophthora* species caused stem lesions of varying lengths on different host trees, except for species in the Pinaceae family, which had low susceptibility to the tested *Phytophthora* spp. Two-year-old bare-root seedlings of *B. pendula*, *Q. robur*, *F. sylvatica*, and *P. sylvestris* appeared to be susceptible to *P. cactorum* infection [30]. Inoculation trials in Finland using a Danish isolate, which was isolated from *B. pendula* in 2009, revealed that *P. cactorum* caused relatively small lesions on *Rhododendron* sp. and *P. abies*, moderate lesions on *B. pendula*, and no infections on *Q. robur* or *P. sylvestris* [31]. In an in vitro study using two-month-old *B. pendula*, roots inoculated with *P. cactorum* often showed dark discolorations, loss of fine roots, and decreased branching [32], even though discolorations are not a specific symptom of *Phytophthora* infections [33]. The symptoms of the aboveground parts included reduced height growth, lower chlorophyll fluorescence, significantly longer dark or brown discolorations in the stems, and a higher proportion of brownish and wilting leaves [32]. Furthermore, inoculation trials on three-month-old *B. pendula* and *A. glutinosa* seedlings showed that *P. cactorum* was able to kill 40% of the *B. pendula* seedlings, but caused only small lesions on 40% of *A. glutinosa* seedlings [34]. However, in the inoculation trials, *P. cactorum* was found to cause low-to-moderate symptoms on *Rhododendron* sp. and *P. abies*, and no symptoms on *P. sylvestris* [31]. *P. cactorum* was also able to cause lesions on non-wounded *B. pendula* seedlings [35]. In stem inoculation trials, Orlikowski et al. [36] showed that *A. glutinosa*, *B. pendula*, and *Prunus padus* were highly susceptible to *P. cactorum*. *Acer saccharinum*, *Corylus avellana*, *Q. robur*, *Rubus caesius*, *Sorbus aucuparia*, and *Tilia cordata* were moderately susceptible, while *Sambucus nigra* and *Sorbus aucuparia* were not susceptible. Interestingly, *P. cactorum* can be detected in *B. pendula* seven years after outplanting, however, at this stage, the effect of stem lesions on seedling mortality or on the number of leader shoots is limited [37]. Bunyaviruses were shown to significantly reduce hyphal growth and the production of sporangia and their size, but not the pathogenicity of *P. cactorum* [38].

Occurrence: In Sweden, *P. cactorum* was first recognized as one of the root parasites causing damping-off disease in forest nurseries in 1961 [39]. Since the beginning of the 1990s, the oak population has been declining in Sweden [40], and in 2003, *P. cactorum* was found to be associated with oak decline in southern Sweden [41]. Later, *P. cactorum* was isolated from the diseased *F. sylvatica* in the city of Malmö and Stora Köpinge municipality in 2016 [42]. Recently, *P. cactorum* was detected on *F. sylvatica* and *Q. robur* in forest nurseries (close to the rivers Säveån, Kävlingeå, and Ätran) (composing 26.3% of all detected *Phytophthora* spp.), in urban *F. sylvatica* forests (near the river Lagan) (15%), and in natural forests affecting *F. sylvatica* (near the river Ronnebyån), *A. alba*, and *P. abies* (near the river Ätran) (30%) [43]. In Finland, *P. cactorum* was found for the first time in necrotic stem lesions of *B. pendula* seedlings in forest nurseries in 1991 [33] and in stem lesions of *A. glutinosa* seedlings in 1995 [34]. It was also detected on symptomatic *Rhododendron* sp. seedlings during surveys that were carried out between 2004 and 2010 [31]. Irrigation water used in Finnish forest nurseries was shown to be the possible source of *P. cactorum* inoculum [44]. The Finnish isolates of *P. cactorum* were shown to have a 17.5 °C optimal growth temperature [45], i.e., much lower than the 25−30 °C reported in other studies [46][47], and that these isolates survived −5 °C temperatures on agar medium for up to 14 days [45]. The observations above suggest that Nordic isolates of *P. cactorum* can be better adapted to local conditions and, in the future, may pose a threat to *B. pendula* seedlings in forest nurseries and reforestations.

