Progression of Ash Dieback in Norway Related to Tree Age, Disease History and Regional Aspects

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Abstract

Ash dieback, caused by the ascomycete *Hymenoscyphus fraxineus*, has been spreading throughout Europe since the early 1990s, threatening European ash at a continental scale. Little is known about the development of the disease in individual forest trees and in different age classes. In this study we monitored ash dieback on trees of different diameter classes in five permanent plots in ash stands in south-eastern Norway from 2009 to 2016, and from 2012 to 2016 in three plots in western Norway with a shorter disease history. Our results showed that more than 80% of the youngest and more than 40% of the intermediate future crop trees in the plots in south-eastern Norway were dead by 2016, while the disease development in large, dominant trees was slower. Although less damage has been observed in the plots in western Norway, the trend for the juvenile trees is the same as in south-eastern Norway with rapidly increasing damage and mortality. Most dead trees in south-eastern Norway were found at sites with high soil moisture and showed symptoms of root-rot caused by *Armillaria* species. Infected trees, both young and old ones, are weakened by the disease and appear to be more susceptible to other, secondary pathogens, especially under unfavourable site conditions.

Keywords: Ash dieback, *Hymenoscyphus fraxineus,* monitoring, year-to-year disease development, crown damage

Introduction

Ash dieback was first reported from Poland in the beginning of the 1990s (Przybył 2002), and has since spread to most areas in Europe where European ash (*Fraxinus excelsior*) occurs (Timmermann et al. 2011, McKinney et al. 2014). The cause of the disease is the pathogenic ascomycete *Hymenoscyphus fraxineus* (syn. *H. pseudoalbidus*, anamorph *Chalara fraxinea*) (Kowalski 2006, Queloz et al. 2011, Baral et al. 2014). Fruit bodies of the fungus are formed between late June and late September (under east Norwegian climatic conditions) on ash leaf litter overwintered in the forest floor, releasing vast amounts of ascospores with a seasonal peak from mid-July until mid-August (Hietala et al. 2013). The spores are infecting the compound leaves, and fungal hyphae are thought to spread to branches and stem before leaf shed late in the season (Gross et al. 2014). Infection initially causes necrotic lesions in leaves and petioles, and later in the bark of branches and stems, leading to leaf wilting, defoliation and shoot or even top dieback (Gross et al. 2014).

Ash dieback threatens European ash at a continental scale, and European ash is now red-listed in many European countries, including Norway (Henriksen and Hilmo 2015). Trees of all ages and at all sites, also outside forest stands, are affected. Younger trees are usually killed faster by ash dieback than intermediate or older, dominant trees, but there is large variation in susceptibility and disease development among individual trees, irrespective of age class. As a consequence of ash decline, a shift in forest species and biodiversity and changes in forest management can be expected in the long run (Pautasso et al. 2013). In forest management, special concern is expressed for the fate of the future crop trees, the next generation of ash trees (Keßler et al. 2012). Furthermore, insect and fungal species associated with European ash may be impacted indirectly when their host is declining (Pautasso et al. 2013, Cross et al. 2016, Thomas 2016).

European ash is commonly distributed in Norway from the Oslo fjord area in the east along the coast in southern and western Norway, with fragmented populations up to ca 64°N around the Trondheim fjord region in Mid-Norway (Figure 1), where the species reaches its northernmost European distribution border, but scattered occurrences of (mostly planted) ash trees are found even farther north. It grows up to 720 m a.s.l. in the temperate broadleaf and mixed forest biome in Norway, mostly in mixture with other deciduous tree species. Larger, pure stands of ash are rare in Norway, although Scandinavia's largest ash forest is found west of the Oslo fjord (Fjugstad nature reserve, monitoring plot FU in Figure 1). Until the first half of the 20th century, ash was widely planted in Norway and the fast-growing, yet strong and flexible hardwood was used for manufacturing of e.g. skis, tool handles and parquet floors. The importance and thus the economic value of ash wood products declined through the second half of the 20th century. Ash received again increasing attention in some regions in Norway at the beginning of this century due to its drought tolerance, and some forest owners west of the Oslo fjord planned to replace Norway spruce with European ash at drought-exposed sites – before ash dieback invaded the country and altered the prospects.

