Growth Performance of Dense Natural Regeneration of *Fraxinus excelsior* under Attack of the Ash Dieback Agent *Hymenoscyphus fraxineus*

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Abstract

Ash dieback, caused by the ascomycete *Hymenoscyphus fraxineus*, is a tree disease, which currently devastates European ash populations. Only a very small fraction of ash individuals exhibits a high degree of quantitative genetic resistance and is likely to survive the disease. We investigated the growth performance of differentially diseased saplings in order to assess the impact of ash dieback on individual competitiveness in dense natural ash regeneration. The research took place on three sites in south-western Germany. From summer 2013 to winter 2014 / 2015, 20.4% of the monitored ash saplings died. In general, shorter trees were more severely diseased. There were no differences in shoot length between healthy or moderately infected trees, whereas shoot length was significantly reduced in trees with more than 50% of symptomatic shoots ($p \leq 0.006$). These highly impacted trees significantly lost tree height to the disease, whereas only marginal height reduction could be detected for lesser affected trees. Our results indicate that trees resistant enough to maintain at least 50% of their crowns are generally able to survive competition in dense regeneration. Thus, promotion of natural ash regeneration could be an effective measure complementary to breeding for resistance to preserve ash as a tree species in the forests.

Key words: Ash dieback, *Fraxinus excelsior, Hymenoscyphus fraxineus*, Competition, Resistance, Tree diseases

Introduction

The fungus *Hymenoscyphus fraxineus* (syn. *H. pseudoalbidus*, anamorph: *Chalara fraxinea*) is the causal agent of ash dieback (Kowalski 2006, Queloz et al. 2011, Baral et al. 2014), a severe and devastating disease of European ash (*Fraxinus excelsior* L.) in Europe. It is suggested that *H. fraxineus* is native to Far East Asia and invasive to Europe (Zhao et al. 2012, Baral and Bemmann 2014, Gross et al. 2014). The disease emerged in the early 1990´s in Poland and has now been recorded in most parts of the natural range of *F. excelsior* (McKinney et al. 2014). In south-western Germany, ash dieback has first been recorded in 2009, but there is evidence that earlier infections occurred in 2006 (Metzler 2010).

Main symptoms are leaf necrosis, dieback of twigs and branches and collar rots that lead to high host mortality after several years of infection. Not only high economic cost resulting from the disease, but also serious ecological consequences following the collapse of populations of this important broadleaf tree species are expected (Jönsson and Thor 2012, Pautasso et al. 2013, Mitchell et al. 2014). However, in a small fraction of ash individuals the presence of high quantitative resistance against the disease has been detected. In several clonal trials and progeny trials, the resistance was demonstrated to be genetically determined and heritable (McKinney et al. 2011, Pliūra et al. 2011, Kirisits and Freinschlag 2012, Kjær et al. 2012, Stener 2013, Lobo et al. 2014, Pliūra et al. 2014, Enderle et al. 2015, Lobo et al. 2015, Muñoz et al. 2016). Selective tree breeding in seed orchards may enable the establishment of more resistant populations of ash (McKinney et al. 2014). However, for sustainable conservation of the species, adequate genetic diversity in the populations must be retained. Kjær et al. (2012) estimated that approximately 1% of the ash individuals have the potential of producing offspring with less than 10% crown damage. Thus, tree breeding in seed orchards would be a labor-intensive and expensive solution.

In general, *F. excelsior* has a very high potential of regeneration. On suitable sites, young ash trees can grow very rapidly (Wardle 1961, Jaworski 1995). Up to an age of 20 years they are able to survive in stagnant conditions in deep shadow and react to sudden light exposure with good growth (Miegroet and Lust 1972). For example, Wardle (1959) observed a living 14-year-old ash sapling with a total stem length of 29.6 cm in the shadow of a dense layer of dog's mercury (*Mercurialis perennis)*. On suitable sites, these features make ash trees very competitive. In natural ash regeneration, densities of 100,000 plants per ha are not uncommon (Roloff and Pietzarka 1997) and can reach 150,000 individuals per ha (Tabari and Lust 1999). Strong intraspecific competition in such stands results in high evolutionary selection. It is likely that susceptibility to ash dieback diminishes the individual competitiveness of young trees and therefore acts as a decisive factor in early selection. Thus far, observed resistance against ash dieback is partial and quantitative and it is likely that even trees with a high degree of resistance will be moderately affected by the disease during their lifetime. If these trees are able to maintain their competitiveness, stands of dense natural ash regeneration may become a rich source of genetically diverse and comparatively resistant ash trees. Under this condition, silvicultural promotion of ash regeneration could be an effective measure complementary to breeding in seed orchards to conserve the tree species. However, little is known about the influence of ash dieback on the competitiveness of individual trees. From infested natural regeneration stands in Lithuania, ash was reported to have a smaller mean height compared to other tree species on the same sites (Lygis et al. 2014). Moreover, it is known that crown damage due to ash dieback is negatively associated with diameter increment (Skovsgaard et al. 2010, McKinney et al. 2011, Metzler et al. 2012, Stener 2013, Enderle et al. 2013, Lobo et al. 2014). In contrast, in a progeny trial the mean height of young trees increased steadily during two growing seasons, even after temporal height loss when diseased leader shoots had died (Pliūra et al. 2014). It is currently unknown whether moderately diseased individuals will be able to compete with other tree species.

