An overview of ash (Fraxinus spp.) and the ash dieback disease in Europe

Rasmus Enderle1*, Jan Stenlid2 and Rimvydas Vasaitis2

Address: 1 Institute for Plant Protection in Horticulture and Forests, Julius Kuehn Institute, 38104 Braunschweig, Germany. 2 Department of Forest Mycology and Plant Pathology, Swedish University of Agricultural Sciences, 75007 Uppsala, Sweden.

*Correspondence: Rasmus Enderle. Email: rasmus.enderle@julius-kuehn.de

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Abstract

Ash dieback, caused by the invasive fungal pathogen Hymenoscyphus fraxineus, has become a serious threat to ash trees (Fraxinus spp.) and ash-related ecosystems in Europe. The fast emergence and expansion of this new disease has called for an intensive investigation, which resulted in a large number of research projects in Europe. Recently, as a result of the European cooperation and exchange programme FRAXBACK, numerous reports containing detailed information about the situation of ash dieback in different countries and related research have been published. For this review, we performed a systematic analysis of these country reports. We focussed on differences and similarities between European regions and countries regarding the importance, genetics and resistance of ash, the spread, monitoring, impact and management of the disease and on factors that have an influence on its severity. By including most recent scientific literature, this review provides a concise yet substantial overview about ash and ash dieback in Europe.

Keywords: Ash dieback, Fraxinus, Hymenoscyphus fraxineus, Invasive species, Emerging disease, Forest pathology

Review Methodology: The main source of information for this review is the FRAXBACK book [1] and references therein. Further information was gathered from a special issue on ash dieback of the journal Baltic Forestry [2] and by online searches (e.g. Google, Google Scholar and Web of Science).

Introduction

Ash dieback is a lethal disease of ash trees (Fraxinus spp.) in Europe. It is caused by an invasive ascomycete, Hymenoscyphus fraxineus Baral et al. (syn. H. pseudoalbidus Queloz et al., anamorph: Chalara fraxinea T. Kowalski), which is native to Far East Asia [3–5]. First symptoms of ash dieback have been observed in the early 1990s in north-eastern Poland [6, 7 and references therein, 8], but a genetic study suggests that the introduction of the pathogen to Europe had occurred one to three decades earlier [3]. The disease spreads fast and is today present in most part of the ash distribution range in Europe, causing a dramatic decline of native trees that belong to the genus Fraxinus. Leaves and petioles are infected by airborne ascospores that can be transported over long distances [5, 7]. The fungus can spread to woody tissues through the petiole–shoot junction [9], where it causes bark necroses and locally kills shoots and twigs. The successive crown decline caused by every year occurring infections often is lethal to the trees. Another important yet little understood factor of mortality is the symptom of root collar necrosis, which is most likely caused primarily by H. fraxineus and often is followed by root and but rot. In this regard, wood-decay fungi, particularly fungi of the genus Armillaria, play a presumably secondary yet decisively aggravating role [10–15].

The European dimension of the ash dieback epidemic did soon demand for an international approach to address challenging research questions. Within the European Cooperation in Science and Technology (COST) programme, an action called FP1103 FRAXBACK was conducted from 2012 to 2016, providing a platform for more than 200 scientists from 38 countries and different disciplines to exchange and interact. As a main outcome of this action, a comprehensive book (299 pages) [1] containing detailed country reports about the situation and research regarding ash dieback was published in 2017.
Importance of Ash in Europe

There are four species of ash native to Europe. Common ash (Fraxinus excelsior L.) is the most widely distributed species and present in all European countries except Island, Malta and Portugal, but rather scarce in the Mediterranean. Here, narrow-leaved ash (Fraxinus angustifolia Vahl) and manna ash (Fraxinus ornus L.), which are restricted to more southern parts of Europe, are of higher importance. F. ornus is not very susceptible to ash dieback [21] and a rather small tree, although of economic importance in southern Europe [22]. The fourth species, Fraxinus polliasae Wilmott ex Pallis, grows rarely in steppe and steppe-forest zones in south-eastern Europe, as does a subspecies of common ash, F. excelsior ssp. coriariaefolia [23]. The susceptibility of the latter two taxa to ash dieback is unknown. This review focuses on F. excelsior and F. angustifolia.

