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Wood increment and earlywood vessel size of pedunculate oak and their relation with climatic factors in Latvia

Academic dissertation

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Table of Contents

Summary

Climate is one of the main factors that determines ecosystem composition and distribution of species. Under climate change, a shift in species distribution has been observed, which may lead to shifts in ecosystem structure and distribution, and economical consequences. Such shifts may be modelled and predicted, however detailed information, both spatial and temporal, on species response to climate and its variability is necessary. Trees, which are dominant living forms in forest ecosystems, are widely used for such purposes due to their long lifespan and high bioindication potential. During life of a tree environmental conditions are recorded in tree-rings via differences in growth. Highest sensitivity of tree growth can be observed on borders of their distribution, due to strict limiting factors. Latvia is located in the boreo-nemoral forest zone, where several broadleaved species, such as oak, occur close to their northern distribution limit, and shift of these species may occur under warming climate. Use of oak in dendrochronological (climatological) studies is simplified due to rather easy crossdating and a long lifespan. For these reasons oak have been widely studied in Central and Western Europe; however there is insufficient information in the Baltic States.

A network of 43 sapling sites located across Latvia was established; oak dominated stands (sites) with age more than 100 years and area more than 1 ha, were chosen. In most of these sites ~10 oak were cored from opposite sides of stem. Tree-ring widths (TRW) were measured. Additionally, mean cross-section area of earlywood vessel lumen (VLA) was measured, as this proxy has been recently shown to contain strong environmental (climatic) signals. For both proxies crossdating was applied to ensure quality of measurements. Agreement between time-series of individual trees within a stand was higher for TRW, while VLA showed better agreement between sites. There was no significant relationship between variation of proxies, showing different sources of variation. Residual chronologies for each proxy for each stand were established to assess high-frequency variation; its similarity in Latvia (between stands) was determined using PCA. Results showed that high frequency variation of proxies was affected by continentality and west-east gradient was observed. According to this gradient, two regions of Latvia: western and eastern part, were distinguished. Effect of climatic factors on high frequency variation of proxies was determined by Pearson correlation and response function analysis. Effect of climatic factors on TRW depended on habitat, as none of factors showed significant effect in all sites within a region. However, in the western region the effect of temperature in spring and the beginning of summer was more common; while effect of August precipitation and effect of previous year July and August temperature was more common in eastern region. VLA showed a common significant effect of temperature in the dormancy period throughout Latvia. Regional chronologies (based on PCA division) of TRW showed similar climatic signals as observed for stands; however, effect of temperature in previous year July and August was stronger in the western region. Regional chronologies of VLA mainly showed the same signals as observed for stands. During the 20th century climatic signals have changed. VLA has been loosing sensitivity for February and March temperature, while sensitivity to December temperature has increased. In the western region TRW has lost sensitivity to February and March temperature, while effect of temperature in previous year July has increased. In the eastern region TRW has increased sensitivity to August precipitation and previous year July and August temperature (negative effect), suggesting effect of drought; however lack of a relationship with drought indices and increased sensitivity to July temperature (positive effect) contradict this idea. Tree age also affected of climatic signals of TRW. With increasing age, effect of precipitation increased, likely due to increasing maintenance costs and VLA. Several intermediate strength pointer years were identified and associated with weather extremes for each proxy. Pointer years in VLA (mainly negative) were caused by extreme cold in dormancy period. Negative pointer years in TRW were associated with extremely cold winters, while positive pointer years occurred in years with warm winters and abundant precipitation in summer. During the past 30 years TRW has significantly decreased while VLA in the eastern region has significantly increased, while at the same time loosing sensitivity. These changes might have been an effect of a rapid and severe weather shift in December of 1978 on insufficiently cold hardened trees.

Kopsavilkums

Matisons, R. 2013. Parastā ozola koksnes pieaugums, pavasara koksnes traheju izmērs un to saistība ar klimatiskajiem faktoriem Latvijā.