The presence of ash dieback in Norway was confirmed for the first time in 2008 (Talgø et al. 2009) and was at that time already widespread in south-eastern Norway. Based on older stem lesions it was concluded that the disease must have been present in the region at least since 2006 (Solheim et al. 2012). Ash dieback has since been spreading along the coast in Norway at a considerable pace, reaching the southernmost parts of the west coast in 2008/2009. By 2013, ash dieback had spread through most parts of the continuous distribution range of European ash in Norway. In 2016, only the region around the Trondheim fjord was still free of the disease (Solheim and Hietala 2017).

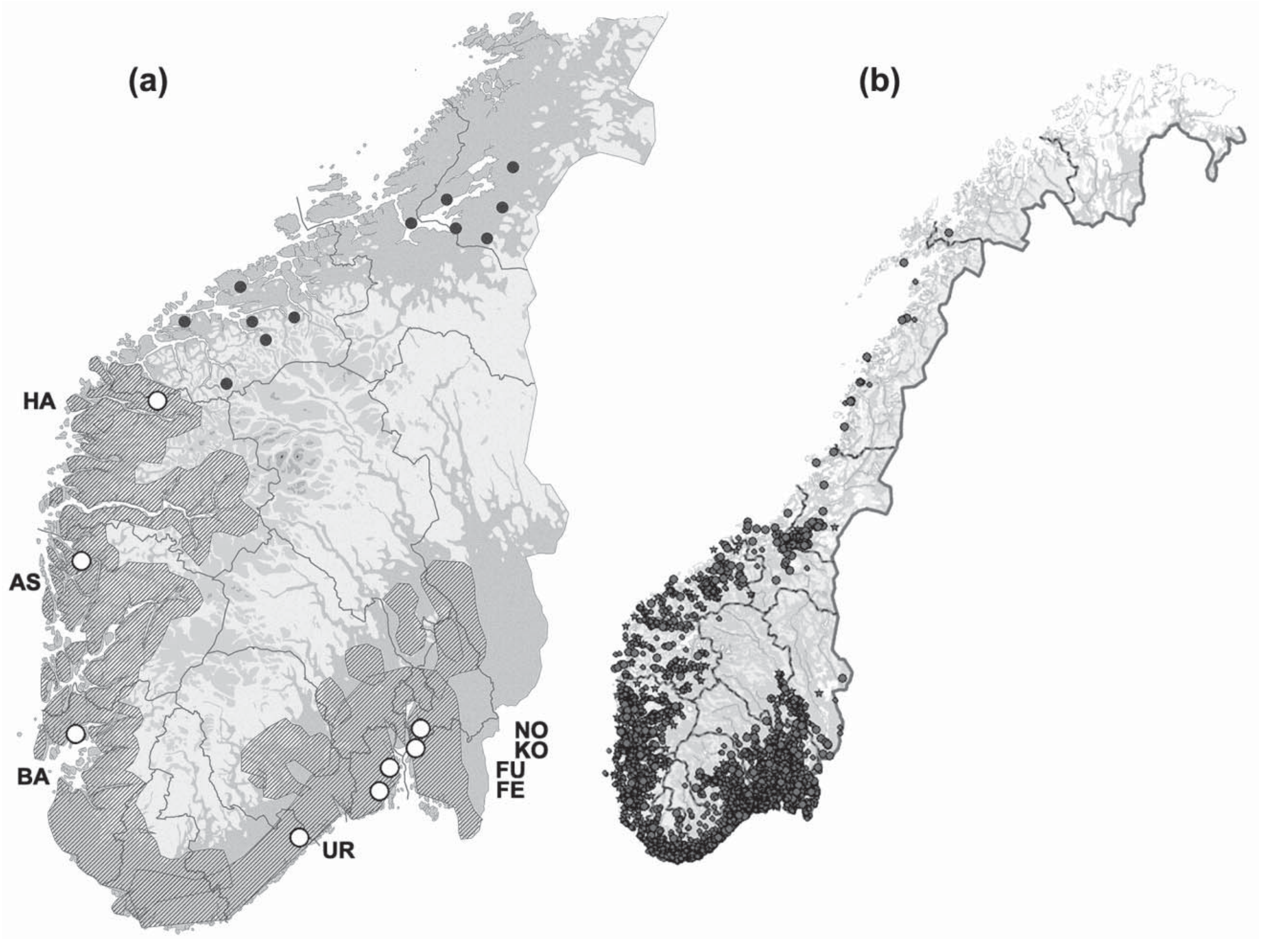

Figure 1. (a) Location of monitoring plots (white dots) and distribution of European ash in forested areas in Norway (shaded area: continuous ash populations; small black dots: fragmented ash populations) according to EUFORGEN 2009 (www.euforgen.org). (b) Single observations of European ash in Norway including park and garden trees according to the Norwegian Biodiversity Information Centre/GBIF Norway 2016 (www.artskart.artsdatabanken.no)

The objectives of the present study were (i) to evaluate disease development in individual ash trees of varying age and to confirm the intensity of ash dieback in ash stands in Norway, and (ii) to compare disease progression in regions with different lengths of disease history. To meet these aims, we assessed disease symptoms such as defoliation and other crown damage parameters annually in trees of different diameter classes on five permanent monitoring plots in south-eastern Norway with a disease history presumably back to 2006, and in three plots in western Norway with a shorter disease history (Table 1).

Materials and methods

