Environmental and Silvicultural Characteristics Influencing the Extent of Ash Dieback in Forest Stands

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Abstract

Extensive investigation of the impact of ash dieback in forest stands in the Czech Republic was conducted in 2013. Data on the defoliation of ash trees were collected from 1169 forest stands within the entire area of the Czech Republic. A set of 37 variables acquired from different databases (State Forests, GIS, Digital Terrain Model) describing silvicultural, environmental and landscape characteristics were used as explanatory variables.A generalized linear model (GLM) explained nearly 26% of the disease data variability. In the model, the extent of the disease was positively affected by the density of stocking, site class, vertical terrain heterogeneity, temperature and the presence and width of watercourse and negatively affected by mean tree height, the altitudinal zone of the forest, and the distance to the nearest ash stand. The model confirmed an important role of tree species composition of stands with ash. The disease extent was the highest in the presence of *Quercus robur* and the lowest in presence of *Acer* spp. and *Abies* spp. This finding is probably due to the different chemical composition of mixed litter and the leaching and translocation of nutrients from maple litter into ash petioles, which could accelerate decomposition, whereas fungistatic tannins and secondary metabolites from fir litter could inhibit microbial growth. The extent of the disease also significantly differed according to edaphic series of forests, and GLM models were successfully developed for them. These models differed from each other and explained 23–37% of disease variability; other factors influencing disease extent were also determined: distance to water, SD of slope, ash area, standing volume, aspect, TPI, landforms and the presence of other tree taxa such as *Pinus* spp., *Quercus petraea*, *Fagus sylvatica* and *Betula pendula*.The results indicated that the disease extent is substantially affected by environmental and stand characteristics and that the development of effective forest management strategies to address the epidemic in European forests (at least in central Europe) is possible.

Keywords: ash dieback, forest stands, disease impact, environmental factors, silvicultural characteristics, litter

Introduction

H. fraxineus (T. Kowalski) Baral, Queloz, Hosoya, the causal agent of ash dieback threatens European ash (*F. excelsior* L.) and narrow-leaved ash (*F. angustifolia* Vahl) in Europe (Gross et al. 2014). European ash is highly susceptible to the pathogen, as can be deduced from the high rate of spread and destructiveness of the ongoing epidemic and the results of infection experiments (Gross et al. 2014). The pathogen is highly virulent because it did not co-evolve with its host (Zhao et al. 2012). The collapse of many European populations and ecosystems in which the dominating or keystone species is *F. excelsior* is repeatedly considered to be a possible consequence of pathogen invasion (e.g., McKinney et al. 2011, Gross et al. 2014, McKinney et al. 2014, Pliūra et al. 2014). This pathogen threatens not only ash, but also the organisms that depend on ash (Pautasso et al. 2013).

The control of established ash dieback in forests is practically impossible, and silvicultural recommendations are limited to avoiding the loss of the value of mature ash stands (Gross et al. 2014). Currently, many healthy or affected ash stands are lumbered in Denmark (Kjær et al. 2012 McKinney et al. 2014), the Czech Republic (Forests of the Czech Republic, state enterprise) and apparently in other European countries. The species is expected to suffer severe decimation as a result of not only high mortality following infection but also intensified logging in forestry (McKinney et al. 2014). Artificial re-establishment of ash stands is not recommended due to the high probability of ash dieback (Pliūra et al. 2014). Furthermore the interest among practitioners to plant the species is limited (McKinney et al. 2014).

Most native *Fraxinus excelsior* trees are highly susceptible to the invasion of *H. fraxineus*, and only approximately 1% of the trees have the potential to produce offspring with an expected crown damage of < 10% under the present disease pressure (Kjaer et al. 2012). The repeatedly detected genetically based resistance of common ash to *H. fraxineus* (e.g., Pliūra et al. 2011, McKinney et al. 2012, Stener 2013, McKinney et al. 2014, Pliūra et al. 2014, Enderle et al. 2015, Harper et al. 2016) has led to the general recommendation of selecting and preserving the most resistant genotypes for use in subsequent breeding. The first orchards to preserve the more resistant genotypes were established in different European countries (McKinney et al. 2014, Pliūra et al. 2014, Havrdová et al. 2015). Following a period of high mortality in natural populations, the selection and breeding of the remaining viable ash trees could provide a route for restoring the role of ash in the landscape (McKinney et al. 2014).

The assisted selection of more resistant genotypes improved by breeding together with still undervalued natural selection *in situ* represents a chance for restoring the species and forests in the future. The restoration of damaged or disrupted forests and other ash stands will take several decades and will be complicated by several other factors such as persisting forestry practices, hindered growth of more resistant trees under high infection pressure, the contribution of susceptible trees to the next generation in reducing the strength of selection (the resistance against *H. fraxineus* is apparently polygenic), and the expected future evolution of the pathogen as a reaction to changes in the host gene pool. Thus, the restoration of ash forests and other ash stands should be facilitated by appropriate methodology.

The appropriate management strategies are still unknown and need to be elaborated (Pliūra et al. 2014). Successful strategies must include thorough knowledge of the biology and epidemiology of the disease (Sakai et al. 2001) however, the effects of only a few environmental and silvicultural factors have been studied in *H. fraxineus* (Gross et al. 2014). The disease extent (crown dieback and collar rot) connects with site humidity (Husson et al. 2012, Enderle et al. 2013, Marçais et al. 2016) and the pathogen is sensitive to high temperatures and dry climate (Hauptman et al. 2013). On mature trees, disease progress is slower than on seedlings or young trees (Kirisits and Freinschlag, 2012; Kowalski and Holdenrieder, 2008). Dieback is more frequent on trees of average or below-average size and the extent of canker in the crown depended on site conditions (Skovsgaard et al. 2010). However, no extensive epidemiological study has been conducted till now. The aim of the present, in cooperation with State Forests of the Czech Republic, was to analyse the distribution and impact of the disease in forests with ash within the area of the Czech Republic and to identify silvicultural, environmental and landscape characteristics potentially affecting the disease epidemiology.

Methods

Study area

The field work was conducted in the entire territory of the Czech Republic, covering 78,866 km^2 with altitudes of 115 – 1603 m.a.s.l. (the mean altitude was 430 m) between 48° 33´ – 51° 03´ N and 12° 06´ – 18° 52´ E. The Czech Republic is located on the territory of four geomorphic provinces: the Bohemian Massif comprising 3/4 of the territory in the west and middle of the country, the Western Carpathians in the east, the Western Panonian Basin in the southeast, and the Middle-European Plain in the northeast of the country. The most common soil types are brown earth in the middle and higher altitudes and chernozem in the lowlands. The area was originally covered mainly by mixed deciduous temperate forests, whereas today´s forestry practices favour the cultivation of coniferous trees. Forests cover 34% of the area, and *Fraxinus* spp. Account for 1.4% of these forests, thus, *Fraxinus* spp. cover approximatelly 36,000 ha (Anonymous 2014).