In most European countries, ash trees account for 1–2% of the forest area or standing volume stock [8, 23–28]. At the northern distribution range, the share of ash trees is even smaller [29–31], while ash trees hold a slightly higher proportion in forests of central Europe [21, 32–34]. Of particular importance is ash in England and Wales, where the proportion of this tree species in woodland ranges from 4.5 to 12.7% [35], and on the Island of Ireland, where ash is an omnipresent landscape component as a major part of hedgerows and woodland patches [36].

The economical importance of ash in Europe was much greater in ancient times and before the onset of the industrialization, when its wood was indispensable because of its toughness and bending properties and was used widely, e.g. for tools, arms and transport [37]. As a pollarding tree, ash has also been a source of fodder for livestock [29, 37]. In the last century, the use of ash timber has often been replaced by steel or other modern materials. However, ash timber is still a favourite for furniture, certain sports equipment, tool handles and some other goods (e.g. [25, 33]). An example in this respect is the hurl (used in traditional Gaelic sports hurley and camogie), which is crafted from ash wood [36]. Overall, the economic contribution of ash to forestry is considered significant in many regions of Europe, as is indicated in almost all country reports of the book [1]. Moreover, ash is very important from an ecological point of view. It provides critical ecological services, such as wildlife habitat and niche, stabilization of water balance and stream banks, production of high quality litter and as a component in slowing zones for forest fires [24, 25, 35, 38]. A large number of organisms are associated with or even entirely dependent on ash [21, 29, 30, 35, 39]. In forestry, ash was popular also because of its robustness, its drought tolerance, fast growth (on rich sites) and prolific regeneration. In the decades before the outbreak of the epidemic, forestry deliberately increased the proportion of ash in many regions [25, 26, 33].

The importance of ash is also demonstrated by a British study, which identified a wide range of national stakeholders for ash from government, the private sector and civil society that either have an influence on or a special interest in the ash dieback epidemic [40]. However, stakeholders in Romania tend to underestimate the importance of ash and the implications of ash dieback, as was concluded from a survey by Drăgoi et al. [41].

Gene Flow, Genetic Structure and Diversity of H. fraxineus

Several population studies demonstrated that in Europe there is low allelic diversity and little to no genetic differentiation between H. fraxineus populations [26, 29, 31, 34, 35, 42, 43]. Genetic differentiation was even small between long-established populations (from Lithuania) and populations from the epidemic front (in Switzerland), and there was no reduced genetic diversity in the front populations [26, 34]. Also between populations in the UK and Continental Europe there was only little genetic differentiation [43]. The uniform genetic structure throughout Europe indicates high-genle flow and a recent bottleneck due to a very small founder population. In fact, analyses of the coding regions of core eukaryotic genes in Asian and European isolates suggest that the European population was founded by two divergent haploid individuals [44]. This finding is supported by comparisons of European and eastern Asian populations, where much higher genetic diversity and similarly high-genle flow was observed [3, 34, 35]. An ancestry analysis indicates that the Russian Far East is the source of the European populations [3].

It can be assumed from expansion rates and gene flow analyses that viable ascospores are transmitted by wind

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over long distances. However, on a small scale, along a tree species mixture gradient in Germany, some slight population differentiation was observed, which may have reflected recent colonization history [45]. Moreover, an increase of genetic diversity of *H. fraxineus* was observed along an altitude gradient in Poland [8, 46]. Population studies also indicate that the fungus is outcrossing and high-genotypic diversity was detected within the European populations [26, 29, 34, 35, 42]. These results may explain part of the variations in virulence, growth rates, temperature optima for growth and exoenzyme profiles, which have been observed among isolates [47–49].