Monitoring of ash dieback in Norway has been conducted at eight study sites; five situated in south-eastern Norway and three at the Norwegian west coast (Figure 1). Four of the monitoring plots in south-eastern Norway were established in 2009 (NO, KO, FU, FE) and the southernmost (UR) in 2010, while the western plots (BA, AS, HA) were established in 2012 (Table 1, Timmermann et al. 2013). All plots are situated in ash dominated forest stands, with stand area ranging from a few 100 m^2 to almost 30 ha (Table 1).

In four plots, showing distinct age classes, 10 large, dominant trees with varying degree of crown damage and 40 healthy appearing young trees were subjectively selected, 50 trees in all (Table 1). In the other four plots, with more even age distribution, 40 trees in total were selected. All trees were marked and numbered for long-term monitoring.

Weather and climate data for each monitoring plot were obtained from the nearest weather observation station providing long-term measurements (the same weather station was used for NO and KO, and for FU and FE, respectively. Data were retrieved from the online weather service www.yr.no). In 2015, mean annual temperature and total annual precipitation was in the range from 7.1 to 8°C and 1035 to 1622 mm in the eastern region, and from 8 to 8.7°C and 1716 to 3102 mm in the western region. Mean summer (June–August) temperature and average summer precipitation in 2015 was 15.0°C and 365 mm in the east, and 13.7°C and 363 mm in the west. In the winter months (December–February), mean temperature and average precipitation was 1.3°C and 325 mm in the east, and 3.5°C and 1016 mm in the west (Table 1).

Visual assessments of crown condition and damage symptoms were conducted on individual trees once per year on every plot (between 15th of June and 15th of August) based on standardized methods developed by ICP Forests (UNECE 2010). Parameters assessed were defoliation, leaf discolouration, shoot and leaf wilting, dead branches and tops, dieback, fruiting, and epicormic shoots. A field calibration was performed in 2012 before monitoring in western Norway started to ensure that assessments were done similarly by the two field workers.