Plot selection and data collection

The investigated forest stands were uniformly distributed within the entire area of the Czech Republic at altitudes of 150 – 900 m a. s. l. in the area. The data were obtained in cooperation with fieldworkers of the State Forest of the Czech Republic from a total of 1169 ash stands covering the full ecological niche of *Fraxinus* spp. in the area (Figure 1). The field investigations were conducted between 1st July and 31st August 2013 and terminated before the first premature leaf fall caused by ash dieback beginning at the end of August in that year.

Disease detection was performed using information leaflets describing characteristic symptoms of the disease (Havrdová et al. 2013). The percentage of crown defoliation in the surveyed ash stands was observed. Because the

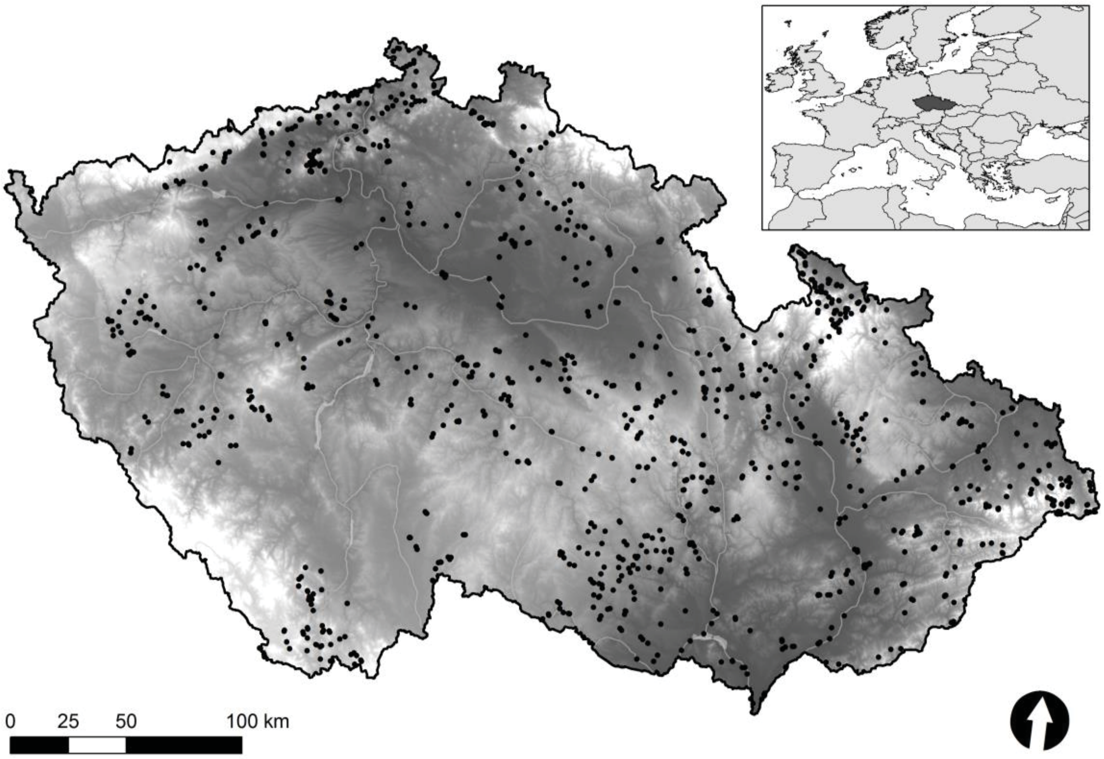

Figure 1. Investigated plots in the Czech Republic

data collection was performed by many people, the data collection methodology was simplified as much as possible. Five damage classes were used to describe ash defoliation: no characteristic symptoms (0%), little crown defoliation (1–10%), medium crown defoliation (11–25%), considerable crown defoliation (26–50%), and high damage (51–100%). The average values of these categories were used for presentation: 0.0, 5.0, 17.5, 37.5 and 75.0% respectively.

Information about silvicultural and forest characteristics such as forest altitudinal zone, age, mean tree height, density of stocking, ash area, site class, standing volume, presence of understory and presence of particular tree species, and forest edaphic series representing trophic and hydric properties (Viewegh et al. 2003) and exact coordinates were obtained from the database of the State Forests of the Czech Republic. In the Czech Republic, the edaphic series are divided into eight categories: extreme (stunted forests), acidic (oligotrophic), nutrient-rich (mesotrophic), humus-enriched (nitrophilous), water-enriched (continually wet with carbonated and oxygenated water), gleyed (alternately waterlogged), wet (permanently waterlogged) and peaty. Because some series were less abundant, the extreme and acidic series were merged into one category and the wet and gleyed series were merged into another category on the basis of similar properties for statistical purposes. The peaty category was omitted because it was not present for ash. Ecological characteristics, including the mean annual temperature, mean annual precipitation, presence and width of watercourse, distance to water and distance to nearest ash stand were acquired using Geographical Information Systems. Information describing landscape morphology, including the mean vertical heterogeneity, mean aspect, mean slope, standard deviation (SD) of slope, topographic position index (TPI; index of the local terrain), SD of TPI and landforms, were obtained using Digital Model of Relief the Czech Republic. An overview of particular variables is presented in Table 1.

Statistical analysis

The statistical analyses were performed using the R plus statistical package (R Core Team 2014). Preliminary data analysis consisted of the evaluation of pair correlations between all continuous variables. Highly correlated variables were identified in the correlation matrix and only one variable was maintained for subsequent analysis from each such group.

To evaluate the mutual influences of individual variables on crown dieback, a general linear model was used,

$$y_i^{\frac{1}{2}} = \beta_0 + \sum_{j=1}^{m} \beta_j x_{ji} + \varepsilon_i \quad [1]$$

Table 1. Overview of the investigated variables with the codes used in evaluation