**Gene Flow, Genetic Structure and Diversity of Ash in Europe**

The genetic structure of European *F. excelsior* populations is still shaped by the ice ages, despite the predominantly outcrossing nature of the species. After the last ice age, the present range was recolonized from glacial refugia in Iberia, Italy, the eastern Alps and the Balkan Peninsula, as was clearly shown by analyses of chloroplast DNA (cpDNA) variation of 62 populations throughout Europe [50]. In western and central Europe, admixture of populations from different refugia and high-gene flow during the recolonization process led to relatively high homogeneity, allelic richness and genetic diversity [36, 51]. For example, 96% of the variation was detected within Irish *F. excelsior* populations with little evidence of population structuring [36].

Results of a recent reciprocal transplanting experiment along a transect from Scotland to the Pyrenees led to an assumption that there is little local adaption in western Europe, as some populations grew well at all sites while local populations never performed best [35]. On the other hand, restricted postglacial gene flow caused by a rapid population expansion in the mountainous topography has likely caused rather strong genetic differentiation over short distances and less genetic diversity within populations in south-eastern Europe, as was suggested by a microsatellite study [51]. There is evidence that the present northern range of common ash was colonized from south-eastern Europe and similarly is characterized by rather limited gene flow and low-allelic richness [29, 31, 50, 52]. It is feared that these more fragmented populations are particularly vulnerable to presumable genetic effects of ash dieback such as loss of allelic structure and inbreeding [31]. In Lithuania, for example, it is very likely that the density of flowering trees and thus the effective population size has already decreased to a degree that compromises the remaining level of genetic diversity and possibilities for successful regeneration of ash populations [26].

When compared with other central European populations, higher genetic variation was detected in south-eastern Germany, where phylogenetic lineages from different refugia meet [33]. The transgression zone between the central and eastern European lineage along Hungary, Slovakia, Czech Republic and Poland could be detected in a corridor of 36 km width when analysing maternally inherited cpDNA, whereas the analysis of bi-parentally inherited nuclear gene markers detected an average width of the transgression zone of 275 km [27]. Another study in Germany confirmed that, while seed dispersal is rather restricted, there is considerable pollen flow at the landscape level [53]. In former times it was believed that *F. excelsior* trees from floodplain forest and from dry, calcareous sites form two ecotypes, but such distinction could never be proved by reciprocal transplants or progeny trials [21, 30]. There are inconsistent results concerning differences in observed heterozygosity between groups of differently susceptible *F. excelsior* trees in Germany and Poland [54, 55].

Similarly to *F. excelsior*, cpDNA analyses of *F. angustifolia* and *F. ornus* populations indicate distinct glacial refugia in southern Europe, with the south-eastern populations being relatively polymorphic [56]. Overall cpDNA diversity in these two species was lower than in *F. excelsior*. Generally, just like *F. excelsior*, *F. angustifolia* is a species with high intrapopulation genetic variation and low differentiation among populations [22]. Only little is known about local inbreeding or outcrossing rates and their impact on the genetic structure of *F. angustifolia* and *F. ornus* [38].

**Genetic Resistance of Ash to *H. fraxineus***

Throughout Europe, there is a remarkable consistency in reports of genotypic differences in susceptibility of *F. excelsior* and *F. angustifolia* to ash dieback. Typically, about 1% of trees show no or only insignificant symptoms (Figure 1) and are considered resistant (or tolerant, depending on definition). Remarkably consistent is also the high degree of genetic control of this quantitative resistance, as was indicated by heritability values in a number of studies from several countries (Table 1). Heritability is defined as the proportion of the total variance due to genetic effects (e.g. [57]). Further evidence for genetic control of the resistance is provided from clonal seed orchards in Austria, the Netherlands, Croatia and Slovakia for both *F. excelsior* [21, 58] and *F. angustifolia* [21, 58–60]. There is also indication that development and severity of ash collar necroses are under considerable genetic control ($h^2$ (narrow-sense heritability) = 0.49 for prevalence and $h^2 = 0.42$ for necrosis width) [61]. Based on these studies it can be assumed with very high certainty that throughout the European populations there is a small proportion of ash trees with genetically controlled resistance. However, there was no significant correlation of damage data between parent ash trees and their offspring in natural regeneration in two heterogenic Austrian ash stands, indicating that environmental conditions and the interaction of genotypes with these play an important role in situ [61, 62].