Table 1. Overview over study sites and monitoring plot data. TS15 and PS15: Mean temperature and total precipitation for summer months 2015 (Jun.–Aug.). TW15 and PW15: Mean temperature and total precipitation for winter months 2015 (Dec.–Feb.). Deviations from standard reference period 1961–1990 are shown in parentheses. Weather and climate data were obtained from the online weather service www.yr.no. ADB infect.: Presumable year of first ash dieback infections in the surroundings of each monitoring plot

Plot ID	Plot start	Coordinates	Plot area (m^2)	Stand area (ha)	No of trees	Altitude (m a.s.l.)	TS15 (°C)	PS15 (mm)	TW15 (°C)	PW15 (mm)	ADB infect.
NO	2009	59.680847 N 10.776908 E	378	3.4	50	100	14.8 (-0.5)	349 (117)	0.7 (5)	214 (77)	2006
KO	2009	59.536433 N 10.711131 E	1036	1	50	40	14.8 (-0.5)	349 (117)	0.7 (5)	214 (77)	2006
FU	2009	59.361899 N 10.457551 E	792	26.7	50	40	15.3 (-0.2)	327 (80)	1.9 (5.1)	319 (94)	2006
FE	2009	59.198004 N 10.235486 E	595	0.1	40	100	15.3 (-0.2)	327 (80)	1.9 (5.1)	319 (94)	2006
UR	2010	58.783128 N 09.121598 E	114	0.02	40	100	14.9 (0.2)	420 (134)	1.3 (4.3)	441 (166)	2006/7
BA	2012	59.345577 N 05.838939 E	n.a.	n.a.	50	20	13.7 (0.8)	425 (19)	3.4 (3.4)	1079 (615)	2007/8
AS	2012	60.615296 N 05.468731 E	n.a.	n.a.	40	15	14.1 (0.2)	430 (-40)	4.2 (2.5)	1218 (641)	2010
HA	2012	61.861023 N 06.339424 E	n.a.	n.a.	40	110	13.1 (-0.5)	235 (15)	3 (3.2)	751 (376)	2013

In the result part, defoliation scores, considered to be the most important damage variable (UNECE 2010), were used to group the trees into five damage classes (Table 2), comparable to the classes used by McKinney et al. (2011). Growth measurements were carried out twice. Diameter at breast height (DBH, all trees > 50 mm) and tree height (only for dominant trees) were measured in 2009 (south-eastern plots) and 2014 (all plots), and the trees were grouped in three diameter classes according to their DBH in 2014: Juvenile or small trees with DBH ranging from 10 to 50 mm, intermediate, future crop trees with DBH 50 to 125 mm and large, dominant trees with DBH above 125 mm (Table 3). Although tree heights are overlapping between diameter classes, diameter reflects tree age to a certain degree, especially for the youngest trees (K. Andreassen, pers. comm.).

Table 2. Grouped damage classes according to percentage of defoliation

Damage class	Defoliation (%)
1 Healthy trees	0–10
2 Slightly damaged	11–25
3 Moderately damaged	26–50
4 Severely damaged	51–99
5 Dead trees	100

Table 3. Diameter classes according to measurements of diameter at breast height (DBH) in 2014, tree height and number of trees in the plots in south-eastern Norway (SE) and western Norway (W)

Diameter class	DBH	Height	No of trees	
	(mm)	(m)	SE	W
Juvenile	< 50	1–10	111	64
Intermediate	50–125	8–16	67	34
Dominant	> 125	12–34	52	32

The percentages of ash trees in the different damage classes were calculated for each diameter class. Annual mean values are presented combined for the five plots in south-eastern Norway, and combined for the three plots in western Norway. One-way analysis of variance with least significant difference *post hoc* test was used to analyze significant differences in defoliation between years for means of each damage class by using the SPSS program (IBM SPSS Statistics 22.0). Differences with $P < 0.05$ were regarded as statistically significant.

Results

Disease progression in south-eastern Norway 2009-2016

In 2009, 86.1% of the juvenile trees on the monitoring plots in south-eastern Norway appeared healthy (0–10% defoliation) or only slightly damaged (11–25% defoliation), and 4.6% were severely damaged (50–99% defoliation) (Figure 2a). In 2016, the proportion of healthy or slightly damaged trees was significantly reduced to only 8.1%, while 89.2% of the young trees were severely damaged or dead, representing a significant increase in dead trees and a mortality rate of 82%. Only few year-to-year changes within each damage class were significant. At plot level, disease development among the juvenile trees has been devastating in plot NO during the monitoring period, leaving 35 of 38 juvenile trees dead by 2016, one dying and two severely damaged.

