Natural Regeneration of Common Ash in Young Stands in Latvia

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Abstract

Due to the dieback caused by ascomycete *Hymenoscyphus fraxineus*, common ash (*Fraxinus excelsior* L.) regeneration currently occurs only naturally and is crucial for existence of the species. Hence, in this study, we assessed the success of the natural regeneration and health condition of common ash in 90 diverse young stands. Additionally, the age structure of ash advance growth (saplings and seedlings) was characterized in four plots, initially dominated by ash. Ash was abundant in the advance growth in the studied plots with the mean density of 4185 ± 401 trees ha^{-1}. Ash advance growth density and health condition decreased with increasing height and age. From the 7533 accounted regeneration ashes, 75% were considered as healthy, 15% damaged and 10% were already dead. Ash regeneration density was the highest and the degree of *H. fraxineus* damage was the lowest in young stands on drained mineral soils. The best ash health condition was found in the densest stands with increased number of advance growth and undergrowth individuals. The highest ash mortality (ca 20%) was found in pure young stands. In the young stands, which were previously formed by ash, regeneration density was relatively low (4319 ± 592 trees ha^{-1}), but the mortality intermediate (ca. 10% of all trees). In contrast, in the stands dominated by black alder and birch, the density of ash advance growth was higher – 7300 ± 6300 and 6933 ± 2711 trees ha^{-1}, respectively, but the number of dead ash was lower (ca. 5%). Ash appeared more susceptible to the disease in the dense and unmanaged stands, as the health condition of ash regeneration was positively related to the number of tendings. A significant correlations between diameter, age and height of ash was observed, yet the analysis of the dimension showed, that the ash regeneration after harvesting and/or dieback has been occurring at different rates.

Keywords: *Fraxinus excelsior*; advance growth; establishment; young stand; ash dieback; natural succession; hemiboreal forest zone

Introduction

Intensive dieback of common ash (*Fraxinus excelsior* L.) caused by the ascomycete fungus *Hymenoscyphus fraxineus* (T. Kowalski) Baral, Queloz, Hosoya, comb. nov. has been observed in Europe since the mid-1990s (Kowalski 2006). The Baltic countries were among the first regions, where the ash dieback was described (Bakys et al. 2009, Stener 2013); yet in Latvia, the disease was confirmed only in 2007 (Kenigsvalde et al. 2010). According to the national inventory conducted in 2009, one third of all ash forest in Latvia has been lost (Kenigsvalde et al. 2010). At present, common ash forms ca. 0.5% (14582 ha) of the total forest area, of which ca. 25% are young stands. Due to the rapid spread of the dieback (Kirisits and Freinschlag 2011, Pliūra et al. 2011), ash planting has been stopped as economically non-sustainable (Kirisits et al. 2011, Bakys 2013). Nevertheless, ash has been regenerating naturally in Latvia (Laiviņš and Mangale 2004) and all Europe (FRAXIGEN 2005, Dobrowolska et al. 2011). In the United Kingdom (Wardle 1961) and Sweden (Dobrowolska et al. 2011), ash has been considered as a pioneer species, while in Denmark it is considered as intermediate between the pioneer and permanent component of forest (Ahlberg 2014). In Central Europe, ash has been associated with invasive species (Wagner 1990, FRAXIGEN 2005), while in northern Europe the term "fraxinisation", which represents the successful self-regeneration of ash, has been used (FRAXIGEN 2005). Still, during the last 10 years, the situation has radically changed, e.g. in Sweden, ash is now a Red listed species (Gärdenfors 2010). Therefore, the assessment of the natural regeneration pathways of ash is necessary to improve the management of existing stands aiming to maintain existence and better health condition of the species by applying silvicultural activities.

In many European countries, the damaged ash stands are transformed every year and certain part of those territories is left for the natural regeneration, subjecting ash to competition with other species that causes stress. In rich and moist sites, the most common competitors to ash advance growth (saplings and seedlings) are the early successional or pioneer species such as grey alder (*Alnus incana* (L.) Moench), silver birch (*Betula pendula* Roth.) and, in some cases, common aspen (*Populus tremula* L.) (Lygis et al. 2014). Natural regeneration of ash differs amongst site with diverse soil types. Prior to the dieback in Latvia, the best regeneration of ash was observed on mineral and drained mineral soils, especially in stands dominated by ash (Sakss 1958, Laiviņš and Mangale 2004). Due to the different views on the *H. fraxineus* spread and aggressiveness in diverse growing conditions (Kirisits et al. 2011, Stener 2013, Bakys 2013, Bakys et al. 2013), it has been unclear, how the dieback of mature ashes affects its natural regeneration, spread and health condition. At present, there is a large uncertainty about the development of ash forests, as since the onset of the disease, only a few studies dealing with the regeneration of damaged stands have been conducted (Ahlberg 2014, Lygis et al. 2014). Still, the optimistic forecasts suggest that, after a certain period of time, ash should recover from the dieback (Pliūra et al. 2011). The aim of this study was to evaluate the density and health condition of different young stands of common ash in Latvia. We hypothesised that the intensity of the damage was higher in the denser stands on the drained soil types. We also assumed that the susceptibility to damage has been affected by the ash advance growth dimensions.