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phenological mismatch (see section different genotypes is probably due to disease escape or 
neighbouring crowns of two F. excelsior (Sweden), where the ash dieback pathogen arrived probably 2001 or 2002 [73]. Only minor parts of the left crown are still alive, because epicormic shoots, which were produced to compensate for dead twigs, gradually became diseased as well. In contrast, despite similar infection pressure for much more than a decade, the right tree is barely affected by ash dieback. It can be assumed that it possesses a relatively high degree of genetic resistance to ash dieback.

Although some part of the variation in the health status of different genotypes is probably due to disease escape or phenological mismatch (see section ‘Influencing factors’), inoculation experiments clearly indicate that an active defence is involved [66]. The mechanisms that play a role in this defence are still virtually unknown. Different gene expression markers and a coding single-nucleotide polymorphism were associated with resistance to ash dieback and indicate a role of MADS box transcription factors (named after genes MCM1, AGAMOUS, DEFICIENS, and SRF) and iridoid glycoside [74, 75]. Fourier-transform infrared spectroscopy of phenolic extracts from bark tissue proved to be a relatively effective method to identify resistant individuals of ash, although on its own is not indicative regarding underlying resistance mechanisms [76]. However, such technologies can significantly advance efforts in selection and breeding for resistance.

Spread and Monitoring of Ash Dieback

According to Hietala et al. [77], the strong saprobic competence of H. fraxineus in defending the sporulation niche against abiotic stress and microbial competition, which enables production of a large amount of sexual spores, may be a main reason for the successful and invasive spread of this pathogen in Europe. The authors further assume that the ability to produce conidia may be connected to its invasion success, although the biological role of these asexual spores needs further investigation.

Our present knowledge of the spatiotemporal spread of the epidemic throughout Europe is based on dates of observations of symptoms and pathogen records, which is, however, biased by the spatiotemporally uneven presence of forest pathology experts and their individual awareness of the disease. For example, H. fraxineus was first detected in England in 2012 on imported nursery stock, but mortality dating of ash trees indicated that ash dieback was already active in England in 2004 or 2005 [78]. A rough overview of the historical spread of ash dieback throughout Europe was given by McKinney et al. [19], showing a more or less concentric expansion from the epicentre of the disease, which is believed to be located in north-eastern Poland [8]. It is quite likely that the disease in its early stage can be overlooked and that the first introduction remained localized for a prolonged period. The subsequent concentric range expansion is documented in some countries on a regional scale, e.g. in Norway, Switzerland, France and Italy, typically with continuous steps of about 30–70 km per year [31, 34, 79, 80]. It is believed that this pattern of disease spread is mainly due to wind dispersal of airborne ascospores. In contrast, irregular or even inverse disease spread occurred in numerous other countries (e.g. [21, 27, 30, 33]), and there is broad agreement that this is an effect of anthropogenic movement of plant material, i.e. the trade of ash plants. It is probable that even to the UK, despite its isolated geographic situation, H. fraxineus was introduced by both wind dispersal and imports of infected plant material [43].

Large parts of central and eastern Europe have been infested before the first description of the causal agent in 2006 [6] and even larger areas before the correct identification of its teleomorph in 2011 [81]. This is why in mainland Europe there were no official attempts to limit the spread of the disease. H. fraxineus had been listed in the EPPO Alerte List from 2007 to 2014, but has never been listed as a regulated organism (A1 or A2 List) in the Plant Health Directive of the European Union [82]. Only on the British Isles, legislations were changed in order to limit or prevent further introductions from mainland Europe by control of importation of plant material. Moreover, ash plants on infested sites were removed and destroyed [35, 36]. Although soon it became clear that there is no hope that these measures can lead to eradication of H. fraxineus, they were continued in Ireland in order to slow spread and build-up of the disease within the island [36]. Measures to prevent possible outbreaks of ash dieback were also taken in the northern Apennines, Italy, by the Regional Phytosanitary Services of Tuscany and Emilia Romagna [79]. There are concerns that introduction of further pathogen genetic diversity to Europe may cause increased disease severity. It is thus recommended to regulate imports of live ash plants and material that may contain ash leave debris from eastern Asia [44].