Abbreviation	Description of the variable	Units	Category (in categorial variable)
Silvicultural variables			
Defoliation	Crown defoliation		0%; 5% (1–10%); 17.5% (11–25%); 37.5% (26–50%); 75% (51–100%)
Edaphic series	Edaphic series		extreme, acidic, nutrient-rich, humus enriched, water enriched, gleyed, wet
Alt. zone	Forest altitudinal zone		1st oak, 2nd beech-oak, 3rd oak-beech, 4th beech, 5th fir-beech, 6th spruce-beech
Age	Mean age	year	
Height	Mean tree height	m	
Stocking	Density of stocking	%	
Ash area	Ash area	m^2	
Site class	Site class	m	
Volume	Standing volume	m^3 u.b.	
Understory	Understory		1 (1–10); 2 (11–20); 3 (21–30) year old
Abies	Presence of species Abies	%	*Abies alba, A. grandis*
Acer	Presence of species Acer	%	*Acer pseudoplatanus, A. platanoides, A. campestre*
Alnus	Presence of species Alnus	%	*Alnus glutinosa, A. incana*
Ash	Presence of species Ash	%	*Fraxinus excelsior, F. angustifolia*
Betula	Presence of species Betula	%	*Betula pendula*
Carpinus	Presence of species Carpinus	%	*Carpinus betulus*
Fagus	Presence of species Fagus	%	*Fagus sylvatica*
Larix	Presence of species Larix	%	*Larix decidua*
Picea	Presence of species Picea	%	*Picea abies, P. pungens*
Pinus	Presence of species Pinus	%	*Pinus silvestris, P. nigra, P. strobus*
Populus	Presence of species Populus and Salix	%	*Populus tremula, P. alba, P. nigra, Salix* spp. etc.
Quercus1	Presence of species Quercus	%	*Qurcus robur, Q. rubra*
Quercus2	Presence of species Quercus	%	*Quercus petraea*
Salix	Presence of species Salix	%	*Salix caprea*
Tilia	Presence of species Tilia	%	*Tilia cordata, T. platyphyllos*
Ulmus	Presence of species Ulmus	%	*Ulmus minor, U. laevis, U. glabra*
Landscape variables			
Heterogeneity	Mean vertical heterogeneity	m	
Aspect	Mean aspect	degree	N (337.6–22.5˚); NE (22.6–67.5˚); E (67.6–112.5˚); SE (112.6–157.5˚); S (157.6–202.5˚); SW (202.6–247.5˚); W (247.6–292.5); NW (292.6–337.5˚)
Slope	Mean slope	degree	
SD slope	SD of slope	degree	
TPI	Topographic Position Index	index	
SD TPI	SD of TPI	index	
Landform	Landforms		canyons, deeply incised streams; convex concave shapes on slope; plains; open slopes; mountain tops
Ecological variables			
Temperature	Mean annual temperature	ºC	
Precipitation	Mean annual precipitation	mm	
Watercourse	Presence and width of watercourse		presence watercourse; width of watercourse < 1m; width of watercourse > 1m
Dist. to water	Distance to water	m	
Dist. to ash	Distance to nearest ash stand	m	

where y_i is rate of crown dieback in i^{th} stand, the coefficients β_j express the effect of individual factors x_j, β_0 is an intercept and ε_i is an error term [1]. To fulfill the assumption of normality of residuals, a square root transformation of crown dieback rate was performed. In the process of fitting the model [1], a large number of included factors turned out to be insignificant. Thus, a bidirectional step regression method was used to determine a set of factors important to the crown dieback rate. The optimal submodel of [1] was selected by minimization of the Akaike information criterion.

To evaluate the significance of differences among values of categorical variables, a multiple comparison method with Bonferroni correction was used. The results are presented in the form of homogenous groups.

Results

The damage was identified in 945 of the total 1169 investigated forest stands (80.8%). The average value of crown defoliation was 27.36% (± 0.75%). Particular categories of stands according to the extent of defoliation importantly differed in number of stands. The defoliation category of 17.5% was the most frequent, whereas the category with defoliation of 5% was the least frequent (Figure 2).

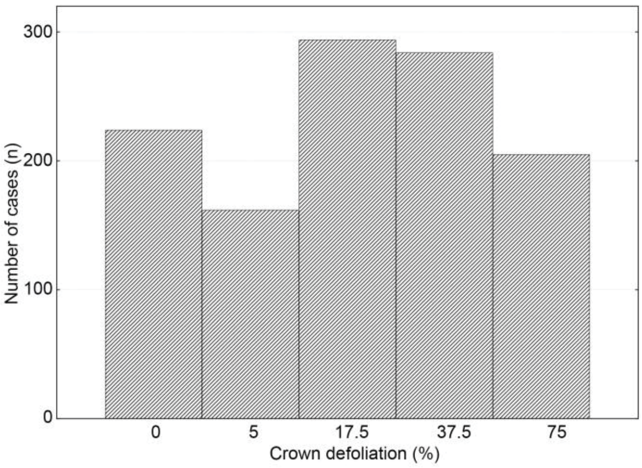

Figure 2. The distribution of forest stands according to the extent of dieback

The most representative of several developed models for all included forest stands was selected (Table 2). The model consisted of 12 significantly contributing environmental variables and explained 25.7% of the disease variability. In the model, the extent of disease was positively affected by the density of stocking, site class, vertical heterogeneity, temperature and the presence and width of watercourse and negatively associated with mean tree height, forest altitudinal zone, and the distance to the nearest ash stand ($P < 0.001$).

The compared edaphic series significantly differed in the proportion of defoliation ($P < 0.001$, Figure 3A, Table 2). The wet and gleyed categories were the least damaged with 23.0% (±2.6) and 11.1% (±3.0) defoliation, respectively, whereas the nutrient category with 34.1% (±1.6) defoliation and the extreme category with 37.5% (±21.7) evaluation were the most damaged.

Table 2. The general GLM model of ash dieback in forests of the Czech Republic

Continuous variable	Estimate	*SE*	*t* value	*P*-value	Strength
(Intercept)	-0.142	2.104	-0.068	0.946	
Stocking	0.135	0.064	2.129	0.033	*
Height	-0.104	0.010	-10.839	< 0.001	***
Site class	0.199	0.032	6.149	< 0.001	***
Heterogeneity	0.040	0.012	3.235	0.001	**
Slope	-0.039	0.022	-1.774	0.076	.
TPI	-0.037	0.023	-1.593	0.111	
Dist. to ash	-0.003	0.002	-2.116	0.035	*
Temperature	0.293	0.123	2.383	0.017	*
Abies	-0.048	0.020	-2.343	0.019	*
Quercus1	0.013	0.006	2.378	0.018	*
Acer	-0.015	0.006	-2.349	0.019	*
Carpinus	-0.044	0.024	-1.808	0.071	.
Categorial variable					
Edaphic series	Estimate	Homogeneous groups			
Extreme	0.000	|	|	|	
Nutrient-rich	-0.700			|	
Humus enriched	-1.587		|		
Water enriched	-1.623		|		
Acidic	-2.018		|		
Gleyed	-2.091	|	|		
Wet	-3.800	|			*
Altitudional zone					
1st oak	0.000		|		
2nd beech-oak	-1.211	|			***
3rd oak-beech	-0.981	|	|		**
4th beech	-0.328		|		
5th fir-beech	-0.905	|	|		*
6th spruce-beech	-0.652	|	|		
Watercourse					
without w.	0.000	|			
width of w. < 1m	-0.163	|			
width of w. > 1m	0.750		|		***

Residual standard error: 2.507 on 1143 degrees of freedom, Multiple R-squared: 0.2572, Adjusted R-squared: 0.241, *F*-statistic: 15.83 on 25 and 1143 DF, *P*-value: < 2.2e-16
Significance codes: *** (0.001), ** (0.01), * (0.05), . (0.1)

The model confirmed an important role for the tree species composition of stands with ash. The disease extent was the highest in the presence of *Quercus robur* and the lowest in the presence of *Abies* spp. and *Acer* spp. ($P < 0.05$).