Material and methods

Study sites, sampling and measurements

Ash regeneration was studied in 90 stands (Figure 1) distributed across Latvia. In Latvia, ash occurs in the mixed forests together with other deciduous trees (e.g., aspen, birch, alder, spruce (*Picea abies* Karst.), etc.); pure stands are rare. Ash is distributed quite frequently, but mainly the stands occur in the central part of Latvia, where soils are fertile and the climate milder (Nikodemus et al. 2009). The climate in Latvia can be classified as transitional maritime to continental, the continentality increases eastwards. Accordingly, the territory can be divided into three regions: the western, central and eastern part of Latvia (Figure 1). In these regions, the mean temperature in January is ca. -1.8, -3.2 and -4.5 °C, but in July ca. 17.4, 18.2 and 17.9 °C, respectively. The mean precipitation in July in these regions is about 748, 619 and 665 mm, respectively.

The young stands of common ash, where in previous rotation ash formed ≥ 40% of standing volume, with the age of 5 to 40 years and the size ≥ 1 ha, were selected from the State Forest Service inventory database. All age groups (distinguished by the step of ten years) were presented by 19–25 plots (Table 1). Stands corresponded to four soils types, mostly dry mineral (46 plots) and drained mineral (26 plots). The studied sites have undergone up to four tending events (mostly once or twice).

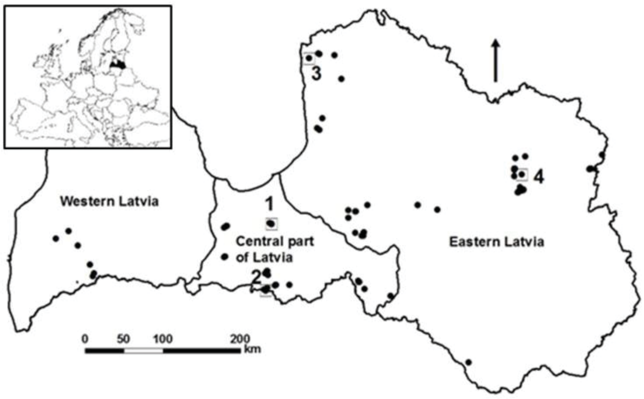

Figure 1. The location of study sites. Dots indicate the studied common ash regeneration plots. Squares denote the plots where stem discs have been collected for the estimates of age (1 – Plakanciems, 2 – Bauska, 3 – Ainaži, 4 – Lejasstradi)

Table 1. Classes of ash height, age and *Hymenoscyphus fraxineus* damage

Class	Age years	Height cm	Degree of ash damage%	Damage visual characteristics
I	< 10	< 50	0 - 10	Tree looks healthy or slightly damaged individual leaves.
II	11 - 20	50 - 100	11 - 25	Damaged several pages, some necrosis of the bark.
III	21 - 30	101 - 150	26 - 60	Fully damaged / dead separate branch; damaged part of the foliage; necrosis of the bark on large areas.
IV	31 - 40	151 - 200	61 - 99	Completely broken up dead part of the crown; partially damaged the entire crown; live separately branches in secondary crown.
V		201 - 250	100	Tree completely dead.
VI		251 - 300		
VII		> 300		

Within each young stand, one 2 × 100 m sampling plot was established along the longest diagonal of the forest district. Within each plot, all trees were accounted and their height was determined with the precision of 0.5 m (Table 1). All species were divided in two groups: advance growth containing all tree species, and undergrowth (shrub species). For each ash, degree of *H. fraxineus* damage was recorded according to five classes described in Pušpure et al. (2015) (Table 1).