Ash dieback and its effects have been monitored in many local trials and forests throughout Europe. An extensive list of studies and sites was provided by Coker et al. [83]. These studies generated much data, which are, however, difficult to compare, because different scoring systems were used and the scoring of ash dieback and its severity is intricate and, in visual assessments, to some degree subjective. Köpina and de Vries [84] compared different methods

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Influencing Factors

Severity of ash dieback in a stand depends on the time of pathogen arrival, the age of ash trees in the stand and several other factors. In numerous monitoring studies a number of factors that were connected to the severity of ash dieback symptoms and the extent of disease-induced mortality have been identified. An overview of factors that were associated with ash dieback is given in Table 2.

As shown there, most of these factors were features of individual trees. Characteristics that are related to age and size of trees are often negatively correlated with the severity of symptoms (i.e. the disease often progresses more slowly on larger or older trees). However, this result depends on the set of investigated trees, which is why such relationship had not been detected in every study (see Table 2 for reference). Moreover, the severity of symptoms is connected to the host tree species, since *F. angustifolia* seems to be slightly less susceptible than *F. excelsior* (and on *F. ornus* only minor symptoms occur on leaves). In a Dutch study, predominantly male ash trees performed better than trees with higher proportions of female flowers. Relatively strong differences in susceptibility were also reported for certain cultivars. Differences in susceptibility between central and western European provenances are only small, but Slovakian provenances apparently differ more, which possibly is connected to higher population differentiation (see the section ‘Gene flow, genetic structure and diversity of ash in Europe’). In Lithuania, autochthonous provenances performed better than foreign ones, which may be due to already commenced natural selection in this long-time infested country, or due to genotype – environment interactions, which were found significant in some trials. Processes of natural selection may also be the reason for young seedlings performing better than regeneration that emerged by sprouting. Trees that are infected by *Armillaria* at the root collar are more likely to be severely damaged in the crown.

The severity of ash dieback symptoms also depends on environmental factors. There is a consensus that moisture and humidity is conducive for the disease. These factors seem to be especially important for the symptom of collar lesion [13]. It was speculated that the formation of apothecia on shoots and roots, which generally occurs only very rarely, may be of higher importance in the wet, maritime climate of Ireland [36]. Although it was not confirmed in a study on veteran trees in Sweden [39], it is a general observation that trees in forests are more severely affected than trees in the open landscape [21], which may be due to higher humidity and infection pressure. On the other hand, there is evidence that drought and high temperature are unfavourable for ash dieback [89].

### Table 1 Heritability values for traits related to ash dieback severity (crown symptoms) as a measure for genetic control of resistance to ash dieback

<table>
<thead>
<tr>
<th>Country</th>
<th>Trial type</th>
<th>Number of sites</th>
<th>Year of establishment</th>
<th>Time of data collection</th>
<th>Species</th>
<th>Heritability value(s)</th>
<th>Reference(s)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Denmark</td>
<td>Progeny</td>
<td>1</td>
<td>2003</td>
<td>2009–2014</td>
<td><em>F. excelsior</em></td>
<td>$h^2$: 0.42–0.53</td>
<td>[63]</td>
</tr>
<tr>
<td>Denmark</td>
<td>Progeny</td>
<td>2</td>
<td>2004</td>
<td>2008–2010</td>
<td><em>F. excelsior</em></td>
<td>$h^2$: 0.37–0.52</td>
<td>[64]</td>
</tr>
<tr>
<td>Denmark</td>
<td>Clonal</td>
<td>2</td>
<td>1998</td>
<td>2007–2009</td>
<td><em>F. excelsior</em></td>
<td>$H^2$: 0.25–0.54</td>
<td>[65, 66]</td>
</tr>
<tr>
<td>France</td>
<td>Progeny</td>
<td>1</td>
<td>1995</td>
<td>2010–2014</td>
<td><em>F. excelsior</em></td>
<td>$h^2$: 0.42</td>
<td>[61]</td>
</tr>
<tr>
<td>Germany</td>
<td>Clonal</td>
<td>4</td>
<td>1991–1995</td>
<td>2012–2013</td>
<td><em>F. excelsior</em></td>
<td>$H^2$: 0.48–0.59</td>
<td>[67]</td>
</tr>
<tr>
<td>Lithuania</td>
<td>Progeny</td>
<td>2</td>
<td>2005</td>
<td>2010</td>
<td><em>F. excelsior</em></td>
<td>$h^2$: 0.40–0.49</td>
<td>[26, 68]</td>
</tr>
<tr>
<td>Lithuania</td>
<td>Clonal</td>
<td>7</td>
<td>2012</td>
<td>2012–2013</td>
<td><em>F. excelsior</em></td>
<td>$H^2$: 0.21–0.65</td>
<td>[26, 69]</td>
</tr>
<tr>
<td>Slovenia</td>
<td>Clonal</td>
<td>1</td>
<td>1989</td>
<td>2009–2012</td>
<td><em>F. angustifolia</em></td>
<td>$H^2$: 0.23–0.50</td>
<td>[70]</td>
</tr>
</tbody>
</table>