Klimats ir viens no galvenajiem ekosistēmu struktūru un izplatību noteicošajiem faktoriem. Mainoties klimatam, ir novērojamas izmaiņas ekosistēmu struktūrā un izplatībā, kas rada arī ekonomiskas sekas. Ekosistēmu mainību ir iespējams prognozēt balsoties uz matemātiskiem modeļiem, taču šim nolūkam ir nepieciešama laikā un telpā detalizēta informācija par sugu reakciju uz klimatu un tā mainību. Koki, kas ir meža ekosistēmu dominējošā dzīvības forma, ir labi modeļobjekti to augstā bioindikatīvā potenciāla un ilgā dzīves laika dēļ. Vides faktori koka dzīves laikā ietekmē augšanu, un šī informācija uzkrājas koksnes gadskārtās. Visaugstākā koku jutība uz vides faktoriem ir novērojama sugu areāla robežu tuvumā, kur ir izteikts limitējošs faktors. Latvija atrodas boreo-nemorālo mežu zonā, kur vairākas platlapju sugas, piemēram, ozols, atrodas tuvu areāla ziemeļu robežai, un klimata pasiltināšanās varētu ietekmēt šo sugu izplatību. Centrālajā un rietumu Eiropā ozols ir plaši izmantots dendrohronoloģiskos (klimatoloģiskos) pētījumos relatīvi vieglās šķērsdatēšanas un lielā dzīves ilguma dēļ; tomēr ozola augšanas gaita ir maz pētīta Baltijas valstīs.

Ozola koksnes veidošanās un klimatisko faktoru saistību novērtēšanai Latvijas teritorijā izveidoja 43 parauglaukumus, kuros ozols ir valdošā suga ar vecumu >100 gadi un kuru platība ir >1 ha. Vairumā parauglaukumu izvēlējās ~10 ozolu, no kuriem paņēma divus koksnes paraugus (urbumus). Paraugiem nomērīja gadskārtu platumus (TRW), kā arī pavasara koksnes traheju dobumu laukumu (VLA), kas, balstoties uz jaunākajām publikācijām, parāda spēcīgu vides (klimata) ietekmi. Abiem mērījumiem veica šķērsdatēšanu un kvalitātes pārbaudi. TRW parādīja augstāku sinhronitāti starp koku mērījumu sērijām audzes ietvaros, bet VLA sērijas parādīja augstāku sinhronitāti starp parauglaukumiem. TRW un VLA savstarpēji neuzrādīja būtiskas saistības, kas liecina par atšķirīgu variēšanas cēloni. Ikgadējās koksnes veidošanās variēšanas raksturošanai izveidoja atlikumu hronoloģijas, un, lai raksturotu līdzību starp mērījumiem no apsekotajām audzēm (parauglaukumiem), veica PCA analīzi. Rezultāti parādīja, ka mērījumu ikgadējā variēšana ir sasaistīta ar kontinentalitāti, veidojot austrumu-rietumu gradientu. Balstoties uz šo gradientu Latvijas teritoriju

iedalīja rietumu un austrumu reģionos. Klimatisko faktoru ietekmi uz koksnes veidošanos raksturoja ar Pīrsona korelācijas un atbildes funkcijas analīzi. Klimata ietekmei uz TRW bija vērojamas lokālas iezīmes, jo neviens no faktoriem nebija būtisks visās audzēs reģionā. Taču rietumu reģionā pavasara un vasaras sākuma temperatūrai bija biežāk novērojama būtiska ietekme, austrumu reģionā būtiska ietekme bija vērojama nokrišņiem augustā un iepriekšējā gada jūlija un augusta temperatūrai. Miera perioda temperatūras ietekme uz VLA bija novērota vairumā audžu visā Latvijas teritorijā. Balstoties uz PCA rezultātiem tika izveidotas reģionālās hronoloģijas, kuras uzrādīja ietekmi no līdzīgiem klimatiskajiem faktoriem, kā konstatēts audžu līmenī. Tomēr TRW reģionālās hronoloģijas uzrādīja spēcīgāku iepriekšējā gada jūlija un augusta ietekmi rietumu reģionā. Ozola koksnes veidošanai būtisko klimatisko faktoru kopums 20. gs. laikā ir mainījies. Februāra un marta temperatūras ietekme uz VLA ir samazinājusies, vienlaikus pieaugot decembra temperatūras ietekmei. Līdzīgi, rietumu reģionā februāra un marta temperatūras ietekme uz TRW ir samazinājusies un iepriekšējā gada jūlija temperatūras ietekme ir palielinājusies. Austrumu reģionā ir palielinājusies augusta nokrišņu (pozitīva) un iepriekšējā gada jūlija un augusta temperatūras (negatīva) ietekme, liecinot par sausumu (ūdens deficītu). Tomēr austrumu reģionā netika konstatēta saistība ar sausuma indeksiem, kā arī novērota pozitīvā jūlija temperatūras ietekme. Klimata ietekmes izpausmi ozolos ietekmēja arī koku vecums: vecie koki ir jutīgāki pret nokrišņiem, iespējams, pamatmaiņas un VLA pieauguma dēļ. Abiem mērījumiem novēroti arī vairāki vidējas intensitātes zīmīgie gadi, kuri saistāmi ar klimatiskiem ekstrēmiem. VLA zīmīgie gadi (vairums no tiem negatīvi) ir saistāmi ar spēcīga sala periodiem miera periodā. Negatīvie zīmīgie gadi TRW ir saistīti ar spēcīgu salu ziemas periodā, bet pozitīvie zīmīgie gadi novēroti gados ar siltu ziemu un nokrišņiem bagātu vasaru. Pēdējo 30 gadu laikā TRW ir būtiski samazinājies, VLA būtiski palielinājies austrumu reģionā, abiem mērījumiem vienlaikus zaudējot jutību. Šīs izmaiņas, iespējams, ir izraisījusi straujā laika apstākļu maiņa 1978. gada decembrī, kad koki vēl nebija adaptējušies salam.