For the intermediate trees disease development has not been as rapid as for the juvenile trees in south-eastern Norway, but also in this group there has been a considerable increase in the number of severely damaged trees and a significant increase in the amount of dead trees from 2009 to 2016 (Figure 2b). Based on defoliation assessments, 70% of the trees in this intermediate diameter class were considered to be healthy or slightly damaged and 12.5% to be severely damaged in 2009. In 2016, 69.7% of these future crop trees were either dead or severely damaged, and only 24.2% still healthy or slightly damaged. The mortality rate for the entire monitoring period was 42.4%. None of the year-to-year changes were significant, except for an increase in dead trees from 2014 to 2015. The decrease in number of healthy future crop trees was significant from 2009 to 2016. However, despite an accelerating mortality rate since 2012, the proportion of healthy trees has been relatively stable since 2013 (around 20%).

Defoliation within the group of large, dominant trees did not increase as much as for the younger trees in south-eastern Norway from 2009 to 2016, and annual changes were not significant for any of the damage classes except for dead trees. The proportion of healthy or slightly damaged dominant trees was fairly stable from 2009 to 2014 (around 60%, Figure 2c), but had decreased to 42.3% in 2016, due to a sharp decline in the number of healthy trees from 2014 to 2016. The proportion of severely damaged and dead trees increased from 16.7% to 46.2% from 2009 to 2016, and the mortality rate for that period was 23.1%.

