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Review

Ash Dieback in Forests and Rural Areas—History and Predictions

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Abstract: Ash trees are an important component of both forests and the countryside. Emerging new diseases like ash dieback poses new challenges to *Fraxinus* spp., which not only have to adapt to global warming but also defend themselves against new threats from pathogenic fungi and insect pests. A new species of fungus, *Hymenoscyphus fraxineus*, has arrived in Europe from Asia and has severely damaged shoots which alters the structure of ash tree crowns. While some older trees have survived, younger trees are dying en masse, so the only hope is that the surviving trees will produce a younger generation that may be more resistant to the new diseases. The fine roots of ash trees are also attacked by pathogenic oomycetes, and others by *Armillaria* spp. The current stressed condition of ash trees in Europe is exacerbated by a new threat from insects. *Agrillus planipennis*, emerald ash borer, migrating from the east (from near Moscow airport) towards the borders of the European Union, killing thousands of ash trees on its way. This raises the question of future prospects for ash cultivation in Europe. This article takes a closer look at the information described in the literature.

Keywords: *Fraxinus* spp.; biological threat; *Hymenoscyphus fraxineus*; *Agrillus planipennis*; climate change threatening growing conditions

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1. Introduction

This article deals with a current problem in Europe, namely the phenomenon of the decline of *Fraxinus excelsior* and *F. angustifolia*. The last species is an important forest tree species in Italy, Slovenia, Hungary, Croatia, Serbia, etc. The first symptoms of increasing common ash dieback were observed in 1992 in north-eastern Poland [1–4]. Ash disease spread throughout the country and soon ceased to be a local phenomenon. The forest area in Poland at the end of 2006 (according to the Forest Condition Report) was 28.9% = 9,026,000 ha, and according to the IBL survey an area of 10,800 ha was affected by ash dieback at that time, i.e., in relation to the total national forest area it was only 0.12%, although the disease occurred in all age classes nationwide [5]. By 2008, the ash dieback phenomenon covered an area of 17,000 ha, and in 2016 it covered only 3200 ha. The decreasing disease incidence did not mean that the health status of this tree species has improved, but is rather the result of changes in the species composition of the stands, in which ash has lost the function of the dominant tree species [6].

In Western Europe, the phenomenon of ash dieback has intensified over the last two decades, and is now found in Lithuania [7], Latvia [8], Estonia, Sweden, Denmark [9], Finland, Norway [10,11], Germany [12], the Czech Republic [13], Slovakia, Austria [14,15], Switzerland [14], France, Hungary [16], Serbia, Romania, Slovenia [17], Italy [18], Poland [19], Belarus [20], and other countries [21,22].

The disease affects both seedlings grown in nurseries and older ash trees growing in plantations (including coppice stands), but it seems to be most dangerous for trees in the young stage [23–26]. Experience from Ukraine showed higher mortality in younger trees under 15 years old [23]. Tree dieback is observed in commercial forests at all age classes (young and mature trees), but is particularly intense in young stands established from artificial regeneration. Seedlings in nurseries also die, as well as urban ash trees. The disease is very much widespread in typical ash habitats. Particularly worrying, ash dieback have been recorded in countries such as Sweden, Austria and Lithuania [3,27,28].

During the examinations of the branches and trunks of the diseased ash trees, especially necrotic tissues, the presence of various fungal species was observed, but for most of them, a direct connection with ash dieback could not be confirmed [1,4,29–32]. Previous research first identified the main cause of ash dieback as the fungus *Chalara fraxinea* [30]. This was a fundamental step that provided the basis for further research aimed to better understand ash dieback. The pathogen, *C. fraxinea*, was then recognised as an anamorph and this cause of ash dieback became known as *Hymenoscyphus fraxineus* in May 2014 (T. Kowalski) [33].

Molecular studies have shown that the pathogen was introduced from East Asia, where it occurs on Manchurian ash *Fraxinus mandshurica* Rupr. [34]. The fungus *H. fraxineus* was detected in forest nurseries in Austria, leading to the conclusion that the disease spreads with infected planting material [35]. *Hymenoscyphus fraxineus* has been confirmed in most European countries and strongly pathogenic properties have been found [10,12,13,19,22,27,32].

Common ash *F. excelsior* is a species with demanding soil requirements, needing fertile, moist sites with neutral pH [36]. For many years, common ash was considered a species resistant to diseases, including pathogenic oomycetes of the genus *Phytophthora* [37]. In 2011, studies were carried out in older dying ash stands in Poland and Denmark, which shed new light on the process of tree death [38]. They confirmed the presence of pathogenic oomycetes in the rhizosphere of ash roots. This experience and the discovery of seedlings infected with new organisms of the genus *Phytophthora* in nurseries [39] were an incentive to investigate their role in the process of tree death. The studies conducted so far have not provided sufficient data on the occurrence of *Phytophthora* spp. in ash stands. There is also a lack of information on the effects of extreme weather events, such as excess water (leading to local flooding of forest stands) combined with infections by shoot and root pathogens.

2. Common and Narrow-Leaved Ash General Characteristics and Value

Fraxinus angustifolia is a second most abundant ash species in Europe, and also severely affected by ash dieback. In some European countries, the narrow-leaved ash is the main ash species with a high economical and ecological value, and there are a lot of research available on this topic.

Fraxinus excelsior covers western, central and southern Europe from the coasts of the Atlantic Ocean in the west to the Volga region in the east (Figure 1). Common ash is absent from northern and central Scandinavia, a large part of the Iberian Peninsula, Corsica, Sardinia, Sicily and the southern tip of the Apennine Peninsula, as well as the Peloponnese and Crete. In Asia, common ash occurs only in small areas in the southwestern part of the continent [40].

In Poland, common ash does not grow higher than 1000 m above sea level, as it is very sensitive to frost. At higher altitudes, it is found in the southern and south-eastern part of its range, i.e., in the Alps up to an altitude of 1630 m and in Iran even up to an altitude of 2200 m above sea level [41].

Due to the wide range of its natural occurrence, common ash colonizes areas with different soil conditions. Forest stands with a significant proportion of this species occur in the most fertile habitats, but are also found in drier and calcareous habitats. Fertile, moist, humus-rich soils are best suited [41,42]. It prefers deep soils, preferably near watercourses, with a high water table [36,43,44] and it grows well on permeable and alkaline soils [9]. Despite demanding habitat requirements, *F. excelsior* is found in many forest sites, and hence *Querco-Carpinetum stachyetosum*, *Q-C. corydaletosum*, and *Q-C. allietosum* are important components of *Fraxino-Ulmetum* elm and ash riparian forests in black soil and floodplains. The greatest importance of common ash are in the alder and ash riparian forests of *Circaeo-Alnetum* (=*Alno-Fraxinetum*), and the *Carici (remotae)—Fraxinetum submontane* riparian forests and the mountain riparian forests of *Alnetum incanae*. Common ash also functions as an admixture species in the *Salici-Populetum* (classified as riparian forests) [45] and occurs on less water-rich sites, where it is largely dependent on rainwater [41,46].