Phytophthora cambivora Clade 7a

Key woody hosts: *Abies alba*, *Acer platanoides*, *Aesculus hippocastanum*, *Alnus glutinosa*, *Castanea denatata*, *C. crenata*, *C. sativa*, *Fagus sylvatica*, *Quesrcus robur*, *Taxus brevifolia*, *Platanus orientalis*, *Juglans regia*, *Malus domestica*, *Rhododendron* sp., *Pieris* sp., *Prunus* sp., *Ulmus* sp.

Symptoms: canker, collar and root rot, bleeding cankers

Aggressiveness: *P. cambivora* is an invasive pathogen that survives and spreads in different environments. Its ability to survive as a saprotroph in the soil and to produce oospores (resting structures) increases its invasiveness. It was described as a causal agent of ink disease on chestnut trees [48][49][50]. The infection causes root destruction, which leads to leaf chlorosis and wilting in the canopies. Depending on environmental conditions, the disease may lead to a quick or to a progressive dieback of infected trees [48][51]. Inoculation tests on *Abies* seedlings also showed the ability of *P. cambivora* to infect and cause characteristic canker symptoms [52].

Occurrence: In Sweden, the first detection of *P. cambivora* was in association with oak health deterioration [41]. It was found together with *P. cactorum* in soil samples in one of ten surveyed forest stands. Later, *P. cambivora* was detected in soil samples collected near *F. sylvatica* trees with bleeding stem cankers in Bokskogen near the city of Malmö (**Figure 1**b) [42]. Nowadays, *P. cambivora* is present in nurseries, urban areas, and natural forests, and is mainly associated with *F. sylvatica* decline and bleeding cankers on the stems [43]. Inoculation of the stems showed that the Swedish isolate of *P.*

cambivora is highly pathogenic to *F. sylvatica*, *B. pendula*, *Tilia cordata*, *Q. robur*, and *Populus trichocarpa. P. trichocorpa* is a non-native tree species in Sweden but it is important for biomass production. Therefore, the establishment of new *P. trichocarpa* plantations for energy should take place using clones more tolerant to *Phytophthora* infections [30]. In Norway, *P. cambivora* was detected for the first time on a 15-year-old *Abies procera* in 2004 [52]. The symptoms included cankers on the stems up to 1.5 m above the ground and dieback of the basal branches. There were 25% of trees that were already dead or dying. Infections of *P. cambivora* on *F. sylvatica* were observed for the first time in 2011, resulting in bleeding cankers [53]. The infected trees were in the areas of Larvik and Ås, which represent the northern limit of *F. sylvatica* distribution, showing that a northern location is not a limiting factor for the spread and infection by *P. cambivora*. The infected trees had a circumference between 40 and 310 cm, and the majority of the cankers were at the height of 0.1−2 m above the ground. Additional symptoms included crown dieback, chlorotic foliage, epicormic shoots, and cracked bark. The infection frequency in some areas around Larvik was up to 4.9% in 2012, but it was up to 9.2% in Ås in 2014 [53]. In addition to *P. cambivora*, *P. plurivora* and *P. gonapodyides* were detected in the water near the diseased trees in Larvik, and both species proved to be pathogenic on *F. sylvativa*. Today, *P. cambivora* can be considered an established species in different environments. To limit its spread, monitoring should take place in nurseries and on seedlings used for outplanting [54].

Phytophthora cinnamomi Clade 7a

Key woody hosts: *Abies* sp., *Castanea sativa*, *Quercus* sp., *Chamaecyparis lawsoniana* (266 genera in 90 families; commonly hardwood trees, including more than 1000 species [55]).

Symptoms: root rot, heart rot, wilt; causes ink disease of chestnut in conjunction with *Phytophthora cambivora.*

Aggressiveness: It is currently the most important *Phytophthora* pathogen of forest trees, and it is also destructive to woody ornamentals, especially rhododendrons and other Ericaceae, and orchard crops, including avocado. It is now widespread, owing to the international trade of plants, and continues to be destructive in the forests of Australia, Mediterranean countries, Mexico, and the SE United States, and is of increasing concern in the forests and wildlands of western North America. With the changing climate, *P. cinnamomi* is expected to expand its range and cause more damage, particularly in Europe and North America.

Occurrence: In Sweden, *P. cinnamomi* was detected in the rhizosphere soil of *Rhododendron luteum* ‘Whitethroat’ and *Stewartia pseudocamellia* growing in the same nursery, thereby representing the first record of this pathogen in a commercial stock of ornamental plants in the country [56].