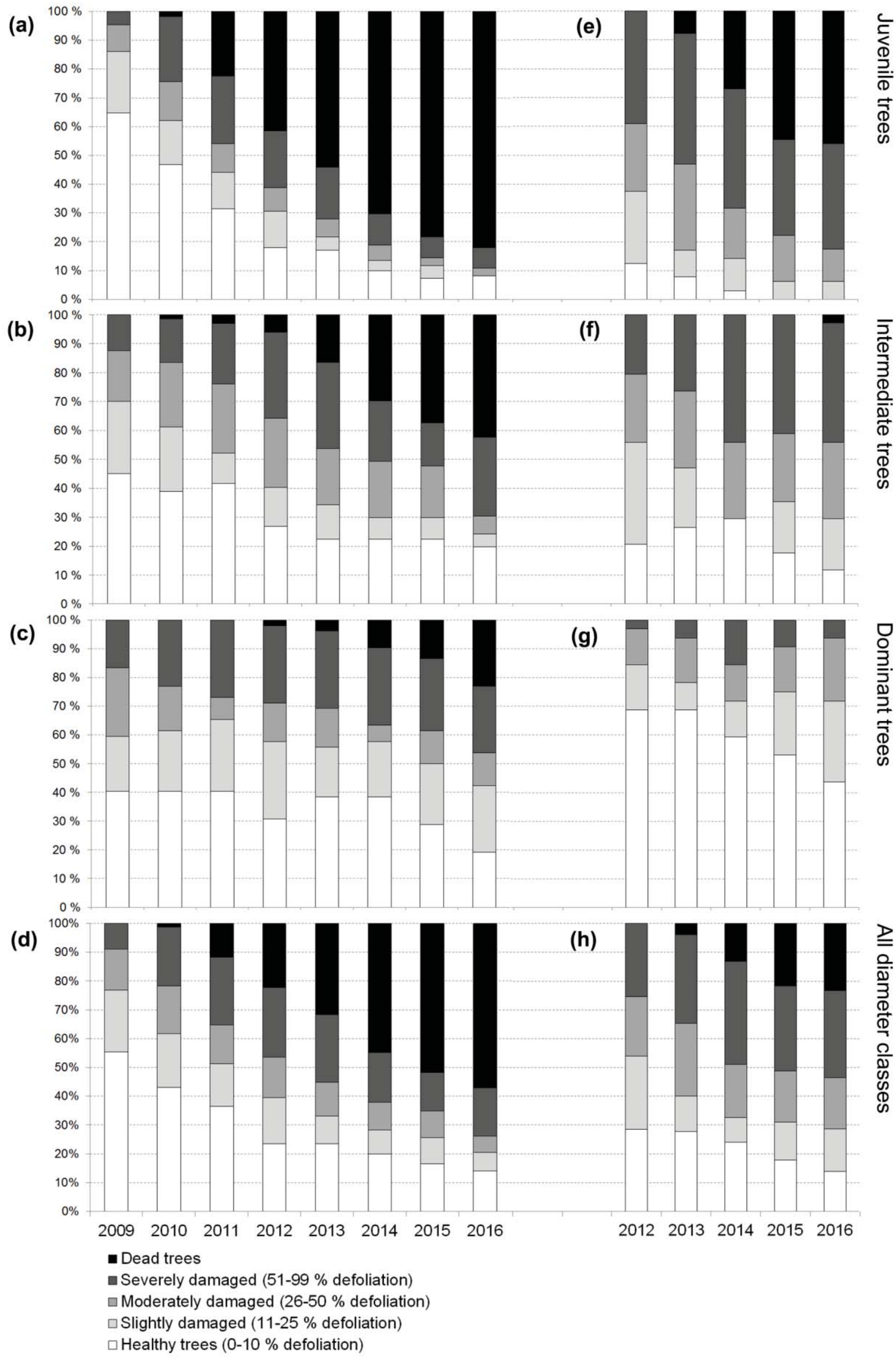

Figure 2. Percentage of ash trees in each damage class. (a–d) Plots in SE Norway 2009–2016; (e–h) plots in W Norway 2012–2016. (a, e) Juvenile trees; (b, f) intermediate trees; (c, g) dominant trees; (d, h) all diameter classes

Of all assessed trees in all diameter classes on the monitoring plots in south-eastern Norway, 76.8 % were considered to be healthy or slightly damaged in 2009, and only 8.9 % to be severely damaged. In 2016, only 20.5 % were still healthy or slightly damaged, 16.6 % severely damaged and 57.2 % were dead (Figure 2d). The increase in number of dead trees from 2009 to 2016 was significant in all diameter classes.

Disease progression in western Norway 2012-2016

In 2012, 37.5% of the juvenile trees on the three plots in western Norway were considered to be either healthy or slightly damaged, and 39.1% severely damaged (Figure 2e). In 2016, no healthy trees were found (a significant decrease) and only 6.3% were slightly damaged. The proportion of severely damaged juvenile trees remained more or less unchanged during the monitoring period, while there was a strong and significant increase in dead juvenile trees to 46% in 2016.

No significant changes in defoliation could be detected for the intermediate trees in the western plots during the monitoring period. However, there was a trend of an increasing proportion of severely damaged trees, which doubled from 2012 to 2016 (to 41.2%, Figure 2f), and the first dead tree in this diameter class was observed in 2016.

No significant differences were found for defoliation in the large, dominant trees in the monitoring plots in western Norway, and no clear trends are visible yet (Figure 2g). The annual changes in the different damage classes were rather small, and no dead trees were found yet in this diameter class. Still, the proportion of healthy trees decreased from 68.8% in 2012 to 43.8% in 2016.

Of all assessed trees in all diameter classes on the monitoring plots in western Norway, more than half (53.8%) were considered to be healthy or slightly damaged in 2012, and 25.4% to be severely damaged. In 2016, only 28.7% were still healthy or slightly damaged, 30.2% severely damaged and 23.3% were dead (Figure 2h).

