

Health Condition of European Ash in Young Stands of Diverse Composition

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Abstract

During the recent decades, the ascomycete *Hymenoscyphus fraxineus* has been spreading across Europe causing dieback of European ash (*Fraxinus excelsior*) and threatening the existence of the species. Still, several studies have suggested positive effect of stand diversity on ash health condition. The aim of this study was to evaluate the effect of stand composition and structure on the health condition of ash in young stands in Latvia. Among the tested stand properties, number of shrub species and tree height were the main factors affecting ash health condition, yet their effect differed regionally. In the eastern part of Latvia, richness of shrub species in forest stands showed positive relationship with ash health, while the taller trees displayed worsening health condition. In the western part of Latvia, the relationships were inverse. Such differences in the biotic relationships might be related to the differences in climate, hence spread and development of the pathogen, and/or genetically determined susceptibility of different populations of ash.

Keywords: *Fraxinus excelsior*; *Hymenoscyphus fraxineus*, species diversity; dieback; mixed stands; populations

Introduction

Since the 1990s, dieback of European ash (*Fraxinus excelsior* L.), caused by the ascomycete *Hymenoscyphus fraxineus* (T. Kowalski), has been marching across Europe, devastating most of the stands and threatening the existence of the species (Pautasso et al. 2013, Gross et al. 2014). Accordingly, numerous efforts have been made to understand the mechanisms of the dieback and to improve the resistance of ash stands (Skovsgaard et al. 2017). The fungus affects trees, irrespectively of size and age, subjecting them to infestation by the secondary agents and decreasing their lifespan severely (Bakys et al. 2009, Schumacher et al. 2010); still, some studies have shown that ash has suffered less damage in mixed, compared to pure stands (Dobrowolska et al. 2011, Schumacher 2011, Stener 2013, Pušpure et al. 2017). Higher resilience of European ash in the mixed stands has been related to chemical, physical, and biological barriers limiting the spread of the primary and secondary pathogen(s) (Loreau et al. 2001, Jactel et al. 2005, Pautasso et al. 2005, Kosawang et al. 2018). Additionally, some population-related differences in the susceptibility of European ash to the pathogen suggest genetic aspect of the resistance (Pliūra et al. 2015). They, however, are modulated by weather conditions (Papic et al. 2018), hence by the dynamics of development of the pathogen (Hietala et al. 2013, Dvorak et al. 2016), thus adding complexity to the species-host interactions.

The aim of this study was to assess the effect of composition and structure of young stands on the health condition of European ash in the hemiboreal conditions in Latvia. We hypothesised that the health condition of ash was related to species richness of woody plants within a stand, yet the effect might differ regionally (between meta-populations, or due to the climate).

Material and Methods

Study sites and measurements

In total, 35 young stands (26–36 years old), where European ash formed >30% of standing volume and had area ≥ 1 ha, were selected from the national forest inventory database. The stands were scattered across the western and eastern part of Latvia and represented two local provenance regions (Hewitt 1999, Jansons and Baumanis 2005; Figure 1), differing by the tree growth responses to the environment. The stands were growing in hemiboreal lowland conditions (altitude <250 m a.s.l.) on mesotrophic silty soils (*Oxalidosa* type); the topography of the sites was flat. The climate was temperate, yet it was milder in the western part of Latvia. The mean annual temperature (\pm standard deviation) in the western and eastern part of Latvia was 7.8 ± 1.8 and 6.2 ± 1.5 °C, respectively. In the western part of Latvia, the mean monthly temperature ranged from 2.1 ± 2.6 to 18.1 ± 0.4 °C, and, in the eastern part of Latvia, from 3.8 ± 2.2

to 16.8±0.5°C in January and July, respectively. The mean annual precipitation in the western and eastern part of Latvia was 690±78 and 740±71 mm, respectively.

In each stand, a 2×100 m sampling plot was established along the longest diagonal of forest patch, and height of all trees within it was measured with the 0.2 m precision. For each ash tree, the degree (percentage) of *H. fraxineus* damage was recorded according to five grades, where “1” represented trees with slight or no damage, and “5” represented recently dead trees (Pušpure et al. 2015). The survey was made by the same person in August 2017.

