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Ash dieback in Germany: research on disease development, resistance and management options

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Abstract
Ash dieback caused by *Hymenoscyphus fraxineus* reached Germany at the latest in 2002. Various projects investigating the disease and the genetic resistance in *Fraxinus excelsior* have since then been carried out in the country. This review summarizes these studies, depicting in detail the drastic progression of the disease and its devastating impacts. The potential of the genetic resistance against ash dieback is discussed on the background of the genetic structure of German ash populations. In the end, recommendations for the management of diseased ash populations in Germany are given, which aim to preserve the species, retain genetic resources of ash and propose alternative tree species for typical ash habitats.

Keywords: Ash dieback, *Fraxinus excelsior*, *Hymenoscyphus fraxineus*, Resistance breeding, Forest disease management, Genetic diversity

Introduction

Ash dieback is a severe disease that currently devastates the European populations of *Fraxinus excelsior* L. and *Fraxinus angustifolia* Vahl. The causal agent is the ascomycete *Hymenoscyphus fraxineus* Baral et al. (anamorph: *Chalara fraxinea* T. Kowalski). Most likely it originates from Far East Asia where it lives non-pathogenically on Asian *Fraxinus* species (Marčiulynienė et al. 2013, Zhao et al. 2013, Baral and Bemmann 2014, Gross et al. 2014b, Zheng and Zhuang 2014). In contrast, it causes necroses on leaves and twigs on the mentioned European species, resulting in massive crown dieback after several years of infection (e.g. Bakys et al. 2009, Kirisits et al. 2009, Skovsgaard et al. 2010, Gross et al. 2014a). Moreover, the fungus is able to colonize the bases of stems (Husson et al. 2012). In combination with other fungi and particularly *Armillaria* spp., this leads to severe basal lesions and collar rots (Lygis et al. 2005, Skovsgaard et al. 2010, Bakys et al. 2011, Husson et al. 2012, Enderle et al. 2013). The disease already led to massive salvage felling and mortality and endangers the future utilization of ash in European forestry. However, high genetic resistance against ash dieback is present in a small fraction of ash individuals, possibly providing a solution to sustain ash species in European forests (e.g. McKinney et al. 2014).

Ash is strongly infested by ash dieback in Germany, where the dramatic consequences of the disease and the lack of knowledge about management options gave rise to a number of research projects. This review summarizes the importance of ash and the spread of ash dieback in Germany. Moreover, studies about the development and impact of the disease and the genetics of ash including genetic resistance in German forests are presented. The review also summarizes management options that are currently recommended in Germany. German research about *Hymenoscyphus fraxineus* and the compounds produced by this fungus (e.g. Junker et al. 2014, Halecker et al. 2014) is not part of this review.

Importance of ash in Germany

In Germany, *Fraxinus excelsior* is the only native ash species and the only ash species with noteworthy relevance in forestry. Moreover, European ash is a popular ornamental tree species in gardens, parks, hedges and avenues. Other ash species such as *F. ornus, F. angustifolia* and *F. pennsilvanica* only play a minor role as ornamental trees in urban areas.

According to the third National Forest Inventory (NFI, data kindly provided by Gerald Kändler), which was conducted in 2012, ash covered an area of about 250,000 ha in Germany, which corresponds to 2.4 % of the total forest area. The ash stock was estimated at 74.7 million solid cubic meters (including bark). Although ash trees can be found all over Germany, its abundance is unevenly distributed. Only on calcareous soils, in flood plain forests and ravine forests ash is a main tree species and thus of special importance in certain regions. About a quarter of the total German ash area (25.3 %) and ash stock (23.8 %) is located in the federal state of Baden-Württemberg in south-western Germany (third NFI).

The ability of natural ash regeneration to dominate and outcompete admixed tree species on certain sites in Germany is called "Vereschung" (Fraxinisation). It has been discussed as a problem in former times, especially because of the high light transmission of ash dominated canopies in mature stands that promotes the emergence of undesired dense layers of grasses and herbaceous plants (e.g. Miegroet 1956, Börth 1990, Wagner 1990, Rysavy and Roloff 1994). In recent decades, however, German forest policies aimed to increase the area of ecologically stable mixed forests (e.g. Mantel 1990, Schriewer 2001, Baumgarten and von Teuffel 2005). In the course of this forest conversion, ash as a native, robust and ecologically and economically valuable tree species had been increasingly planted and its regeneration had been promoted. Moreover, facing climate change, the high drought tolerance of ash had been considered advantageous (Schmidt 2007, Anon 2008). Overall, the area covered by ash in Germany increased by 17.4 % from 2002 to 2012 (second and third NFI). Only in the federal states of Schleswig-Holstein and Mecklenburg-Western Pomerania the area covered by ash slightly decreased during this period of time, which possibly is connected to the relatively early infestation of these states by ash dieback.

The importance of ash in Germany is reflected by a high number of certified seed stands (e.g. 155 stands in Bavaria). Seeds had been harvested regularly until the outbreak of ash dieback. Forestry now runs the risk of losing this economically and ecologically valuable tree species for mixed forests due to the increasingly severe ash dieback.