Discussion and conclusions

The development of ash dieback in individual trees has been monitored on permanent plots in south-eastern Norway since 2009 and in western Norway since 2012. Our monitoring data have shown that disease progression has been fast, even in areas with a short disease history. While there are numerous earlier reports about mortality of ash in relation to ash dieback, there are few prior studies where the health condition of ash has been monitored annually, and related to the duration of disease exposure. The current survey showed that the extent of crown damage has continuously increased in all diameter classes, and that tree mortality has been high, especially among the youngest trees in south-eastern Norway, the region with the longest disease history in the country. But also intermediate and old, dominant trees are attacked, damaged and eventually killed. Diseased large trees can survive for many years due to their extensive foliage and gradual decline in crown condition, usually with small annual changes in defoliation and dieback. Infected mature ash trees often develop epicormic shoots from the stem or main branches to compensate for foliage loss due to the disease. This stress reaction can lead to a temporary increase in foliage, even though the tree crown is severely damaged by ash dieback.

Monitoring projects performed in the Czech Republic 2009–2015 (Vacek et al. 2015) and in Bavaria in southern Germany 2010–2014 (Lenz et al. 2016) found similar patterns in disease development for different age classes and accelerating mortality especially for understorey trees after four years of monitoring. A study conducted in France with 15–20 year-old ash trees showed a mortality rate of only 3% in the period 2010–2014 (Muñoz et al. 2016), while an Austrian survey performed on mature ash trees (Keßler et al. 2012) reported slow disease progression and a low mortality rate (1%) during the monitoring period between 2007 and 2010. In contrast, mortality rate for the mature, dominant trees in our study in south-eastern Norway was 23% from 2009 to 2016, and 42% for the intermediate trees in the same region and period. Even when considering a shorter period (2009–2013), mortality rates in south-eastern Norway were 4% and 16% for mature and intermediate trees, respectively.

Juvenile trees with small DBH are easier killed or severely damaged by the disease than larger trees since a single necrosis on the stem may lead to dieback of the top or even the whole tree, while it will take several years and multiple infections to kill major branches in old trees (Cech 2008). Earlier studies conducted at the monitoring plot NO have shown that during summer enormous amounts of ascospores are released by *Hymenoscyphus fraxineus* ascocarps growing on ash leaf litter (Timmermann et al. 2011, Hietala et al. 2013). It is therefore reasonable to assume that infection pressure for smaller, juvenile trees is much higher than for tall, dominant trees having their foliage 10 or 20 metres above ground. This assumption was confirmed by field experiments conducted in Belgium (Chandelier et al. 2014), where spore traps where placed at different heights in an infected ash stand. Spore density was decreasing significantly with increasing height, and was found to be 5- to 100-times lower at only 3 m height than at the ground. Juvenile trees are also more exposed to competition with other vegetation and thus more predisposed to die off if they in addition are infected by ash dieback (Cech 2008). Healthy appearing juvenile trees in our monitoring plots often have been found dead in the subsequent season.

Large differences between individual trees in crown condition and disease development have been observed in all age classes at our monitoring plots. Although ash dieback has been present in south-eastern Norway for around 10 years and has done large damage to trees of all age classes in the monitoring plots, some trees are still healthy. There is no spatial clustering in the occurrence of trees with different degree of damage in a stand, as healthy, damaged and dead trees are found right next to each other. Both findings indicate that there might be individual, genetically determined differences in resistance to ash dieback and thus possible material for future breeding, thereby supporting the observations of earlier field surveys (Kirisits and Freinschlag 2012, Gross et al. 2014, McKinney et al. 2014). Recent evidence indicates that ash trees without signs of crown damage in stands affected by ash dieback are equally susceptible to leaf infection by ascospores as trees highly affected by shoot dieback and defoliation, and that both healthy and damaged trees support the build-up of pathogen infection pressure in a stand (Cross et al. 2016).

