Tree-ring Width of European Ash Differing by Crown Condition and its Relationship with Climatic Factors in Latvia

ILZE PUŠPURE, LINDA GERRA-INOHOSA, ROBERTS MATISONS* AND MĀRIS LAIVIŅŠ

LSFRI "Silava", Rigas str. 111, Salaspils, Latvia, LV2169

**Corresponding author: robism@inbox.lv, tel. +371 29789581*

Pušpure, I., Gerra-Inohosa, L., Matisons, R. and Laiviņš, M. 2017. Tree-ring width of European ash differing by crown condition and its relationship with climatic factors in Latvia. *Baltic Forestry* 23(1): 244-252.

Abstract

The spreading dieback of European ash (*Fraxinus excelsior* L.) that is a serious threat to the existence of the species in Europe, has been related to climatic changes. Still, not all trees in stands are damaged equally, suggesting that sensitivity to weather conditions might have affected the susceptibility to the disease. Climate-growth sensitivity of ash with visually healthy and damaged crowns growing in four stands in the central and eastern part of Latvia was assessed by dendrochronological techniques. The patterns of tree-ring width variation showed high diversity amongst trees, stands and regions; differences were observed between the damaged and healthy trees. Tree-ring patterns showed higher diversity amongst the healthy trees in the central part of Latvia, but, in the eastern part of Latvia, amongst the damaged ones. Mainly, the damaged trees were ca. 10–15 years older than the healthy ones suggesting age related differences in susceptibility, which might be related to vigour. The damaged and healthy trees differed also by growth trends, suggesting affiliation to different crown class, particularly at younger age. The sets of the significant climatic factors differed between the central and eastern part of Latvia. In the central part of Latvia, ash was mainly affected by the precipitation and daily temperature difference in the summer preceding formation of the tree-ring. Although the damaged trees were more sensitive to daily temperature difference and precipitation in the preceding August, the healthy trees were also additionally affected by maximum temperature in the preceding August. In the eastern part of Latvia, the sets of the significant factors were site specific, however, trees were mainly affected by temperature in the preceding autumn and current spring. In one site, the damaged ashes were more sensitive to temperature in July and September, while in other site the damaged trees were more affected by precipitation in July; the healthy trees were additionally affected by precipitation in September and temperature in April. Hence, the susceptibility to the disease appears partially related to the climatic sensitivity of trees.

Keywords: *Fraxinus excelsior*; ash dieback; dendroclimatology; climate-growth relationships; tree-ring width; radial growth patterns.

Introduction

The dieback of ash, which has been spreading across the Europe (Kowalski et al. 2010, Timmermann et al. 2011), is considered as a serious threat to the existence of the species (Kowalski 2006, Bakys et al. 2009a). The dieback is a rapid process, as the infected tree might die within a few years after the first symptoms, such as reduction of crown, appear or, in some cases, symptoms might not be even visible (Bakys et al. 2009b, Timmermann et al. 2011, Enderle et al. 2013). Although the mechanisms of ash dieback are not completely understood, it is considered to be caused by a complex of factors including climate and pathogens (Pautasso et al. 2010, Skovsgaard et al. 2010). The fungus *Hymenoscyphus fraxineus*, has been considered as a initiator of the dieback process (Kowalski 2006), which promotes further infestation and damage by the secondary agents (Kowalski et al. 2010, Skovsgaard et al. 2010, Bakys et al. 2011). The fungus, which attacks root system of ash (Bakys et al. 2008) affecting physical stability (susceptibility to uprooting) and water relations (increasing risk of water deficit) (Tulik et al. 2010), is considered to infest stressed trees, e.g. by unfavourable weather conditions (Thomsen and Skovsgaard 2006, Pautasso et al. 2010). Still, not all trees within a stand are damaged equally (Kirisits and Freinschlag 2011, Pliūra et al. 2011), suggesting different resistance to the disease (McKinney et al. 2011, Stener 2012). Hence, the sensitivity to climate might be one of the factors affecting the susceptibility of ash to the dieback. Similar has been observed for the declining pedunculate oak (*Quercus robur*) in Southern Finland, which showed different climate-growth sensitivity also before the decline (Helama et al. 2009).

Climate is one of the main factors affecting vigour and growth of trees, which are archived in the variation of wood increment (Fritts 2001). Hence, detailed information about the sensitivity of tree growth to climatic factors can be obtained from a retrospective analysis of the variation of tree-ring width (TRW) (Speer 2010). As tree growth has an explicit biological i.e., age trends (Fritts 2001), the effect of climatic factors is commonly assessed from the high-frequency variation of TRW (Cook et al. 1992). Considering that a tree-ring forms during a certain period of the vegetation period, combined effects of several factors might be recorded in TRW (Cook 1992, Schweingruber 1996).

The aim of this study was to assess the variation of TRW of ash with different crown condition and its relationship to climatic factors at the inter-annual scale. We hypothesized that the damaged trees had different growth patterns and were more sensitive to climatic factors than the healthy ones, and that the sets of the significant factors differed.

Material and methods

Studied sites, sampling and measurements

Four mature stands dominated or co-dominated by ash with different crown condition located in the central and eastern part of Latvia near Ukri (UKR), Rundāle (RND), Gulbene (GBN) and Barkava (BAR) (Figure 1) were studied. Sites in these regions were selected, as differences in growth have been observed for other species (Matisons et al. 2012, Baumanis et al. 2001). All of the stands were situated on a flat terrain in a normal moisture conditions on loamy soil. According to the national classification by Bušs (1976), site type in all stands was *Aegopodiosa*. The elevation of stands was ca. 35 and 110 m above the mean sea level in sites in the central (UKR and RND) and eastern (GNB and BAR) part of Latvia, respectively. The maximum age of ash in the BAR, GBN, RND and UKR sites, as determined from the obtained wood samples, was ca. 70, 190, 110 and 100 years, respectively. Advanced regeneration occurred in all stands.