Disease history of ash dieback in Germany

The first remark in the literature about ash dieback in Germany (Heydeck 2005) reports the incident of typical ash dieback symptoms affecting young *F. excelsior* trees in 2002 in the federal states of Brandenburg, Mecklenburg-Western Pomerania and Saxony-Anhalt (north-eastern Germany). Such widespread distribution in 2002 allows the presumption that the pathogen was already present in Germany some years before. And indeed, already in 2000 / 2001, disease symptoms have been recorded in Mecklenburg-Western Pomerania (pers. com. Paul Heydeck) and Hamburg but not assigned to ash dieback. *Chalara fraxinea* was reported in 2007 for the first time in Germany (Schumacher et al. 2007). Meanwhile, the disease is distributed in all German federal states (Fig. 1). In Schleswig-Holstein, Saxony and Bavaria, disease symptoms were observed in 2005, and *H. fraxineus* was proved to be the causal agent in 2006, 2008 and 2008, respectively. Ash dieback reached Lower Saxony and Baden-Württemberg at the latest in the year 2006, while the pathogen was laboratory-confirmed in 2006 and 2009, respectively. In North Rhine-Westphalia ash dieback was observed in the year 2007 and confirmed in 2008. In Hesse and Thuringia first symptoms and evidence of *H. fraxineus* were reported in 2008 and 2009, respectively. First but unassigned symptoms of ash dieback were recorded in Saarland in the year 2008 and 2009, but the presence of *H. fraxineus* was verified in 2010. The last federal state where ash dieback was observed is Bremen (in the year 2012). In the beginning of the infestation of new areas, the disease and especially disease induced mortality was realised only in young plantations, nurseries or natural regeneration. There was some time lag, until symptoms in adult trees attracted attention (e.g. Schumacher et al. 2007, Metzler 2010). Like on the European level, in Germany no alert or quarantine status could be established during the cryptic dissemination of the disease before it became obsolete. Trade and transportation of ash plant material undoubtedly contributed to the fast spread of the pathogen within Germany.

Development and impact of ash dieback

Ash dieback in provenance trials

In south-western Germany, the development of ash dieback has been monitored in a provenance trial in four different stands consisting of more than 1900 *F. excelsior* trees in total that belong to eight provenances from southern Germany (Metzler et al. 2012, Enderle et al. 2013, Erbacher 2015).

Figure 1 First reports and laboratory-confirmed evidence (bold) of ash dieback caused by *Hymenoscyphus fraxineus* in Germany (●) and percentage of ash in forest areas in German federal states (except city states) according to the German National Forest Inventory 3 (2012): ■ = 0.3 % ash, ■ = 1-1.7 % ash, ■ = 2.1-2.4 % ash, ■ = 3.1-3.6 % ash, ■ = 4.9 % ash. Map created by the Northwest German Forest Research Station in 2016, Dep. Forest Protection B4, compiled by Gitta Langer. Data of the National Forest Inventory 3 (BWI 2012) was provided by Gerald Kändler, FVA-BW. Background source: GeoBasis-DE/BKG2010.

The trial was established in 2005 with three years-old saplings. When data collections started in July 2009, it was possible to record earlier affections of trees retrospectively. Since then they have been repeated every year. Tree individual disease affection was classified according to the number of infected twigs. Results are presented in Figure 2 that shows a massive disease progress. Mortality increased exponentially and reached 28.3 % in 2015. On the other hand, only 1.7 % of the trees in 2015 were symptomless in the crowns. Unfortunately, two of the stands were flooded in July 2014 and data collection was thus carried out in mid-August. During this time, premature leaf fall had already occurred, and the assignment of the trees to the classes 0 – 3 was hampered and thus probably to some part inaccurate.

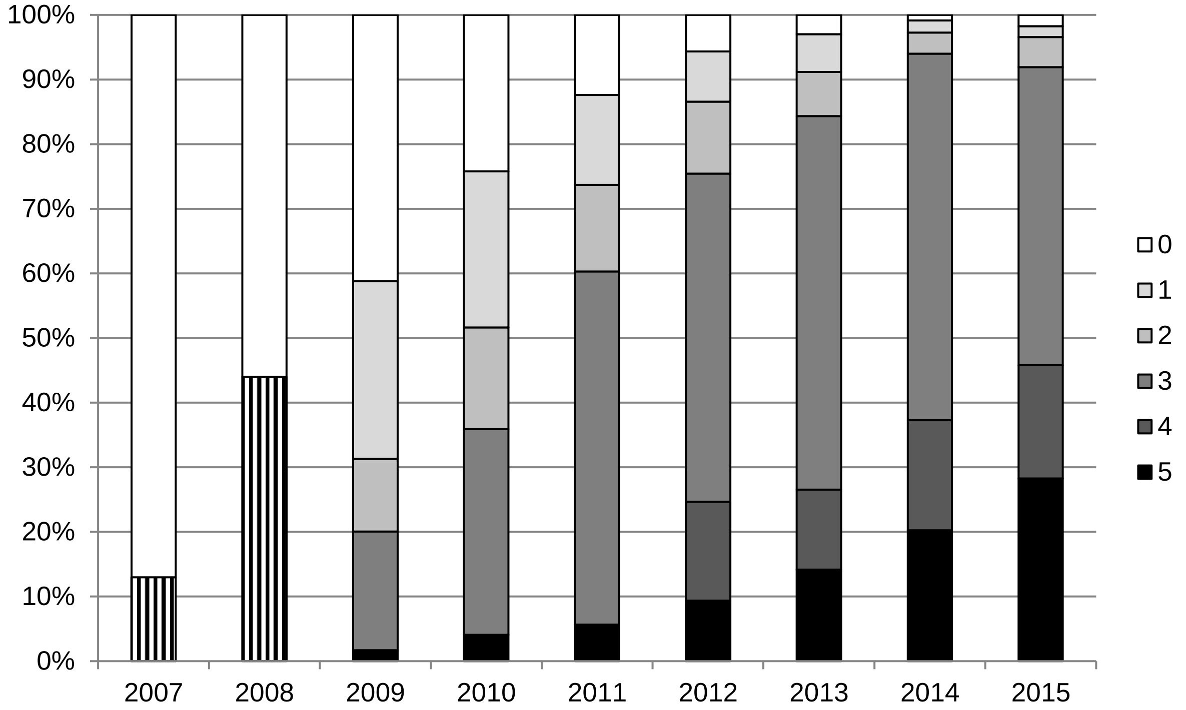

Figure 2 Development of the proportion of trees in classes of disease intensity in a provenance trial from 2007 to 2015, updated from Enderle et al. 2013. For retrospectively analysed years, data are only distinguishing between healthy and affected (hatched bars) individuals. Class 0: healthy, class 1: less than three symptomatic shoots, class 2: less than five symptomatic shoots, class 3: five or more symptomatic shoots, class 4: more than 50 % symptomatic shoots (has been applied since 2012), class 5: dead.