The aim of this study was to investigate the severity and development of ash dieback in dense natural regeneration stands of *F. excelsior* in south-western Germany and its influence on height growth and tree height in order to gain knowledge of individual competitiveness of differently susceptible ash trees. It was intended to create knowledge that enables better assessment of the fraction of ash saplings that is able to survive in the long term in dense natural regeneration stands under attack of ash dieback. Such assessment is necessary when evaluating the prospects of natural selection leading to enhanced resistance in future ash populations. The knowledge can facilitate assessing the silvicultural management options, such as promotion of ash regeneration, that aim to mitigate the future impact of the disease.

Methods

Investigated stands

Data was collected in three stands with dense natural regeneration in south-western Germany, where generally high competitiveness can be expected for ash. Coordinates, elevation above sea level and climate information of the stands are presented in Table 1.

Table 1. Stand characteristics of investigated study sites.

	Stand 1	Stand 2	Stand 3
Latitude	48°19′12′′	48°35′21′′	49°16′23′′
Longitude	9°7′10′′	7°58′3′′	9°53′4′′
Elevation [mamsl]	870	140	480
Mean annual precipitation [mm]	1065	913	929
Mean annual temperature [°C]	6.0	10.2	7.9

Stand 1 was located in the Swabian Jura on shallow, moderately humid but good drained Cambisol on bedrock of Jurassic limestone. It was a 100- to 125-years old beech forest (*Fagus sylvatica*), mixed with about 5% sycamore maple (*Acer pseudoplatanus*), 5% *F. excelsior* and 3% other tree species. In the understory, there was a dense layer of natural regeneration consisting of ash (53%), beech (39%), maple (6%) and some other woody species (2%). Ash regeneration was in general higher than the beech regeneration. The vast majority of beech was smaller than one meter. Advance regeneration in this stand emerged after a winter storm had produced gaps in the canopy in 1990, but the vast majority of the regeneration arose following harvesting operations in 2001, 2004 and 2005.

Stand 2 was located in the upper Rhine valley on nutrient rich, wet soils (flood plain forest). It was established in 1990 on a former agricultural land by planting black alder (*Alnus glutinosa*), sporadically mixed with ash. Dense, understory natural regeneration was present in an area of about 0.5 ha in the alder plantation, which was located in the vicinity of an adjacent ash-dominated mature stand. The regeneration consisted of 99% ash and 1% other woody plants (*Viburnum-, Alnus-* and *Prunus* spp.). There was a dense cover of herbaceous plants, mainly policeman's helmet (*Impatiens glandulifera*), *Mercurialis perennis* and common nettle (*Urtica dioica*).

Stand 3 was located on heavy, calcareous clay on bedrock of lower Keuper in the Swabian-Franconian mountain forest. The former old-growth stand was partially damaged during a storm event in 1999 and clear cut in 2005 after a severe bark beetle outbreak. Subsequently, some parts of the area were re-planted with pedunculate oak (*Quercus robur*), but most of these plants soon were outcompeted by strongly emerging natural regeneration of ash. In 2014, ash was the major tree species in the stand (91%), forming a dense layer that exceeded five meters in height in most parts of the stand. Admixed woody species in the regeneration were *Quercus* spp. (4%), sycamore maple (2%) and some other species (3%).

Data collection

The data collection in stands 1 and 2 occurred in July 2013 and was repeated in January 2015 to follow the development of ash dieback. Hence, the period of investigation included one complete growing season. In both of these stands, 15 circular plots with a radius of 1.5 m were investigated and the centre was permanently marked. In three plots in stand 1, the regeneration was damaged during harvest of mature trees in autumn 2014. Thus, data from only 12 plots were analysed in stand 1. In stand 3, data collection occurred in 14 plots in December 2014, and no repeated assessment was conducted. The locations of the plots were chosen randomly, with the following criteria: a minimum number of 15 trees per plot, which corresponds to a density of about 21,000 trees per ha, a maximum tree height of 5 m and a minimum distance between plot margins of 5 m. In the plots, all ash trees were assessed. For all other woody plant species present in the plots, the number of trees per species was recorded. Ash trees that were broken or obviously affected by factors other than ash dieback (e.g. browsing by game) were counted, but not further investigated.