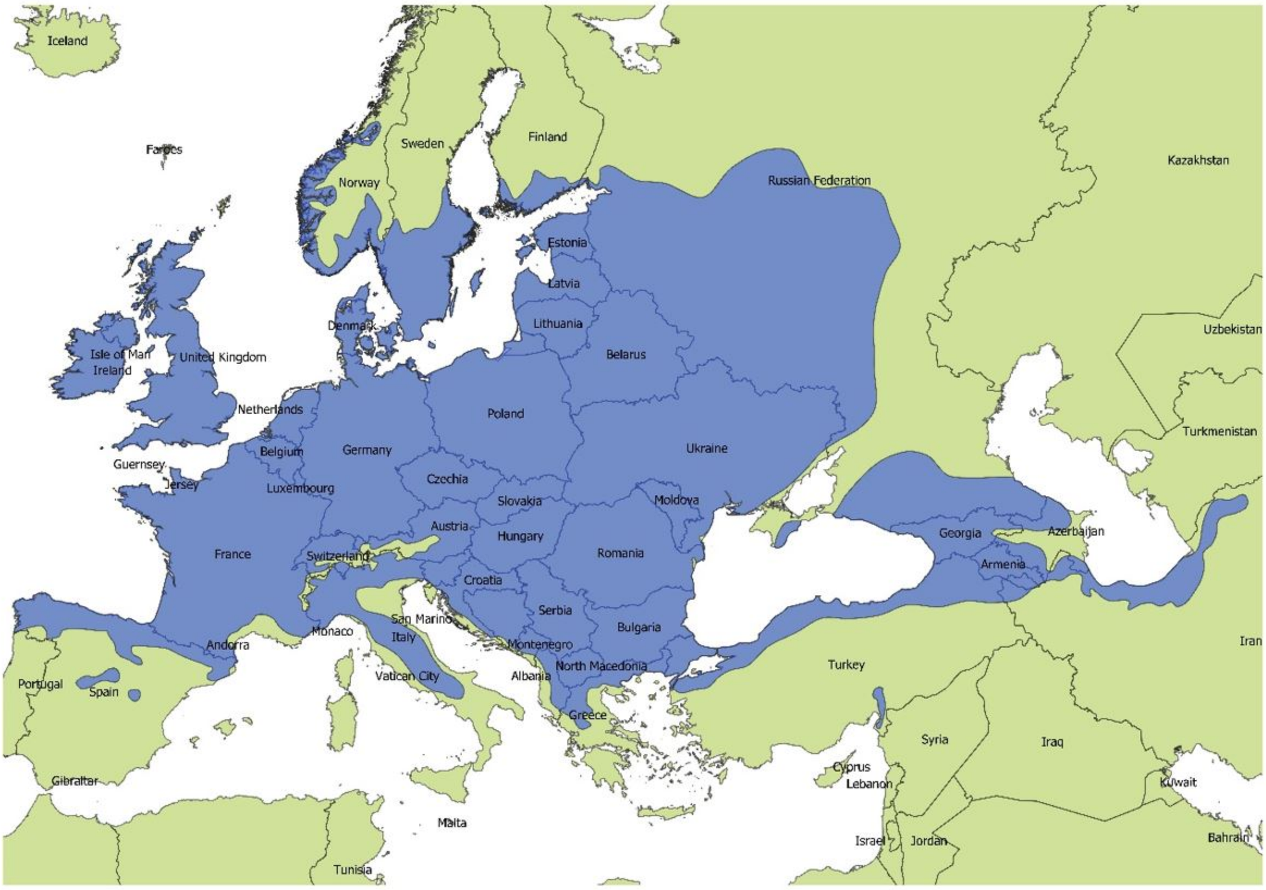

Figure 1. Common ash *Fraxinus excelsior*—range of occurrence (EUFORGEN 2016).

Ash grows well in the soil acidity range of pH 5–8, growing best at pH 7–8 [47]. Common ash, as the major species in *Fraxinus* forms the strongest trees. Under optimal conditions, trees usually reach heights from 30 to 35 m with DBH from 1 to 1.5 m [40]. In Poland, the tallest specimens are found in the Białowieża Forest, where they grow up to 45 m high and reach a stem girth of 2 m [41,45]. After 2002, however, a sharp decline of tree vitality was recorded in the Białowieża National Park [48,49], both in its Polish and Belarusian parts.

Common ash trees easily colonize fertile habitats as a pioneer species on bare or recently disturbed land [45] because of its dispersal strategies [50], and in some countries, it becomes frequent on agricultural fallow land [51]. Due to its rapid growth, the trees provide merchantable lumber at 70 to 80 years old, with a DBH of about 30 cm and a height of up to 28 m [43].

In the first years of growth, common ash can tolerate shading for extended periods and retains the ability to develop rapidly when light conditions improve [50,52]. Young trees grow very slowly when light conditions are inadequate, but they do not die, and trees that are several years old but only around 30 cm have been observed. In such a situation, the shoots can sometimes become prostrate and take root [41]. Ash trees can survive up to 30 years in the shade, because of the differentiation of the leaves into shade-tolerant or sun leaves [25]. It is considered a relatively tolerant species to pollution [53]. In common ash, the phenomenon of "sexual variability" is observed, i.e., the ability to produce different flower types (male, female or hermaphroditic) in one individual [52].

In general, the fruits of ash trees are not available every year and do not germinate the following year (go through dormancy), [54] causing problems in the supply of seedlings each year. In addition, ash fruits can be attacked by insects and fungi, yet they do not contain a large proportion of *H. fraxineus* (a few percent) [55]. However, even if we can observe a year with numerous flowers, we cannot be sure that the fruits are of good quality (vigour). This is an important issue as problems with fruiting of ash trees have been reported in some countries.

Ash shoot dieback, which has been observed throughout Europe since the early 1990s, is a problem for both forestry and nature conservation (Figure 2). As common ash rarely forms solid stands, little commercial attention has been paid to it [9]. The current proportion of common ash in the total forest area of Europe is small and amounts to less than 1% [56]. Outside the forest, common ash is a valued shade and roadside tree and is common along avenues in the rural landscape. However, due to late leaf development, depletion of soil nutrients around the occupied area, lack of use by bees and faster growth than other trees, the ash has seen little use as a park tree [57]. Common ash has always been valued and used because it is considered a particularly "healthy" tree to which positive bio-energetic effects are attributed [58]. Ash wood has long been widely used because of its desirable properties and aesthetic appearance [52]. In the past, ash wood was used to make spears, lances for cavalry, and skis, and the leafy branches were fed to animals [59]. The wood was used to build railway carriages, to furnish luxury carriages, but also to build skeletons of entire carriages [60].

Figure 2. Pathogen *Hymenoscyphus fraxineus* atacks all age classes of ash trees. (**Left**) 30 years and (**Right**) 100-year-old ash trees *(F. excelsior* L.).

The manufacturers of the first airplanes used ash for wing ribs and propeller structures for aircraft. The wood industry still uses heavy, flexible and hard ash wood in the furniture industry as veneer material, and in carpentry, for sporting goods and making tool handles [58,61].

3. The Phenomenon of Ash Dieback in Europe

By November 2010, ash dieback had been reported in 22 European countries [3,23]. The presence of the fungus *Hymenoscyphus fraxineus* (anamorph—*Chalara fraxinea*) was confirmed in all of these countries. At that time, ash dieback was not reported outside of Europe [28]. Until 2012, this pathogen was not included in the list of the European Union Plant Protection Directive, which allowed the free movement of ash planting material and wood within the European Union [62].

Currently, the disease has been confirmed in at least 26 countries, and its current south-western limit extends to central France [26]. In Norway, the disease spreads at a rate of 30 km/year, in Latvia at 40 km/year and in north-eastern Italy at 50–60 km/year [8]. In 2011, the British Isles' common ash is highly valued and the fourth most common deciduous tree species [62] was still considered free of ash dieback [3]. A year later, however, the pathogen was introduced to England with seedlings from the Netherlands [63].

Of the over 80 million common ash trees growing in the UK, up to 90% of them are at risk [24,64]. Attempts to burn the infested trees on the islands to control the disease have failed. The case of ash dieback in the UK became a matter of public interest, even making it to government meetings and the BBC media. This forced the government to take urgent remedial action [24]. One of the solutions implemented in England was to extensively educate the public on how the disease was spread and how to recognise and monitor it, including through mobile phone applications. Educational videos on the symptomatology and aetiology of the disease were made available via social media (You Tube), and a game was organised on Facebook in which participants had to match the DNA sequence of *H. fraxineus* [65]. To underline the importance of the problem, a computer program was developed to visualise the hypothetical decline of the ash trees. Numerous studies have also been carried out in the British Isles; the scientists showed that 953 species of organisms are associated with ash tree populations, 44 of which are obligate [66].