Phytophthora citrophthora Clade 2a

Key woody hosts: *Citrus* sp., *Aesculus hippocastanum*, *Buxus* sp., *Castanea sativa*, *Chamaecyparis lawsoniana*, *Juglans regia*, *Rhododendron* sp. (in total, 88 genera in 51 families).

Symptoms: root rot, stem necrosis, canker, fruit rot, twig blight, seedling blight

Aggressiveness: *P. citrophthora* causes brown rot disease of citrus and is an economically important pathogen of citrus crops. It can also cause a dieback of rhododendron and other ornamental plants.

Occurrence: In Sweden, *P. citrophthora* was found in a nursery of *Rhododendron catawbiense* in 2018 [43]. In Norway, it was detected on *Chamaecyparis lawsoniana* [57].

Phytophthora cryptogea Clade 8a

Key woody hosts: *Abies concolor*, *A. fraseri*, *A. procera*, *Chamaecyparis* sp., *Cupressus* sp., *Juglans regia*, *Malus domestica*, *Pinus mugo*, *P. nigra*, *P. contorta*, *Pseudotsuga menziesii*, *Rhododendron catawbiense*, *R. maximum* (in total, 141 genera in 49 families).

Symptoms: damping-off, foot rot, stem rot, leaf rot, wilt.

Aggressiveness: *P. cryptogea* is primarily a soil-borne plant pathogen in the temperate regions, but it also exists in nature (fresh water) as a saprotroph. It is most active at temperatures between 10 °C and 20 °C [55]. It is a serious plant pathogen in many countries, causing great damage to ornamentals produced in nurseries, greenhouses, and hydroponics. *P. cryptogea* is an aggressive soil-borne pathogen of fir species, which are produced as Christmas trees [58] [59].

Occurrence: In Sweden, *P. cryptogea* was detected in soil samples associated with symptomatic *F. sylvatica* trees in a nursery (near the river Ätran) and in an urban forest (near the river Alsterån) [43]. It was also found in soil samples in Christmas tree plantations and, together with *P. megasperma*, demonstrated a high aggressiveness to *P. abies* and *A. nordmanniana* trees [60].

Phytophthora gonapodyides Clade 6b

Key woody hosts: *Chamaecyparis lawsoniana*, *Corylus avellana*, *Fagus sylvatica*, *Juglans regia*, *Malus domestica*, *Quercus* sp., *Rhododendron* sp.

Symptoms: stem bleeding cankers, root rot

Aggressiveness: *P. gonapodyides* is considered as a weak parasite with saprophytic abilities usually associated with aquatic environments, such as rivers, riparian areas, and wetlands [55]. However, some isolates of *P. gonapodyides* can be highly virulent [36][61]. Their aggressiveness appears to be stimulated by prolonged root flooding and cool soil conditions. *P. gonapodyides* can hinder seed germination and cause root rot and stem lesions in *Q. robur* and *Q. ilex* [62][63].

Occurrence: In Sweden, the first report of *P. gonapodyides* was in 2016, when the pathogen was isolated from characteristic bleeding cankers on *F. sylvatica* trees growing in Pildamms Park in the city of Malmö (**Figure 1**c) [64]. It was suggested that recent changes in local climatic conditions, such as high summer precipitation coupled with mild winter temperatures, could favor the multicyclic spread of *P. gonapodyides* via zoospores and/or that the increased average age of *F. sylvatica* stands contributed to their higher susceptibility [64]. *P. gonapodyides* was also reported in a nursery (Lagan area) in association with *F. sylvatica* seedlings [43]. In Denmark, *P. gonapodyides* was recovered from rainwater ponding in an old declining *F. excelsior* stand [36].

Phytophthora inundata Clade 6a

Key woody hosts: *Aesculus hippocastanum*, *Olea* sp., *Salix* sp., *Vitis* sp.

Symptoms: root and collar rot of trees or shrubs in wet or flooded areas

Aggressiveness: *P. inundata* is responsible for wilting and the root rot of olive trees [65]. It can also act as an opportunistic, albeit aggressive root pathogen. On *A. nordmanniana*, it caused poorly developed roots and brown to reddish discoloration under the bark at the stem base and downwards. The foliage exhibited drought symptoms, with leaves that were pale green, yellow, or brown [57].