Differences between provenances in crown damage were evident in the beginning of the study (Metzler et al. 2012, Enderle et al. 2013), but became less and less pronounced in the course of disease progress. In 2015, these differences were rather negligible, although still statistically significant (Erbacher 2015).

The presence of collar rots in the trial was recognized in 2011 for the first time and has been recorded systematically since 2012. Molecular investigation of bark samples from collar rots in that year indicated that the involved honey fungus belonged to *Armillaria gallica*. Analyses of the distribution of collar rots in the provenance trial revealed a strong spatial dependency with range from 3.3 m to 11.0 m in different stands. This suggests an influence of micro location conditions on collar rot prevalence. Moreover, collar rot prevalence was highest in the wettest parts of the stands, indicating that collar rot formation is favoured by soil moisture. There was no evidence for differing susceptibility to collar rot between the provenances.

The proportion of living trees with collar rot was 32.6 % in 2012, 46.9 % in 2013, 49.7 % in 2014 and 51.2 % in 2015 (Enderle et al. 2013, Erbacher 2015). Recently, it was shown that susceptibility to collar rot is genetically determined (Muñoz et al. 2015). The little increase of collar rot infections in the last years raises hope that the remaining trees in the trial exhibit relatively high genetic resistance against infections at root collars or are surrounded by micro location conditions that prevent from collar rot formation. By now, collar rot is the most important mortality factor in the provenance trial. Collar rot was present in 92.5 % of the trees that died between 2014 and 2015 and in 84.4 % of the trees that died between 2013 and 2014 (Erbacher 2015).

In a 28 year old provenance trial in Bavaria including fourteen provenances from Germany, two from Switzerland and one from Romania (established in 1988 (Kleinschmit et al. 2002)) ash dieback has been observed since 2011 in every second year. Altogether 592 trees were monitored and damage was recorded following the classification scale elaborated by Lenz et al. (2012). Mortality of the trees increased severely up to 18.6% in 2015, whereas healthy trees dropped down to 3.5% (Figure 3).

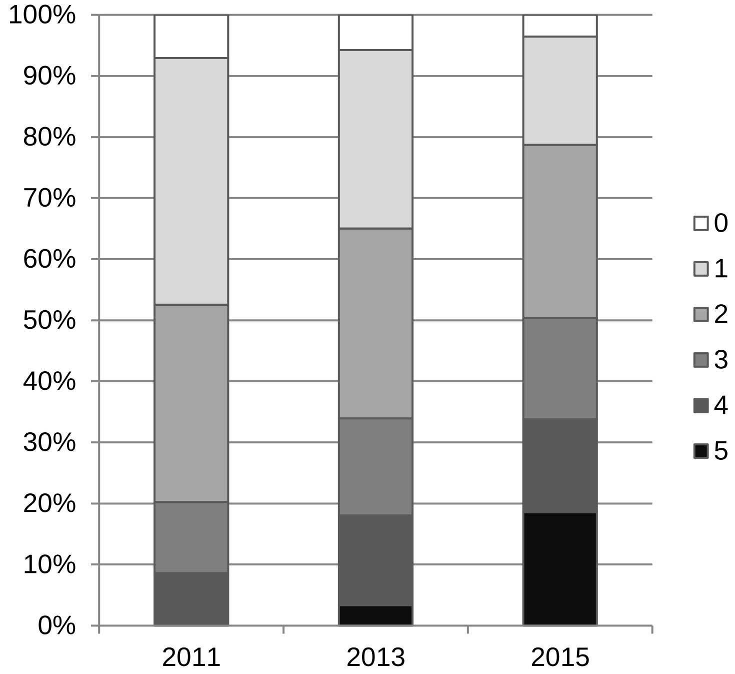

Figure 3 Observation of disease intensity in a provenance trial in Bavaria installed in 1988. Each tree was classified into one of six classes, starting from class 0 for trees with no symptoms to class 5 with 100% damage.

Ash dieback in stands of differing age in southern Germany

In south-eastern Germany, the development of ash dieback, its disease expansion and severity was examined on 22 study sites, capturing differences not only between habitats, but also between age classes (Lenz et al. 2016). The sites included eight mature stands with a total of 230 trees, six pole stands with 584 trees and eight young growth stands with 579 trees. For vitality determination a scoring system was applied that uses six vitality classes (from 0 to 5, Lenz et al. 2012). Depending on their crown defoliation, ash trees belonging to the vitality classes 0 and 1 were less affected, trees within the vitality classes 2 and 3 moderately to seriously affected and trees of the vitality classes 4 and 5 were dying or already dead. Figure 4 shows the development of tree vitality over a period of five years. In 2010, no disease-free areas were found anymore. As we cannot determine how long the fungus has already been present in the different stands and because the initial degree of infestation differed massively (Figure 4), a comparison between the stands is rather difficult. Generally, mortality rates were higher in young growth stands and pole stands compared to mature stands. The development of vitality in some ash stands was not assessed in 2015, because of high mortality rates. With the exception of one young growth stand (No. 24) where only 16 % of the trees were assigned to the vitality classes 4 and 5, all other stands showed mortality rates from more than 50 % up to 95 % in 2014. Three from six pole stands were massively affected by the disease, exhibiting mortality ranging from 37 % to 78 % in 2014. In all mature stands a drastic shift from vitality classes 0 and 1 to 2 and 3 could be observed. Compared to pole and mature stands, the average vitality decreased much faster in most of the young growth stands, even though these stands were already more diseased in the beginning of the monitoring (Lenz et al. 2016). The monitoring will be continued in future. In summary, decreasing vitality accompanied by increasing mortality could be detected in all examined ash stands, regardless of age and habitat. Surprisingly, no correlation between the extent of the mortality and the geographical position of the stands was observed, although the disease was first detected in the southern part of the area of investigation.