Ash dieback has not been found in southern Italy [67]. Little is known about the decline of ash trees in eastern and south-eastern Europe (France, Spain) [23]. In parts of northern Europe, it is already present, e.g., in Ireland [68], and there are no recent data from Russia (with the exception of Kaliningrad Oblast), Moldova or Bulgaria [3].

In 2010, Sweden listed the *Fraxinus excelsior* in the Red Book of Threatened Species [46], and 60 species of organisms associated with ash were already on this list. If the disease continues to spread and intensify, some of these organisms will probably be on the verge of extinction [69]. In Sweden, according to data from 2009, up to half of the ash trees were affected by ash disease [70]. The problem is not only the disease itself, but also the belief by forest owners that removing dying trees en masse will contain the spread of the pathogen [63]. In Sweden, a nationwide mobile phone monitoring program has been launched to encourage citizens to report the location of healthy ash trees [9].

In Norway, ash dieback was first reported in 2008 but infection with *H. fraxineus* probably occurred there at least two years earlier [3,71], and in 2015 the common ash was listed as an endangered species in the Red Book of Plants [72]. Although low temperatures were initially considered a damaging factor [71], tree deaths due to infection with *H. fraxineus* were confirmed in 2009. Since then, Norway has been divided into three zones: Quarantine, Surveillance and Disease-free. As a preventive control measure, a ban on importing ash wood, cuttings and plant parts (also from quarantine zones) into observation zones where the disease is not present has been introduced. Nursery stock for renewal is checked for disease symptoms before being released for sale [3].

In Denmark, the first symptoms of ash dieback were noticed in 2003, when Danish foresters observed damage to the branches of young ash trees. Soon the problem was reported nationwide, but the cause remained unknown. Only in 2006 was it confirmed that the symptoms were caused by the *Chalara fraxinea*. The planting of new common ash forests was almost completely stopped, and the economically important species gradually began to disappear from Danish forests [73]. Efforts are also being made in Denmark to select common ash genotypes that are resistant to ash shoot dieback [9].

In Latvia, common ash is the most common deciduous tree species in the forests [74]. In 2003, forests were designated under the EUFORGEN program to protect the gene pool of the common ash. In 2007, however, a massive dieback of the trees was observed, which is why these stands could no longer fulfill the task of conserving genetic resources. Until the introduction of the disease to Latvia, common ash was the most common deciduous tree species (readily cultivated among the hardwoods), and now it only occupies about 0.5% of the total forest area and is no longer the dominant species in most stands [75]. In Latvia, the area of common ash stands decreased by 40.6% [8]. In the case of stands of younger age classes, the area decreased by more than four times, disrupting the age structure of the population to such an extent that the proportion of younger age classes fell from 43% (at the beginning of the 21st century) to 15% in 2015. Currently, the intensity of ash dieback in Latvia has decreased [74], and observations show that it is progressing at a rate of about 40 km per year [8].

In Lithuania, ash dieback was first detected in 1996 in forests in the northern part of the country. Soon the decline spread to the whole country. From 2001 to 2012, the area of common ash decreased from 2.7 to 1.7%. Virtually all remaining Lithuanian common ash stands have been decimated, and their health is still deteriorating [7].

The national forest monitoring network recorded the beginning of the mass drying of ash trees in Belarus in 2003. At that time, 6.8% of trees died at the permanent registration points, and in 2004, 12.2% died. More than 80% of ash forests are classified as plantations with impaired stability, and only 12% are recognised as biologically sustainable [49]. According to the forest management data, almost all recorded ash stands in the "National park "Białowieża Forest" are affected by root rot and stem pests, which leads to the disappearance of ash stands as a formation of Białowieża forests.

In Germany, ash dieback disease symptoms were already observed in Brandenburg in 2002 [76]. The investigations started in Bavaria in 2008, resulting in numerous confirmations of the occurrence of *H. fraxineus*. Common and narrow-leaved ash *Fraxinus angustifolia* Vahl. trees of all ages were found to be affected, both in forest nurseries and in forests growing in different locations, as well as in urban plantations [77].

Ash dieback in Slovenia was first observed in 2006 in the north-eastern part of the country. In 2007 and 2008, typical disease symptoms appeared throughout the country. In 2009, due to the spread of the fungus *H. fraxineus* and the problems in obtaining healthy seedlings in Slovenian nurseries, it was decided to replace common ash with other tree species such as sycamore maple or poplar [78].

In Austria, the phenomenon of ash dieback was first confirmed in plantations in 2005 [14], although ash trees with characteristic disease symptoms had already been found in 1997 [79]. By 2007, the disease was very widespread, and the observed symptoms of ash dieback were consistent with those in other European countries [14].

In Ukraine, the disease has been observed since 2010, but the health of ash trees there had already deteriorated significantly four years earlier, especially those growing on the outskirts of the forest. However, the disease spreads quite slowly, especially in the eastern part of Ukraine [23]. In 2014–2015, the mortality of common ash trees was observed in all age groups. Hot and dry summers prevailing in the south and south-east of Ukraine were likely not conducive to the development of the disease, in contrast to the cooler climate of the western and northern parts of the country [80].

In the Czech Republic, the weakening of common ash trees has been observed since the mid-1990s, but the presence of the pathogen was confirmed only in 2007 [81]. Natural forests, commercial plantations, forest nurseries, riparian vegetation, avenues and urban plantations were all affected. Trees of all ages died, but the most severe losses were suffered by young trees. Young stands up to 50 years old were significantly more affected by ash shoot dieback than mature stands [60].

In Hungary, *H. fraxineus* was first detected in the western part of the country in 2008, although the pathogen was probably already present in the area three years earlier. Originally, the damage to the trees was attributed to low temperatures. This pathogen was also found on the narrow-leaved ash. In 2008–2009, the cause of tree death was already present throughout Hungary and occurred in both younger and older stands, but caused more frequent damage to younger forest stands (two- to ten-year-olds) [16].

In general, the common ash was considered to be more susceptible to the disease [62] than the narrow-leaved ash [28,77], but new findings (for example, from Croatia), show that narrow-leaved ash is highly susceptible to the ash dieback, and the least susceptible is manna ash (*F. ornus* L.) [82]. Symptoms of the disease were also found in black ash (*F. nigra* Marsh.), green ash (*F. pennsylvanica* Marsh.) and white ash (*F. americana* Marsh.) [28]. Manchurian ash (*F. mandshurica* Rupr.), along with *F. chinensis* Rox., are included in the group of natural hosts of the fungus *H. fraxineus*, although the disease does not usually lead to the death of these trees [83], and the pathogen has even been found in healthy specimens of *F. mandshurica* growing in far eastern Russia [82]. *H. fraxineus* has also been found in healthy Manchurian ash trees in China and Japan. Artificial inoculations of Manchurian ash seedlings with the fungus showed the possibility of tissue infection, but the damage observed was minor and did not lead to plant death [82].

Following Koch's postulates, *H. fraxineus* was re-isolated from infected tissue with mild disease symptoms [82]; it is worth emphasizing again that the infected tissue in question is the one from Manchurian ash. This is why, in Europe, the fungus is considered to be an alien that has become an invasive species causing a mass mortality of trees. For this reason, in Europe, it is the East Asian and North American ash trees that tolerate the disease the most and show only mild symptoms. Perhaps it was the diseased, asymptomatic Manchurian ash trees transported to Estonia that brought the disease to Europe [82], although Manchurian ash had been cultivated there for a long time and other ash species were not diseased [83]. Also in Sweden, common ash trees planted next to infected Asian ash trees showed no signs of dieback [82].