In order to estimate the degree to which the ash trees were affected by ash dieback, trees were divided into classes of disease intensity. Infections of shoots and branches by *H. fraxineus* are easily recognizable by typical bark necroses, bark discolorations and abnormal branching structures (e.g. Kowalski and Holdenrieder 2008, Kirisits et al. 2009, Skovsgaard et al. 2010). The following classes were used (according to Enderle et al. 2013): class 0: no symptomatic twigs (completely healthy); class 1: 1 – 2 symptomatic twigs; class 2: 3 - 4 symptomatic twigs; class 3: 5 or more symptomatic twigs; and class 4: more than 50% of the twigs are symptomatic. The division of trees into classes was conducted regardless of the location of the infected twigs in the tree crown. As infection of the apical shoot (the leader) may have a special influence on tree growth and is crucial for the development of high quality timber, infections of apical shoots were noted additionally. Completely dead ash trees were counted and their height was measured.

As indicators for the individual competitiveness, the total tree height and the living tree height were recorded, such that a loss of height due to the disease could be calculated. The total height of all ashes was measured with a levelling staff. When the highest part of the tree was dead, the height of the highest living tip of the tree was also measured. As an additional indicator for competitiveness, the shoot growth of the present year of the highest living shoot was measured as the distance from the tip of the shoot to the first bud scar. In Figure 1, the method of measurement is sketched.

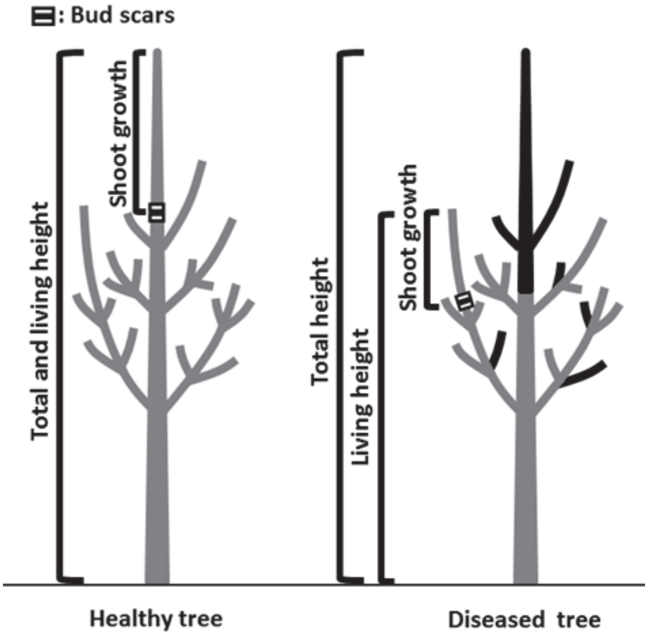

Figure 1. Sketch of the measurement method used to determine total height, living height and shoot growth on a healthy and a diseased tree. Black colour represents diseased or dead parts of the trees; grey colour represents healthy parts

Statistical analysis

Of special interest in this study was the situation of ash trees that had a chance to overcome other competitors. A main factor influencing competitiveness of young ash is their tree height in relation to their neighbours; smaller trees are more likely to be over-topped and hence to be outcompeted. Thus, analyses were conducted additionally for the stratum of trees of above-average height, to which belonged all ashes, including dead trees, with a height higher than the overall mean of total height of the respective plot.

The height growth of young ash trees depends mainly on the light regime (Petritan et al. 2007) and is also influenced by other local micro conditions such as density and water and nutrient supply (e.g. Kerr and Cahalan 2004 and references therein). The mean shoot growth varied considerably between the plots and stands. Assuming relatively homogeneous micro-local conditions within the small plots, we eliminated the plot effect in order to compare the impact of ash dieback on individual shoot growth regardless of local conditions. For this purpose, we chose a ranking approach, because shoot growth was not normally distributed in the plots. The relative rank of shoot growth was determined for each investigated ash tree as follows:

$$[1]\ Rr_i = \frac{Rp_{ij}*100}{n_j} - \frac{100}{n_j*2}$$

where Rr_i is the relative rank of the shoot growth of tree *i* with the plot effect eliminated, Rp_{ij} is the rank of shoot growth of ash tree *i* within plot *j* and n_j is the number of ash trees in plot *j*. *Rr* can have values between 0 and 100. The range of *Rr* is wider in plots with a higher number of trees than in plots that have only few trees. In other words, the tree with the highest shoot growth of a plot with a high number of ashes was assigned a higher relative rank than the highest tree of a plot with a rather small number of ashes. The arithmetic mean of *Rr* is 50 (per plot and in total). For each tree, the loss of height was calculated as the difference between total height and living height as a percentage of the total height. None of the variables were normally distributed, so Mann-Whitney tests were used to investigate the significance of differences of variables between classes of disease intensity. For these tests, the classes of disease intensity 0 to 2 were combined, because of the small number of trees in these classes. The tests were performed using SPSS 21 (IBM, Chicago, USA).

Results

In 2013, there were 1,145 ash trees within the 27 plots of stand 1 and 2. A fraction of these ashes (1,037 trees) were examined in more detail (Table 2). Over the period of investigation, the total number of trees remained unchanged in the stands with repeated measurement, while the number of living ash trees decreased from 867 trees in 2013 to 690 in 2015 (Table 2). This corresponds to a mortality of 20.4% during the period of investigation. The reduction was especially evident in stand 1. The proportion of dead ashes increased from 14.8% to 23.7% over this period of time.