To assess the relationship between ash height, diameter, age and the degree of damage, four of the studied young stands (two six-year old and two eight-year old), were selected (Figure 1, indicated by squares). In each stand, one 2 × 100 m sampling plot was established. In the sampling plots, all ashes were sampled, the cutting was done at the soil level and their height was measured with the precision of one cm. From each stem, a sample at its base (stem disc) was taken. The degree of *H. fraxineus* damage was recorded according to the five classes as described above. The number of felled trees per stand ranged from 108 to 160; at least 10 ashes in each height class were sampled. In the laboratory, stem discs were grinded and tree-rings were counted under a microscope.

Growth inventory in the study stands was conducted from mid-June to September 2015 when the damage of *H. fraxineus* was clearly visible and identifiable (Lygis et al. 2014). Ash samples were collected in August 2015. Dominant canopy species in previous rotation were determined according to the national inventory 2015; mostly they were ash (48% of all plots), ash with silver birch (14%) and grey alder (7%) admixture, spruce (8%) ect. The dominance of species in the advance growth was distinguished according to Simson (2006) (the dominant species comprises ≥ 50% of the total number of advance growth individuals and exceeds other species by 20%; the codominant species comprises 25–50% of all individuals). Soil types were distinguished according to data from the National State Forest Service inventory. Peat soils were considered if thickness of peat layer exceeds 30 cm.

Data analysis

To assess the effect of region and species composition on ash regeneration, generalized linear models (GLM) were applied. Differences in ash density according to soils and stand age (classes) were determined by the generalized linear mixed models (GLMM). The region (western, central and, eastern part of Latvia) as well as site was included in the models as the random factors. In both models, Gaussian distribution with "log" function was used. The models were based on the mean values for sampling plots. The GLMM method was also used to determine the factors (ash height and age, soil type, ash density, dominant species in advance growth, number of tending events) affecting ash health condition. For the tested factors, the central part of Latvia, aspen and dry mineral soils were chosen as the reference levels, to which other levels were compared. Such reference levels were chosen as the largest ash forests occur in the central part of Latvia, ash grows best on the mineral soils (Sakss 1958) and its health condition is the best in the stands with admixture of aspen. The significance of the GLMM was evaluated using the Likelihood ratio test (West et al. 2006). The relationships between ash density and height (classes from I to VI, Table 1), between health condition and height, and between the number of undergrowth and advance growth species were quantified by a bootstrapped (Johnson 2001) Pearson correlation analysis. The relationships between the ash diameter, age and height, were evaluated using a linear model. The differences in ash diameter, height and age between the sites and health classes were assessed by one-way ANOVA. The mean values of the gradation classes were compared using the Tukey HSD post-hoc test. The distributions of the dimensions of trees were compared by the chi-square test. All analyses were calculated at the significance level $\alpha = 0.05$ in the program R v. 3.1.2 (R Core Team 2014) using libraries "lme4" (Bates et al. 2014) and "lmerTest" (Kuznetsova et al. 2015).

Results

Species composition and ash regeneration

In total, 11 advance growth and 23 undergrowth species were accounted in the studied young stands, which had the mean density of 18410 ± 1040 trees ha^{-1}. The proportion of the advance growth and undergrowth individuals was 48.4 vs. 51.6. The undergrowth was dominated by two species – bird-cherry (*Padus avium* Mill.) (55% of total number of species, 5163 ± 638 shoots ha^{-1}) and hazel (*Corylus avellana* L.) (15%, 1399 ± 172 shoots ha^{-1}) (Figure 2). The advance growth density differed greatly and ranged from 1050 to 22900, with the mean value of 7150 ± 558 trees ha^{-1}. The highest advance growth density was observed for ash with 4185 ± 401 (ranging from 50 to 17750) trees ha^{-1} followed by grey alder (1620 ± 321 trees ha^{-1}), silver birch (681 ± 114 trees ha^{-1}) and aspen (687 ± 134 trees ha^{-1}) (Figure 2).

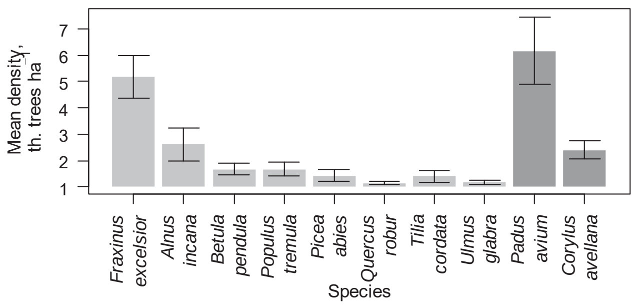

Figure 2. Mean density of the main understorey (advanced- and undergrowth) species

Ash advance growth density was similar amongst the regions (p-value = 0.06), age groups (p-value = 0.29), soil types (p-value = 0.58) and stands with different canopy species in the previous rotation (p-value = 0.06) (Figure 3a-d), yet some tendencies were observed. Ash density decreased with the increasing ash height and age. The density in the age group I was 5405 ± 951 trees ha^{-1}, while in the group IV 3036 ± 486 (Figure 3b). Although the correlation between ash advance growth density and ash height (up to three meters) was not significant (r = -0.08, p-value = 0.30), the highest density occurred in the height group I – 1857 trees ha^{-1}, but in the following groups, it decreased three time.