In Estonia, the phenomenon of tree death was found in the species *Fraxinus sogdiana* Bunge, and it was the first case where the disease was confirmed in ash trees from Central Asia [83]. Furthermore, Drenkhan et al. [83] noted that there are twenty ash species naturally occurring in Eurasia, reaching as far as Estonia, and that this could be a potential route of spread for the pathogen.

H. fraxineus attacks Asian species of ash but does not kill them because it has co-evolved with them. Trees that co-evolved have natural resistance mechanisms, whereas European ash species are therefore sensitive to infection by this fungus. In addition, the climate in Central Asia may not favor the development of the pathogen as much as in Europe.

It is not yet certain whether the current spread of the pathogen is limited to the eastern range of the host trees or also to the western range. It is doubtful that the pathogen accompanied its host during the transcontinental spread of ash from East Asia to Europe and survived only in northeastern Poland in a latent form until 1992, when the phenomenon of mass ash shoot death was first described in Europe [83]. *H. fraxineus* was probably brought to Central Asia together with the Manchurian ash.

4. *Hymenoscyphus fraxineus*—The Cause of the Decline of the Common Ash Tree

In 2006, ash shoot dieback affected almost 11,000 ha in Poland [5] and was already reported in eastern Poland in the forest districts of Czerwony Dwór and Borki in the early 1990s [3]. In 2006, however, the discovery of Prof. Tadeusz Kowalski, who first described the fungus *Chalara fraxinea*, pointed to the new species as the cause of ash dieback, which was later confirmed by other researchers [14,30]. In 2008, based on genetic studies and in vitro analyses of colony characteristics, the fungus was found to form fruiting bodies on petioles of fallen leaves from the previous year. The fungus was described as *Hymenoscyphus albidus* (Robergere ex Desm.) W. Philips [84]. However, *H. albidus* has been known in Europe since 1851 and has not shown pathogenicity to common ash. This leads to speculation about mutations and the emergence of new pathogenic strains of the fungus, or the introduction of a closely related, morphologically similar species.

Confirmation of the introduction of a new related species was conducted by a team from the Swiss Federal Institute of Technology Zurich (ETH) in collaboration with the Department of Forest Phytopathology in Cracow [28]. Investigations showed that two phylogenetic subgroups were distinguishable within known isolates of *H. albidus* [85]. The pathogenic subgroup was represented by the species *Hymenoscyphus pseudoalbidus* (whose anamorph is *Chalara fraxinea*, described in 2006). It was assumed that *H. pseudoalbidus* displaced the non-pathogenic fungus *H. albidus* from the environment [28].

However, studies in the southeast of the Czech Republic showed the presence of inoculum in the air of both species, indicating their coexistence in the environment, and that *H. albidus* is still found at individual sites in Norway, Belgium and France [81]. Attempts to inoculate plants with the fungus *H. albidus* showed no pathogenicity on common ash or green ash [86].

Until 2011, the two names *Chalara fraxinea* and *Hymenoscyphus pseudoalbidus* were used interchangeably. However, according to the decision of the International Botanical Congress of 2011, dimorphic fungi should have only one name. Genetic studies have shown that the causal agent of ash dieback is closer to the genus *Hymenoscyphus* than to *Chalara*. Since the term "fraxinea" was widely used in the literature, it was decided to combine it with the taxonomically correct "*Hymenoscyphus*" [33]. Currently, the accepted name of the fungus is *Hymenoscyphus fraxineus* (T. Kowalski) Baral, Queloz, Hosoya, comb. Nov.; basionym: *Chalara fraxinea* T. Kowalski; synonym: *Hymenoscyphus pseudoalbidus* Queloz et al. The term ash cup was adopted as the Polish name because the fungus in the teleomorphic stage produces characteristic "cups" (Figure 3) with a diameter of 1.5 to 3.0 (7.0) mm [87].

Figure 3. Ash cup—fruiting body of the *H. fraxineus*.

Before Baral and Zhao [34] revealed the difference in the structure at the base of asci in the two fungal species, it was believed that a distinction between *H. albidus* and *H. fraxineus* based on morphological characteristics was not possible [88]. Recent studies indicate that *H. fraxineus* is most likely an invasive species [3], as it was found to be genetically and morphologically identical to *Lambertella albida*, which has been known in Japan since 1993 [69,88]. This name is often used in the literature as a synonym for the species *H. fraxineus* [82]. The speculation that the pathogen was introduced was supported by the finding of greater genetic diversity of this fungus in Japan than in Europe, and the lack of natural resistance of common ash trees in interactions with the pathogen [69].

Modeling of the spread of the pathogen showed that the climate in south-western Europe is too warm (it was not found in Spain). The assumption is that the disease will continue to spread northwards [89].

Scientists in Asia have reported the presence of *H. fraxineus* in China; it has also been found in South Korea [88], and it is thought to occur naturally in Central and East Asia [83], as a saprotroph [82]. In this area, there are fungal species belonging to the same genus, but their pathogenicity has not been reported so far; however, should they be accidentally introduced into Europe, they could pose a new threats to European forests [90]. The sexual reproduction of the pathogen ensures genetic diversity of the pathogen, which allows it to adapt to changing environmental conditions and successfully compete with other fungi [69], which may be how trees that initially appear to be resistant eventually become diseased [26]. Samples of plant material from a herbarium in Switzerland show that the pathogen has been introduced to Europe several times in the past, but has only recently become successfully established [3].

In light of the current scientific knowledge, it is recognised that the fungus *H. fraxineus* is present throughout Poland [87] and forms apothecia on foliage from the previous year (including under laboratory conditions).

Despite evidence that urea and carbendazim are effective in limiting the growth of the pathogen in in vitro experiments (in cultures in Petri dishes), there are still no effective methods of protection against this pathogen [16,24]. The use of urea may prove practical (e.g., for the protection of individual trees), as it is relatively cheap and non-toxic to the environment, and also promotes the development of numerous organisms hostile to the fungus [91].

4.1. Transmission Routes and Biological Cycle of H. fraxineus

The species *H. fraxineus* spreads in the air by ascospores that reach maturation at night, under high humidity [3], and are released in the early morning from April to October, in central Europe, with the greatest intensity in August [81,92]. Ascospores are produced in apothecial cups on the fallen leaves of dead seedlings [92], and their production is favoured by high humidity [23,81]. Under such conditions, the spores can remain airborne even when fruiting bodies are no longer present. A similar process of spore dispersal also occurs for *H. albidus* [81]. Studies have also shown that the species *H. fraxineus* prefers cooler conditions; its optimal growth on solid media is between 20 °C to 22 °C, and hyphal growth stops above 28 °C [89]. The fungus penetrates the host through epidermal cells [93] and can develop in the living part of the bark, phloem or xylem [19], although no preference has been for specific tissue types [87,93]. Tissue necrosis occurs at the infection sites [23,69], while the pathogen develops in various tissue types and in different directions [87,93].

In nurseries, the incubation period of the fungus in host plants lasts about 10–14 days and the first tissue necroses appear after two weeks, while clear disease symptoms may only appear after several months [62].

The disease symptoms are usually observed under natural conditions in summer or autumn (in the year of infection or spring of the following year) [62]. *Hymenoscyphus fraxineus* is a primary pathogen because the fungus is isolated from infected tissues only at the beginning of the infection development [94], and then there is the fungus retreat place for secondary pathogens, especially species of *Phomopsis* and *Fusarium*, which quickly colonise the dead tissues previously killed by *H. fraxineus* [69,87]. This situation limits the possibility of isolating the *Chalara* conidia produced in phialides of the anamorphs known as *C. fraxinea* [87].