In total, in stand 1 and 2, 5.9% of the living ashes (51 ash trees, Table 2) showed no ash dieback symptoms (disease intensity class 0) in 2013. This fraction decreased to 4.6% in 2015 (32 ash trees, Table 2). Meanwhile, the proportion of ashes with more than half of the crown affected (disease intensity class 4) increased from 37.0% to 50.0% during the period of investigation. The disease in stand 2 was less severe than in stand 1 for both years ($p <$ 0.001; Mann-Whitney test) (Figure 2). Moreover, decreased disease intensity was observed in the stratum of the higher trees (in 2013 $p = 0.001$; in 2015 $p < 0.001$; Mann-Whitney test). Especially, the portion of trees in disease intensity classes 4 was smaller in the stratum of above-average height.

In the 14 plots of stand 3, there were 341 ash trees, of which 338 trees were examined in more detail (Table 2). Here, 48.5% of the ash trees were already dead. Of the living trees, 76.4% were assigned to disease intensity class 4 and 21.3% to class 3. Only one tree was assigned to class 2 and three trees to class 1. No tree was considered completely healthy. Similar to trees in stand 1 and 2, trees of above-average height were healthier than trees belonging to the stratum of below-average height in stand 3 (Figure 2).

Table 2. Number of trees and ash trees in the plots separated by year and stand

Year	2013			2014 / 2015			
Stand	Stand 1	Stand 2	Both stands	Stand 1	Stand 2	Stand 3	All stands
Total number of:							
ash trees in the plots	542	603	1145	455	570	341	1366
ash trees examined	497	540	1037	423	510	338	1271
ash trees dead	83	87	170	169	74	164	407
living ash trees with symptoms of dieback	414	453	867	254	436	174	864
ash trees healthy	12	39	51	3	29	0	32
trees (all species) in the plots	1026	610	1636	1063	582	374	2019
Mean tree number per plot (all species)	85.5	40.7	60.6	88.6	38.8	26.7	49.2
Mean ash tree number per plot	45.2	40.2	42.4	37.9	38.0	24.4	33.3
Mean percentage composition of ash [%]	52.8	98.9	70.0	42.8	97.9	91.2	67.7

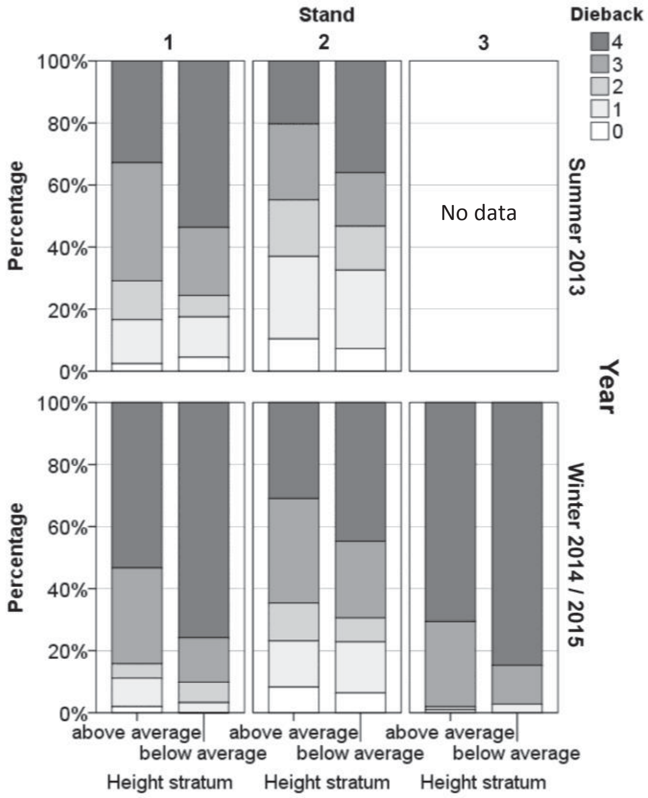

Figure 2. Percentage of ash trees in classes of disease intensity (dieback), differentiating for stand, year and stratum of relative tree height

The mean total height of living ash in stands 1 and 2 increased by 14.0% from 163.4 cm to 186.2 cm during the period of investigation. The trees were shortest in stand 2 and tallest in stand 3 (Figure 3).

The mean height of dead trees was smaller, but increased by 12.4% from 126.3 cm in 2013 to 141.9 cm in 2015. The total height decreased with increasing disease intensity (Figure 3). The differences in total height between classes of disease intensity were not that evident when considering only the stratum of the above-average relative height. The living height was significantly reduced for trees of disease intensity class 4 compared to all other classes, regardless of if all trees or only trees of above-average height were considered. Consequently, a considerable loss of height was characteristic to these ashes (Figure 3). Mean loss of height for trees of disease intensity class 4 was smallest in stand 2 in 2015 and highest in stand 1 in 2013 (Figure 3).