Abbreviations

AC – autocorrelation

EPS – Expressed Population Signal

EV – earlywood vessels

GLK – Gleichläufigkeit

IC – interseries correlation

ICs – interseries correlation between mean time-series of sites

LEGMC – Latvian Environment, Geology and Meteorology Centre

NAO – North Atlantic oscillation

p.t.f. – prior to tree-ring formation

PCA – Principal Component Analysis

ScPDSI – self-calibrating Palmer drought severity index

SD – standard deviation

SENS – mean sensitivity

TRW – tree-ring width

VLA – lumen cross-section area of earlywood vessels

List of Figures

sums (lines) for western and eastern regions of Latvia, respectively. Significant correlations are shown by black bars and * (precipitation). Months in uppercase refer to the previous calendar year.

Fig. 12. Response function coefficients between residual chronologies of TRW (A and B) and VLA (C and D) and mean monthly temperature (bars) and monthly precipitation sums (lines) for western and eastern regions of Latvia, respectively. Significant coefficients are shown by black bars and * (precipitation). Months in uppercase refer to the previous calendar year.

Fig. 13. Significant Pearson correlation coefficients between mean monthly temperature and monthly precipitation sums from April of the year previous to tree-ring formation to October of year of growth and residual chronologies of TRW (A western region and B eastern region) and VLA (C western region and D eastern region) for 50-year moving intervals in the period 1900–2009. Dots represent negative correlation. In uppercase – climatic factors in the year prior to tree-ring formation.

Fig. 14. Significant response function coefficients between mean monthly temperature (T) and monthly precipitation sums (P) from April of the year previous to tree-ring formation to October of year of growth and residual chronologies of TRW (A western region and B eastern region) and VLA (C western region and D eastern region) for 50-year moving intervals in the period 1900–2009. Dots represent negative correlation. In uppercase –climatic factors in the year prior to tree-ring formation.

Fig. 15. Pointer year indices of tree-ring width and sampling depths (number of trees) for A- tree-ring width in western Latvia, B- tree-ring width in eastern Latvia, C- VLA in western Latvia, D- VLA in eastern Latvia.

Fig. 16. Residual chronologies and sample depth of TRW for oak with age 90–130 (black line) and 180–210 years (gray lines) for site MOR.

Fig. 17. Significant Pearson correlation and response function coefficients between climatic factors and residual chronologies of TRW of oaks with age 80–130 (A and B) and 180–210 years (C and D) from site MOR. Months in uppercase correspond to previous calendar year.

Fig. 18. Changes in mean TRW (A) and VLA (B) in western and eastern regions of Latvia during 1950 –2010 and their linear trend lines.

List of Tables

Table 1

Mean yearly temperature and precipitation sums for western, central and eastern regions of Latvia. Data is calculated for Liepāja, Rīga and Rēzekne meteorological stations for the period from 1950–2009 (LEGMC).

Table 2

Coordinates, moisture regime, relief, mean age (mean age of five oldest cored oaks), stand composition (cleared or mixed) of sampling plots and number of cored trees.

Table 3

Mean statistics for all measurement time series: range of measurements (10^{-2} mm for TRW and 100 μm^2 for VLA), mean autocorrelation (AC) calculated for trees in a site, mean sensitivity (SENS), mean EPS (calculated for trees in a site); mean interseries correlation (IC, calculated between trees in site; ICs calculated between mean time-series of sites).

Table 4

Comparison of tree-ring proxies. Correlations between TRW, early- and latewood widths and VLA, potential conductivity and EV density.

Table 5

Statistics of PCA analysis of residual chronologies and pointer year index time-series of TRW and VLA.

Table 6

Proportion of sites showing significant correlation between residual chronologies of TRW and VLA and climatic factors in western, central and eastern regions of Latvia.

Table 7

Statistics of data (time-series) pooled within regional chronologies of TRW and VLA for eastern and western regions of Latvia.