Three other variables that were included in the model had negative but not statistically significant associations with the disease extent: slope ($P = 0.08$), TPI ($P = 0.11$) and

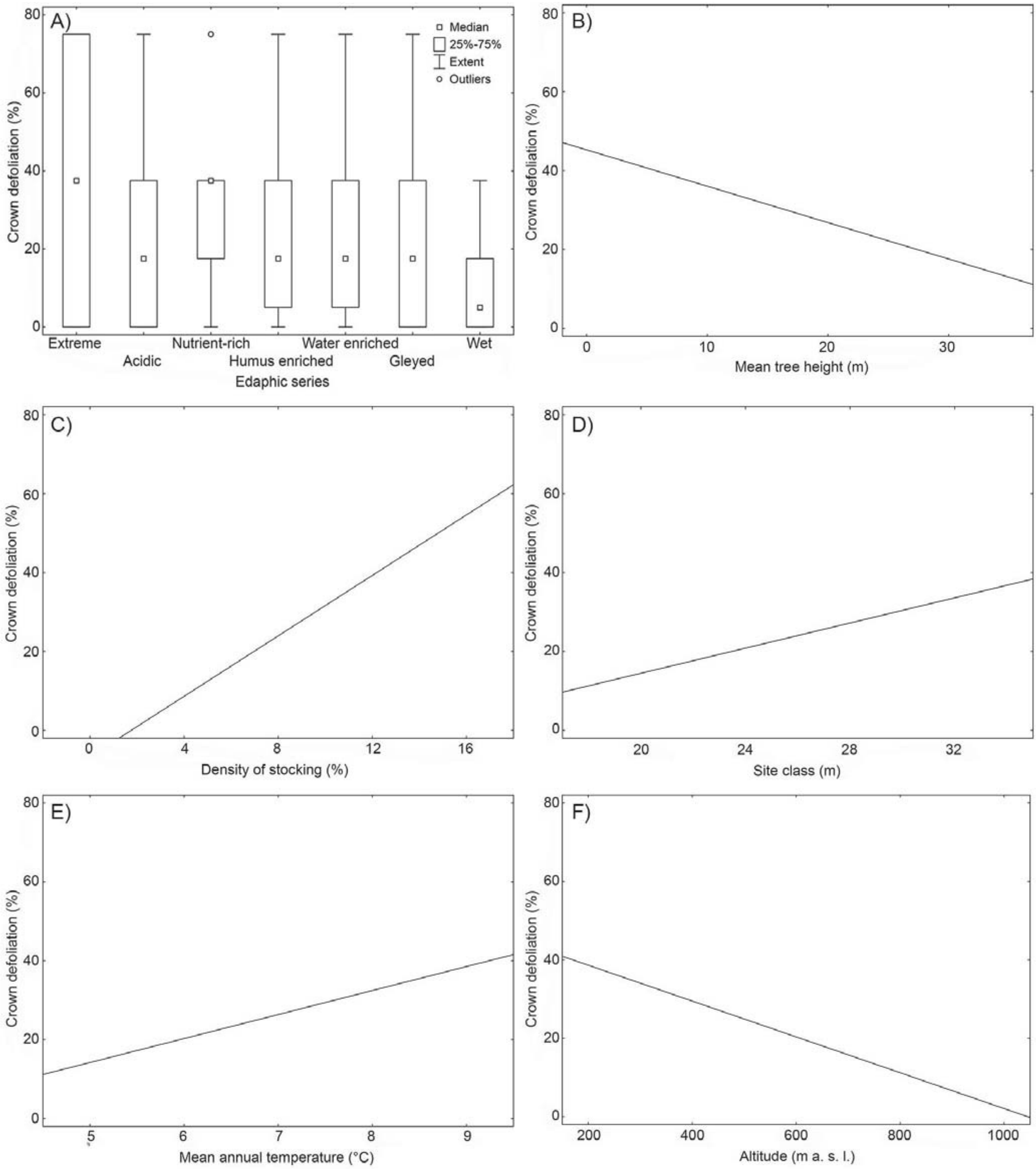

Figure 3. A) Extent of ash dieback in edaphic series in forests of the Czech Republic. B) Correlation between the extent of ash dieback and medium tree height. C) Correlation between the extent of ash dieback and the density of stocking. D) Correlation between the extent of ash dieback and site class. E) Correlation between the extent of ash dieback and the average annual temperature. F) Correlation between the extent of ash dieback and altitude

the presence of *Carpinus betulus* ($P = 0.07$; Table 2). The negative effect of *Picea* spp. was not identified and, moreover, its partial correlation to disease extent was also insignificant (Table S1).

Overall, the dataset of 35 explanatory variables for the extent of crown damage was evaluated. Twelve variables were included in the GLM model of the disease extent (Table 2); however, four other variables with significant relation to the extent of ash dieback were not incorporated in the model: ash area and the presence of ash with a positive correlation to the disease level and age and the presence of alder which were negatively correlated. The overview of the partial correlations of all quantitative variables is included in the correlation matrix in Table S1. Selected variables with the most influence on the extent of ash dieback are presented in Figure 3.

Five particular GLM models were successfully developed for the edaphic series –nutrient, enriched by humus, enriched by water, wet and gleyed and extreme and acidic series. The last series were merged into pairs (wet and gleyed and extreme and acidic series, respectively) due to the lower number of stands in some series and their resemblance. The models differed from each other in the composition of explanatory variables. These models described 23.2–36.7% of the disease variability (Table 3).

The GLM model for nutrient edaphic series was developed for 272 stands with ash explained 27.9% of the disease variability and contained 9 explanatory variables. Six variables significantly contributed into the model: forest altitudinal zone, mean tree height, the presence and width of watercourse, distance to water, site class and the presence of *Pinus* spp.

The GLM model for the humus-enriched series was constructed with data from 162 stands and explained 36.0% of the data variability. The model contained a total of 8 variables, and 6 of these variables were significant: ash area, mean tree height, standing volume, site class, aspect and landform.

The model for the series enriched by water (alluvial or bottomland series) was based on data from 351 stands and explained 25.6% of the variability of the data in the series. The model contained 11 explanatory variables and seven of them significantly contributed to the model: mean tree height, site class, vertical heterogeneity, distance to the nearest ash stand, temperature, the presence of *Q. petraea* and the presence of *Fagus sylvatica*.

Table 3. Overview of GLM models for particular edaphic series and their groups

Variables	General model	Extreme + Acidic	Nutrient-rich	Humus enriched	Water enriched	Gleyed + Wet
(Intercept)					-	-
E.s. wet	-					
2nd beech-oak	-		-			
3rd oak-beech	-					
5th fir-beech	-					
Height	-	-	-	-	-	-
Stocking	+					
Ash area				+		
Volume				-		
Site class	+		+	+	+	
width of w. > 1m	+	+	+			
Dist. to water			-			
Dist. to ash	-				-	
Temperature	+				+	+
Heterogeneity	+				+	
SD Slope		+				+
TPI						+
Aspect NE				+		
Aspect SW				+		
Landf. Tops				-		
Abies	-	-				
Pinus			-			
Quercus1	+					
Acer	-	-				
Quercus2					+	
Fagus					+	
Betulus						+
Multiple R-squared	0.257	0.232	0.279	0.360	0.256	0.367

+ (positive) and – (negative) influence on the disease impact

The model for the wet and gleyed series was based on 122 stands, explained 36.7% of the disease variability and contained 10 explanatory variables. Five of these variables (mean tree height, temperature, SD of slope, TPI and the presence of *Betula pendula*) contributed significantly to the model.