The annual shoot growth was highly variable in all stands and ranged from less than 1 cm to 134 cm (the highest shoot growth was detected on a tree of disease intensity class 4). The mean shoot growth was smallest in stand 1 and largest in stand 3 (Figure 4). The mean shoot growth of ashes of disease intensity class 4 was smaller than that of the other disease intensity classes. These differences between the classes were significant for stand 1 and 2, but not for stand 3, where the smallest number of ash trees were present. Shoot growth did not differ significantly between classes 0 to 2 and 3. Similar results were found when the relative rank of shoot growth (*Rr*) was considered (Figure 4). For trees of above-average height, the difference between class 4 and the other classes was not always significant. Moreover, the difference between the disease intensity classes was not significant for the trees in stand 3, where relatively small numbers of trees were present in this stratum and in the classes of lower disease intensity. By testing the data of shoot growth and *Rr* combined for all stands, class 4 was distinguished clearly from all other classes, which did not differ significantly from each other (Table 3).

In the stands 1 and 2, the proportion of living ashes with an infected stem leader remained constant (79.5% in 2013 and 80.3% in 2015) and was slightly reduced for the stratum of above-average height (70.3% in 2013 and 70.9% in 2015). In stand 3, 94.1% of the stem leaders were diseased. Approximately half of the trees of disease intensity class 1 had infected stem leaders. This proportion increased with increasing disease intensity, up to 100% for trees of class 4 (Figure 5). Within the classes 1 to 3, infection of stem leaders was connected to a significant reduction of shoot growth, indicating that shoot growth was more influenced by diseased stem leaders than by other infected twigs.

Table 3. P-values of comparisons of classes of disease intensity for shoot growth and the relative rank of shoot growth (*Rr*) combined for all stands according to Mann-Whitney tests. Above diagonal: summer 2013. Below diagonal: winter 2014 / 2015. Significant differences are labelled by * (Bonferroni correction: $p \leq 0.005$)

	Shoot growth					*Rr*				
Class	0	1	2	3	4	0	1	2	3	4
0	1	0.084	0.263	0.131	< 0.001*	1	0.187	0.567	0.151	< 0.001*
1	0.663	1	0.438	0.627	< 0.001*	0.653	1	0.293	0.861	< 0.001*
2	0.680	0.918	1	0.761	< 0.001*	0.956	0.597	1	0.328	< 0.001*
3	0.994	0.411	0.425	1	< 0.001*	0.708	0.199	0.513	1	< 0.001*
4	0.004*	< 0.001*	0.004*	< 0.001*	1	0.006	0.001*	0.001*	< 0.001*	1