The highest number of ash was observed in the stands on the drained peat (mean 4584 ± 917 trees ha^{-1}), dry mineral (4275 ± 565 trees ha^{-1}) and drained mineral soils (4269 ± 846 trees ha^{-1}), but the lowest in the stands on wet mineral soil (1880 ± 331 trees ha^{-1}) (Figure 3c). The GLM analysis showed that the ash advance growth density was not significantly (p-value = 0.59) affect by the species composition. Yet the highest density of ash advance growth occurred in the stands where black alder (7300 ± 6 300 trees ha^{-1}) and birch (6933 ± 2711 trees ha^{-1}) were the main species, but the lowest (less than 2000 ash trees ha^{-1}) in stands dominated by lime and aspen (Figure 3d).

Incidence of Hymenoscyphus fraxineus in ash undergrowth

Of the 7533 accounted young ashes, 75% (5644 trees.) were considered as healthy, 15% (1134 trees) were damaged to varying degree, while 10% (755 trees) were dead. The degree of damage differed significantly (p-value < 0.001) among the regions (Figure 3a). The best ash health condition was observed in the central part of Latvia, where 78% of ash was healthy and 8% was dead, but the worst – in the western part of Latvia, where only 49% were healthy and 27% of ashes were already dead.

The degree of damage increased with age and height of ashes that was confirmed by the GLMM analysis (Figure 3b, 4). Significant correlation (r = 0.28, p-value < 0.001) was observed between disease intensity and height of ash. Up to 3 m height, 81% of ashes were healthy, but 4% were dead, while above the height of 3 m, these numbers were 54% and 33%, respectively. The age of young ash also had a significant (p-value < 0.001) effect on the occurrence of the disease. In the age group I, 81% of all ash trees were healthy, but in the group IV, it decreased to 58%, while the amount of dead trees was 3% and 24%, respectively.

The incidence of *H. fraxineus* damage differed significantly (p-value < 0.001) among the stands on different soils (Figure 3c). Similarly to ash density, health condition was the best in stands on the dry mineral and drained soils, e.g. 79% of ashes on drained mineral soils and 76% on dry