Data Analysis

The relationships of ash health condition with the structure and composition of stands were assessed by the mixed ordinal regression. Tree was considered as observation and sampling plots were used as random intercepts. In the models, 1) height of trees, 2) mean height of trees in a plot, 3) number of tree, 4) shrub species in a plot, 5) forest type, 6) region (the western or eastern part of Latvia; Figure 1), 7) proportion of ash within a plot, 8) stand density, 9) dominant species of a plot, 10) species diversity in a plot (Shannon diversity index), and their combinations were tested as the linear predictors of ash health conditions. Considering that development of the pathogen is affected by climatic factors (Hietala et al. 2013, Dvorak et al. 2016), mean air temperature, precipitation sum and standardized precipitation-evapotranspiration index (Vicente-Serrano et al. 2010) for the July–August and May–August periods (Dvorak et al. 2016) in 2017 were also tested. Gridded climatic data were used (Harris et al. 2014). The best combination of predictors was determined by manual stepwise-forward selection; up to seven factors were tested simultaneously. The performance of the models was assessed by the Akaike information criterion (AIC) and conformity with biological realism; the significant predictors were tested for multicollinearity (Fox and Weisberg 2011). The distribution of tree and shrub species between the western and eastern part of Latvia was compared by the χ^2 test. Data analysis was conducted in R v. 3.5.1 (R Core Team 2018), using packages ‘ordinal’ (Christensen 2018) and ‘car’ (Fox and Weisberg 2011).

Results

The studied stands were formed by 7–15 tree and shrub species. The most common tree species, besides European ash, were *Alnus glutinosa*, *A. incana*, *Corylus avellana*, *Padus avium*, *Picea abies*, *Tilia cordata*, and *Betula* spp. The distribution of the most common species significantly (p -value < 0.01) differed between the western and eastern part of Latvia; the abundance of *A. glutinosa*, *C. avellana*, *P. abies*, and *T. cordata* was higher in the eastern, while the abundance of *A. incana*, *P. avium*, as well as European ash was higher in the western part of Latvia. The density of the

studied stands ranged from 4,400 to 74,900 trees ha⁻¹, and ash formed 40–100% of all trees. The mean height of all trees in the studied stands ranged from 1.07 to 4.73 m, yet the mean height of ash trees ranged from 0.45 to 7.54 m; trees were ca. 65% higher in the eastern part of Latvia. The mean health grade of ash ranged from 1.0 to 4.1 indicating diverse levels of dieback among the stands, yet the mean health grade was higher (worse health condition) in the eastern than in the western part of Latvia, 2.4 and 1.7, respectively.

Among 156 combinations of the factors tested, the combination of tree height and number of shrub species in a stand were the best predictors of ash health condition, yet both their effects were highly significantly (p -value < 0.01) interacted by the provenance regions (Table 1). The next best model displayed notably weaker performance (AIC was 5201 vs. 4727 of the best model). Although the regions differ by climate, the tested climatic factors were excluded during the selection process, likely as in 2017, the differences between the regions were small (e.g. 0.3 °C for July–

Table 1. Description of the best mixed ordinal regression model predicting health condition of European ash in young mixed stands based on stand and tree properties

Fixed effects estimates			
	Estimate	Std. error	z-value
Number of shrub species	-0.68	0.32	-2.12
Region (western)	-5.76	1.78	-3.23
Tree height	0.17	0.02	6.68
Number of shrub species × region (western)	1.09	0.38	2.89
Region (western) × tree height	0.09	0.03	3.07
Threshold coefficients			
Health grade	Estimate	Std. error	z-value
1 vs. 2	-2.38	1.40	-1.71
2 vs. 3	-0.11	1.39	-0.08
3 vs. 4	0.41	1.39	0.29
4 vs. 5	0.68	1.39	0.49
Random effects			
Stand (intercept)	Variance	Std. error	
	1.321	1.149	
Model analysis of deviance table, type II test			
	Likelihood ratio, χ^2	Degree of freedom	p-value
Number of shrub species	0.14	1	0.71
Region	0.48	1	0.49
Tree height	245.04	1	< 0.001
Number of shrub species × region	9.12	1	< 0.01
Region × tree height	9.43	1	< 0.01

August temperature). In the stands in the western part of Latvia (Figure 1), the number of shrub species was positively related to the health grade of European ash (Figure 2A), indicating worse health condition in more diverse stands. The opposite was observed in the eastern part of Latvia, and the effect of shrub species richness there was even stronger. Nevertheless, tree height showed positive relationship with the health grade of ash, particularly in the eastern part of Latvia, implying that health condition was worse for the larger trees (Figure 2B). Only slight effect (the regression line was almost horizontal) of tree height was observed in the western part of Latvia, where the mean tree height was lower. Some models, in which the effect of the dominant species of stand showed a p -value of ca. 0.06,