Although conidia can also develop on fallen tree trunks, their growth on seedlings is unlikely [3,87]. However, later in vitro studies showed that conidia can germinate on ash leaves and infect seedlings via leaves or roots in the soil. Seedlings inoculated with conidia also show necrosis and wilting of leaves and even death [95].

Despite the low germination frequency of the conidia, they could play an important role in the rapid spread of the pathogen. *H. fraxineus* can grow in plant debris on the ground [95]. An important factor limiting the spread of the pathogen *H. fraxineus* is the low resistance of the ascospores to UV radiation and their low nutrient supply; thus, long distance natural invasion from areas of natural occurrence (e.g., by ascending air currents and further into the stratosphere) seems unlikely [69].

Tree dieback moves faster along valleys and is consistent with bird migration routes [8]. Therefore, there is a high probability that birds using infected leaves to build their nests may carry pathogen spores on their feathers over long distances (Oszako, unpublished).

An obstacle to the spread of the fungus may be a thick layer of dry leaves of other species (e.g., beech) and a poorly developed undergrowth. Such conditions lead to a lack of development of *H. fraxineus* apothecia on leaves fallen onto such substrates [87].

Scientists disagree on whether diseased trees (with symptoms of dying) and dead trees are reservoirs for inoculum. According to Kowalski [87], trees with symptoms of dieback, with local necrosis or withered branches, do not produce spores that could threaten neighboring healthy trees. Therefore, they do not compose a reservoir of infectious material. On the other hand, the primary inoculum is from the leaves of the previous year, where *H. fraxineus* conidia are formed in autumn and winter [96], while ascospores are formed on the fallen leaves in the following summer. Under natural conditions, the fungus can survive in the petioles for up to five years after leaf fall [97].

4.2. Symptoms of Tree Infection by H. fraxineus

Infected trees show some symptoms resembling frost damage from a distance [63], such as loss of foliage, leaf discolouration and necrosis, reduced fruiting, etc. [98]. A characteristic symptom and one of the earliest is frequent discolouration near the central vein of leaves. The growth of hyphae through plant tissue leads to the death of successive shoots, and this can even cover entire tree crowns. The most important symptom is the wilting of leaves (as hyphae develop inside vessels and parenchyma of whorl rays, and interfere with the transport of water and assimilates), and the subsequent tissue necrosis is visible on the surface of the shoot bark [87,92]. This leads to the death of parts of the shoots located above the infection site (Figure 4).

Figure 4. Damage to young ash trees infected by ascospores of *H. fraxineus*.

Diseased ash trees tend to drop their leaves by early autumn and many trees are deprived of photosynthetic tissues by the end of September [78,87]. In younger trees, cancerous changes can be observed on the trunks, rarely in connection with sap secretions from diseased tissues (Figure 5).

Figure 5. Canker lesions on the stems of young ash trees in the Wolica Reserve (Chojnów Forest District) caused by the fungus *H. fraxineus.*

The wood in the affected areas is characterised by tissue discolourations [87]. Kowalski [87] also lists the symptoms of the death of the underground parts, such as the rotting of small roots and their blackening, unhealed necrosis (tissue discolouration starting from the infection sites), often near the root collars [87]. These symptoms are similar to the damage caused by pathogens of the genus *Phytophthora*. *H. fraxineus* infects the roots only sporadically and only of seedlings, which show a grey-brown discolouration of the underground parts of the root collars [24,87] with sporadic fruiting bodies [99]. In heavily infected plants, the pathogen has also been isolated from the roots [93], although it was previously believed that the pathogen (then recognised as *H. pseudoalbidus*) did not infect roots [77]. This was confirmed by later studies, which showed that the fungus not only infects seedling roots but also moves within xylem to above-ground parts [95].

In Sweden, it was observed that tree health deteriorated rapidly within two years (from healthy to severely damaged to death) [63]. However, many specimens (in older age classes) improved, which was also confirmed by observations in Denmark, where ash trees with larger stem girths were less affected. This could indicate that older trees were able to overcome *H. fraxineus* infections and survive [63].

It has also been found that ash clones that develop buds earlier (which correlates positively with their health) are less susceptible to infection by *H. fraxineus* [7], and earlier discolouration and shedding of leaves in autumn also showed a positive correlation with health [26]. Susceptible individuals were characterised by prolonged growth in the summer [93].

Laboratory studies have shown that the fungus can produce toxins called viridiols [28,69,100], but these have not been found in samples of shoots and wood from infected trees [69], nor has it been demonstrated that such substances can cause necrosis of ash tissues [101]. *Hymenoscyphus fraxineus*, rather, has not been found to infect forest trees other than ash or to occur as an endophyte in living roots, shoots and leaves [87], although there is a risk of infection from related plants such as the olive [95], since they both belong to the *Oleaceae*.

5. Pathogens of Small Ash Roots of the Genus *Phytophthora* spp.

A characteristic feature of organisms belonging to the genus *Phytophthora* is the content of cellulose instead of chitin in the cell wall, which distinguishes them from fungi [102]. Furthermore, they have motile conidia and have been classified in the kingdom *Chromista* [103].

In the last decade, only a few studies have examined the influence of pathogenic oomycetes of the genus *Phytophthora* on disease in common ash [104,105]. As soil pathogens present in ash stands, they can infect and destroy small roots responsible for the uptake of water with mineral salts [103]. This genus includes the most important pathogens of nurseries and plantations of ornamental plants. The most widespread *Phytophthora* species in Poland since the 1960s is *P. plurivora*. Later (after 1990), many new species were brought to Poland, facilitated by the development of trade and the abolition of controls within the European community [105].

Mass introduction of oomycetes from nurseries into forest ecosystems (together with seedlings and the soil adhering to them) can result in large-scale tree dieback, as had occurred in California, Oregon and Washington State, USA [106]. In Europe, pathogenic oomycetes led to the decline of black alder, especially along watercourses [104].

The occurrence of *Phytophthora* species in water bodies poses a real threat to many plant species living in their natural environment, as well as to nurseries that draw water for plant irrigation from natural surface waters such as rivers, water reservoirs, etc. [105].

Based on the close relationship between *Phytophthora* and the aquatic environments [103], common and narrow-leaved ash arenarrow-leaved ash as well are particularly susceptible to this pathogen, especially during periodic flooding. The species *P. citricola* (now *P. plurivora*), *P. cambivora* and *P. megasperma* have been isolated from Polish rivers flowing through forest and agricultural areas [107]. Even in winter, when water temperatures are around 5–7 °C, these organisms were found to cause necrotic patches on leaves collected in traps [108]. The destructive nature of this group of pathogens is underlined by its name, which derives from the Greek *phyto*—plant and *phthora*—destroyer. The control of *Phytophthora* with pesticides or antibiotics is often ineffective, and these therapeutic methods may lead to the masking of disease symptoms which provides a false impression of disease.

5.1. Ash as a Potential Host for Phytophthora Species

During investigations in nurseries in northern Germany [77], representatives of *Phytophthora* were not included in the group of major causal agents of ash dieback, but *P. ramorum* Werres, De Cock and Man in ’t Veld was shown to infect a number of forest tree species, such as. *Fagus sylvatica* L., *Quercus rubra* L., *Pseudotsuga menziesii* Mirb., and potential hosts such as *Acer pseudoplatanus* L. and *Fraxinus excelsior* [106].

Laboratory tests have shown that *P. ramorum* is capable of infecting ash leaves and shoots [106]. Common ash is also on the list of hosts of *P. citrophthora* (R.E. Sm. and E.H. Sm.) Leonian and *P. plurivora* Jung and Burgess. (formerly *P. citricola*). Isolation of the latter species from ash tissue during the growing season is difficult or even impossible due to the high concentration of microbial growth inhibitors produced by plants [31].