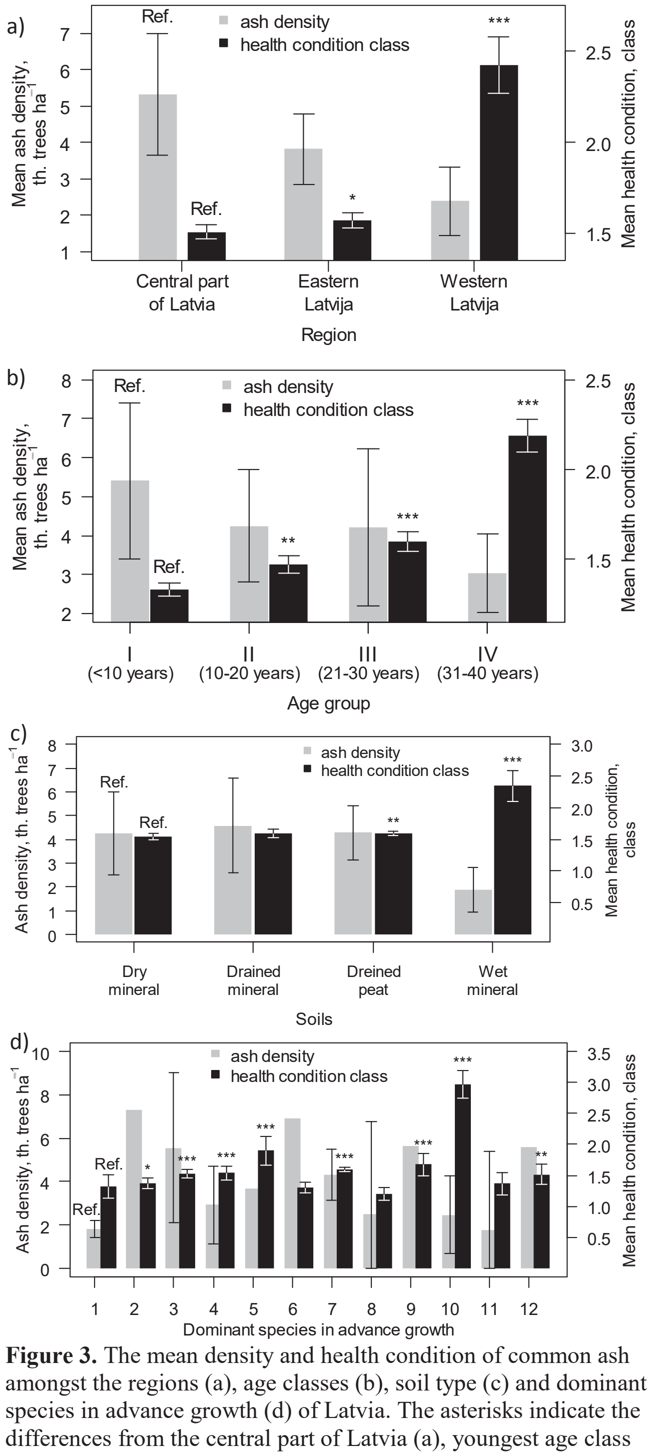

Figure 3. The mean density and health condition of common ash amongst the regions (a), age classes (b), soil type (c) and dominant species in advance growth (d) of Latvia. The asterisks indicate the differences from the central part of Latvia (a), youngest age class (b), dry mineral soil (c) and *Populus tremula* (d) used as the reference level (Ref.). Significance codes: * - p ≤ 0.05, ** < 0.01, *** - p ≤ 0.001. Dominant species in advance growth: 1 – *Populus tremula*, 2 – *Alnus glutinosa*, 3 – *A. incana* ,4 – *A. incana/F. excelsior*, 5 – *Acer platanoides*, 6 – *Betula pendula*, 7 – *F. excelsior,* 8 – *F. excelsior/B. pendula*, 9 – *Picea abies*, 10 – *P. abies/F. excelsior*, 11 – *Tilia cordata*, 12 - *T. cordata/F. excelsior*

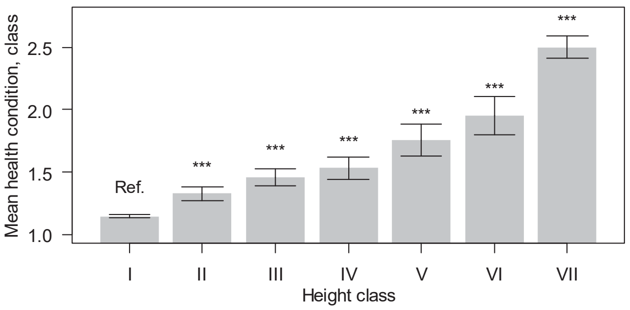

Figure 4. Ash health conditions in he studied young stands depending on tree height compared to the smallest height class, used as the reference level (Ref.). Significance code: * - p ≤ 0.05, ** < 0.01, *** - p ≤ 0.001

mineral soils had minimal or no symptoms. The highest degree of the damage of ashes was observed in stands on the wet mineral soils, where only 54% of trees were healthy and 27% were dead.

Although the relationship between ash density and ash health condition differed among sites, a significant (*p*-value < 0.001) negative logarithmic relationship between the mean health condition class and ash density was observed (Figure 5). Ash density was < 2000 tree ha^{-1} when the mean health class exceeded 4.3 (Figure 5). Analogically, negative correlations were observed between the ash density and the density of advance growth and undergrowth density, r = - 0.23 and - 0.24, respectively. The highest ash mortality was observed in the pure stands where 20% of ash was dead. In contrast, in stands where ash was in the admixture, its health condition was better and 82–95% of ash trees were healthy and only 1% was dead.

Health condition of ash significantly differed (*p*-value < 0.001) among the young stands with diverse dominant species (Figure 3d). The main species in the advance growth composition in the plots where ash (53% of the plots), grey alder (10%), grey alder/ash (9%) and spruce/ash (6%), yet the greatest *H. fraxineus* damage was observed in young stands formed by spruce/ash (40% of ash were dead), maple (*Acer platanoides* L.) (14%) and spruce (12%), but the lowest in ash/birch (87% of ash were healthy), birch (87%) and aspen (89%) young stand.