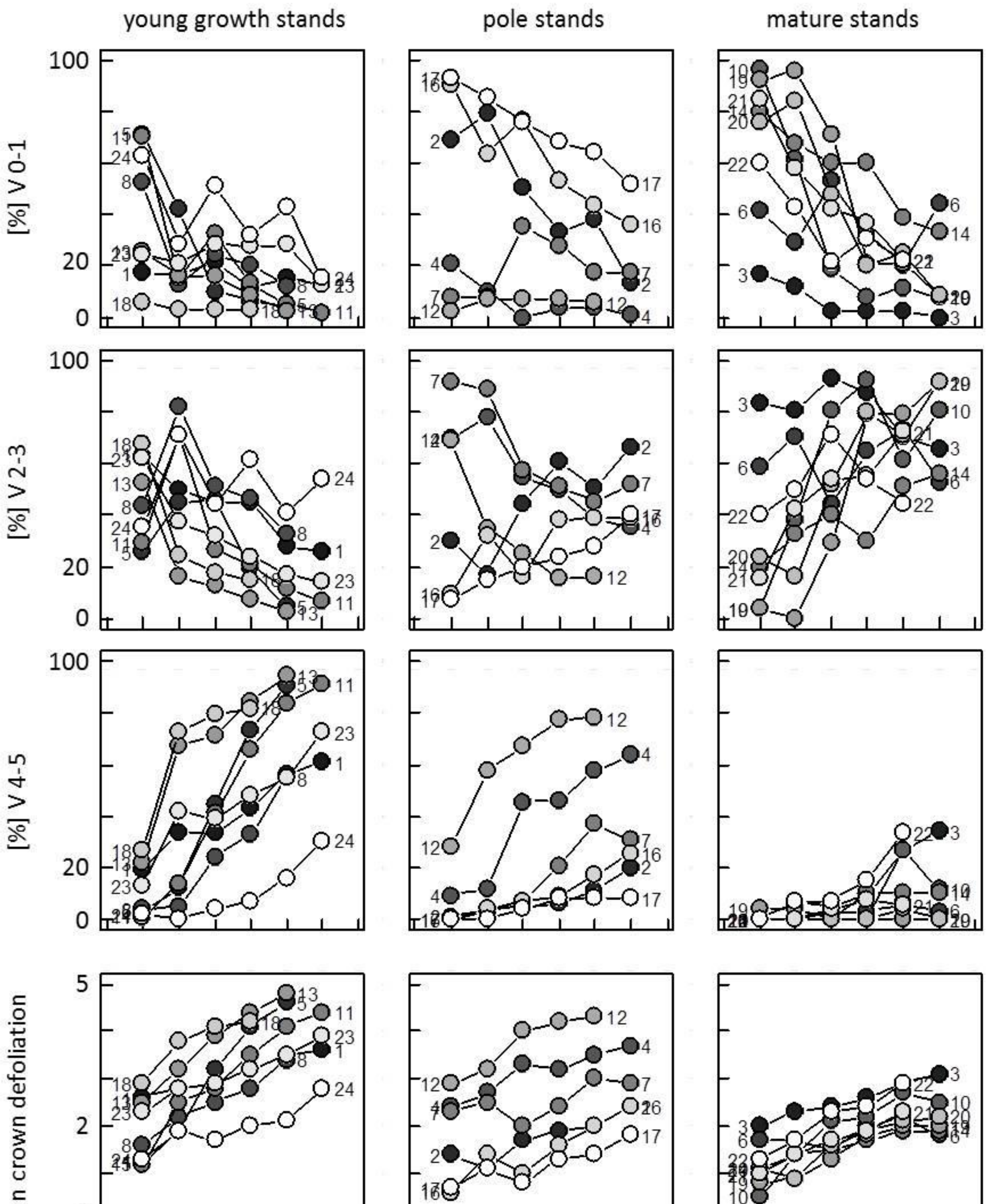

Figure 4 Proportions of trees in classes of crown defoliation V 0-1 (healthy or slightly diseased), V 2-3 (moderately diseased) and V 4-5 (dying or dead) are illustrated for young growth-, pole and mature stands from 2010-2015. The development of the mean crown defoliation (classes 0-5) for each study site is shown at the bottom. Numbers indicate different study sites (updated from Lenz et al. 2016).

Ash dieback in north-western Germany

In north-western Germany, infections and mortality due to ash dieback were monitored in five ash stands of differing age (Langer et al. 2015a). High fractions of infected trees in this and additional ash stands in 2013 and following years demonstrate the fast spread of the pathogen (Table 1). Strong infestations take place in young and old ash stands, natural regenerations and in urban greens, resulting in high mortality. For example, a site afforested with saplings exhibited an infection rate of 80 % one year after planting (Langer et al. 2015a) and 100 % after five years, and mortality added up to 73 %. Especially in Schleswig-Holstein, but also in the other federal states, tree mortality is increasing and often connected with collar necroses. The latter are often associated with *H. fraxineus* or *Armillaria* root rot (Langer et al. 2015b). Therefore, salvage cuttings, especially because of traffic safety responsibilities, had been necessary since 2009 (Langer et al. 2015a). In all investigated sites, the proportion of infected trees and the mortality increased drastically (Table 1). Natural regeneration stands exhibited the highest fraction of healthy trees, but nevertheless were prone to high mortality (Table 1).

Table 1 Mortality and proportions of diseased trees (with regard to crown symptoms) in several ash stands in north-western Germany. na = not applicable because data not compiled.