5.2. Symptoms of Plant Infestation by Oomycetes

A typical symptom of infestation of plants by oomycetes is the infection of the bark of the root collars. From a distance, brown sap exudates can be observed coming from the cracks on the stems, accompanied by necrosis of the tissue under the bark. The general symptoms include wilting of leaves and their discolouration as well as a reduction in size (atrophy), defoliation, death of branches and consequent thinning of crowns [103]. The greatest threat from *Phytophthora* spp. is to nurseries and forestry crops, but they also cause damage to mature trees, sometimes over many years [103]. There are several other research studies on *Phytophthora* associated with ash published by the teams of

Orlikowski [31,38], Milenković [109], Duraes [110], and Akili [111]. The isolates were found to be pathogenic when inoculated onto the stem bases of young *F. excelsior* [31] and *F. angustifolia* seedlings [111]. They also isolated *Phytophthora* species near mature ash trees in decline [38]. About 400 samples were collected in different stands in Serbia from 46 hosts, and 20 hosts were positive for the presence of *Phytophthora* species, including *F. excelsior* [109]. Roots infected with *Phytophthora plurivora* and a mixed inoculum of *P. plurivora*, *P. megasperma* and *P. hungarica* showed progressive root losses, when fine roots were scanend during the four-month incubation period with WinRHIZO software (Regent Instrument version 2017a [109]. The mortality of *F. excelsior* was also associated with *P. plurivora* in Spain [110].

6. The Role of *Armillaria* spp. and Other Fungi in the Decline of Ash Trees

Important secondary pathogens of the common ash are *Armillaria* fungi, which infect individuals weakened by damage caused by *H. fraxineus* [3,46,92]. Crown transparency caused by fungal infections resulted in better exposition of remaining shoots for sun, and an accumulation of sugars transported to the roots finally created favourable conditions for infection by root pathogens [46]. *Armillaria* spp. are pathogens of weakened hosts, and prevent trees from regenerating and enhancing their decline [69]. As a rule, *Armillaria* spp. destroy the root system of the trees, whose shoots may have been infected by *H. fraxineus*, whereupon the health of the trees deteriorates drastically during a growing season. Common and narrow-leaved ash trees affected by *Armillaria* root rot can also fall over in still weather [112]. Infection by *Armillaria* root rot is secondary, since trees often have dying shoots with apparently healthy root systems and no visible signs of stem rot [46]; however, they eventually succumb to *Armillaria* root rot later. The assumption is that shoots were infected by ash dieback, which weakened them, and then they became infected by *Armillaria* root rot which led to their death [112].

Armillaria root rot also attacks younger trees [28], which is why stands up to 40 years old die faster than older ones [9]. In Germany, the mortality rate of younger age classes in common ash was as high as 95% [112]. The same study from 2010–2014, conducted in south-eastern Germany, showed that while older stock took longer to die, the deterioration over four years occurred regardless of age [112].

Fungal species other than *H. fraxineus* also occur on necrotic areas on twigs, branches and trunks of ash trees with dieback symptoms. The most common are *Alternaria alternata, Cytospora pruinosa, Diaporthe eres, Diplodia mutila, Fusarium avenaceum, Fusarium lateritium* and locally *Fusarium solani, Phoma exigua* and *Valsa ambiens* [113]. Pathogens that have a significant impact on ash health include *Botryosphaeria stevensii* [98] and species of *Cytospora* and *Phomopsis* [114]. Various reports on the pathogenicity of known opportunistic fungi found in necroses on ash trees (*Diaporthe, Fusarium*, etc.) [115] and rot fungi such as *Ganoderma* [116] or Lentinus tigrinus [117] are also found on dying ash trees. Narrow-leaved ash trees can be attacked by *Diplodia fraxini* [118], which causes the same symptoms as *H. fraxineus*.

Kosawang et al. [119] argue that fungal endophytic communities of tolerant ash species can protect them from ash dieback and that selected endophytes have the potential to act as biocontrol agents. These hypotheses were tested by isolating members of the fungal communities of five tolerant ash species and identifying them by their ITS regions. The endophyte candidates were tested in an in vitro antagonist assay with *H. fraxineus*. Of the total 196 isolates, 9 fungal orders, 15 families and 40 species were identified. Fungi of the orders *Pleosporales* (e.g., *Boeremia exigua* and *Diaporthe* spp.) and *Hypocreales* (e.g., *Fusarium* sp.) were found in most communities, indicating that they are common taxa. The in vitro antagonist test revealed five species with high antagonistic activity against *H. fraxineus*. These endophytes were identified in the region ITS as *Sclerostagonospora* sp., *Setomelanomma holmii, Epicoccum nigrum, B. exigua* and *Fusarium* sp. Three of these taxa have been previously described as antagonists of plant pathogenic microbes and are of interest for future studies on their potential as biological control agents against ash dieback, especially for valuable ash trees in parks and urban areas. On the other hand, recently identified endophytic fungi associated with the ash dieback causative agent were shown to have different behaviour because they encode the pathogenicity genes on European ash which are in common with pathogenicity signatures of *H. fraxineus* [120].

Monitoring of the health status of *F. excelsior* trees in Bosnia and Herzegovina revealed unusual symptoms [121]. These included the appearance of necrosis and cankers in the lower parts of the trees, followed by the formation of fruiting bodies, but none of these symptoms were found in the crowns. After taking samples and isolating the necrotic parts from the base of the boot, the pathogen *Neonectria punicea* was isolated and identified on the basis of the characteristics of pure cultures, the morphology of the fruiting bodies and multilocus sequencing. In [122] studies, macroscopic symptoms attributed to crown death and canker were strongly associated. In addition, the disease was associated with symptoms of *Armillaria gallica*, but no associations were found for symptoms of *Neonectria galligena, Pseudomonas syringae* subsp. savastanoi pv. fraxini, *Hylesinus fraxini*, or *H. varius* when these were considered together. Dieback occurred more frequently in trees of average or below average size, suggesting that the resistance of individual trees decreases as growth potential or vigour decreases. The extent of canker infestation in the crown depended on site conditions and possibly on silvicultural measures. The development of phytosanitary prescriptions for silviculture should primarily target young stands, as these are the most critical stages of stand development.

The lack of availability of certified chemicals approved by the FSC (Forest Stewardship Council) and PEFC (Programme for the Endorsement of Forest Certification Schemes) to control the above-mentioned pathogens limits the possibilities to protect ash trees [98]. Research conducted in Poland at the Chojnów Forest Inspectorate [123] on the use of phosphites as a means of promoting tree resistance to pathogens may prove helpful in addressing this issue.

7. The Role of Animals in the Decline of the Common Ash

Animals can strongly affect valuable natural regeneration [45], which can resist disease processes in the first years of growth [114]. European bison can burn the bark of old ash trees, especially directly at the root with their urine. European and Canadian beavers can also prevent the regeneration of ash trees [58]. However, the greatest economic damage is caused by roe deer which include common ash as a very important part of their diet [98]. It is worth emphasizing that deer debark young trees, causing wounds—potential entry points for fungi. Deer, including protected elk, are capable of completely destroying the natural regeneration of ash and severely damaging seedlings in artificial regeneration [45,58].

8. Insect Pests and Their Significance for the Disease Process of Ash Trees

For Dutch elm disease, the main vectors for the spread of the pathogen are *Scolytus multistriatus* and *S. scolytus*, but as far as we know for common ash diseases, none of the major ones have significant insect vectors. Insects may spread hyphae, ascospores, conidia or all of the above between neighboring trees, which reduces the efficiency of disease control methods [124]. Kowalski [87] found that *Hylesinus orni* did not transmit *H. fraxineus* from dying trees to living ash trees, which supports the minimal role of insects in the transmission of this pathogen from dying trees to living ones. The fungus does not form apothecia on stems and branches and these are therefore not a source of inoculum spread by insects [99].