$h^2$, broad-sense heritability; $h^2$, narrow-sense heritability. The values are based on studies with different settings and plant materials.
The disease risk is considered to be low in warm areas of southern Europe and global warming is expected to alleviate the disease to some extent in the future [89, 90]. Thinning can change the microclimate and possibly alter conditions of infection and reduce disease severity. However, in young even-aged ash stands in Denmark, disease severity was the worst in unthinned plots, but otherwise unrelated to stand density [91]. Pruning of diseased branches reduces the probability of stem infections, although such control tactic may not be economical [92]. Interestingly, old trees that had been pollarded some decades ago are less affected than other more recently or not at all pollarded veteran trees [39]. Although some fungal ash endophytes with high in vitro antagonistic activity against H. fraxineus have been identified [93–96], an influence of endophytic mycobiomes on the health status of ash trees (i.e. the susceptibility to ash dieback) or on the establishment of the pathogen has not yet been demonstrated [77, 94, 96, 97].

Impact of Ash Dieback on Timber Logging

An obvious reaction to ash dieback is increased timber logging due to salvage cuttings. Published data on this increase, however, are relatively rare and often of rather indirect nature. Swedish national forest inventory data reveal a notable decline of the standing timber stock since 2009, which is probably due to increased cuttings in stands damaged by ash dieback [29]. In Lithuania, where symptoms of ash dieback were first observed in 1996, heavy salvage cutting (selective felling and clearcutting of more than 1500 ha of ash stands) commenced in 2001 [26]. Annual salvage cutting reached its maximum in 2006 (about 3500 ha) and smoothly decreased down to about 1000 ha in 2015. At this time, 18 years after the first observation of symptoms, the former area of ash stands was reduced by more than 50% [26]. Clearcutting was also carried out in other countries. For example, as an ultimate option, immature but heavily devastated ash stands often have been clearcut in Austria [21, 98]. In Grafenegg (Austria), where ash dieback arrived about 2005, logging of ash more than doubled by 2011, quadrupled by 2014 and sextupled by 2015 when compared with 2008. A similar exponential increase in timber logging is reported from state owned forests in Baden-Württemberg, Germany [98], and from Denmark [19, 98]. In Wallonia (Belgium), a very sharp increase in the number of ash timber lots greater than 50 m³ was recorded in 2015 [32]. In summary, it can be said that sharp increases of ash timber logging commenced 5–8 years after ash dieback symptoms were detected in a region or country for the first time.

Management of Ash Dieback

Silvicultural strategies in response to ash dieback were reviewed comprehensively by Skovsgaard et al. [16], who concluded with the main advice to retain tolerant-appearing ash trees wherever reasonable within the context of management objectives and overall forest structure in order to preserve these genetic resources (i.e. heritable resistance). However, there are reports from numerous countries that forest owners do not always

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Table 2
Factors that are associated with symptom severity or mortality due to ash dieback according to references in the FRAXBACK book [1]