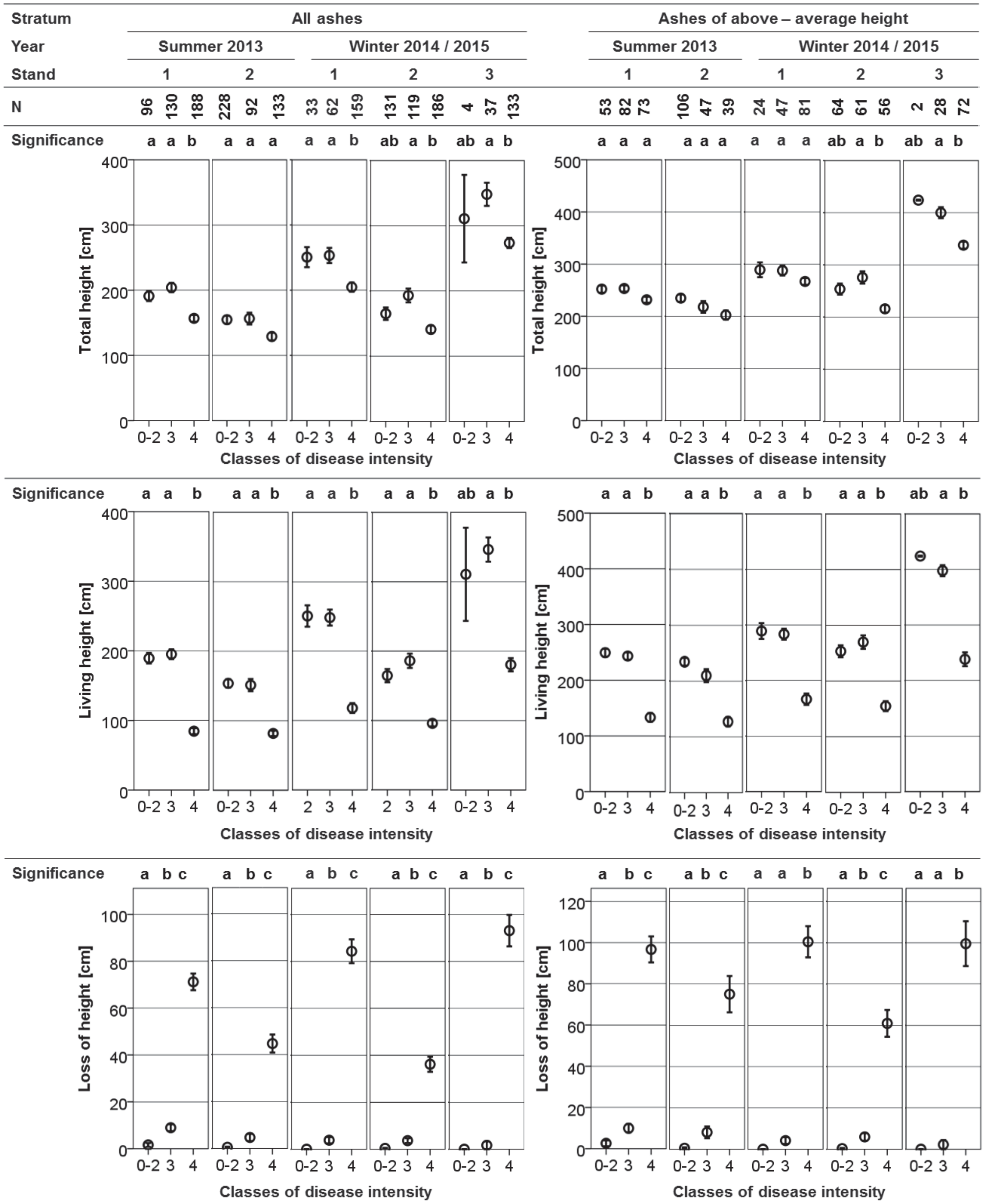

Figure 3. Mean ± standard error of tree height variables separated by classes of disease intensity for all ashes and for the ashes of above-average height in the different stands and years of investigation. The classes of disease intensity 0 to 2 are combined because of the small number of trees in these classes. Groups of trees with differing letters differ significantly according to Mann – Whitney tests with Bonferroni alpha correction ($p < 0.017$)