The climate in the studied sites is determined by the dominant western winds, which bring cool and moist air masses from the Baltic Sea and the Atlantic. The weather conditions are harsher in the eastern part of Latvia. The mean annual temperature is ca. +6.4 and +5.5 °C; the mean monthly temperature ranges from -4.3 to +17.5 °C and from -6.2 to +17.4 °C in January and July in the central and eastern part of Latvia, respectively. The vegetation period, when the mean diurnal temperature is above +5°C, extends from mid-April to mid-October; it is usually 10–15 days longer in the central part of Latvia. The mean annual precipitation is about 610 mm in all sites. The highest monthly precipitation sums occur in the summer months, usually resulting in a positive water balance (Klavins and Rodinov 2010). Climatic changes are reflected as an increase of temperature in the autumn-spring period, which is extending the vegetation period (Lizuma et al. 2007). In the same time, summer precipitation regime is becoming more variable (Avotniece et al. 2010).

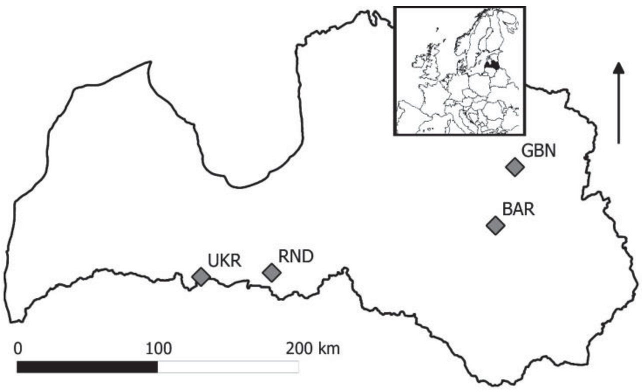

Figure 1. Location of studied sites near Barkava (BAR), Gulbene (GBN), Rundāle (RND) and Ukri (UKR)

In each stand, 10 dominant ashes with visually healthy crowns (crown reduction, i.e. dry branches, ≤ 15%) and 10 ashes with damaged crowns (crown reduction 30–60%) were selected. From each tree, two increment cores from the opposite sides of stem were collected with a Pressler increment corer at ca. 1.4 m height, avoiding reaction wood if trees were tilt. The sampling was done at the end of May 2015, when leaves had fully flushed. In the laboratory, increment cores were air dried and mounted on fixation planks for grinding. Sandpaper of four roughness grits (120, 140, 320 and 400 grains per inch) was applied, using hand sanding machine. The polished surface of samples was rubber with chalk to increase the contrast between early and latewood and to aid the recognition of tree-rings. The TRW was measured by a Lintab 5 measurement system (RinnTECH, Heidelberg, Germany) with the precision of 0.01 mm.

Data analysis

All of the measured chronologically ordered series of TRW were crossdated (i.e. their dating and synchronicity compared against each other) and their quality was checked by graphical inspection and statistically, by the program COFECHA (Grissino-Mayer 2001). Series showing low agreement with the rest of the dataset ($r < 0.35$) were omitted from further analysis. The TRW series of the healthy trees were used as a reference for crossdating of the damaged trees. The crossdated series were then averaged for trees and their quality was verified. For description of the datasets, expressed population signal, signal to noise ratio (Wigley et al. 1984), Gleichläufigkeit, interseries correlation (based on detrended series) and the first order autocorrelation coefficients were calculated.

For assessment of high-frequency variation of TRW, residual chronologies based on the crossdated datasets were produced by the program ARSTAN (Cook and Holmes 1986) for each site and group of trees (damaged and healthy). Double detrending, firstly by a negative exponential curve and secondly by the cubic spline with rigidity of 64 years and 50% frequency cut-off level, was applied. The relationships between climatic factors and high-frequency variation of TRW was assessed by a bootstrapped Pearson correlation analysis (Johnson 2001) conducted for the common period from 1934 (1948 for the healthy trees in the RND site) to 2010. The significance of correlations was determined at $\alpha = 0.05$, performing 10000 iterations. The climatic factors showing significant correlations with TRW were tested for collinearity. The tested climatic factors were the minimum, maximum and mean temperature, potential evapotranspiration (PET), precipitation sums and mean daily temperature difference for months. The climatic window from January in the year preceding formation of tree-ring to September in the year of tree-ring formation (21 months) was used. Climatic data were obtained from the high-resolution gridded datasets provided by the Climatic Research Unit of UEA for the closest to the sites grid entries (Harris et al. 2014). The statistical analysis were conducted in the program R (R Core Team 2014) using the library “dplR” (Bunn 2008).

Results

After the crossdating and quality checking, from 75 to 100% of the series per group/site were maintained for further analysis. The crossdated datasets covered the periods beginning from 1824 to 1948 in GBN and RND sites, respectively (Table 1). Generally, TRW series showed better agreement in the central part of Latvia, as shown by higher values of interseries correlation and expressed population signal. The agreement of TRW of the healthy trees was better in sites in the eastern part of Latvia, where values of interseries correlation (0.35 vs. 0.15), Gleichläufigkeit (0.62 vs. 0.58) and expressed population signal (0.75 vs. 0.55) were higher. The opposite was observed in sites in the central part of Latvia, where the environmental signal was stronger, as shown by a higher signal to noise ratio (4.8 and 2.3, respectively). The agreement of TRW was considerably weaker, hence the noise was considerably stronger for the damaged trees in the BAR site, compared to the rest of the datasets. The value of expressed population signal exceeded 0.85 only for the damaged trees in the UKR site. Nevertheless, common tendencies, such as the decreased TRW in 1940, 1963, 1984, 1990 and 2006 were observed in all chronologies (Figure 2).