<table>
<thead>
<tr>
<th>Factor</th>
<th>Symptoms are more severe on/at ...</th>
<th>Reference(s)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Characteristics of individual trees</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Host species</td>
<td>F. excelsior compared with F. angustifolia (depending on site)</td>
<td>[27, 84]</td>
</tr>
<tr>
<td>Gender</td>
<td>male trees</td>
<td>[58]</td>
</tr>
<tr>
<td>Provenance</td>
<td>Not applicable</td>
<td>[25–27, 33, 66]</td>
</tr>
<tr>
<td>Cultivar</td>
<td>Not applicable</td>
<td>[25, 58, 84]</td>
</tr>
<tr>
<td>Leaf yellowing/leaf shed</td>
<td>later shedding trees</td>
<td>[66]</td>
</tr>
<tr>
<td>Spring phenology</td>
<td>later flushing trees</td>
<td>[25, 26, 29, 87]</td>
</tr>
<tr>
<td>Diameter at breast height (DBH)</td>
<td>(inconsistently) trees of smaller DBH</td>
<td>[26, 29, 39, 80]</td>
</tr>
<tr>
<td>Crown surface projection</td>
<td>trees with smaller crowns</td>
<td>[8]</td>
</tr>
<tr>
<td>Age</td>
<td>(inconsistently) younger trees</td>
<td>[25, 33, 88]</td>
</tr>
<tr>
<td>Seeding versus sprouts</td>
<td>sprouts</td>
<td>[26]</td>
</tr>
<tr>
<td>Armillaria root rot</td>
<td>Armillaria-infected trees</td>
<td>[26]</td>
</tr>
<tr>
<td>Site conditions</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Altitude</td>
<td>lower altitudes</td>
<td>[25]</td>
</tr>
<tr>
<td>Shade, woodland, open, grazed</td>
<td>(inconsistently) shaded, forested sites</td>
<td>[21, 39, 84]</td>
</tr>
<tr>
<td>Temperature</td>
<td>low to moderate temperature</td>
<td>[28, 79]</td>
</tr>
<tr>
<td>Drought, arid climate</td>
<td>less dry sites</td>
<td>[21, 23, 28, 79]</td>
</tr>
<tr>
<td>Moisture, humidity</td>
<td>more humid sites</td>
<td>[21, 79]</td>
</tr>
<tr>
<td>Soil type</td>
<td>not specified</td>
<td>[27]</td>
</tr>
<tr>
<td>Management</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Pollarding, pruning</td>
<td>Inconsistent results</td>
<td>[39, 58]</td>
</tr>
<tr>
<td>Thinning</td>
<td>Not significant</td>
<td>[29]</td>
</tr>
</tbody>
</table>

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follow this advice, which may be due to the lack of information [39], economic reasons [26] or general loss of interest and expectation regarding forestry with ash [21, 25, 26, 33]. The latter often is connected to the experience of observing declining trees that appeared resistant in the early stages of the disease.

Generally, official recommendations for disease management in the ash dieback-affected countries are in line with the strategies that are proposed in the silviculture review [16], but there are regional adaptations and emphases of certain aspects. For example, measures to prevent disease spread and inoculum build-up (i.e. destruction of infected plants, plant material and leaf litter) were carried out extensively in the British Isles, although with low impact [35, 36]. In contrast, in continental Europe there were only a few local attempts to slow down the spread of the disease, e.g. in order to prevent outbreaks in the Apennines in Italy [79]. Awareness of the risks rose too late for efficient quarantine measures in large parts of Europe, where the disease spread before fundamental knowledge was available.

In most infested countries nursing and planting of new ash trees is not recommended and has decreased sharply since the onset of the disease [24, 25, 29, 32, 33, 58, 66]. In Poland, the production of ash plant material even was banned completely [8]. On the other hand, large numbers of ash plants were still produced in Slovakia (up to 873,000 plants in 2015), where 150,000 to 175,000 trees were annually planted in the forests [27]. In 2017, planting of ash was still subsidized in Flanders, Ireland and Greece [22, 24, 36]. At the northern limit of the range of F. excelsior, planting of healthy seedlings from local sources is considered to be the best option to prevent loss of genetic diversity on the one hand and loss of local adaption on the other [31], which both is crucial in these areas (see the section ‘Gene flow, genetic structure and diversity of ash in Europe’). A similar strategy is also proposed in so far not infected areas, i.e. in Portugal, with the aim to increase among- and within-population genetic diversity and hence prepare ash populations for invasive pathogens such as H. fraxineus [38].