Occurrence: There are no reports from Sweden. In Norway, *P. inundata* and *P. megasperma* were reported from Christmas tree plantations of *A. nordmanniana* and *A. lasiocarpa* in 2004, respectively [57]. Approx. 70% of *A. nordmanniana* and 25% of *A. lasiocarpa* were symptomatic. As the site was grassland for decades with no history of Christmas tree cultivation, it was suggested that the disease followed imported transplants [57].

Phytophthora megasperma Clade 6b

Key woody hosts: *Aesculus hippocastanum*, *Castanea sativa*, *Juglans regia*, *Prunus domestica*, *Pseudotsuga menziesii*, *Sorbus aucuparia*

Symptoms: root rot, crown rot, storage rot, seedling damping-off, fruit rot, foot rot, stem canker, tuber rot, collar rot, sudden wilt, apoplexy, stunting, chlorosis. The symptoms of *P. megasperma* on *A. lasiocarpa* were pale yellow foliage and girdling at the stem bases [57].

Aggressiveness: It is primarily a root-rotting organism, causing the most serious losses on fruit and broadleaf trees. It appears to be restricted to more temperate regions of the world, however, its oospores can survive for up to 5 years, either free in the soil or in host tissue [66]. Prolonged wet conditions and heavy clay soils and soil impaction layers, which allow the maintenance of high soil water content, are often needed for the development of disease epidemics by *P. megasperma* [67].

Occurrence: In Sweden, *P. megasperma* was isolated from roots of a symptomatic *P. abies* seedling [60]. In Norway, *P. megasperma* was reported in association with *A. lasiocarpa* [57]. Both species *P. cryptogea* and *P. megasperma* may become problematic for Christmas tree and bough production, especially in saturated soils, which favor disease development.

Phytophthora pini Clade 2c

Key woody hosts: Pinaceae

Symptoms: root rot, canker

Aggressiveness: There is only limited information about this species. It can cause root rot and rapid mortality of olive trees [68]. Inoculations of *P. abies* seedlings using both wound-mycelia and zoospore suspension showed that after seven days, *P. pini* caused 100% disease incidence and a high frequency of severe symptoms [45].

Occurrence: In Sweden, *P. pini* was reported in commercial nurseries (near rivers of Säveån and Mölndalsån) in association with *R. catawbiense* [43]. In Finland, it was also detected on *Rhododendron* sp. [31].

Phytophthora plurivora Clade 2c

Key woody hosts: *Acer platanoides*, *Aesculus hippocastanum*, *Alnus glutinosa*, *Fraxinus excelsior*, *Quercus robur*, *Quercus petrea*, *Tilia cordata*, *Fagus sylvatica*, *Rhododendron* sp.

Symptoms: stem cankers, collar and root rot, dieback. *P. plurivora* can cause wilting and discoloration of current year shoots (on *P. abies* seedlings), bark necroses, fine root losses, and dieback on at least 45 woody host species [31][45].

Aggressiveness: *P. plurivora* is a highly aggressive plant pathogen, which has a worldwide distribution and a high diversity of hosts. *P. plurivora* is a hemibiotrophic organism that possesses the ability to infect living tissues and to continue its life cycle on dead tissues. In inoculation trials, *P. plurivora* was able to cause relatively large lesions or, in many cases, stem girdling on *Rhododendron* sp., *B. pendula*, *A. incana*, *A. glutinosa*, and *P. abies*, showing a high virulence on several woody plants and especially on *P. abies* as compared to other *Phytophthora* spp. tested [31]. The disease incidence on *P. abies* was also shown to be dependent on a particular isolate and inoculation method, as there were 83.3−100% disease incidence using wound inoculation with living mycelia and 0−77.8% using zoospores [45]. In *P. abies* shoot tissues, *P. plurivora* can grow both inter- and intracellularly, which is largely in the vascular tissues [45]. *Pinus sylvestris* and *Q. robur* showed no symptoms after four weeks of *P. plurivora* inoculation [31][69]; however, in other studies, this pathogen caused extensive bark lesions on *Q. robur* after a longer time [70]. In stem inoculation trials, Orlikowski et al. [36] showed that *A. saccharinum*, *A. glutinosa*, *B. pendula*, *C. avellana*, *P. padus*, *R. caesius*, and *S. nigra* were highly susceptible to *P. plurivora*, while *Q. robur*, *S. aucuparia*, and *T. cordata* were moderately susceptible. In addition to stem inoculations, soil infestation trials may also be needed to examine the susceptibility of fine roots of different tree species to *P. plurivora* and other *Phytophthora* spp. [31].