Table 1. Statistics of the crossdated datasets of tree-ring width (TRW) of ask with the damaged and healthy crowns in sites near Barkava, Gulbene, Rundāle and Ukri. A – stand age, D– mean diameter of trees, S – mean sensitivity, N – number of crossdated trees, IC – mean interseries correlation, AC – autocorrelation, GLK – Gleichläufigkeit, EPS – expressed population signal (Wigley et al. 1984), SNR – signal to noise ratio

	N	Period	A, years	D, cm	Min. TRW, mm	Max. TRW, mm	Mean TRW, mm	St. dev. TRW, mm	S	IC	AC	GLK	EPS	SNR
Barkava (BAR)														
Healthy	8	1933–2014	91	32.9	0.68	5.69	2.53	0.90	0.20	0.39	0.70	0.63	0.79	3.67
Damaged	10	1928–2014	91	28.9	0.10	10.00	1.99	0.99	0.22	0.09	0.80	0.58	0.42	0.71
Gulbene (GBN)														
Healthy	10	1824–2014	195	48.6	0.17	5.39	1.48	0.61	0.18	0.31	0.77	0.60	0.72	2.53
Damaged	10	1831–2014	195	43.9	0.12	4.77	1.38	0.56	0.19	0.23	0.79	0.58	0.69	2.20
Rundāle (RND)*														
Healthy	9	1948–2014	68	27.2	0.46	6.24	2.05	0.81	0.21	0.36	0.73	0.60	0.82	4.49
Damaged	10	1916–2014	112	34.2	0.16	6.35	1.79	0.88	0.19	0.36	0.83	0.60	0.83	4.90
Ukri (UKR)														
Healthy	7	1933–2014	106	33.2	0.53	5.28	1.99	0.99	0.19	0.40	0.86	0.60	0.81	4.32
Damaged	8	1925–2014	106	29.5	0.20	5.80	1.65	0.89	0.17	0.44	0.87	0.64	0.86	5.73

* – uneven aged stand.