Tending and early thinning is recommended in Poland in order to increase tree vigour, which helps ash trees to survive the disease, by fostering the growth of crowns and root systems [8]. In Germany, such early promotion is recommended only for resistant appearing ash trees [33], whereas in Lithuania pre-commercial thinning is recommended only in heavily damaged stands with low proportions of ash [26].

For the management of middle-aged stands there are different concepts that depend on the severity of the disease and the proportion of ash. Generally, stands should be thinned as usual to promote canopy development while focusing on retaining resistant appearing trees and species other than ash. Foresters in Sweden are advised to mark the healthiest ash trees in order to avoid cutting these in error and to enable somewhat objective observations of the development of the disease over time [29]. In Norway it was recommended to preferably remove susceptible ash trees in order to lower the local overall infection pressure and to reduce their genetic influence on the next tree generation [31]. However, new research demonstrated that trees with higher levels of crown damage produce much less amounts of propagules than healthier trees [99]. This relationship is stronger for seeds than for pollen, so it seems recommendable to focus particularly on diseased male trees when thinning. Valuable timber should be harvested before wood quality deteriorates. If, however, it can be expected that the damage will become too large to allow for silvicultural control of stand development, salvage felling of larger parts of the stand or even clearcutting may be the only options.

Replacement of ash trees that have died or have been felled due to the disease can be achieved by either natural forest regeneration or planting. Natural regeneration of ash can be used and even fostered, e.g. by retaining some relatively healthy ash individuals as seed trees, as is recommended in Lithuania and Estonia [18, 26]. Since planting of new ash trees is, if at all, recommended only exceptionally (see above), the choice of alternative tree species needs to be considered carefully. Especially in monocultural ash woodlands, which often is the case in Ireland, it is suggested to aim for a transition to more mixed species forests, in order to build a greater degree of resilience [100]. There is a consensus that replacement in forests by non-native Fraxinus species is not a preferable option, even if these species are more resistant to ash dieback [16, 18, 21, 23, 25, 30, 33]. Instead, recommendations for alternative tree species are mainly based on specific site adaption and thus differ between regions and countries. In Great Britain, the ability of tree species and species mixtures to substitute the ecosystem functions of ash is considered as an additional important criterion [35, 101].

**Conclusion**

Ash species native to Europe provide important ecosystem services and are considered of high value both as ornamental trees and as a forest component. In many places, particularly in central Europe and the British Isles, wood production with F. excelsior or F. angustifolia contributes significantly to local economy. There is little genetic differentiation of ash populations in western and central Europe, but some population differentiation is characteristic to its eastern and, due to local adaptation, particularly to its very northern range. The European population of H. fraxineus is characterized by extremely low genetic variation and local differentiation, which is a result of its recent introduction, its subsequent rapid spread and effective sexual outcrossing. The disease spread both by wind dispersal of ascospores and by human-mediated transportation of infected plant material. Large parts of
the continent were infested before the identification of *H. fraxineus* as the causal agent of ash dieback, and sharp increases of ash timber logging typically commenced 5–8 years after ash dieback symptoms were detected for the first time in a region.

Severity of ash dieback is influenced by individual tree characteristics (e.g. tree age) and site conditions (e.g. moisture or humidity), but there is rather little and inconsistent evidence for an influence of forest management practices. Strategies for disease management, which differ slightly between countries, thus aim mainly for the retention and propagation of resistant or tolerant trees. Heritability values for ash crown damage and other disease-related traits from numerous clonal trials and progeny trials were consistently high, regardless of their location in Europe. This is an indication for strong genetic control of these traits, although it was not yet possible to demonstrate a connection of tree health between parent trees and natural regeneration under heterogeneous conditions.

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**References**


http://www.cabi.org/cabreviews


64. Kjær ED, McKinney LV, Nielsen LR, Hansen LN, Hansen JK. Adaptive potential of ash (Fraxinus excelsior) populations


http://www.cabi.org/cabreviews