Occurrence: In Sweden, the earliest report of *P. plurivora* was from alder trees in Asslebyn (Bengtsfors locality) in Sept 2012 [43], even though the species was likely found during surveys near the city of Nyköping [21]. In 2016, *P. plurivora* was detected in soil samples and bleeding stem lesions of *F. sylvatica* in the city of Malmö (**Figure 1**c) [42]. It is one of the most abundantly detected *Phytophthora* species in natural forests and urban areas with declining and symptomatic *F. sylvatica* and *Q. robur* trees (**Figure 1**d) [43]. *P. plurivora* was also found to be highly virulent on *F. sylvatica* and *Q. robur* seedlings, causing large lesions, thus, it should be considered as a high-risk species to Swedish forests with a potential to severely destabilize the broadleaf forest ecosystems [64]. *P. plurivora* was also reported from Denmark and Norway as a disease agent of several deciduous tree species [27][71][72]. In Norway, *P. plurivora* was reported on *F. sylvatica* in a park in Oslo and in Ålesund [53]. Interestingly, the infection process for some *F. sylvatica* trees was rather fast and took only two years before the tree was dead. In Finland, surveys in 2005 on symptomatic *Rhododendron* sp. resulted in the detection of *P. plurivora* (originally identified as *P. inflata*) [31][69].

Phytophthora pseudosyringae Clade 3a

Key woody hosts: *Quercus* spp., *Fagus sylvatica*, *Alnus glutinosa*, *Carpinus betulus*

Symptoms: root and collar rot, stem bleeding cankers

Aggressiveness: It is an aggressive pathogen on several broadleaf tree species.

Occurrence: In Sweden, *P. pseudosyringae* was reported causing basal cankers and dieback on horse chestnut in June 2014 in Sankt Jörgens Park in the city of Gothenburg [73].

Phytophthora quercina Clade 3b

Key woody hosts: *Quercus* spp.

Symptoms: rot of fine roots, overall oak decline

Aggressiveness: *P. quercina* is often associated with other *Phytophthora* spp. [40], shows adaptation to different site conditions and soil pH, and has a high host specificity i.e., a high aggressiveness to different oak species [46][63]. *P. quercina* is also well-adapted to temporary dry conditions, possibly due to its particularly thick oospore walls [46]. Oaks with *P. quercina* or other *Phytophthora* spp. in their rhizosphere have ca. 50% higher probability of exhibiting severe aboveground disease symptoms than oaks without *Phytophthora* spp. [74]. Jönsson et al. [75] showed that Swedish isolates of *P. quercina* had the capacity to induce fine-root dieback of *Q. robur* seedlings growing in acid, N-rich but otherwise nutrient-poor forest soils (dominant in Sweden), as well as in high pH, nutrient-rich soils under the mesic water regime. Their aggressiveness, together with a high infection rate (all the seedlings were infected) showed a potential capacity of *P. quercina* to infect plants in acid forest soils [75]. In addition, the stress-induced susceptibility of the seedlings and/or increased aggressiveness of the pathogen in the forest soil could be factors accounting for differences of root dieback between soil types [75].

Occurrence: The decline of European oaks mainly occurs in trees older than 100 years, and in this process, trees may survive for a long time. It is only under exceptional circumstances that oaks may die in large areas [63][76]. A similar decline of oaks (in particular, *Q. robur*) has occurred in Sweden during the recent decades [40]. The reason for this loss was unclear until the three different *Phytophthora* species were recovered from 11 out of 32 oak stands in the southernmost part of the country, with *P. quercina* being the most frequent species [41]. However, a weak association was found between the occurrence of *P. quercina* and the vitality of mature oak stands [77]. Thus, the decline of oaks in southern Sweden can probably be attributed to several different site-specific factors, such as infection by *P. quercina* or unusual weather events, which interact with a number of biotic and abiotic factors, leading to oak decline [78]. Later, Jönsson-Belyazio and Rosengren [79] summarized that *P. quercina* contributes to oak decline in southern Sweden. A conceptual model for the development of *Phytophthora* disease in *Q. robur* suggested that the link between the root damage caused by *Phytophthora* species and overall tree vitality is in the assimilation and allocation of carbon within the plants [80]. More recently, *P. quercina* was also found in both urban (Mölndalsån area) and natural forests (Säveån and Lyckebyån areas), but not in forest nurseries [43].