Location	Forest type	N trees	Tree age 2013	Proportion of diseased trees [%]			Mortality [%]		
Year				2013	2014	2015	2013	2014	2015
Hesse, Neueichenberg	Natural regeneration	543	Ø 5	35	55	80	6	14	38
Hesse, Schotten	Mixed broadleaf forest (natural regeneration)	358	24-125	100	100	100	13	14	22
Lower Saxony, Göttingen	Natural regeneration	489	Ø 3	21	50	71	4	12	23
Lower Saxony, Göttingen	Mixed broadleaf forest (natural regeneration)	318	19-170	100	100	100	0	0,3	1,5
Lower Saxony, Stroit	Afforestation	157	4	99	100	100	62	73	na
Lower Saxony, Stroit	Afforestation	447	15	na	96	99	na	35	39
Lower Saxony, Goseplack	Afforestation	2336	15	100	na	na	36	na	na
Lower Saxony, Riefensbeek	Afforestation	2337	15	100	na	na	7	na	na
Lower Saxony, Elm	Mixed broadleaf forest (natural regeneration)	116	32-134	100	100	100	0,9	3	4
Schleswig-Holstein, Lauenburg	Mixed broadleaf forest (natural regeneration)	220	29-155	100	100	100	15	18	25
Schleswig-Holstein, Scharbeutz	Afforestation	2350	15	100	na	na	54	na	na
Schleswig-Holstein, Satrup	Mixed broadleaf forest	60	93-145	100	100	100	23	23	30

Ash dieback in sample points of the National Forest Inventory

The latest NFI of Germany was conducted in 2012 at permanently marked random sample points in a systematic grid. According to the data of this inventory, ash trees were present at 1.373 sample points of the NFI that are located in the Federal State of Baden-Württemberg in south-western Germany. In July and the first week of August 2015, a special inventory focussing on ash dieback was conducted at a random subsample of 529 of these sample points in order to gain representative data of ash dieback severity in a supra-regional area (Enderle et al. 2015a). This inventory included 1.627 adult ash trees (DBH greater than 7 cm) and 698 regeneration ash trees (taller than 0.5 m and DBH smaller than 7 cm). For every adult tree, crown defoliation and the portion of epicormic shoots of the living crown were assessed in percentage classes. The portion of epicormic shoots turned out to be a suitable indicator for individual susceptibility towards ash dieback (Enderle et al. 2015b). Moreover, the presence or absence of collar rot was recorded for every tree with DBH greater than 7 cm. The data of the regular NFI 2012 was used as a basis to calculate the volume of wood in cubic meters for the respective categories of ash dieback symptoms. For the regeneration trees, ash dieback severity was scored according to the number of infected shoots.

In total, 39.2 % of the total ash stock of Baden-Württemberg, that was 17.8 million cubic meters in 2012 according to the NFI, consisted of ashes with crown defoliation higher than 60 %. Considering these trees as insufficiently vigorous, this means that almost 7 million cubic meters will have to be harvested within the next few years or will decay unused. Ash trees with proportion of epicormic shoots higher than 60 % even accounted for 62.2 % of the total ash stock, giving an indication of the volume of trees that are too susceptible to survive in the long term. Ash trees exhibiting collar rot accounted for 17.5 % of the ash stock. On the other hand, 6.7 % of the ash stock consisted of trees with little crown defoliation and portion of epicormic shoots (less than 25 %) and without collar rot. This fraction of trees might be resistant enough to survive sustainably, although formation of new collar rots is still possible.

The volume of wood consisting of trees that had been harvested or died between the last two inventories (2012 - 2015) was 55.1 % higher for ash than for other tree species on the investigated sample points. Ash trees that died naturally accounted for 10.8 % of this volume, whereas trees of other species that died naturally accounted for only 2.3 % of this volume. This depicts the problem that the timely harvest of the now frequently dying ash trees is not always feasible.

The high sample size allowed the comparison of ecoregions, which revealed considerable differences in the severity of the disease. Crown defoliation and portion of epicormic shoots were smallest in the ecoregion “Neckarland”. Also collar rots were relatively rare in this ecoregion. Forests of the Neckarland are located mainly in colline altitudes of the Keuper Uplands with moderate precipitation. In the ecoregion “Upper Rhine valley”, where ashes exist mainly in flood plain forests, the volume of ashes with collar rots accounted for 42.7 % of the stock, which is the highest proportion of all investigated ecoregions.

The total number of regeneration ash trees decreased drastically by 56.4 % within the three years since the last NFI. The reduction was especially high in the Upper Rhine valley, were ash trees occur mainly in flood plain forests. Here, regeneration trees already weakened by ash dieback are exposed to strong competition by herbaceous plants, particularly when the canopy layer partly disintegrates due to the disease. Of the remaining regeneration trees, 31.9 % were not affected by ash dieback, 14.6 % were diseased at less than 50 % of their twigs, 17.6 % were diseased at more than 50 % of their twigs and 35.8 % of the trees were dead. This proportion of healthy trees is considerably higher than in earlier studies from south-western Germany (Enderle et al. 2016) and is rather comparable to results of a survey in Lithuania (Lygis et al. 2014). However, the vast majority of healthy trees (91.5 %) were smaller than 130 cm in height. Possibly, the high fraction of healthy young ash trees is already a result of commencing evolutionary adaption to the disease.

Genetics of ash populations and resistance

Population structure and genetic diversity of ash in Germany

Several studies used molecular markers to investigate the genetic structure of German ash populations (Höltken et al. 2003, Heuertz et al. 2004a, 2004b, Heblel et al. 2006a, 2006b, Fussi and Konnert 2014). Northern Germany is dominated by one chloroplast haplotype, which is typical for central Europe (Heuertz et al. 2004b). Higher chloroplast variation was detected in southern Germany, especially in populations from south-eastern Bavaria (Fussi and Konnert 2014), where four chloroplast types have been detected by Heuertz et al. (2004b) in the same region. Historical contact of different chloroplast lineages from different refugia in Italy, the eastern Alps and the Balkan Peninsula could explain this pattern (Heuertz et al. 2004b).

The results of genetic studies in Germany revealed a high genetic variation within and high genetic differentiation between ash populations (Hebel et al. 2006b, Fussi and Konnert 2014). High genetic variation within stands was also found in Italy (Ferrazzini et al. 2007) and generally higher genetic variation was detected in central and western Europe than in south-eastern Europe (Heuertz et al. 2004a). In contrast, genetic differentiation was higher for populations in south-eastern Europe than in central Europe (Heuertz et al. 2004a).