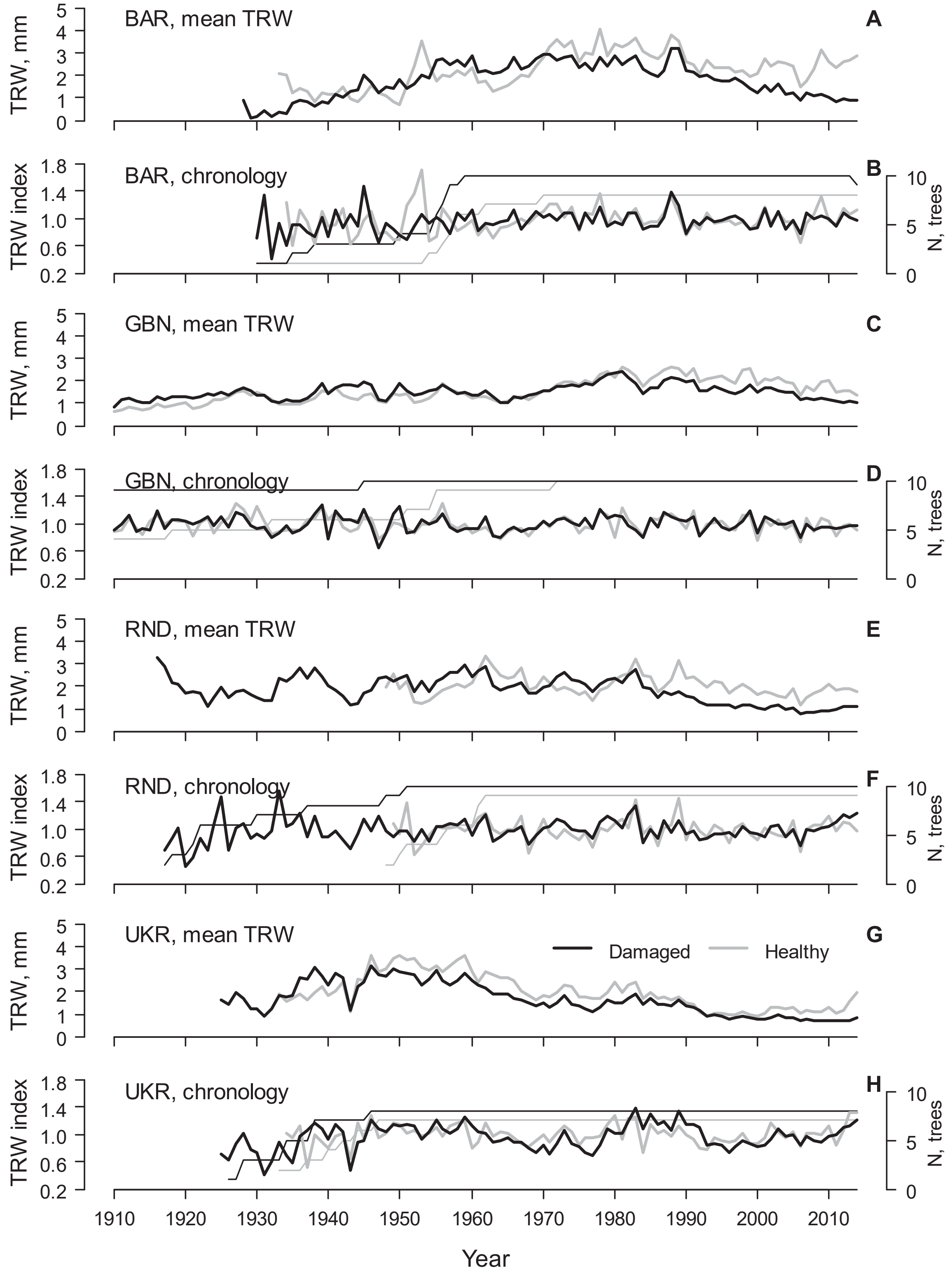

Figure 2. Mean series (A, C, E, G), residual chronologies (thick lines) and sample depth (thin line) of tree-ring width (TRW) (B, D, F, H) of ash with damaged (black lines) and healthy (grey lines) crowns for sites near Barkava (BAR), Gulbene (GBN), Rundāle (RND) and Ukri (UKR), respectively. Curves are based on crossdated datasets. For GBN site, only data for period from 1910 to 2014 are shown

In most of the cases, the healthy trees were younger, had higher mean TRW and contained less autocorrelation (0.77 vs. 0.82) than the damaged ones (Table 1). The damaged trees showed growth suppression during a few recent decades, although in some sites, they have been growing faster than the healthy trees at younger age (Figure 2).

The indices of chronologies generally ranged from ca. 0.60 to ca. 1.40, but the range tended to become narrower during a few recent decades (Figure 2). The agreement among the chronologies was weak, as the mean values of correlation calculated between them was 0.26, although Gleichläufigkeit was 0.63. The correlation between chronologies of the healthy and damaged trees ranged from 0.36 to 0.70 in the BAR and GBN sites, respectively. Nevertheless, the agreement between the chronologies of trees with different crown condition increased with age, particularly during the recent decades, as shown by the mean values of correlation coefficients of 0.50 and 0.65 at the beginning and at the end of the 20th century, respectively (not shown).

From the tested 132 climatic factors, 18 significantly correlation with TRW of ash (Figure 3). The number of significant correlations was higher in sites in the central than in the eastern part of Latvia (23 and 13, respectively). The values of correlation coefficients were generally low and did not exceed 0.32, except for precipitation in March (r = 0.48). The climate-growth relationships were quite individual, particularly in the eastern part of Latvia, as the sets of the significant correlations differed amongst the sites. In the central part of Latvia, TRW was affected by climatic factors (precipitation and daily temperature difference) related to the previous vegetation season (May–August), as well as some correlations with precipitation in February and March of the current year were observed. In the eastern part of Latvia, TRW of ash appeared mainly sensitive to weather conditions (maximum and mean monthly temperature) in the previous autumn (September and October) and in the current vegetation season (April–September). Generally, temperature and its mean daily difference had a negative effect on TRW, as shown by the prevailing negative correlations, while precipitation had a positive effect.

Only a few pronounced and systematic differences in the sets of the significant climatic factors were observed between the healthy and damaged trees (Figure 3). The damaged trees in the central part of Latvia displayed stronger correlation to the mean daily temperature difference and precipitation in August of the preceding year. The healthy trees showed additional sensitivity to the maximum temperature in previous August. In the RND site, TRW of the healthy trees showed the strongest of the observed correlations with precipitation in March. In the UKR site, the healthy trees showed stronger correlation with PET in May of the preceding year. In the eastern part of Latvia in the BAR site, the damaged trees were more affected by temperature in July and September of the current year, while the healthy trees were additionally affected by temperature in September and October of the preceding year. In the GNB site, the healthy trees were affected by precipitation in previous September and temperature in April of the current year, but they were less sensitive to precipitation in previous July.