Infected trees, both young and old ones, are weakened by *H. fraxineus* and thus more susceptible to other, secondary diseases like e.g. root-rot caused by *Armillaria* (Skovsgaard et al. 2010), as well as to competition and unfavourable abiotic site conditions such as water-logging, or nutrient deficiency. A combination of all or some of these factors might contribute to the death of the trees, making it difficult to determine the primary cause of death. In plot NO, the cause of death of newly dead trees was assessed in 2014, and most dead trees that had clear symptoms of ash dieback in the crowns in previous years showed signs of *Armillaria* rot in the roots, but no obvious symptoms of *Hymenoscyphus*-infections could be found in the roots or root collar. In 2016, all newly dead, dominant trees in monitoring plots NO and FU showed signs of *Armillaria* infection. Lenz et al. (2016) concluded in their study from Bavaria that *Armillaria* rot in ash trees contributed considerably to the acceleration of mortality. A large-scale crown reduction by *H. fraxineus* in a stand can be anticipated to cause significantly reduced water transpiration from trees. In stands with high soil moisture content this may in turn cause oxidative stress in roots, which again predisposes the trees to infection by *Armillaria* species, fungi commonly associated with trees on water-logged sites (Wargo and Harrington 1991). Furthermore, a degrading root system caused by *Armillaria* rot, alone or in combination with collar lesions affecting the vascular tissue, will impair water and nutrient uptake of the tree and hence contribute to accelerating decline in crown condition (Chandelier et al. 2016). Several studies (Cech 2008, Keßler et al. 2012, Vacek et al. 2015) reported increasing defoliation and dieback on sites with high soil moisture compared to drier, better drained sites. This is in accordance with the results from our monitoring plots where the highest mortality rate for both young and old trees has been registered at a water-logged site (plot NO). At this plot, 50% of the dominant and 90% of the juvenile and intermediate trees were dead in 2016. In contrast, at the most well-drained site at a south-faced slope (plot KO) situated only 16 km air-line distance south of plot NO, most of the dominant trees were still healthy or only slightly damaged in 2016, while 55% of the younger trees were dead. High humidity in the field layer and forest floor is presumably crucial for the formation and activity of *H. fraxineus* ascomata; it remains to be examined to what extent the sporulation period and infection pressure of this pathogen differ between sites that vary in soil moisture, and how this is reflected in the progression of ash dieback in a stand.

Based on observations of older lesions, the first infections of ash dieback in the surroundings of plot BA in western Norway might have taken place as early as 2007 (Solheim 2012, Solheim and Hietala 2017), and in the area nearby plot AS in 2010. In these two plots, clear symptoms of ash dieback were present in 2012 when monitoring started here, and respective damage was recorded in the consecutive years. The northernmost plot (HA) was established one year before ash dieback reached that area, and consequently less damage than in the other western plots and only few clear signs of ash dieback have been detected in this plot so far. However, the presence of *H. fraxineus* in this plot was confirmed by microscopy analysis of fruit bodies sampled in 2015, and the disease has also advanced farther north since 2013 (Solheim and Hietala 2017).

Due to different length of disease history, the ash trees in the west Norwegian plots have experienced varying development of the disease as well, both between the three plots in this region and compared to the south-eastern region. Differences in defoliation patterns in western Norway are larger between plots than between age classes. Plot BA in south-western Norway has the longest disease history of the western plots. As a consequence, most of the dead trees are found on this plot. In contrast, little damage and only two dead trees are found in the northernmost plot (HA) with the shortest disease history. Half of the dominant trees in the west Norwegian sample are found at this site, and all of them were still healthy or only slightly defoliated in 2016. Most of the foliage damage observed in plot HA is caused by mining insects and not by ash dieback (H. Nyeggen, pers. comm.). In the third west Norwegian plot (AS), situated in between the two other plots both in terms of geography and disease history, crown damage is quite extensive, but only a few trees have died so far.

In conclusion, our monitoring data showed that there are clear differences in the progression of ash dieback in trees of different age, *irrespective* of their disease history, but also between stands in different regions *depending* on their disease histories. Our results indicate that development and severity of ash dieback may be correlated with soil moisture in stands and with *Armillaria* root infections. Better understanding of the genetic background that underlies the differential expression of disease symptoms in ash individuals, and the interactions between *H. fraxineus,* European ash and abiotic and biotic environment, is needed to actively facilitate the survival and eventual recovery of ash populations.

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