Different gene flow intensities during postglacial recolonization might be the explanation for these observed patterns (Heuertz et al. 2004a).

Studies indicate that historical effective seed dispersal occurred mainly over short distances (Heuertz et al. 2004a) and pollen dispersal might have been more effective, since the dispersion of pollen by wind is typical for *F. excelsior*. Nevertheless, the data on pollen dispersal is contradictory, as very limited pollen dispersal has been reported in *F. excelsior* (50% and 95% of pollen dispersed at less than 10 m and 50 m, respectively, Altman and Dittmer (1964) in Heuertz et al. 2001). Douglas (2006) also mentioned that pollen flow and seed dispersal in ash is generally restricted within the stand. These findings could explain the genetic uniqueness of some southern German populations (Fussi and Konnert 2014). However, in some cases gene flow by pollen into fragmented populations can be extensive (46–95%) having two components: a very localized and restricted one and a second one stretching over long distances with dispersal occurring over several kilometres (Bacles et al. 2005). Effective dispersal distances (average 328 m) were greater for fragmented populations than values reported for contiguous populations (Bacles et al. 2005). However, in view of ash dieback, dying trees and / or an active withdrawal of ash can lead to depletion of populations with restricted effective gene flow between the remaining and possibly more resistant trees.

Genetic resistance in populations and individuals

The genetic determinism of the resistance against ash dieback was investigated in four different clonal seed orchards in south-western Germany (Enderle et al. 2015b). In total, the seed orchards comprised 1.726 ramets that belonged to 246 autochthonous clones. The grafts for the clones originated from different nearby regions in south-western Germany. As in former studies, tree individual crown defoliation was assessed in classes in order to score the degree to which the trees were affected by ash dieback. However, some severely diseased trees showed little crown defoliation due to extensive formation of epicormic shoots. Thus, the proportion of epicormic shoots of the living crown was additionally assessed for every tree and interpreted as an indicator for individual susceptibility to ash dieback. The assessments took place in 2012 in all four seed orchards and were repeated in 2013 in two of the orchards. Broad-sense heritability ranged from 0.48 to 0.58 for portion of epicormic shoots and from 0.18 to 0.55 for crown defoliation between the orchards. These results are comparable to other studies from Denmark, Sweden and Lithuania (McKinney et al. 2011, Stener 2013, Pliūra et al. 2014). Differences between the origins of grafts were significant, but very small. Together with the results of the provenance trials, this indicates that the main source of resistance is determined on the level of the individuals, not on the level of populations or provenances.

Fussi and Konnert (2014) reported that ash populations from southern Germany were genetically very different and most of the studied populations displayed symptoms of ash dieback, although in different intensity. Nevertheless, resistance on the population level seems rather unlikely. More likely is that *H. fraxineus* has not arrived in populations, where no symptoms have been discovered yet. In southern Germany, genetic variation between damaged and undamaged subpopulations was compared to see if genetic differences between these two collectives exist (Fussi and Konnert 2014). The authors detected higher proportions of heterozygotic individuals (observed heterozygosity) in the less susceptible groups compared to the susceptible groups, indicating that heterozygotic individuals might be able to withstand ash dieback better than homozygotic individuals. This means a higher variability on the individual level for heterozygotic individuals that might therefor have higher plasticity and reaction capacity against the disease. Namkoong et al. (1998) and Tessier du Cros et al. (1999) earlier suggested that heterozygotic individuals could be more resistant to environmental stresses.

Evolutionary selection in natural ash regeneration

European ash is a tree species, which usually regenerates very successfully. In natural regeneration, densities of more than 100,000 ash trees per ha can be reached (Roloff and Pietzarka 1997, Tabari and Lust 1999), and ash can be very competitive on suitable sites. This fact is worth to consider when searching for management options that aim to increase the resistance against ash dieback in future ash populations. However, ash dieback influences individual competitiveness and changes the processes of evolutionary selection in natural regeneration. To gain a better understanding of selection processes in ash regeneration, individual disease severity was assessed and compared to tree height and annual height growth, which were recorded as indicators of competitiveness (Enderle et al. 2016). The study took place in three sites with dense ash regeneration in south-western Germany with a total number of 1,271 ash trees. Data collections were performed in summer 2013 and winter 2014 / 2015.

In the investigated stands, smaller trees were generally more affected by the disease. The height growth of moderately diseased trees was not reduced compared to completely healthy ashes, but a significant reduction of height growth was evident for trees with more than 50 % crown dieback. Moreover, these trees lost in average 30 % - 40 % of their tree height due to dieback, whereas only minor reduction of height could be detected for less affected trees. The number of living ash trees in the stands decreased by 20.4 % during the period of investigation.

From this study it can be assumed that individual competitiveness is not reduced notably as long as less than half of the twigs of a tree are diseased or dead. However, further research is needed to assess the potential of natural regeneration leading to enhanced resistance by evolutionary selection.

First experiences in breeding for resistance

In order to elucidate the breeding potential and to gain general experience in breeding for resistance against ash dieback, a study was initiated in southern Germany to test the heritability of supposed resistance in the field (Fussi et al. 2016, submitted manuscript). In nine infected mature ash stands, a number of ash trees that visually did not exhibit any disease symptoms were identified in 2010. This can be considered as a first step in a putative breeding program for ash. Scions were collected from these potentially resistant trees and grafted on two years-old root stocks in spring 2012. Following a randomized block design, a field trial was established in Bavaria in winter 2013 / 2014 with 306 of the resulting ramets that belonged to 36 clones. Subsequently, in June 2014 and 2015, individual crown damage was scored by determining the number of infected shoots as a percentage of the total number of shoots per plant.