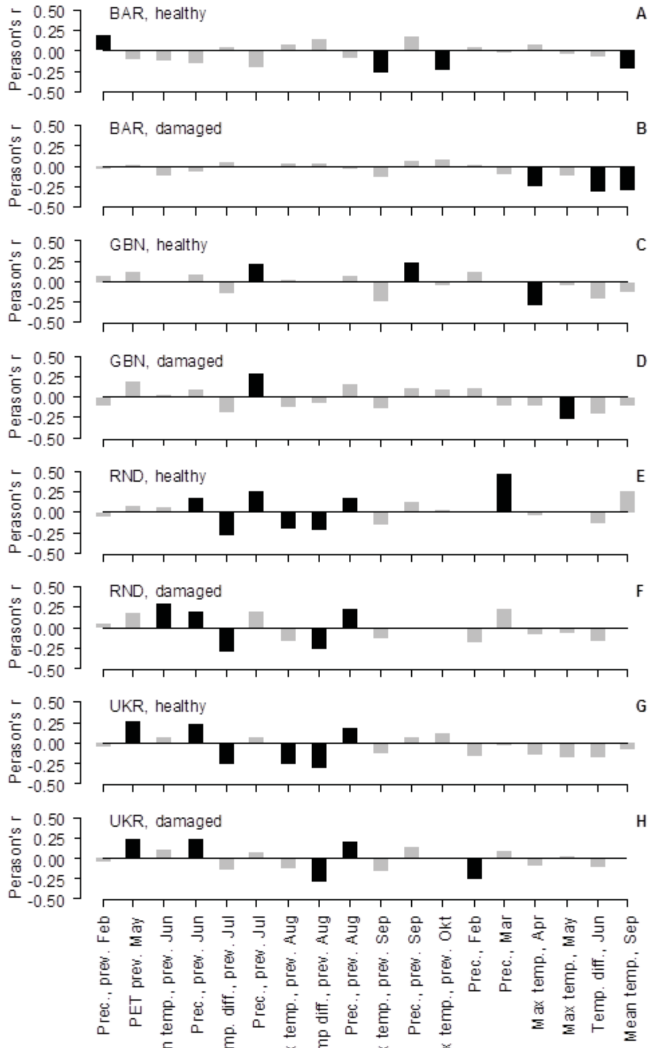

Figure 3. Bootstrapped Pearson's correlation coefficients calculated between climatic factors and residual chronologies of tree-ring width of ash with healthy (A, C, E, G) and damaged crowns (B, D, F, H) for sites near Barkava (BAR), Gulbene (GBN), Rundāle (RND) and Ukri (UKR), respectively. The period from 1934 (1948 for healthy trees in RND site) to 2010 was analysed. The significant correlations (at α = 0.05) are shown in black. Only the significant factors are plotted. PET – potential evapotranspiration

Discussion and conclusions

Most of the TRW series were sufficiently crossdated, as they had common signature years (narrow tree-rings in certain years). Yet the individuality of growth was rather pronounced (Table 1), as the values of expressed population signal were mainly below 0.85 (Wigley et al. 1984). Such individual growth patterns apparently caused the noise in the datasets, hence the values of signal to noise ratio were below 5.8 (Table 1). Pronounced site-specifics in the growth patterns were also evidenced by weak correlation amongst the established chronologies (Figure 2), despite the fact that, in Latvia, ash occurs near its northern distribution limit (EUFORGEN 2009), where distinct effect of a common climatic factor(s) is expected (Fritts 2001). The observed regional differences in agreement of TRW series (Table 1) matched with the current knowledge on the diversity of tree growth patterns between the central (western) and eastern part of Latvia (Baumanis et al. 2001, Matisons et al. 2012). Nevertheless, weaker agreement of the TRW series was observed in the eastern part of Latvia that might be explained by stressed growth under harsher climate, when the effect of competition diversifies growth patterns (Speer 2010). In contrary, individuality of growth has been observed also for trees growing in optimum conditions, where a strict limiting factor is lacking (Fritts 2001). In the central part of Latvia, where climate is milder, ash, apparently, was less suppressed, hence the common signatures in TRW were clearer (Table 1). This is supported by the differences in agreement between the healthy and damaged trees. In the central part of Latvia, trees, which had stronger crown damage, showed better agreement of TRW likely due to higher sensitivity to environmental variability, suggesting the role of climatic factors in the dieback process (Thomsen and Skovsgaard 2006, La Porta et al. 2008). In the eastern part, crown damage, apparently, additionally stressed the trees, diversifying their growth patterns (Speer 2010).

The susceptibility of ash to fungal infection (Enderle et al. 2013) appeared to be age-related, as the healthy trees were mainly younger than the damaged ones (Table 1). With age, maintenance costs increases (Ryan 1990) and less resources might be allocated for production of defence substances (Pallardy 2008). This is supported by higher autocorrelation in TRW of the damaged trees (Table 1), suggesting stronger dependence on nutrient reserves (Fritts 2001). Nevertheless, the differences in growth rates between the tree groups (Figure 2) suggested that the susceptibility to disease might be also related to the social status (i.e., crown classes) of trees (Martin-Bento et al. 2008). The damaged trees, apparently, had a higher social status at the young age, as shown by faster growth (wider tree-rings) during a few earliest decades of their life. In contrast, trees, which grew slower, were less susceptible to crown damage at the older age. In all sites, the damaged trees showed reduction of TRW for ca. three recent decades compared to the healthy ones (Figure 2) suggesting that previously suppressed trees have been infected (Timmermann et al. 2011). Similarly, stronger symptoms of decline has been observed for the suppressed oaks (Helama et al. 2009). Simultaneous reduction of TRW in all sites during the recent decades (Figure 2) might be explained by the effect of weather conditions, such as the extreme drop of temperature in the winter of 1978/1979, striking the insufficient hardened trees and causing shifts in their growth trends (Matisons et al. 2013). The reduction of TRW decreased its annual variation particularly for the damaged trees (Figure 2) due to the suppression of growth (Speer 2010), but the patterns became more similar for both tree groups (Figure 2) suggesting clearer effect of common limiting factor(s).

High-frequency variation of TRW was significantly affected by the tested climatic factors (Figure 3). Still, the rather low values of correlation coefficients might be explained by the individuality of TRW variation within a site due to stresses, when the common response is reduced (Speer 2010). Similarly, the diversity of the significant factors amongst the sites and tree groups, particularly in the eastern part of Latvia (Figure 3), might be explained by the individuality of growth rhythms (Table 1). This apparently explains the number of observed significant correlations. In the sites in the central part of Latvia, the sets of significant climatic factors were similar (Figure 3), suggesting that trees have been able to show clearer reaction to weather conditions. The TRW mainly correlated with climatic conditions in the preceding summer, suggesting effect of nutrient reserves on wood increment (Barbaroux and Breda 2002). In the ring porous species, including ash (Carlquist 2001), nutrient reserves are mainly deployed for early growth (Barbaroux and Breda 2002) that affects water relations of tree in the following vegetation period (Tyree and Zimmermann 2002) and hence the increment. The amount of precipitation in summer showed positive correlation with TRW for all groups (Figure 3), suggesting that in the central part of Latvia ash has suffered water deficit. Shifting temperature conditions can burden assimilation and physiological processes (Pallardy 2008), as certain time is needed for the adjustment of photosynthetic apparatus to current conditions (Berry and Downton 1982), explaining the observed negative correlations between mean difference in daily temperature and TRW (Figure 3). The effect of precipitation and temperature in the preceding August was significant in all sites (Figure 3), as it is the time when the formation of nutrient reserves initiates (Barbaroux and Breda 2002).