Health condition of the young stands was influenced by management. The intensity of ash dieback differed significantly (*p*-value < 0.001) among the stands with different number of tending events performed. The best ash health condition was in the young stands, which were tended four times, as the mean value of disease class score was 1.12, but it gradually increased with the decreasing number of tending events reaching 1.70 for untended stands. All differences among stands with different number of tending events were strictly significant (*p*-value < 0.001).

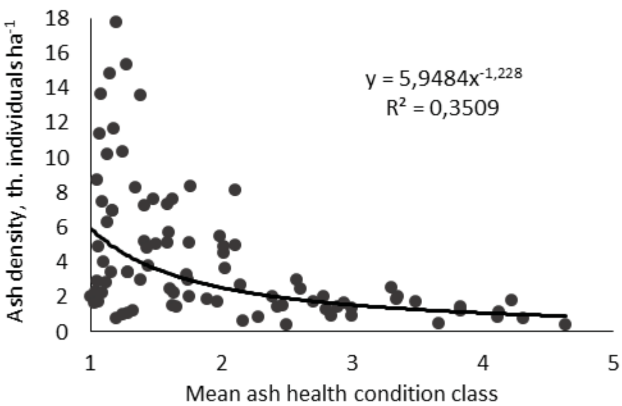

Figure 5. The relationship between the health condition and density of the common ash in the studied plots

Advance growth dimensions

The mean height of ash did not differ significantly (*p*-value = 0.57) among the studied four plots (regions), but the mean diameter (*p*-value = 0.001) and age of ash did (*p*-value < 0.001) (Table 2), although the mean age of ash in the first three height classes (up to 150 cm) was five years. A significant (*p*-value < 0.001) linear relationship between the diameter and height of ash was observed (Figure 6). The relationship between ash age and height was also significant (*p*-value < 0.001), still during the first 5–8 years, the height of ash increased irregularly and individually as rather high variability was present at each age (Figure 6).

Ash height distribution did not differ significantly between the sites (*p*-value = 0.57), but the diameter distribution differed only between Bauska and Lejasstradi sites (*p*-value = 0.02). In contrast, the age distribution was similar only in the same two sites (Figure 7). Ash height was significantly (*p*-value = 0.002) affected by the disease, but significant differences were observed only between the health classes I and II (*p*-value = 0.005).

Table 2. Ash measurement in stem discs collection plots

	Mean density, ash ha^{-1}	Young stand age, years	Mean age, years	Std. Error	Mean height, cm	Std. Error	Mean diameter, mm	Std. Error
Ainaži	4850	8	6.23	0.26	159.77	9.87	264.74	15.81
Bauska	5100	6	7.38	0.32	178.83	11.53	307.83	18.39
Lejasstradi	14850	6	7.23	0.35	166.02	10.32	211.63	13.97
Plakanciems	11650	8	3.77	0.22	175.30	9.50	266.60	16.19

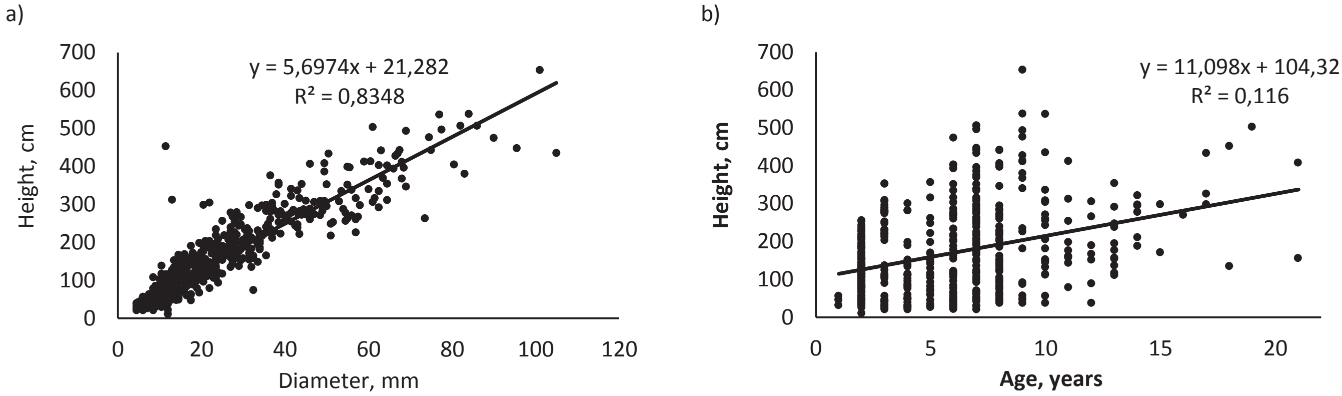

Figure 6. Relationship between the diameter and height (a), and age and height (b) of ash in the studied plots