In 2014, 81.4 % of the ramets and 14 clones were completely healthy. This fraction decreased drastically in the following year, when only 5.6 % of the ramets and no clone were completely healthy. Instead, 11.4 % of the ramets had already died in 2015. There were strong differences in crown damage between the clones but not between the blocks (Kruskal-Wallis tests, $p < 0.001$ and $p = 0.55$, respectively), indicating that the clones differed substantially in their genetic resistance against ash dieback. However, in 2015, only few clones with relatively little crown damage remained. These clones will be further monitored to see if they harbour an adequate potential of resistance for breeding purposes. The relatively high fraction of rather susceptible clones in the trial highlights the importance of thorough determination of the ortets´ degree of resistance. Not more than five years after the pathogen´s arrival in the region (cf. Figure 1) the time of ortet selection (2010) probably was too early. At this time, the amount of pathogen inoculum certainly had not yet been on its maximum, and resistance was not distinguishable from disease absence or disease escape. If possible, ortets for future breeding projects should be selected by thorough observation of the health status over a period of several years under high infection pressure. Younger trees are probably more suitable for the assessment of individual susceptibility, because symptoms can be detected more easily and infection pressure is higher near the ground (Chandelier et al. 2014). Recently identified molecular markers can be used additionally to ensure high degrees of resistance in ash trees that are foreseen for breeding projects (Harper et al. 2016).

Proportion of potentially resistant ash trees

In all examined study sites in Germany, increasing disease progression could be observed that has not come to a standstill yet. As there are currently no efficient treatments known to cure or slow down ash dieback, special attention must be drawn to those trees that withstand the disease for a long period of time under high infection pressure. These trees can be regarded as candidate tolerant trees, although the above described experiences in breeding for resistance reflect the difficulty in assessing a tree´s degree of resistance. Moreover, the identification of candidate trees is much complicated by the symptom of collar rots, which is still not well understood.

According to the studies that are summarized above, the fraction of healthy or slightly diseased trees differs strongly between sites and age classes. In Baden-Württemberg, 6.7 % of the ash stock consists of trees with little crown defoliation and portion of epicormic shoots (less than 25 %) and without collar rots (Enderle et al. 2015a). The current fraction of potential candidate trees in Bavaria has been estimated at 4 % in young plantations and approximately 20 % in mature stands (Lenz et al. 2016). Similar assumptions can be drawn from data that was collected in the provenance trials. However, as the periods of investigations were rather short and because of the huge lack of knowledge concerning collar rots, these estimations are still subject to considerable uncertainty.

However, in natural regeneration that emerged after the infestation, the fraction of healthy trees is much higher (Enderle et al. 2015a, Langer et al. 2015a). This could already be the effect of commencing natural selection towards higher resistance in ash populations.

Ongoing and planned research in Germany

Research regarding ash dieback in southern Germany is foreseen to focus on breeding for resistance and processes of natural selection in autochthonous ash populations, including the genetic component of collar rots. Health stages of ash trees in the provenance trials will be further evaluated. In spring 2016, seedlings produced from seeds of healthy mother trees will be planted in the field. This offspring consists of half-siblings that will provide information on the potential inheritance of resistance of the mother trees and are potential trees for further breeding. But also the pathway of infection leading to collar rots and site characteristics that favour or hamper collar rot formation are intended to be further investigated. A project that compares early infection stages in leaves from susceptible and resistant trees by microscopy has already been initiated in order to gain knowledge about the resistance mechanisms in leaves.

In north-western Germany, it is intended to follow further disease development and its general impact. Mortality and infection rates due to ash dieback as well as the disease progression will be further monitored in at least 12 stands of different age-classes and forest types. The stands are long term observation plots of growth and yield in eastern Schleswig-Holstein, in the eastern and southern highlands of Lower Saxony and the Vogelsberg region in Hesse. The plots already existed before ash dieback appeared. Mixed hardwood stands with in total 1,000 ash trees of different ages ranging from 24 to 157 years are observed. The proportion of ash in the stands ranges from 3 % to 95 %. Disease severity has been assessed annually since 2013 on every numbered ash tree according to a 1 to 5 scoring system (Langer et al. 2015a). It is planned to analyse correlations between tree age, percentage of ash, competition, increment of diameter at breast height and the disease status. The aim of this study is to find conclusions for the maintenance of mixed hardwood stands with ash and to get an idea of the development of stand structure under progressive disease.

Management options to mitigate the impact of ash dieback

Silvicultural management options

Once the devastating effects of ash dieback became obvious in Germany, the forest research institutes of the respective federal states developed independently different recommendations for the management of the disease. Recently, these recommendations to forest practitioners were pooled in a single nationwide publication (Metzler et al. 2013). However, the implementation of the recommended actions is not mandatory in Germany. The following paragraphs give a short summary.

Generally, seed collection, nursing and planting of ash is not recommended. Especially, it is not reasonable to produce healthy but susceptible saplings in nurseries by the application of fungicides. Although detailed data on production of ash plants in Germany do not exist, it is estimated to have dropped down to a 5-10% level in 2015 as compared with the production ten years ago (pers. communication G. Wezel 2016). Existing natural ash regeneration, however, should be utilized in general, although it may be necessary to plant additional site-adapted admixture species if regeneration is dominated by ash. Basically, no further management actions are necessary until the envisaged knot free stem length is reached, but promotion of less competitive admixed tree species and sound looking and resistant appearing ash individuals may be meaningful. Regular thinning in older stands is still strongly recommended. Here again, the promotion of admixed tree species and sound looking ash individuals should be the main objective. Resistant appearing ash trees should never be felled, because it is essential for the conservation of ash to allow these trees to reproduce. Otherwise, fragmentation of ash populations and a crucial loss of genetic diversity must be expected.