The conidia of *H. fraxineus* are "sticky", and if they are spread by insects, this would explain the genetic differentiation between upland and lowland populations of *H. fraxineus* [95]. In recent years, pests that feed on tree buds and leaves and have not caused major losses so far have become more important [125]. There is an evidence of several insect species that may play important roles in the observed phenomenon of ash dieback. These include the following foliar pests: *Stereonychus fraxini*, *Prays curtisellus*, *Operophtera brumata* and *Vespa crabo*, which feed on shoots. *S. fraxini* occurs in all developmental stages of the common ash. Damage to the leaves leads to considerable weakening of the trees, making them less resistant to fungi and various abiotic factors. Xylo—and cambiophagous insects in turn—kill trees weakened by other factors [125].

Investigations carried out in ash stands of younger age classes show that the most important insect species are: *Hylesinus fraxini* and *Hylesinus orni*, while in older trees, under thick bark, feeding grounds of *Hylesinus crenatus* were found [124]. There is a risk that secondary pests of ash trees, which were not previously of economic importance, will gain importance due to the high number of weakened trees, although secondary pests seem not to influence the increase in ash dieback [112].

Clearly more important than the European insect species is the emerald ash borer *Agrilus planipennis*, which originated in East Asia and has decimated ash trees (*F. pensylvanica, F. nigra* and *F. americana*) in the USA [126,127], and is now approaching central Europe from Russia. In North America, the range of this insect is expanding at a rate of 80 km/year [128]. It is estimated to have contributed to the death of about 150 million ash trees in the United States alone in recent years [58]. In 2003, its introduction into western Russia was confirmed, from where it is spreading westwards at a rate of 13–31 km/year, both naturally (by flight) and with human involvement (including transport on roads) [128]. Due to its high tolerance to different environmental conditions, this insect can survive in the entire range of common ash. Observations so far show that common ash is just as susceptible as American ash [127]. The introduction of this insect into Poland, in combination with the currently unsatisfactory health situation of local ash populations, could lead to the extirpation of common ash in many parts of the country.

9. Abiotic Factors Favoring the Weakening and Death of Trees

The most serious environmental factors for common ash that increase the susceptibility of trees to diseases and pests are as follows: changes in soil acidity (pH), frost, high air temperatures, drought, water inundation and excess atmospheric nitrogen [98,129]. There are also theories linking the death of the common ash to the release of radioactive cesium after the accident at the Chernobyl nuclear power plant [130]. Although this theory was controversial, it was published in the specialised press by scientists from Lithuania.

9.1. The Influence of Habitat Conditions on the Health Status of Ash Trees

When ash dieback appeared, it was thought to be related to a maladaptation of the common ash to its changing environment but it turned out that more ash trees died in favourable habitats than in ones less optimal for growth, and that they showed greater resistance to harmful factors in less suitable conditions [130]. This observation was confirmed by studies on the influence of habitat conditions on the development of common ash roots in the upper soil layers [44] in the Rudka, Olecko and Lębork forest districts. In the course of these investigations, "a significantly weaker development of ash roots in the ash-alder habitat" was detected, and "twice as many fine ash roots were found in the wet forest habitat than in the admixture species". The density of dead fine roots in relation to the density of living roots was higher in typical wet ash habitats. Water shortage in the wet forest habitat could cause a faster death of fine ash roots than in the more dry habitat [130], and this might be due to the adaptation of trees to less favourable habitat conditions [44,130]. However, the presence of root pathogens, such as *Phytophthora* spp., has not been investigated, even in the light of recent studies on the possibility of alder damage by *P. alni*.

Investigations carried out in Austria showed that trees without symptoms of *H. fraxineus* infection had a denser root system [79]. Perhaps the roots were better nourished by the undamaged foliage of the trees. Investigations in Poland [87] carried out in common ash stands of younger age classes, revealed the highest proportion of dead trees in moist forest sites, while no damage was found in drier forest sites; in wet mixed conifer forests, the percent of damaged trees was only 6%.

In the Staszów Forest Inspectorate, common ash trees did not show visible disease symptoms in drier forest sites, which is consistent with the hypothesis that ash trees on less suitable sites have a higher resistance to dieback. Recent studies on ash dieback even recommend not planting ash trees on flood-prone sites [9]. Nevertheless, common ash can die regardless of age [19,130], according to studies in the Rokita Forest Inspectorate (Poland), and in all forest sites they occupy [114,131].

Hungarian experiences [16] showed that *H. fraxineus* more frequently attacked trees growing on frost-prone, well-watered sites with deep soil, as well as on drier sites exposed to extremely low temperatures. In Slovenia, disease symptoms were observed to increase on sites with higher relative humidity, lower temperatures and no direct sunlight [78].

During the research in the Srokowo Forest District in the Regional Directorate of State Forest in Olsztyn (Poland) [47], it was found that common ash symptoms became more visible when the acidity of the soil was below pH 4.2 or above pH 8, although in Latvia, healthy ash stands were found on both acidic and slightly alkaline soils and the soil pH around damaged stands was close to the limits considered appropriate for this species [74]. The change in soil pH may be due to the disturbance of water conditions and the type of water management from flow to stagnation. The drying out of the uppermost soil layers has a negative effect on the health of the roots [44].

The resistance of common ash to pathogens may also deteriorate due to a large amount of water in the soil, limiting the formation of endomycorrhizae [44]. In this context, the activity of beavers blocking water courses causes damage to root systems and negatively affects soil acidity [45].

Regular flooding of forest stands favours the development and spread of *Phytophthora* spp. [103]. The incidence of common ash decreases in long-term floods, especially during the growing season. Common ash is considered tolerant flooding for a maximum of 15–20% of the growing season. The health of the trees also depends on the depth of flooding, with an upper tolerance limit of 1.5 m [132], which has the most negative effect on young trees in the youngest age class.

9.2. Significant Impact of the Changing Climatic Conditions on Common Ash

The long-term changes in climatic conditions in the second half of the 20th century were characterised by a continuous increase in average winter temperatures, a seasonal shift in precipitation from summer to winter and a tendency towards heavy rainfall. For many regions of Central Europe, climate models predict a further intensification of these trends [133] and of the recently observed acceleration of climate change and its associated consequences. In particular, the increase in average temperature and hydrological changes can affect the health of the common ash [134]. Current issues with this species may be associated with climate change, particularly long-term droughts [135]. One of the likely effects of climate change in Europe will be shifts in distribution ranges of many tree species [136]. Against this background, some scientists have provided very positive outlooks about the future of common ash, describing it together with beech [137], pedunculate oak, sessile oak and fir as species that will survive unfavourable changes in contrast to pine, spruce, larch and silver birch [134]. However, ash dieback remains an unsolved problem across Europe, although there are hopes for heritable resistance and natural selection [64]. Other studies indicate that long-term droughts due to climate change in less humid habitats can lead to the local extinction of species with high moisture requirements, which include the common ash [136]. This is all the more true as it is the most important deciduous tree species in Poland, which is classified as moderately resistant to drought stress [138]. Climate warming may also have an impact on the establishment of foreign fungal and insect species in Poland, which could prove to be another threat to native flora, including common ash trees, under the new conditions [136,139]. Laboratory studies on *H. fraxineus* find that the optimal temperature for its development is 20–22 °C and that temperatures above 30 °C limit its growth and development [114,131,140].