In the sites in the eastern part of Latvia, TRW of ash was mainly negatively affected by temperature (Figure 3), but the mechanisms of influence shifted during the season. In autumn, raised temperature can increase respiration, causing losses of stored nutrients (Ögren et al. 1997). In September, increased temperature, apparently, might also increase evapotranspiration (Traykovic 2005) causing water deficient, as positive correlation with precipitation was observed (Figure 3). This applies to current and previous September temperature. The negative effect of temperature in current spring might be explained by earlier onset of the active period or earlier leaf flush, subjecting trees to damage from late frosts (Gu et al. 2008), which are quite common in the eastern part of Latvia (Avotniece et al. 2010).

In the context of regional and local diversity, the sets of the significant factors between the healthy and damaged trees differed slightly (Figure 3), suggesting that climatic sensitivity had non-drastic effect on susceptibility to the disease and crown reduction (Figure 2), although the effect of weather extremes might not be visible in the residual chronology (Schweingruber 1992). Still, some regional or stand differences were observed (Figure 3). In the central part of Latvia, the damaged trees were more affected by water deficit and temperature regime in the preceding August, as shown by higher values of correlation (Figure 3). Stronger relationships with climatic factors suggested that under unfavourable conditions, i.e. warm and dry summers, which are becoming more frequent (Avotniece et al. 2010), trees are more stressed hence predisposed to the infection and damage. Nevertheless, negative effect of the maximum temperature in the preceding August was observed for the healthy trees (Figure 3), which apparently have been able to react to additional factor, probably due lower stress (Speer 2010). On the other hand, the negative effect of maximum temperature in August, which is the second warmest month (Lizuma et al. 2007), might be related to slower growth of the healthy trees before 1970s (Figure 2). In the RND site, only the healthy trees showed positive relationship with precipitation in March, which had the highest value of correlation coefficients (Figure 3). Precipitation in March is usually in the form of snow, and its effect might be explained by the insulating properties of snow layer, which influences soil temperature, decreases soil freeze (Hardy et al. 2001) and hence winter mortality of fine roots (Tierney et al. 2001), affecting water relations of a tree later in spring (Tyree and Zimmermann 2002). The absence of such relationship might suggest that the damaged trees have had less sensitive root system before the infection. The effect of potential evapotranspiration in the previous May in the UKR site (Figure 3) might be related to excess of soil water at the beginning of vegetation season, which influence root respiration (Pallardy 2008). Still, the differences in reaction to this factor between the healthy and damaged trees is difficult to explain. Probably, it might be related to slower growth of the health trees at younger age, when they have been more influenced by this factor. In the eastern part of Latvia in the GBN site, where trees were the oldest, TRW was influenced by precipitation (Figure 3) that might be explained by the age-related sensitivity to water deficit (Carrer and Urbinati 2004). The damaged trees showed stronger correlation to precipitation (Figure 3), suggesting increased susceptibility to water deficit, hence they were more stressed in the dry years that, presumably, led to the infection by fungus and reduction of crown (Kowalski et al. 2010). In the BAR site, the differences in sets of the significant factors are difficult to explain and might be caused by the district individuality of growth patterns (Table 1).

Although located near its northern distribution limit, in Latvia, ash showed site-specific growth patterns and climatic sensitivity, probably due to the stresses caused by the pathogen(s). This also approves the complexity of ash dieback process. In all sites, ash of different crown conditions was affected by the climatic factors related to water deficit in summer, suggesting that under the changing climate, growth of ash might become even more stressed. The sensitivity of growth was higher under more continental conditions. Trees with different crown condition, apparently differed by social status, as the damaged trees grew faster at young age, but the TRW of the healthy trees was the highest at medium age. Still, the damaged trees showed growth reduction during recent three decades. The susceptibility to disease also appeared age-related, as the damaged trees were older than the healthy ones, likely due to the increasing maintenance costs. Still, some differences in climatic sensitivity were observed. In general, trees with the damaged crowns were more affected by the climatic factors, suggesting that climatic stresses have been at least partially involved in the development of the disease. Nevertheless, the healthy trees also showed effect of some climatic factors not observed for the damaged ones, suggesting influence of e.g. microclimate and microtopography on the susceptibility to the disease. For better understanding of the role of tree water relations in ash dieback, analysis of wood vessels might be useful.

Acknowledgements

This study was funded by the joint stock company "Latvijas Valsts Meži" project "'Ash forest destruction and regeneration in Latvia" (5.5.-5.1_0017_101_14_28) and by the Forest Sector Competence Centre project "Methods and technologies for increasing forest capital value" (No L-KC-11-0004)".

References

Avotniece, Z., Rodinov, V., Lizuma, L., Briede, A. and Kļaviņš, M. 2010. Trends in frequency of extreme climate events in Latvia. *Baltica* 23: 135–148.

Bakys, R., Vasaitis, R., Barklund, P., Ihrmark, K. and Stenlid, J. 2009a. Investigations concerning the role of *Chalara fraxinea* in declining *Fraxinus excelsior*. *Plant Pathology* 58: 284–292.