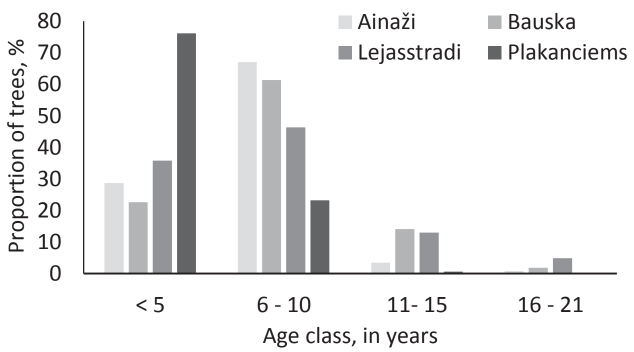

Figure 7. The age distribution of common ash in the understory of the studied plots

The best health condition was observed for the lowest trees. Similarly, ash diameter was affected by the disease (p-value < 0.001); smaller diameter trees were healthier. Ash health condition class differed significantly among the age classes (p-value < 0.001) and decreased with age.

Discussion

This study showed that the density of advance growth and undergrowth (18410 ± 1040 ashes ha^{-1}) was similar as observed before the decline (15 – 30 th. shoots ha^{-1}) (Sakss 1958), though growing conditions might have altered due to changing climate . The floristic composition of regeneration of ash stands, appeared little affected by the dieback as the same species have been observed before (Sakss 1958) and after (Figure 2; Lygis et al. 2014) the outbreak of the disease. Still, the proportions of regenerations species have been altered. In the studies stands, increased proportion of the undergrowth species was observed (Figure 2), suggesting ongoing changes in the stands. Although ash dieback can facilitate development of the undergrowth species, which consumes nutrients and alter light climate stressing ash (Keer 1998, Givnish 2002, Royo and Carson 2006, Skovsgaard et al. 2010), ash advance growth density was higher in stands with dense undergrowth (r = ca. -0.23). In the stands with the densest undergrowth (> 15 th. individuals ha^{-1}), ash advance growth also had the best health condition, likely due to higher species diversity.

Ash advance growth density (Table 2) was considerably higher than recently observed in the neighbouring Lithuania (Lygis et al. 2014) (4185 ± 401 vs. 599 trees ha^{-1}, respectively), suggesting regional differences in intensity of the dieback. Considering that the disease was spreading from south, better ash health condition in Latvia might be related to longer time available for the adaptation (Pliūra et al. 2011). Yet it was lower than before the outbreak of the disease in Europe, when more intense natural regeneration of ash (150000 young ashes ha^{-1}) occurred (Sakss 1958, Tabari and Lust 1999, Lygis et al. 2014). Nevertheless, Ahlberg (2014) suggested that in Denmark optimal ash advance growth density is 1500 individuals ha^{-1}, when the interspecific competition is the lowest. Ash advance growth density was inversely related to the disease intensity (Figure 5) that might be explained by the increased mortality and differences in the resistance of young ash. Similar relationships due to rapid development of the disease was observed by Enderle et al. (2013).

Ash density decreased with increasing age and height (Figures 3b, 4) as the density of the stands younger than 10 years was ca. 5000 trees ha^{-1}, but at the age of 31–40 years, it was only up to 56% of that density, thus following the reverse-J shape distribution of the natural regeneration. Normally, ca. 40–50% of the recruiting young ashes die annually, but under intensive disturbance, e.g. dieback, mortality can reach up to 85% (Harmer et al. 2005). Ash is a gap specialist, which is shade-tolerant at the sapling phase, but is light-demanding when reaches canopy (Petriţan at al. 2009, Kerr and Cahalan 2004), hence insufficient light conditions decreases its competitiveness with other species (Niemelä et al. 1992, Guzman and Dirzo 2001) and resistance against pathogens (Bakys at al. 2013) thus increasing mortality. Probably, the density of young stands was also decreased by the dieback, as a considerable part of seedlings might be weakened and outcompeted by the herbaceous vegetation (Wardle 1961, de la Cretaz and Kelty 2002), especially in fertile sites (Dobrowolska et al. 2011). Still, the amount of dead seedlings (10% of total number) was lower compared to Lithuania (Lygis et al. 2014), supporting regional differences in health condition of ash. Skovgaard et al. (2010) showed that in a planted stand, small- and medium-sized trees were more susceptible to the disease. However, in this study in the naturally regenerating stands, the opposite was observed as the smaller ashes (height ca. 160 ± 50 cm and diameter ca. 23 ± 7 mm, which comprised 39% of all measured) were the most healthy (Figure 4), but the largest ashes (H > 240 cm, D > 45 mm which comprised 20% of all measured) were the most damaged, suggesting age-related increase in susceptibility to the disease.