The last GLM model was prepared for acidophilous and the extreme series. The model was prepared on the basis of 262 stands and was the least successful among the developed models – it explained 23.2% of the disease variability. The model contained 12 variables and 5 of them had significant effects in the model: mean tree height, the presence and width of watercourse, SD of slope, the presence of *Abies* spp. and the presence of *Acer* spp. Particular GLM models are schematically shown in Table 3.

The analysis of particular GLM models (Table 3) found that some explanatory variables play an important role in the all or the majority of models. The variable playing an important role within the entire ecological niche of *F. excelsior* and its pathogen is mean tree height. The variables that significantly explained some disease data in at least two or three models are site class, the presence and width of watercourse, SD of slope, and temperature. Other variables (forest altitudinal zone, ash area, standing volume, distance to watercourse, distance to other ash stand, vertical heterogeneity, TPI, aspect, landforms and the presence of some tree species) were significant in one of the developed models (Table 3).

Table 4. Overview of GLM models for stands divided according to the presence and width of watercourse

Variables	Without watercourse	Width <1m	Width >1m
(Intercept)		-	
2nd beech-oak	-		
3rd oak-beech	-		
4th beech	-		
5th fir-beech	-		
6th spruce-beech	-		
Height	-	-	-
Volume	+		
Site class	+	+	
Dist. to water			-
Dist. to ash			
Temperature		+	+
Heterogeneity	+	+	+
Aspect SW	+		
Abies			-
Carpinus		-	
Multiple R-squared	0.295	0.220	0.222

+ (positive) and – (negative) influence on the disease impact

Because humidity is highly important for spore production, spread and infection in many foliage pathogens (Sinclair and Lyon 2005) including *H. fraxineus* (Hietala et al. 2013; Dvorak et al. 2016) and the influence of water source on the disease is highly significant ($P < 0.001$; Table 2), the disease data were evaluated according to the presence of a watercourse in forest stands. Defoliation was highest (32.2% ± 1.5), in stands with the presence of a watercourse wider than 1 m and was lowest (22.4% ± 1.3) in stands with a watercourse up to 1 m wide. The GLM models explained 22.0 to 29.5% of the data variability: the most successful model was developed for stands without the presence of water. The three models importantly differ in combinations of explanatory variables (Table 4). The model for stands without the presence of water was composed of forest altitudinal zone, mean tree height, standing volume, site class, vertical heterogeneity and aspect with significant value, whereas the models for stands with both types of watercourses were different but more similar to each other and contained mean tree height, temperature, vertical heterogeneity, site class (up 1 m in width), the presence of *C. betulus* (<1 m in width), distance to other ash stand (>1 m) and the presence of *Abies* spp. (>1 m; Table 4).

Discussion

Extensive investigation of ash dieback in Czech forests was performed in 1169 forest stands within the entire area of the Czech Republic in 2013; the average ash defoliation in forest stands was 27.4%. The average crown defoliation registered in the Danish National Forest Inventory increased rapidly from a background level of 10–15% leaf loss to over 40% leaf loss in 2009 (McKinney et al. 2014). This difference between Czech and Danish forests is relatively high and could be due to the differing climate between the two regions. The climate in Denmark is typically oceanic with a high level of precipitation throughout the year, whereas the climate in the Czech Republic is mild and transitional with an increase in continental characteristics in its south-eastern regions (Tolasz et al. 2007). Because spore release and infection processes are influenced by air humidity (Hietala et al. 2013, Havrdová 2015, Dvorak et al. 2016), the difference in disease level in these climatically different areas is understandable.

In total, 224 (19.2%) forest stands included in this study were designated by foresters as "healthy"; however, when a sample of ten "healthy" forest stands throughout the country was thoroughly investigated, the forest stands were found to be diseased, although with very low disease incidence. The other, independent thorough investigation of forest and other stands with ash conducted during 2011–2013 revealed that ca 95% of 1045 trees in 80 investigated plots were more or less affected by the pathogen (Havrdová

2015). Thus, the disease is widespread in the area and affects all or nearly all ash stands in the country.

The most informative GLM model for the disease distribution explained 25.7% of the disease variability in Czech forests. Particular models were also developed for edaphic series with explanatory power from 23.2 to 36.7%. The rest of the (unexplained) variability can be ascribed to the variation in ash sensitivity by genotype (McKinney et al. 2011, Kirisits and Freinschlag 2012, Kjær et al. 2012, McKinney et al. 2012, Stener 2013, Pliūra et al. 2014, Lobo et al. 2015) and provenance levels (Enderle et al. 2013, Havrdová et al. 2016), the variation in pathogen virulence (Kowalski and Holdenrieder 2009, Bakys et al. 2011, Husson et al. 2012), the other non-investigated environmental and stand characteristics (Havrdová 2015) and the error.

A total of 23 explanatory variables describing environmental and stand characteristics were found to significantly influence the disease level in the general model or at least in models for particular edaphic series. The variables that positively affected the disease extent were density of stocking, ash area, site class, the presence and width of watercourse, vertical heterogeneity, temperature, NE and SW aspects, TPI, SD of slope, and the presence of some tree species (*Quercus robur*, *Q. petraea*, *Fagus sylvatica*, *Betula pendula*). The variables that negatively affected the disease extent were mean tree height, standing volume, distance to watercourse, distance to nearest ash stand, altitude, landform (mountain tops and ridges) and the presence of *Abies* spp., *Pinus* spp. and *Acer* spp. Furthermore, the disease extent was influenced by edaphic series.

The set of variables significantly affecting disease distribution and intensity comprised of variables at different ecological scales. For example, edaphic series, temperature and altitude were among the variables with an affect at the large landscape scale. Their including apparently connected with the extremely broad ecological niches of the host (Wardle 1961, Dobrowolska et al. 2011) and of the pathogen, which covers the geographical and altitudinal distribution of the host (Queloz et al. 2011, Baral and Bemmann 2014, McKinney et al. 2014). The finding of the lowest disease incidence in the wet and gleyed series in the present study is consistent with the findings of Schumacher (2011) who reported that stands on wet soil with changing moisture had generally lower infection rates.

The next set of variables affected the pathogen distribution at a medium scale – at a range from dozens of metres to a km – aspect, SD of slope, TPI, landform, vertical heterogeneity, medium tree height and density of stocking. These environmental variables described the landscape and stand morphology; thus, they should be ascertained as indirect variables (Franklin 1995). These variables described the shapes and coarseness of the terrain and environment and affected the microclimate including air humidity near the ground in different ways (Bennie et al. 2008, Geiger et al. 2009, Meentemeyer et al. 2012, Pezzopane et al., 2015). Variables such as the presence of a watercourse and its width and the distance to water also affected air humidity including the amount of horizontal precipitation (Geiger et al. 2009). Humidity is important for spore production and the release of many pathogens (Sinclair and Lyon 2005); the dispersal pattern of *H. fraxineus* ascospores and the disease level is influenced by air humidity (Havrdová 2015, Dvorak et al. 2016). Because the ascospores are drought-sensitive (Aylor 2003, Gross et al. 2014), leaf wetness from morning dew also protects them against desiccation (Hietala et al. 2013). The presence of watercourses in stands (or connected high water table) could create more friendly conditions for ascomata formation and the production of ascospores due to higher soil humidity, which agrees with the finding of Schumacher (2011) that the disease risk was highest for soils with very (all-season) wet conditions.