Bakys, R., Vasaitis, R., Barklund, P., Thomsen, I. and Stenlid, J. 2009b. Occurrence and pathogenicity of fungi in necrotic and non-symptomatic shoots of declining common ash (*Fraxinus excelsior*) in Sweden. *European Journal of Forest Research* 128: 51–60.

Bakys, R., Vasiliauskas, R., Barklund, P., Ihrmark, K. and Stenlid, J. 2008. Fungal attacks to root systems and crowns of declining *Fraxinus excelsior*. *Aktuelt fra skogforskningen* 1: 71–72.

Bakys, R., Vasiliauskas, R., Ihrmark, K., Stenlid, J., Menkis, A. and Vasaitis, R. 2011. Root rot, associated fungi and their impact on health condition of declining *Fraxinus excelsior* stands in Lithuania. *Scandinavian Journal of Forest Research* 26: 128–135.

Barbaroux, C. and Breda, N. 2002. Contrasting distribution and seasonal dynamics of carbohydrate reserves in stem wood of adult ring-porous sessile oak and diffuse-porous beech trees. *Tree Physiology* 22: 1201–1210.

Baumanis, I., Gailis, A. and Liepiņš, K. 2001. Comparisons of Scots pine provenances in Latvia. *Mežzinātne* 11: 52–66, (in Latvian).

Berry, J.A. and Downton, W.J.S. 1982. Environmental regulation of photosynthesis. In: Govindjee (Editor), Photosynthesis: development, carbon metabolism and plant productivity. Academic Press, New York, Vol. 2, p. 265–345.

Bunn A.G. 2008. A dendrochronology program library in R (dplR). *Dendrochronologia* 26: 115–124.

Bušs, K. 1976. Latvijas PSR mežu klasifikācijas pamati [Basis of Forest classification in SSR of Latvia]. LRZTIPI, Rīga 34 pp, (in Latvian).

Carlquist, S.J. 2001. Comparative wood anatomy: Systematic, ecological and evolutionary aspects of dicotyledon wood. Springer, Berlin, 268 pp.

Carrer, M. and Urbinati, C. 2004. Age-dependent tree-ring growth response to climate in *Larix decidua* and *Pinus cembra*. *Ecology* 85: 730–740.

Cook, E.R. 1992. A conceptual linear aggregate model for tree rings. In: E.R. Cook and L.A. Kairiukstis (Editors), Methods of dendrochronology: application in the environmental sciences. Kluwer Academic Publishers, Dordrecht, p. 98–104.

Cook, E.R. and Holmes, R.L. 1986. Guide for computer program ARSTAN. In: R.L. Holmes, R.K. Adams, and H.C. Fritts (Editors), Tree-ring chronologies of Western North America: California, eastern Oregon and northern Great Basin. University of Arizona Press, Tucson, p. 50–65.

Cook, E.R., Briffa, K., Shiyatov, S. and Mazepa, V. 1992. Tree-ring standardization and growth trend estimation. In: E.R Cook and L.A. Kairiukstis (Editors), Methods of dendrochronology. Kluwer Academic Publishers, Dordrecht, p. 104–123.

Enderle, R., Peters, F., Nakou, A. and Metzler, B. 2013. Temporal development of ash dieback symptoms and spatial distribution of collar rots in a provenance trial of *Fraxinus excelsior*. *European Journal of Forest research* 132: 956–876.

EUFORGEN 2009. Distribution maps, *Fraxinus excelsior* L. www.euforgen.org/Documents/Maps/PDF/Fraxi nus_excelsior.pdf. Accessed 11.11.2015.

Fritts, H.C. 2001. Tree-rings and Climate. The Blackburn Press, Caldwell, 582 pp.

Grissino-Mayer, H.D. 2001. Evaluating crossdating accuracy: a manual and tutorial for the computer program COFECHA. *Tree-Ring Research* 57: 205–221.

Gu, L., Hanson, P.J., Post, W.M., Kaiser, D.P., Yang, B., Enami, R., Pallardy, S.G. and Meyers, T. 2008. The 2007 Eastern US spring freeze: Increased cold damage in a warming world? *BioScience* 58: 253–262.

Hardy, J.P., Groffman, P.M., Fitzhugh, R.D., Henry, K.S., Welman, A.T., Demers, J.D., Fahey, T.J., Driscoll, C.T., Tierney, G.L. and Nolan, S. 2001. Snow depth manipulation and its influence on soil frost and water dynamics in a northern hardwood forest. *Biogeochemistry* 56: 151–174.

Harris, I., Jones, P.D., Osborn, T.J. and Lister, D.H. 2014. Updated high-resolution grids of monthly climatic observations—the CRU TS3.10 Dataset. *International Journal of Climatology* 34: 623–642.

Helama, S., Läänelaid, A., Raisio, J. and Tuomenvirta, H. 2009. Oak decline in Helsinki portrayed by tree-rings, climate and soil data. *Plant and Soil* 319: 163–174.

Johnson, R.W. 2001. An introduction to bootstrap. *Teaching Statistics* 23: 49–54.

Kirisits, T. and Freinschlag, C. 2011. Ash dieback caused by *Hymenoscyphus pseudoalbidus* in a seed plantation of *Fraxinus excelsior* in Austria. *Journal of Agricultural Extension and Rural Development* 4: 184–191.

Klavins, M. and Rodinov, V. 2010. Influence of large-scale atmospheric circulation on climate in Latvia. *Boreal Environment Research* 15: 533–543.

Kowalski, T. 2006. *Chalara fraxinea* sp. Nov. associated with dieback of ash (*Fraxinus excelsior*) in Poland. *Forest Pathology* 36: 264–270.