However, these were in vitro tests with artificial substrates which are physiologically different from fungi colonizing host tissues. In vivo growth may be more sensitive to temperature fluctuations than growth in pure cultures on artificial media [140]. However, the optimal growth temperatures and intolerance to high temperatures suggest that progressive increases in average annual temperatures due to climate change are likely to limit the development of *H. fraxineus*, which in turn could slow or stop the further spread of ash dieback.

10. Breeding Aspects and Their Impact on Ash Dieback

As early as the 1980s in Europe, attention was drawn to the over-exploitation of common ash trees in the past, as well as the conversion of their stands to alders which were planted in some unsuitable habitats [45]. The death of common ash as a result of *H. fraxineus* in natural stands is less intense than in artificial plantings [25,28]. In the Staszów Forestry Inspectorate (Poland), the proportion of dead trees in the artificially regenerated stands was eight times higher than in the self-seeded stands. Crown damage with more than 50% foliage loss was more frequent in older trees from plantations [28].

Similar results were obtained in the Łosie Forest Inspectorate [87] where stands with high re-establishment rates may contribute to strong competition between trees, and lead to tall and branchless stems [130]. Under high density, strong competition between trees (for water, light, etc.) in turn leads to stress and susceptibility to fungal infections.

According to observations in Austria, ash trees suffering from ash dieback and female specimens were more susceptible to fungal infections [79], although there are male, female and hermaphrodite specimens of the common ash [141]. Based on other research [125], it is important to systematically regenerate ash naturally in suitable habitats, which is contrary to the current forestry practice of abandoning the cultivation of this species.

11. Conclusions

Ash dieback, which can now be observed throughout Europe, began in north-eastern Poland in 1992, and at that time nothing was known about its causes. It is possible that *Hymenoscyphus fraxineus* arrived in Europe by chance when the Manchurian ash was introduced from East Asia.

Today, there are several places in Estonia where Manchurian ash grows, and the first plantings date back to 1865. It is possible that the diseased, asymptomatic Manchurian Ash transported to Estonia was the vector of the disease to Europe, but other ash species were not diseased and the large-scale dieback of the native European ash has only recently begun.

Literature is not available about plantings of the above-mentioned species in Kaliningrad and Belarus, which are also within or close to the now suspected single epicenter of the disease and which also belonged to the Soviet Union at the time; thus, they were subject to the free movement of living plant material. It is possible that the current climate change, i.e., the increase in the average annual temperature over the last 100 years, is the reason why the fungal pathogen is only now becoming active.

In addition to *H. fraxineus*, other fungi have been frequently found in the necrotic tissue of ash trees and are involved in the phenomenon of ash dieback, and these can increase the size of necroses in ash trees weakened by *H. fraxineus*. Such pathogens include *Botryosphaeria stevensii, Cytospora pruinosa, Fusarium lateritium, Massaria* sp. and fungi of the genus *Phomopsis*. The root systems of weakened trees are attacked by *Armillaria* sp. (causing white wood rot).

The honey fungus *sensu lato* is described as a weak pathogen that impairs the regenerative capacity of trees and hastens their death. The health of ash trees deteriorates drastically within one growing season when the root system and shoots are destroyed by the pathogen *H. fraxineus*. Ash trees affected by root rot can even fall over in calm weatherand fungi of the genus *Heterobasidion* and are also among the pathogens that have a significant impact on the health of ash trees.

The role of insects in ash shoot dieback depends on the health of the ash trees; diseased specimens are infested by *Hylesinus orni*, which, however, has not been demonstrated to be a disease vector. The risk of transmission of the fungus *H. fraxineus* is minimal, as the fungus does not form apothecia on stems and branches and these therefore do not constitute a source of innoculum. Several insect species, foliar pests, may play an important role in the observed ash shoot dieback, e.g., *Stereonychus fraxini*. Leaf damage leads to considerable weakening of the trees, making them less resistant to fungi and various abiotic factors. Xylophagous and cambiophagous insects, in turn, kill trees weakened by other factors. In young stands, *Hylesinus fraxini* and *Hylesinus orni* are of the greatest importance, while in older trees, the black stag beetle has been found under the thick bark. Of these three species, the black ash bark beetle is the most common and abundant. There is a risk that secondary pests of ash trees, which were previously of little economic importance, would become more important due to the large number of weakened trees, but this has not yet been observed. Far more significant than the European insect species is the emerald ash borer (*Agrilus planipennis*), native to East Asia, which is decimating ash trees in North America (in 2002, it was confirmed to have killed 150 million ash trees in the USA); it is now spreading from the Moscow area (where it arrived in 2003) both naturally (by flight) and by human intervention (including transport on roads) at a rate of about 13–34 km/year. The common ash tree is as susceptible as the American ash tree. Should it reach Europe, the species could be completely wiped out in certain areas of the country because of the increasing mortality from diseases. Another serious limitation in the fight against the emerald ash borer is that the first symptoms of its destructive activity become visible only six years after its appearance in a new area.

Prolonged periods of drought as a result of climate change can lead to the extinction of species with high moisture requirements, including ash, in less humid areas. This is all the more true as ash is classified as moderately resistant to drought among the main deciduous tree species. However, ash is not indifferent to hydrological changes; it is already suspected that the current problems of this tree species are due to past climate changes, with prolonged droughts being an important factor. Against this background, some scientists are very positive about the future of ash, pointing out that it will survive negative changes together with beech, English oak, sessile oak and fir, in contrast to pine, spruce, larch and silver birch. However, this point of view is questionable, as ash shoot dieback is still an unsolved problem throughout Europe, although laboratory studies on the thermal preferences of the main causal agent of ash shoot dieback (*H. fraxineus*) indicate that the optimal temperature for its development is around 20–22 °C and that temperatures above 30 °C limit the development of this pathogen. Therefore, if the average temperature is raised above the above-mentioned optimum for the development of *H. fraxineus*, ash shoot dieback could possibly be prevented.

The chance of ash returning as a forest-forming tree species is currently low. It makes sense to continuously monitor the health status of ash, e.g., by cultivating ash in forest nurseries, on small plots and also on small forest crops mixed with other species. If an improvement in the health status of the ash trees is noticed, it is possible in this way to react at an early stage and to change the previous approach accordingly. In summary, 30 years after the first reports of ash shoot dieback in Europe, further research is needed to find plants that are resistant or at least tolerant to the disease through natural selection.

Recently, Harper et al. [142] identified molecular markers able to predict low susceptibility to ash dieback, suggesting that the pre-priming of defence responses in ash trees may decrease susceptibility to the disease. The sequencing of whole genomic DNA from infected ash trees, different single nucleotide polymorphism (SNP) loci, were identified to be related to ash dieback resistance and were frequently close to putative homologue genes involved in the regulation to pathogen responses in other plant species [143]. Overall, the ash breeding programme and natural selection or hybrid breeding programmes seem to be promising tools for the growth of ash species more resistant to ash dieback [144].

Furthermore, ash dieback caused by *H. fraxineus* should be monitored from a broader environmental perspective. Ash trees are used as windbreaks and are often located along roads bordering agricultural fields, whose crops could become potential hosts for this pathogen and further complicate the epidemiological situation. There are few examples of phytopathogenic fungi and oomycetes having common hosts in forestry and agriculture (e.g., *Fusarium circinatum*, *Phytophthora ramorum* and *Phytophthora cinnamomi*).

Although *H. fraxineus* has not yet been reported to infect agricultural crops, there is a potential risk, especially in the context of global climate change. In addition, there is a related *Hymenoscyphus* spp. (e.g., *H. fructigenus*) that can parasitise fruit from both fruit trees and forest trees, suggesting that this fungus can colonise different environments. For all these reasons, it is necessary to intensify comprehensive monitoring in different environmental niches and to search for sustainable products for the efficient management of ash dieback.

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