Slope usually has a negative effect on air humidity (Geiger et al. 2009), but its standard deviation, which was included in the GLM model of ash dieback in two series, affected air humidity positively. Undoubtedly, this quantity could also describe the terrain coarseness on slopes as vertical heterogeneity in flat landscape forms. Moreover, the slopes closing the valleys and gorges impeded the air circulation and affected the local climate (Geiger et al. 2009).

TPI usually affects the disease level negatively (general model in this study, Havrdová 2015). However, in the wet and gleyed series, the disease level increased in locations with higher TPI, i.e. in places elevated above the surrounding waterlogged areas. The cause of this association is unknown, but this series is relatively less affected by the pathogen and the higher disease impact in drier stands of this series could be caused by the better persistence of ash petioles in drier conditions than in the waterlogged or seasonally flooded conditions. This finding is also in agreement with the findings of Schumacher (2011).

The study also revealed the significant influence of terrain aspects on the disease intensity in one series. The NE aspect is typified by long term sustainable higher air humidity (Geiger et al. 2009), whereas in the most heated SW aspect the strengthened upward airflow can also strengthen the infection pressure of ascospores. These findings generally agree with the outcomes of Havrdová (2015).

The presented outcomes confirmed the importance of air humidity indirectly, but the set of influencing variables (vertical heterogeneity, medium tree height, density of stocking, etc.; Geiger et al. 2009) was nearly the same as in Havrdová (2015), where the correlations between measured air humidity and these variables were confirmed. The direct influence of precipitation on the disease level was not confirmed, but it could be supposed. The influence of precipitation could be confirmed on the whole-European scale especially in the oceanic-continental climate gradient as discussed above in the comparison with the Danish (McKinney et al. 2014) and Czech forests. Undoubtedly, precipitation plays an important role in disease epidemiology, based on the large amount of new infections in extremely wet summers (for instance in 2011) and the limited number of new infections in dry summers (especially 2015) as we repeatedly observed in the previous decade in the area. Likely, the potential influence of precipitation in presented models could be overshadowed by extreme variability in the length and intensity of wet and dry periods in last years (Daňhelka et al. 2015) or by many other environmental variables affecting air humidity in ash stands (Havrdová 2015) and its elucidation needs further investigation or deeper statistical evaluation.

The other variables of medium scale described the stand characteristics – site class, ash area and density of stocking. These variables were partially intercorrelated and positively influenced the disease level in stands (Table 2, Table S1). The quantity site class describing site productivity is defined as the height of a dominant tree (Avery and Burkhart 2002). These variables positively affected the possibility of colonization of the stands (host area, its concentration and biomass) and, moreover, the amount of *in situ* developed inoculum. The influence of these variables was in concordance with the ash dieback epidemic requiring a sufficient accumulation of susceptible host individuals (Schumacher 2011, Gross et al. 2014) or, better, accessible biomass.

The distance to the nearest ash stand and the mean tree height negatively affected the disease level. Both variables described the distance of the susceptible host tissues (mainly foliage) from the inoculum source. In the first case, a source of primary inoculum was in another stand, whereas in the second case, the distance of the source of "secondary" inoculum on the plant debris on the soil surface from sensitive living tissues directly in the stand was described. The distance of susceptible hosts was highly important to the spreading potential of the pathogen and was determined to be fundamental in landscape models describing spactial patterns of important tree diseases including SOD (Meentemeyer et al. 2011, 2012). Tree height negatively affected the disease level. The younger and smaller trees were usually damaged to a larger extent (Kowalski and Holdenrieder, 2008; Schumacher, 2011; Kirisits and Freinschlag, 2012) because their crowns were closer to the source of inoculum on the ground. Moreover, the infection pressure is lower and leaf quality and/or microclimatic conditions are less suitable for infection in the crown of higher trees (Gross et al. 2014). Standing volume was negatively correlated with the extent of the disease in one series (Table 3). This finding is likely due to the relationship of the standing biomass to the mean tree height, which is important in the epidemiology of ash dieback as elucidated above.

The last group of variables probably influenced the pathogen on a small scale via litter chemistry (Madritsch and Cardinale, 2007) because the disease level was affected by the coincidental presence of other tree species in the stand with ash. The disease level was significantly lower in the presence of *Abies* spp., *Pinus* spp., and *Acer* spp., whereas the extent of the disease was higher in the presence of *Quercus* spp., *Fagus sylvatica* and *Betula pendula*. The influence of these tree species is probably mediated via physical and chemical characteristics of litter and by differences in decomposition rates. For example, maple litter is more quickly decomposed than oak litter (Blair et al. 1990). The decomposition process in one type of litter can accelerate the decomposition of another type in the mixture by translocation of nutrients through diffusion of a water film and/or active transport through invertebrate-microbial interactions (Blair et al. 1990). The difference between the effects of *Acer* spp. and *Quercus* spp. on the disease level could be explained by the different rates of ash petiole degradation in mixed litter with different compounds. On other sites, the coniferous litter containing high amounts of secondary compounds such as tannins, lignin, waxes and terpenoids can leach secondary metabolites and tannins into the surrounding and could directly inhibit microbial growth and activity there (Kraus et al. 2003, Madritsch and Cardinale 2007, Ushio et al. 2013) and thus could also inhibit the development of *H. fraxineus* in mixed litter. The decomposition rate is also affected by C:N ratio in litter, which is the most advantageous in maple litter, worse in oak liter and the less favorable in pine litter (Madritsch and Cardinale 2007). Likely, the structure and size of fallen leaves could also affect the level of diffusion of different compounds into ash petioles. Likely, fine coniferous needles could more tightly surround ash petioles in forest floor, thus the compounds translocation could be more effective in this case than in leaves of oak and other broadleaved trees with relatively higher content of tannin. The significant negative effect of *Abies* spp. and *Pinus* spp. on the disease extent was confirmed in the study, whereas the effect of *Picea* spp. was also negative but not significant.

Conclusions

Extensive analysis of the influence of environmental and stand characteristics on the presence and extent of ash dieback in forest stands in the Czech Republic was conducted. The data on the defoliation of ash trees were collected from 1169 forest stands within the entire area of the Czech Republic in 2013. A set of 37 variables acquired from different databases (State Forests, GIS, Digital Relief Model) describing environmental and stand characteristics was used as explanatory variables.

The general developed model (GLM, R plus) explained nearly 26% of the disease variability. In the model, the extent of the disease was positively affected by 12 variables. Density of stocking, site class, vertical heterogeneity, temperature and the presence and width of watercourse positively affected the disease impact, whereas mean tree height, forest altitudinal zone, and the distance to the nearest ash stand negatively influenced the disease impact. A direct influence of precipitation was not confirmed. However, a set of environmental and silvicultural characteristics (such as density of stocking, vertical heterogeneity, the height of trees, and the presence and width of watercourse) were determined to be variables that indirectly influenced air humidity near the ground and the infection process indirectly.