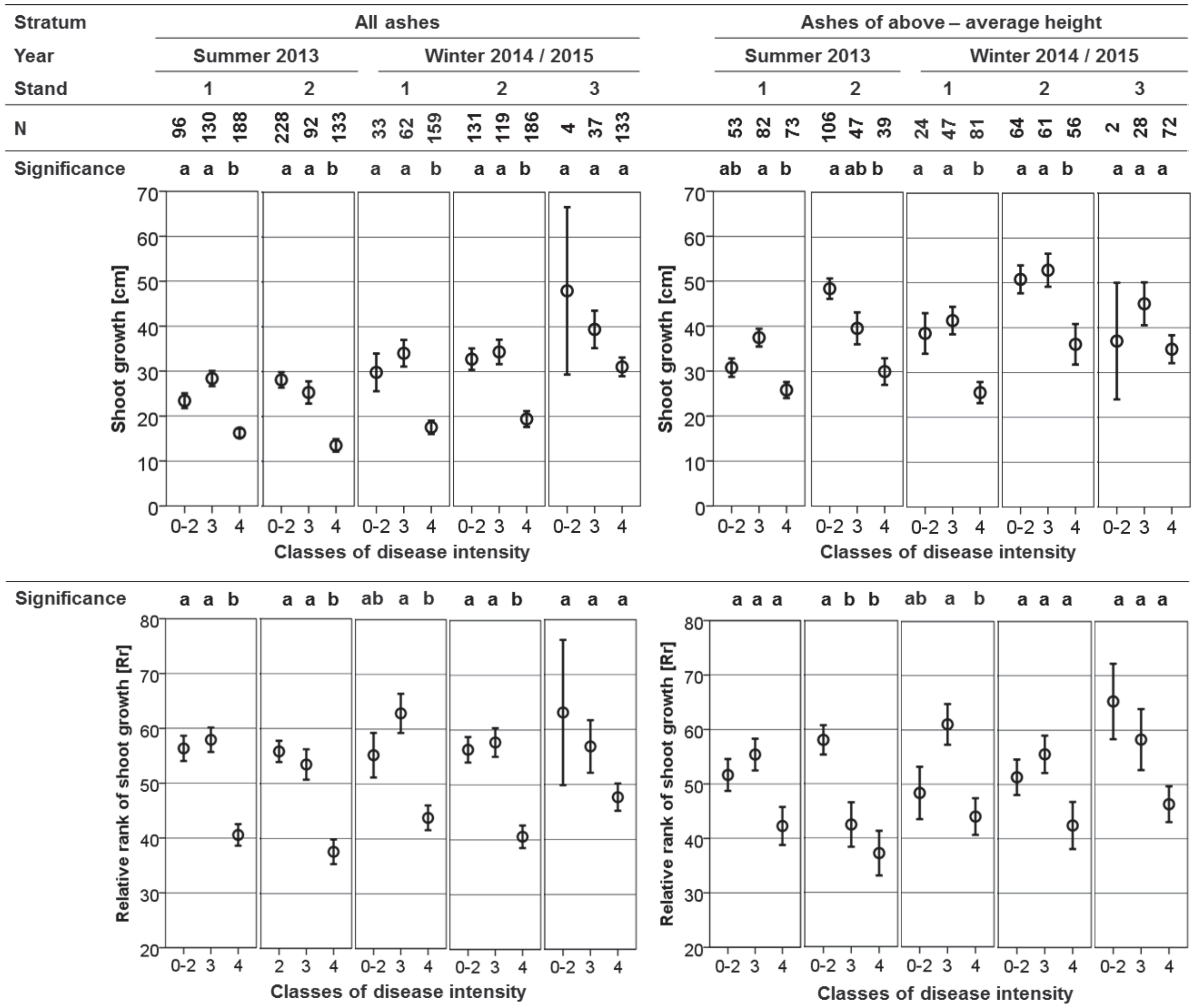

Figure 4. Means ± standard errors of shoot growth variables separated by classes of disease intensity for all ashes and for the ashes of above-average height in the different stands and years of investigation. The classes of disease intensity 0 to 2 are combined because of the small number of trees in these classes. Groups of trees with differing letters differ significantly according to Mann – Whitney tests with Bonferroni alpha correction ($p < 0.017$)

Discussion

Overall, the disease severity in the natural regeneration stands was similar to the disease intensity in a provenance trial located in south-western Germany (Enderle et al. 2013). As in the provenance trial, disease intensity increased with time.

The worst health condition was found in stand 3, which is located in the region where the oldest evidence for ash dieback, a necrosis occurring in 2006, in south-western Germany was found (Metzler 2010). The high disease severity in stand 3 may be due to its relatively long disease history. Furthermore, a criterion for the selection of the plot locations was a maximum tree height of five meters. In most areas of stand 3, regeneration was taller, so the investigated plots cannot be considered as a random sample of this stand. Dieback was more severe in smaller ash trees, and thus a bias towards an overestimation of ash dieback severity is likely in stand 3.

The proportion of asymptomatic trees was much smaller than in a Lithuanian study, where 43.6% of ash seedlings (not sprouts) in natural regeneration stands were asymptomatic (Lygis et al. 2014). This could be connected to the longer disease history in Lithuania, where processes of natural selection in favour of more resistant trees might already have commenced, as was indicated by results of a study of a Lithuanian progeny trial with different European provenances (Pliūra et al. 2014). But a smaller infection pressure must be assumed for Lithuanian stands, given the decreased number of remaining ash trees. On the other hand, the proportion of dead trees is comparable between the Lithuanian and the present study. However, the amount of dead trees is difficult to interpret, as the time of death is unknown, and trees which died a longer time ago may not have been found anymore. The reduction of living ash of 20.4% in the stands with repeated measurements allows a better understanding of the mortality rate, which was considerably higher in stand 1 than in stand 2 (Table 2). The competition due to the high density of woody plants in stand 1 might have led to this result. Natural self-thinning depends on the maximum number of living stems, the mean stem diameter and the species (Reineke 1933) and must be considered thoroughly when interpreting the influence of ash dieback on the mortality.

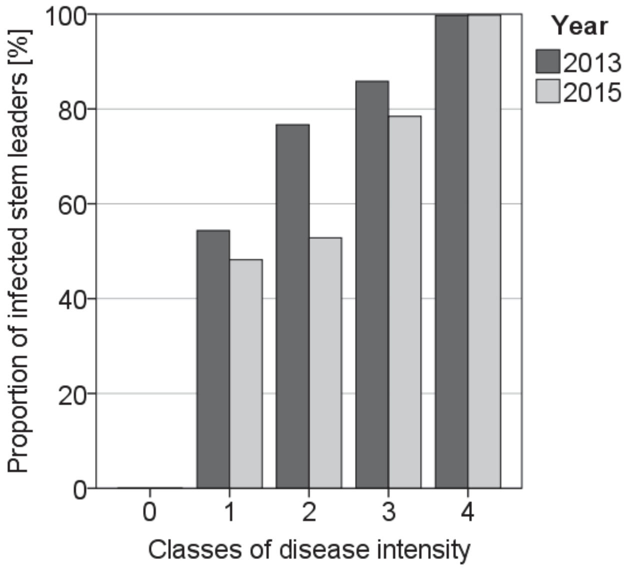

Figure 5. Percentage of living trees with infected stem leader in stands 1 and 2 by classes of disease intensity, differentiating for year

The shoot growth differed between the years of investigation, which is probably connected to the season of data collection. In 2013, fieldwork was conducted in July, when the growing season was not yet over and the yearly shoot growth might not have been completed in all individuals. In 2015, data collection took place in January. This has to be considered when interpreting the presented data, as there is high variation of disease activity between seasons (Bengtsson et al. 2014). However, the repeated measurements clearly demonstrate that patterns of height and height growth in differently diseased trees remained stable for more than one complete growing season.