Although diverse opinions about the effect of site type on the susceptibility to *H. fraxineus* damage persist in Europe (Bakys et al. 2013), in Latvia, higher susceptibility of ash was observed in the wet sites, as previously shown by Gross et al (2014). Ash is susceptible to prolonged waterlogging (Wardle 1961), hence the most abundant ash regeneration with the best health condition was observed in stands growing in well-drained and dry mineral soils (Figure 3c). The positive effects of drainage system on ash health condition has been emphasized in Denmark (Ahlberg 2014), Germany (Schumacher 2011) and other countries (Dobrowolska et al. 2011) as in the over-moist sites, trees have been more stressed, hence less resistant to disease.

Ash regeneration (mean 8064 trees ha^{-1}) and health condition (82–95% of ash trees were healthy) was better in the mixed stands. In Central Europe, establishment and development of ash seedlings is influenced by the canopy species composition (Götmark et al. 2005). Similarly, lower degree of damaged ash and better increments have been observed in mixed rather than pure stands (Dobrowolska et al. 2011, Schumacher 2011, Stener 2013). The lowest ash sampling mortality was observed in stands where certain satellite species occured (Givnish 2002). Likewise, in this study, the most abundant ash regeneration with the best health condition, was observed in stands formed by black alder and birch 7300 ± 6300 and 6933 ± 2711 trees ha^{-1}, respectively (Figure 3d), as demonstrated previously (FRAXIGEN 2005, Dobrowolska et al. 2011, Ahlberg 2014). Although ash is considered to have the lowest regeneration in sites with acidic humus layer (Tabari et al. 1999, Dufour and Piegay 2008), we found rather high regeneration density also in stands formed by spruce (5650 ± 2650 trees ha^{-1}). This might be related to decreased competition with other broadleaved species likely due to poor light conditions. Yet, ash health condition was considerably lower compared to broadleaved stands (Figure 3d) likely due to stress caused by root competition between ash and spruce (Lei et al. 2012). Although in mixed stands young ash has rapid development (Le Goff and Ottorino 1996, Keer 2004) thus outcompeting others (Rysavy and Roloff 1994, Dobrowolska et al. 2011), the disease might severely decrease its competitiveness. Hence, decreased ash health condition was observed in stands with maple admixture (Figure 3d) pointing to increased competition, as both species have similar growth strategies (Petritan et al. 2009), but the competitiveness of ash (Urbinati and Cillia 1995) has been weakened. In stands where ash was the canopy species, its regeneration density was lower (4319 ± 592 ash trees ha^{-1}) likely due to intraspecific competition.

High site-specificity of the increments of ash has been observed, as ash dimensions had a wide range within each of the four studied sites (Table 2), suggesting the plasticity of the species. The management of young stands had an effect not only on the height and diameter, but also on the health condition of ash advance growth. In the stands that have undergone several tendings, young ashes had a higher stem diameter and best health condition (Table 2, Figure 5), as the highest susceptible to disease has been observed in dense and unmanaged stands (Cech and Hoyer-Tomiczek 2007, Skovsgaard et al. 2010, Bakys et al. 2013). After thinning, the competition amongst ashes is decreased, thus minimizing biotic (competition) and abiotic (increased moisture) stresses (Niemelä et al. 1992, Guzman and Dirzo 2001). Hence, thinning might be recommended as one of the means to improve ash condition (Guzman and Dirzo 2001, Niemelä et al. 1992, FRAXIGEN 2005) also in Latvia. Though, excessive tending can also promote the disease (Bakys et al. 2013).

Conclusions

Our study showed that after 15 years since the initiation of the ash dieback, natural regeneration has been taking place in sufficient quantities. The floristic composition of advance growth and undergrowth species in the declining ash stands have remained similar with pre-dieback stands, yet the proportion of undergrowth species has increased, apparently altering the succession. It is expected that ash regeneration would continue on dry or drained sites, where the species was more abundant and their health condition was the best. Still, at present, 75% of the studied young ash trees are healthy, but mostly they are two to six years old, hence further monitoring is necessary. Considering current health condition and regeneration density, ash will apparently could remain as an admixture species in rich sites.

Acknowledgements

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