The model confirmed a significant role of tree species composition of stands with ash on ash dieback. The disease extent was larger in the coincidental presence of *Quercus robur* and lower in the presence of *Abies* spp. and *Acer* spp. The influence of these trees is likely to be mediated via chemical characteristics of litter and in differences decomposition rates on ash petioles as a substrate for *H. fraxineus* in mixed litter. The decomposition of ash petioles could be accelerated by the coincidental decomposition of maple litter (for instance by the translocation of nutrients from it) in comparison with another litter type (oak). In contrast, secondary metabolites and tannins from coniferous litter leaching into ash litter could directly inhibit microbial growth and activity.

The extent of the disease also differed by edaphic series (wet and gleyed series were less damaged) and particular GLM models were also successfully developed. These models differed from each other and explained 23–37% of disease variability; other factors influencing disease extent were also determined: distance to watercourse, SD of slope, ash area, standing volume, aspect, TPI, landforms and the presence of other tree taxa such as *Pinus* spp., *Quercus petraea*, *Fagus sylvatica* and *Betula pendula*.

The outcome of this study clearly supports the idea that disease management based on the utilization of sources of resistance could be effectively facilitated by appropriate forest and landscape management. Forest management could be useful, at least in more heterogeneous areas with different forest types with ash and in regions with transitional, Mediterranean or more continental climates, which are typically in central, eastern and southern Europe. Of course, in more homogeneous flat regions in north-western and western Europe (for instance Denmark, the Netherlands, the Northern German Plain), the scale of environmental factors affecting the disease impact could be more restricted than in more variable central European landscape. The oceanic climate in west Europe could also support disease development in comparison with more eastern regions with transitional and continental climates.

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Supplementary material

Supplement Table S1a. Correlation matrix of quantitative variables and stand characteristics; partial correlation coefficients are shown; statistical significance ($P \leq 0.05$) is highlighted in grey

	Defoliation	Age	Stocking	Ash area	Height	Volume	Site class	Heterogeneity	Slope	SD slope	TPI	SD TPI	Dist. to water	Dist. to ash	Temperature	Precipitation
Defoliation	1.00	-0.33	0.19	0.08	-0.31	-0.03	0.16	-0.05	-0.12	-0.05	0.02	-0.04	-0.01	-0.03	0.24	-0.02
Age	-0.33	1.00	-0.32	0.02	0.87	0.28	-0.01	0.16	0.18	0.12	-0.04	0.12	-0.08	0,00	-0.16	-0.04
Stocking	0.19	-0.32	1.00	0.04	-0.23	0.02	0.16	0.03	-0.05	0.02	0.06	0.02	0.03	0.04	0.08	0.02
Ash area	0.08	0.02	0.04	1.00	0.02	0.70	0.04	0.05	-0.13	0.01	0.18	-0.02	-0.01	0.15	0.30	-0.04
Height	-0.31	0.87	-0.23	0.02	1.00	0.30	0.27	0.16	0.14	0.15	-0.12	0.12	-0.11	0.03	-0.11	-0.05
Volume	-0.03	0.28	0.02	0.70	0.30	1.00	0.12	0.13	-0.03	0.06	0.12	0.04	0.01	0.14	0.11	-0.02
Site class	0.16	-0.01	0.16	0.04	0.27	0.12	1.00	0.00	-0.06	0.02	-0.14	0,00	-0.15	0.04	0.14	-0.01
Heterogeneity	-0.05	0.16	0.03	0.05	0.16	0.13	0.00	1.00	0.68	0.64	0.08	0.72	-0.09	0.28	-0.35	-0.03
Slope	-0.12	0.18	-0.05	-0.13	0.14	-0.03	-0.06	0.68	1.00	0.68	-0.17	0.77	-0.08	0.04	-0.48	0.00
SD slope	-0.05	0.12	0.02	0.01	0.15	0.06	0.02	0.64	0.68	1.00	-0.13	0.78	-0.14	0.19	-0.28	-0.02
TPI	0.02	-0.04	0.06	0.18	-0.12	0.12	-0.14	0.08	-0.17	-0.13	1.00	-0.05	0.26	-0.04	0.13	-0.05
SD TPI	-0.04	0.12	0.02	-0.02	0.12	0.04	0,00	0.72	0.77	0.78	-0.05	1.00	-0.13	0.19	-0.25	-0.02
Dist. to water	-0.01	-0.08	0.03	-0.01	-0.11	0.01	-0.15	-0.09	-0.08	-0.14	0.26	-0.13	1.00	-0.08	0.12	0,00
Dist. to ash	-0.03	0.00	0.04	0.15	0.03	0.14	0.04	0.28	0.04	0.19	-0.04	0.19	-0.08	1.00	0.01	-0.04
Temperature	0.24	-0.16	0.08	0.30	-0.11	0.11	0.14	-0.35	-0.48	-0.28	0.13	-0.25	0.12	0.01	1.00	-0.04
Precipitation	-0.02	-0.04	0.02	-0.04	-0.05	-0.02	-0.01	-0.03	0,00	-0.02	-0.05	-0.02	0,00	-0.04	-0.04	1.00
Ash	0.09	-0.12	0.06	0.16	-0.10	0.02	0.02	-0.35	-0.17	-0.28	-0.08	-0.30	0.08	-0.27	0.23	-0.01
Picea	-0.03	0.02	0.07	-0.17	0.04	-0.07	0.05	0.31	0.20	0.19	0.08	0.22	-0.04	0.19	-0.28	0.03
Pinus	-0.03	-0.01	-0.07	-0.06	-0.03	-0.04	-0.09	-0.02	-0.07	-0.03	0.07	-0.03	0.05	0.04	0.04	-0.02
Larix	-0.05	-0.04	0.00	-0.01	-0.04	0.00	-0.06	0.03	0.02	0.03	0.08	0.03	0.00	-0.02	-0.06	0.04
Abies	-0.04	-0.04	0.03	-0.06	-0.08	-0.03	-0.02	0.02	-0.02	-0.01	0.05	-0.01	0.00	0.05	-0.06	0.07
Quercus1	0.05	0.07	-0.12	0.15	0.02	0.05	-0.04	-0.08	-0.16	-0.10	0.10	-0.10	0.03	0.06	0.22	0,00
Quercus2	0.03	0.00	0.03	-0.04	-0.02	-0.02	-0.04	-0.01	-0.05	0.02	0.06	0.02	0.04	0.03	0.10	-0.06
Fagus	-0.01	0.13	0.08	0.00	0.07	0.16	0.00	0.44	0.36	0.35	0.10	0.39	0.02	0.06	-0.23	0.00
Acer	-0.11	0.03	-0.03	-0.06	0.04	-0.01	-0.03	0.09	0.19	0.17	-0.12	0.16	-0.09	0.03	-0.16	-0.01
Alnus	-0.06	0.08	-0.10	-0.11	0.12	-0.06	0.04	-0.09	-0.14	-0.05	-0.18	-0.11	-0.12	0.03	-0.05	0.00
Tilia	-0.02	0.03	0.01	0.04	0.08	0.06	0.05	-0.01	-0.08	0.03	0.07	0.01	0.02	0.08	0.11	-0.03
Betula	-0.03	-0.04	-0.05	-0.04	-0.06	-0.05	-0.11	0.03	0.05	0.01	0.06	0.04	0.00	0.02	-0.10	0.01
Carpinus	-0.03	0.05	0.01	0.01	0.05	0.03	0.01	0.06	0.08	0.12	0.05	0.16	-0.03	0.07	0.13	0.03
Populus	-0.02	-0.01	-0.13	-0.01	0.02	-0.01	0.02	-0.06	-0.11	-0.07	0.02	-0.08	0.02	0.00	0.09	-0.02
Ulmus	0.03	-0.04	0.02	0.04	-0.09	-0.01	-0.02	-0.02	0.01	-0.01	-0.02	0.00	0.00	0.04	0.09	0.00