Kowalski, T., Schumacher, J. and Kehr, R. 2010. Das Eschensterben in Europa – Symptome, Erreger und Empfehlungen für die Praxis [Ash dieback in Europe – symptoms, causes and prognosis]. In: D. Dujesiefken (Editor), Jahrbuch der Baumpflege 2010. Haymarket Media, Braunschweig, pp. 184–195, (in German).

La Porta, N., Capretti, P., Thomsen, I.M., Kasanen, R., Hietala, A.M. and Von Weissenberg, K. 2008. Forest pathogens with higher damage potential due to climate change in Europe. *Canadian Journal of Plant Pathology* 30: 177–195.

Lizuma, L., Kļaviņš, M., Briede, A. and Rodinovs, V. 2007. Long-term changes of air temperature in Latvia. In: M. Kļaviņš (Editor), Climate change in Latvia. University of Latvia, Riga, p. 11–20.

Martin-Benito, D., Cherubini, P., del Rio, M. and Canellas, I. 2008. Growth response to climate and drought in *Pinus nigra* Arn. trees of different crown classes. *Trees-Structure and Function* 22: 363–373.

Matisons, R., Elferts, D. and Brūmelis, G. 2012. Changes in climatic signals of English oak tree-ring width and cross-section area of earlywood vessels in Latvia during the period 1900–2009. *Forest Ecology and Management* 279: 34–44.

Matisons, R., Elferts, D. and Brūmelis, G. 2013. Possible signs of growth decline of pedunculate oak in Latvia during 1980–2009 in tree ring width and vessel size. *Baltic Forestry* 19: 137–142.

McKinney, L.V., Nielsen, L.R., Hansen, J.K. and Kjær, E.D. 2011. Presence of natural genetic resistance in *Fraxinus excelsior* (Oleaceae) to *Chalara fraxinea* (Ascomycota): an emerging infectious disease. *Heredity* 106: 788–797.

Ögren, E., Nilsson, T. and Sundblad, L.G. 1997. Relationship between respiratory depletion of sugars and loss of cold hardiness in coniferous seedlings over-wintering at raised temperatures: indications of different sensitivities of spruce and pine. *Plant, Cell and Environment* 20: 247–253.

Pallardy, S.G. 2008. Physiology of woody plants, third ed. Elsevier, London, 464 pp.

Pautasso, M., Dehnen-Schmutz, K., Holdenrieder, O., Pietravalle, S., Salama, N., Jeger, M.J., Lange, E. and Hehl-Lange, S. 2010. Plant health and global change—some implications for landscape management. *Biological reviews of the Cambridge Philosophical Society* 85: 729–755.

Pliūra, A., Lygis, V., Suchockas, V. and Bartkevičius, E. 2011. Performance of twenty four European *Fraxinus excelsior* populations in three Lithuanian progeny trials with a special emphasis on resistance to *Chalara fraxinea*. *Baltic Forestry* 17: 17–34.

R Core Team 2014. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL: http://www.R-project.org/. Accessed 11.11.2015.

Ryan, M.G. 1990. Growth and maintenance respiration in stems of *Pinus contorta* and *Picea engelmanii*. *Canadian Journal of Forest Research* 20: 48–57.

Schweingruber, F.H. 1992. Dendrochronological information in pointer years and abrupt growth changes. In: E.R. Cook and L.A. Kairiukstis (Editors), Methods of dendrochronology. Kluwer Academic Publishers, Dordrecht, p. 277–284.

Schweingruber, F.H. 1996. Tree rings and environment—dendroecology. Paul Haupt Verlag, Berlin, 682 pp.

Skovsgaard, J.P., Thomsen, I.M., Skovgaard, I.M. and Martinussen, T. 2010. Associations between symptoms of dieback in even-aged stands of ash (*Fraxinus excelsior* L.). *Forest Pathology* 40: 7–18.

Speer, J.H. 2010. Fundamentals of tree-ring research. The University of Arizona Press, Tucson, 333 pp.

Stener, L.G. 2012. Clonal differences in susceptibility to the dieback of *Fraxinus excelsior* in southern Sweden. *Scandinavian Journal of Forest Research* 28: 205–216.

Thomsen, I.M. and Skovsgaard, J.P. 2006. Toptørrea i ask: klimaskade eller svampeangreb? [Crown dieback of ash: Climatic damage or fungal attack?] *Skoven* 38: 408–411, (In Danish).

Tierney, G.L., Fahey T.J., Groffman P.M., Hardy J.P., Fitzhugh R.D. and Driscoll C.T. 2001. Soil freezing alters fine root dynamics in a northern hardwood forest. *Biogeochemistry* 56: 175–190.

Timmermann, V., Børja, I., Hietala, A. M., Kirisits, T. and Solheim, H. 2011. Ash dieback: pathogen spread and diurnal patterns of ascospore dispersal, with special emphasis on Norway. *EPPO Bulletin* 41: 14–20.

Traykovic, S. 2005. Temperature-based approaches for estimating reference evapotranspiration. *Journal of Irrigation and Drain E-ASCE* 131: 316–323.

Tulik, M., Marciszewska, K. and Adamczyk, J. 2010. Diminished vessel diameter as a possible factor in the decline of European ash (*Fraxinus excelsior* L.). *Annals of Forest Science* 103: 1–8.

Tyree, M.T. and Zimmermann, M.H. 2002. Xylem structure and ascent of sap. Springer, Berlin, 304 pp.

Wigley, T.M.L., Briffa, K.R. and Jones, P.D. 1984. On the average value of correlated time series, with applications in dendroclimatology and hydrometeorology. *Journal of Climate and Applied Meteorology* 23: 201–213.