Individual tree vigour, as a measure of individual resistance, is the most important criterion during selection of ash trees for thinning. The best time for the selection of trees for harvest is July, when there is a maximum of foliage and disease related crown defoliation can be assessed. Attention must be paid not only to the crown symptoms, but also to collar rots. Permanent marking of final crop ash trees is not feasible anymore. The timber can be used as usual, because it is not a source of additional pathogen inoculum. If massive decline of the canopy and subsequent invasion of grasses or herbaceous plants is to be feared, appropriate measures for forest regeneration must be taken in due time. In mature stands, the main objective should be to harvest high quality timber before deterioration of wood quality, which is increasingly endangered by the formation of epicormic shoots, insects or rot and blue stain fungi when crown defoliation exceeds about 70 %. Trees with collar rots should be harvested in due time, as well.

However, it must be noticed, that foresters are reluctant in selecting potentially resistant ashes and tend to clearcut heavily affected pure stands. This may be due to the incidentally high numbers of collar rots. Within the following years special attention has to be drawn on practical aspects of preserving resistant ash individuals.

During harvest and thinning, high standards for traffic and occupational safety must be applied, which is endangered by dead branches and collar rots (cf. Metzler and Herbstritt 2014). The work should be conducted by qualified staffs that were explicitly informed about the risks. The use of forest harvest machinery is preferable to motor-manual harvesting.

Ash trees in public green, solitary trees in particular, seem to be much less affected by the phenomenon of collar rot, since basal lesions are rarely observed. Thus, the tree safety aspect is much less serious and the responsible staff can concentrate on crown symptoms which can be cured by removing dead branches, possibly to be repeated every year, depending on the progress of disease and on financial background.

Table 2 Alternative tree species to *F. excelsior* based on flooding tolerance and base claim for floodplain and terrestrial forests.

Species	Habitat		Flooding tolerance	Base claim
	Floodplain forest	Terrestrial forest		
Pseudotsuga menziesii[1]		x	low	low
Picea abies[1]	x	x	moderate	low
Larix decidua[1]		x	low	low
Pinus sylvestris[1]	x	x	moderate	low
Abies alba[1]		x	low	middle
Populus tremula[2]	x	x	high	middle
Populus nigra[2]	x		high	high
Salix spp. [2]	x		high	high
Acer pseudoplatanus[1]	x	x	high	high
Ulmus glabra[1]	x	x	moderate	high
Sorbus aucuparia[1]		x	moderate	low
Sorbus torminalis[1]		x	low	high
Acer campestre[1]	x	x	high	high
Ulmus minor[2]	x	x	high	high
Ulmus laevis[2]	x	x	high	middle
Alnus incana[2]	x		high	high
Populus x canescens[2]	x		high	high
Carpinus betulus[1]		x	moderate	middle
Sorbus aria[2]		x	low	high
Betula pubescens[2]	x		high	low
Fagus sylvatica[1]		x	low	low
Betula pendula[1]		x	moderate	low
Alnus glutinosa[1]	x		high	middle
Populus alba[2]	x		high	high
Tilia platphyllos[1]		x	low	high
Sorbus domestica[1]		x	low	high
Acer platanoides[1]	x	x	high	high
Quercus robur[1]	x	x	high	low
Quercus petraea[1]		x	low	low
Prunus padus[2]	x		high	high
Prunus avium[2]		x	low	high
Malus sylvestris[2]	x	x	high	high
Pyrus pyraster[2]	x	x	high	high
Tilia cordata[1]		x	high	middle

[1] According to BaSIS (Taeger et al 2016a, Taeger et al. 2016b)
[2] According to Walentowski et al. 2004

Alternative tree species

In severely affected ash stands, reforestation efforts with alternative tree species have to be considered, especially if mixed species are not available to compensate for the emerging forest gaps. Depending on the habitat (floodplain or terrestrial forest), different species can be used. In south-eastern Germany the Bavarian State Institute of Forestry has developed a digital information system (BaSIS) to describe site conditions (soil and climate) combined with a modeled cultivation risk assessment of tree species (Taeger et al 2016a, Taeger et al. 2016b). By using this system in addition to the appropriate tree species already described in these areas (Walentowski et al. 2004), several alternative tree species could be found for the possible replacement of ash trees (Table 2).

In addition to native species, exotic tree species are considered by some forest owners. However, these are mostly not welcome in close-to-nature forestry and there may be restrictions in protected areas. For example, in flood plain forests, poplar hybrids showed to be able to fill the gaps of declining ash stands. There are also examples of *Juglans nigra* surviving periodic inundation in good health condition. Depending on the forest ownership several experimental plantings were established in order to find tree species that can replace ash adequately.

Conclusions

Generally, ash has relative low abundance in Germany, but forest policies had aimed to increase its share until the devastating effects of ash dieback became apparent. Within ten years, the disease spread over the whole country. Various studies have been carried out in different regions of Germany to follow up the disease progression and to assess the impact of the disease. They revealed a drastic increase in disease severity, which did not come to a standstill, yet. Only a very small fraction of ash trees is still able to withstand the disease. Mortality is increasingly caused by collar rots. The participation of wood decay fungi in collar rots, especially *Armillaria* spp., represents high risks for occupational and traffic safety and thereby is reason for huge salvage cuttings.

It was shown that resistance against ash dieback in Germany is genetically determined on the individual level and that provenances and populations play a negligible role in resistance. In natural populations, genetic diversity was calculated between susceptible and less susceptible trees. The remaining level of genetic diversity within the group of less susceptible individuals has to be monitored, because it is important for breeding programs to ensure a wide genetic base, particularly since analyses based on microsatellites revealed genetic variation in *H. fraxineus* populations (Bengtsson et al. 2012, Fussi et al. 2012, Gherghel et al. 2013) and genotype dependent differences in the pathogen-tree interaction might be expected. The fraction of highly resistant trees that are possibly viable in the long term is still difficult to estimate, especially because the future impact of collar rots is not yet predictable. However, in natural regeneration that emerged after the infestation, natural selection might already have commenced, as the fraction of healthy trees is much higher. Thus, recommendations for disease management in Germany concentrate on the maintenance of sound looking trees to preserve genetic diversity in ash populations.

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