The health condition of the stratum of the taller trees was significantly better than for shorter trees (Figure 2). On average, a smaller total tree height was recorded for trees of disease intensity class 4 (Figure 3). This could be either due to higher infection pressure (Chandelier et al. 2014) or better infection conditions (i.e. humidity) near the ground. Lobo et al. (2014) found strong negative correlations between the severity of ash dieback and diameter and height in an ash field trial established in 2001 and proposed that these correlations were due to the reduced crown area and the allocation of substantial amount of resources for the formation of epicormic shoots in more susceptible trees. In contrast, better health condition of smaller trees in natural ash regeneration was demonstrated in a recent study from Latvia (Pušpure et al. 2017). Apparently, the relationship between tree height and disease severity depends strongly on the development stage and the disease history of the stand.

The living height of trees of disease intensity class 4 was significantly lower than that of trees of the other classes of disease intensity, which did not differ noteworthy in this criterion (Figure 3). Moreover, marginal loss of height for trees up to disease intensity class 3, but a considerable loss of height for trees of disease intensity class 4 was observed (Figure 3). This result is remarkable, as infections were detected particularly often on the stem leaders (Figure 5). Trees with less than half of the crown affected by dieback can obviously compensate the loss of the upper part of the stem leader easily by enhancing growth of overtaking twigs.

A similar pattern was demonstrated for the shoot growth, where, on average, only trees of disease intensity class 4 showed reduced lengths of shoots (Figure 4). This result was further confirmed by the relative rank of shoot growth (*Rr*). However, for the stratum of trees of above-average height, the shoot growth difference was less pronounced. Also in stand 3, reduced shoot growth of the stratum of trees of above-average height was not significant. This might be due to the comparatively small number of trees in the classes of disease intensity 0 to 2. When the data of all three stands were combined, class 4 was clearly distinguished from all other classes (Table 3).

The largest observed annual shoot growth of 134 cm was recorded on a tree of disease intensity class 4, providing evidence that highly diseased trees can have extraordinary shoot growth, too. It can be hypothesized that this phenomenon may occur when the size of the crown is diminished rapidly by the disease and the few remaining twigs receive a bulk of resources from the still comparatively large root system. The loss of side twigs may even support the growth of the leading shoot. However, we think that these trees will not be able to compete with other trees in the long term, because of new and recurring infections every year linked with the loss of height and energy.

Tree height and height growth both are factors most relevant for inter- and intraspecific competitiveness in dense natural regeneration. Our results indicate that young ash trees maintain their height and height growth, as long as less than half of their crown is affected by the disease. Further research is required to confirm our results, which are based on observations in only three stands and one complete growing season, but our findings provide viable management options that aim to save the species for timber production.

Reports from areas with longer disease history demonstrate successful regeneration of ash under natural infection pressure. According to Lygis et al. (2014), average density of natural ash regeneration in former ash dominated and clear cut stands in Lithuania was only 599 plants per ha, which they traced back to relatively low numbers and the poor condition of seed trees in the clear cuts. Another study reports a sharp increase of advance ash regeneration from 2005 to 2015 in the understory of former ash dominated stands in Latvia (Pušpure et al. 2016). This indicates good prospects for prolific ash regeneration, if mature stands are not clear cut.

In conjunction with breeding programs in clonal seed orchards, stands with generally good site conditions for ash and with dense ash regeneration could become a simple, inexpensive and rich future source for genetically diverse and highly resistant ash propagation material. It is likely that in such stands, several hundreds of trees per ha are resistant enough to sustain in the long-term more than half of their crown. As our results indicate, these trees would have the prospective ability to survive the disease and the competition. However, an element of uncertainty is the serious symptom of collar rot (Bakys et al. 2011, Husson et al. 2012, Enderle et al. 2013, Muñoz et al. 2016). Most surviving trees will probably not be suitable for high quality timber production, as dieback affection in young plants, especially at the stem leader, is connected with a deterioration of stem quality (Enderle et al. 2013).

The symptoms of ash dieback are easily recognizable (e.g. Kowalski and Holdenrieder 2008, Kirisits et al. 2009, Skovsgaard et al. 2010), but it cannot be excluded that individual twigs that died due to other causes, such as shading, were incorrectly assessed as disease symptoms. This might have led to slightly inaccurate assignments of trees to the classes 0, 1 and 2. However, as these classes were combined in analyses, we are sure that this did not have a noteworthy influence on our results.

Conclusion

In this study, the severity of ash dieback and its effect on individual tree growth of *F. excelsior* saplings in natural regeneration was analysed. The influence of the disease severity on the individual competitiveness could thus be clarified. Severe damage due to ash dieback was found in the investigated natural ash regeneration. Repeated measurements showed a drastic increase of disease intensity, and experiences from earlier infested areas suggest further deterioration of the regeneration. However, our results indicate that young ash trees maintain their height and height growth, as long as less than half of their crown is affected by the disease. As these factors are very relevant for competitiveness in dense natural regeneration, it can be assumed that trees with a high degree of resistance are generally able to survive ash dieback and competition in dense natural regeneration in the long term. On suitable sites, silvicultural promotion of ash regeneration thus may be an effective measure complementary to breeding for resistance to maintain a participation of ash in European forests, to mitigate the impacts of ash dieback and to increase the degree of resistance in future ash populations.

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