Phytophthora ramorum Clade 8c

Key woody hosts: *Abies* sp., *Aesculus hippocastanum*, *Alnus* sp., *Betula pendula*, *Fagus sylvatica*, *Fraxinus excelsior*, *Larix kaempferi*, *Notholithocarpus densiflorus*, *Pseudotsuga menziesii*, *Quercus* sp., *Rhododendron ponticum*, *Rhododendron* sp.

Symptoms: lethal stem cankers, shoot dieback, foliage blight

Aggressiveness: *P. ramorum* is one of the most aggressive *Phytophthora* species. It is considered a highly invasive species due to its ability to spread, persist, and reproduce in new environments. The pathogen can infect plants in nurseries situated in close proximity to streams, later causing significant outbreaks on outplanted ornamentals. Spread events appear to be associated with either the movement of infected plant parts, normally from large wild infestations, or the introduction of infected plants, normally from infested ornamental nursery stock [81]. Infected nursery plants, such as *Rhododendron*, *Camellia*, and *Viburnum*, often contribute to long distance dispersal of the pathogen. Inoculation trials on stems showed that in addition to *Rhododendron* sp., *P. ramorum* caused necrotic lesions on *A. glutinosa*, *A. incana*, and *B. pendula*, while *P. sylvestris* and *P. abies* showed no disease symptoms [31][69], even though the pathogen might be able to infect individual *P. abies* needles [82]. Inoculation trials suggest that the damage can be substantial, as used isolates of *P. ramorum* were able to cause stem lesions in over 80% of *B. pendula* and over 30% of *A. glutinosa* seedlings [31].

Occurrence: In Sweden, the first report of *P. ramorum* was in 2002, which was found on 11 plants of *Rhododendron* sp. [83]. In 2017, it was detected on two plants of *Rhododendron yakushimanum* in a nursery in the municipality of Skurup. In 2018, *P. ramorum* was detected on four *Rhododendron* plants in a private garden in the municipality of Klippan. In Finland, *P. ramorum* was detected for the first time in 2004 [69]. It was found on marketed plants of *Rhododendron* spp., which were imported from other EU member states. The same year, *P. ramorum* was also discovered on *Rhododendron* sp. in a Finnish nursery, and detection was also successful in the following years, i.e., 2004−2010, except 2007, showing the persistent establishment of this pathogen despite the annual sanitation measures [31]. In Norway, *P. ramorum* was reported for the first time in 2002 [84]. It was isolated from symptomatic *R. catawbiense* in a nursery in Bergen. In the following years, the number of locations with *P. ramorum* has gradually increased (in 2004, there were 29 new locations, and in 2005, there were 43 locations), showing a broader distribution and/or rapid spread within the country. Apart from

rhododendron, *P. ramorum* was also detected on *Pieris japonica* and *Viburnum fragrans*, and the latter was heavily infected. *P. ramorum* was most likely imported to Norway with symptomless plants and/or with plants that had mild symptoms, which are difficult to detect using random controls [84].

Phytophthora rosacearum Clade 6a

Key woody hosts: *Malus domestica*, *Prunus* spp. (Rosaceae)

Symptoms: pathogenic

Aggressiveness: Not clear

Occurrence: In Sweden, *P. rosacearum* was reported in commercial nurseries (near Kävlingeå) in association with *Prunus laurocerasus* [43].

Phytophthora syringae Clade 8d

Key woody hosts: *Aesculus hippocastanum*, *Fagus sylvatica*, *Camelia* sp., *Rhododendron* sp., *Prunus* sp. (29 genera in 14 families, including *Syringa vulgaris* (Oleaceae) and Rosaceae).

Symptoms: twig blight, fruit rot, root and collar rot, stem canker, wilt, leaf spot, and shoot dieback of lilac

Aggressiveness: *P. syringae* is known to infect nursery plants, particularly apple and pear trees. It infects plants through wounded areas and is most pathogenic during cold and wet weather conditions.

Occurrence: In Sweden, *P. syringae* was found in the soil in the vicinity of horse chestnut growing in Pildamms Park in the city of Malmö [42]. It was also detected in a nursery (near Kävlingeå) and in urban forests (near the Nyköpingsån river) in association with *R. catawbiense* [43].

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