Supplement Table S1b. Correlation matrix of quantitative variables and tree species; partial correlation coefficients are shown; statistical significance ($P \leq 0.05$) is highlighted in grey

	Ash	Picea	Pinus	Larix	Abies	Quercus1	Quercus2	Fagus	Acer	Alnus	Tilia	Betula	Carpinus	Populus	Ulmus
Defoliation	0.09	-0.03	-0.03	-0.05	-0.04	0.05	0.03	-0.01	-0.11	-0.06	-0.02	-0.03	-0.03	-0.02	0.03
Age	-0.12	0.02	-0.01	-0.04	-0.04	0.07	0.00	0.13	0.03	0.08	0.03	-0.04	0.05	-0.01	-0.04
Stocking	0.06	0.07	-0.07	0.00	0.03	-0.12	0.03	0.08	-0.03	-0.10	0.01	-0.05	0.01	-0.13	0.02
Ash area	0.16	-0.17	-0.06	-0.01	-0.06	0.15	-0.04	0.00	-0.06	-0.11	0.04	-0.04	0.01	-0.01	0.04
Height	-0.10	0.04	-0.03	-0.04	-0.08	0.02	-0.02	0.07	0.04	0.12	0.08	-0.06	0.05	0.02	-0.09
Volume	0.02	-0.07	-0.04	0.00	-0.03	0.05	-0.02	0.16	-0.01	-0.06	0.06	-0.05	0.03	-0.01	-0.01
Site class	0.02	0.05	-0.09	-0.06	-0.02	-0.04	-0.04	0.00	-0.03	0.04	0.05	-0.11	0.01	0.02	-0.02
Hetero-geneity	-0.35	0.31	-0.02	0.03	0.02	-0.08	-0.01	0.44	0.09	-0.09	-0.01	0.03	0.06	-0.06	-0.02
Slope	-0.17	0.20	-0.07	0.02	-0.02	-0.16	-0.05	0.36	0.19	-0.14	-0.08	0.05	0.08	-0.11	0.01
SD slope	-0.28	0.19	-0.03	0.03	-0.01	-0.10	0.02	0.35	0.17	-0.05	0.03	0.01	0.12	-0.07	-0.01
TPI	-0.08	0.08	0.07	0.08	0.05	0.10	0.06	0.10	-0.12	-0.18	0.07	0.06	0.05	0.02	-0.02
SD TPI	-0.30	0.22	-0.03	0.03	-0.01	-0.10	0.02	0.39	0.16	-0.11	0.01	0.04	0.16	-0.08	0.00
Dist. to water	0.08	-0.04	0.05	0.00	0.00	0.03	0.04	0.02	-0.09	-0.12	0.02	0.00	-0.03	0.02	0.00
Dist. to ash	-0.27	0.19	0.04	-0.02	0.05	0.06	0.03	0.06	0.03	0.03	0.08	0.02	0.07	0.00	0.04
Tempera-ture	0.23	-0.28	0.04	-0.06	-0.06	0.22	0.10	-0.23	-0.16	-0.05	0.11	-0.10	0.13	0.09	0.09
Precipita-tion	-0.01	0.03	-0.02	0.04	0.07	0.00	-0.06	0.00	-0.01	0.00	-0.03	0.01	0.03	-0.02	0.00
Ash	1.00	-0.57	-0.18	-0.18	-0.12	-0.21	-0.16	-0.27	-0.17	-0.23	-0.12	-0.14	-0.13	-0.07	0.02
Picea	-0.57	1.00	0.02	0.05	0.08	-0.14	-0.06	0.01	-0.05	-0.12	-0.08	-0.04	-0.06	-0.08	-0.06
Pinus	-0.18	0.02	1.00	0.11	-0.01	0.05	0.02	-0.04	-0.05	-0.05	0.02	0.01	0.00	0.01	-0.02
Larix	-0.18	0.05	0.11	1.00	-0.01	-0.03	0.03	-0.02	-0.03	-0.06	0.01	0.00	0.03	-0.02	0.01
Abies	-0.12	0.08	-0.01	-0.01	1.00	-0.03	-0.01	0.05	-0.03	-0.05	-0.02	-0.02	0.00	-0.02	-0.02
Quercus1	-0.21	-0.14	0.05	-0.03	-0.03	1.00	-0.05	-0.08	-0.09	-0.10	0.07	0.01	0.07	0.00	0.05
Quercus2	-0.16	-0.06	0.02	0.03	-0.01	-0.05	1.00	-0.04	-0.06	-0.06	0.02	-0.02	0.11	-0.01	-0.02
Fagus	-0.27	0.01	-0.04	-0.02	0.05	-0.08	-0.04	1.00	0.01	-0.13	-0.06	-0.05	0.01	-0.05	-0.03
Acer	-0.17	-0.05	-0.05	-0.03	-0.03	-0.09	-0.06	0.01	1.00	-0.12	0.02	-0.03	0.03	-0.05	-0.02
Alnus	-0.23	-0.12	-0.05	-0.06	-0.05	-0.10	-0.06	-0.13	-0.12	1.00	-0.08	0.00	-0.02	0.05	-0.02
Tilia	-0.12	-0.08	0.02	0.01	-0.02	0.07	0.02	-0.06	0.02	-0.08	1.00	-0.02	0.10	0.02	0.02
Betula	-0.14	-0.04	0.01	0.00	-0.02	0.01	-0.02	-0.05	-0.03	0.00	-0.02	1.00	-0.02	0.03	-0.03
Carpinus	-0.13	-0.06	0.00	0.03	0.00	0.07	0.11	0.01	0.03	-0.02	0.10	-0.02	1.00	-0.01	0.01
Populus	-0.07	-0.08	0.01	-0.02	-0.02	0.00	-0.01	-0.05	-0.05	0.05	0.02	0.03	-0.01	1.00	-0.01
Ulmus	0.02	-0.06	-0.02	0.01	-0.02	0.05	-0.02	-0.03	-0.02	-0.02	0.02	-0.03	0.01	-0.01	1.00