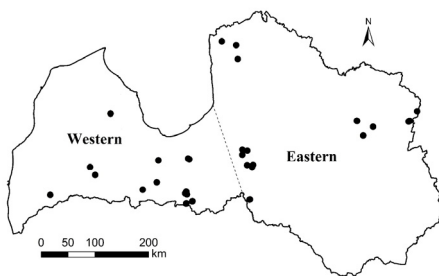


Figure 1. Location of studied stands of European ash. Broken line denotes two parts of Latvia (western and eastern) with differing tree growth (provenance regions)

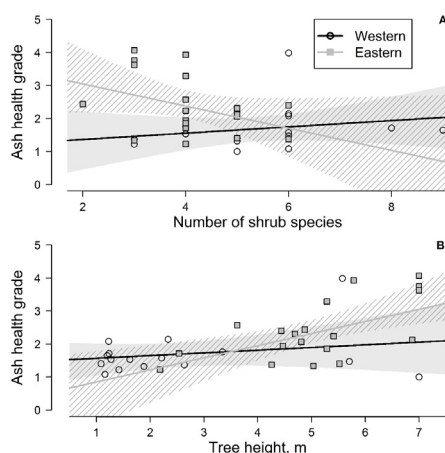


Figure 2. The relationship between health condition (health grade) of European ash in young mixed stands and number of shrub species (A), and tree height (B) in the western and eastern parts (provenance regions) of Latvia. The polygons (envelopes) denote confidence intervals

suggested that the presence of *P. abies* tended to worsen health of ash (not shown).

Discussion

The richness of shrub (woody) species in stand had effect on health condition of European ash in young stands (Figure 2A), as observed previously (Dobrowolska et al. 2011, Schumacher 2011, Stener 2013, Skovsgaard et al. 2017). The richness of shrub species can be related to fertility, as well as history, hence structural diversity of stands (Fescenko et al. 2014). The explicit regional differences in the effect of shrub species richness on ash health condition (Table 1, Figure 2) might be related to the climatic conditions, as suggested by Papić et al. (2018). In the western part of Latvia, warmer climate, apparently, facilitated development of *H. fraxineus* (Kowalski and Bartnik 2010, Dvorak et al. 2016) in longer term, suppressing growth of ash, as

hinted by shorter tree height, and marginal effect of tree height on ash health grade (Figure 2B). Under such conditions, the admixture species, apparently, competed with ash decreasing its vigour, thus explaining positive linkage with the health grade (Figure 2A).

Under cooler climate in the eastern part of Latvia, which is less favourable for *H. fraxineus* (Kowalski and Bartnik 2010), the diversity of shrub species had positive effect on the health condition of ash (Figure 2A), likely acting as mechanical barriers (in mixed stand, ash trees are scattered and the composition of debris is diverse), hindering spread and development of the inoculum of the pathogen (Jactel et al. 2005, Pautasso et al. 2005). Higher species richness also can provide more habitats for antagonists of the disease (Kosawang et al. 2018), acting as biological barriers. Although ashes suffered more damage, they were also taller, indicating better growing conditions under more continental climate, as previously shown by Papić et al. (2018). This suggests, that higher diversity of woody species in a stand might be applied for the improvement of survival of ash as previously suggested by Givnish (2002), at least in the eastern part (provenance region) of Latvia. Unfortunately, considering the numbers of sampled stands and admixture species, it was impossible to determine, which shrub species had the strongest effect on ash health condition. Still, the presence of *P. abies* in stand tended to worsen ash health condition (not shown), likely due to the competition for light, soil, as well as soil acidification (Lei et al. 2012). Also, the understory under *P. abies* is poor, providing weak barriers for the spread of the disease (Pautasso et al. 2005).

Alternatively, regional differences in the relationships of health condition of ash with stand diversity and tree height might be related to the two populations of European ash that colonised post-glacial Eastern Europe (Hewitt 1999), hence genetic components of the resistance to dieback is appeared (Pliūra et al. 2015). Diverse stand composition might be mentioned as another cause of regional differences in health grade. Still, the positive relationship between height and health grade of ash (Figure 2B) suggested cumulative effect of the pathogen as the trees grow.

Conclusion

The hypothesis was verified only partially, as linkage between the richness of shrub species, growth, and health status of ash was observed. The observed relationships suggested that management for higher diversity might be applied to decrease the effects of dieback under more continual climate in the eastern part of Latvia. The negative effect of richness of woody species under milder and warmer climate in the western part of Latvia suggested that decrease of ash health conditions is still expectable due to the warming. Ac-

cordingly, efforts to preserve ash stands should be primarily focussed in the areas with more continental climate.

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