Table 8

Significant Pearson correlation coefficients between residual chronologies of TRW and VLA for western and eastern regions of Latvia, respectively. TRW analyzed for periods 1806 – 1900 and 1901 –2002. October –December corresponds to previous calendar year. p-values: *<0.05, **<0.01, ***<0.001.

Table 9

Extreme pointer years (absolute index value ≥ 0.25) of TRW and related climatic (weather) extremes. Numbers in brackets indicate differences from 100-year mean values.

Table 10

Pearson correlation coefficients between pointer year index (TRW and VLA) and climatic factors in western and eastern regions of Latvia. Significant correlations are shown in bold, p-values for correlation coefficients are shown as: * 0.05, ** 0.01, *** 0.001. In addition, randomization test p-values estimate the proportion of iterations in which a greater difference in pairs of correlation coefficients was obtained. A p-value ≤ 0.05 was considered as a significant difference between correlation coefficients of regions.

Table 11

Statistics of measurement series of oaks of different age: mean sensitivity (SENS), autocorrelation (AC), interseries correlation (IC), EPS.

Table 12

Statistics and comparison of TRW and VLA in western and eastern regions of Latvia for 1950–1979 and 1980–2010 (SD–standard deviation, AC–autocorrelation, IC–interseries correlation).

Preface

Climate is one of the main factors limiting ecosystems and distribution of species. During the past 10000 years, climate has changed gradually several times, altering distribution of forests and other biota (Harrison et al., 2006). During the past 100 years, climate changes have been accelerating, causing biological and ecological impact. The effect of climate change (warming) is various, depending on the region. Increase of temperature can have devastating effect in arid regions, especially when combined with drought, while some warming effects can be beneficial in northern latitudes, by extending the growing period and increasing rate of growth of plants (IPCC, 2007). Forest ecosystems are highly valuable biologically due to their high biodiversity among terrestrial ecosystems and their economic importance as a source of timber. As forests occupy more than half of the territory of Latvia, growth of forests has high economical as well as biological importance. At present forests in Latvia are dominated by boreal species: Scots pine, Norway spruce, birch, aspen and black alder. Stands dominated by other tree species occupy a much smaller area. Latvia is situated in the hemiboreal (boreo-nemoral) forest zone where coniferous and broadleaved species can grow together in one stand. Considering changes in climate (warming), changes in growth of tree species might be forecast, as warmer climate may become more beneficial for nemoral broadleaved species. In this respect, forest management should be modified for conservation of biological diversity and economical sustainability in the future.

For determination of effect of climate changes on forest ecosystems, knowledge about tree species growth-climate interactions and their plasticity over time is necessary (Fritts, 2001). As climate exhibits regional or even local variability, fine geographic coverage is necessary. For these reasons, research should be concentrated on species with highest sensitivity (growing in areas with expressed effect of limiting factors). Species at their northern distribution are usually limited by minimal temperatures in the dormant period and length of growing period, and they are most sensitive to climate change (warming) (Kullman, 2008). Pedunculate oak could be considered as one such species in Latvia, as it is a nemoral species situated close to its northern distribution limit. Although at present pedunculate oak in Latvia is not an important commercial species due to its relatively low occurrence, it might become so in the future if temperature and precipitation increase. In Latvia oak stands are important for biodiversity as they are often inhabited by rare species and species richness is rather high. Thus, changes in oak (and other nemoral species) occurrence and growth may need to be considered in sustainable management. Although there have been many studies in Central and Western Europe on growth-climate relationship of pedunculate oak, less is known in the Baltic Countries and there is a lack of such information in Latvia.

Tree response to variability of environmental factors is reflected in tree-rings. In this respect, the use of dendrochronological methods can provide detailed information about growth of living trees and their relationship with the environment. Retrospective information on older periods of time can be obtained from dead wood and archaeological material by applying cross-dating (Speer, 2010). In such studies tree-ring width is a widely used proxy, but it contains information about many factors and the effect of a single factor can be difficult to distinguish. Wood anatomical proxies that provide information about specific factors are becoming useful with the advance of measurement automation.

The aim of this study was to characterize effect of climatic factors on wood formation of pedunculate oak in Latvia. The objectives were:

1) establish a data network on wood formation of oak in Latvia,
2) test use of earlywood vessels lumen area in extraction of climatic signals,
3) compare tree-ring proxies (width of earlywood, latewood and whole ring, earlywood vessel lumen area, density and potential conductivity) and suggest the most appropriate and informative tree-ring proxies for climate analysis,
4) establish site chronologies and assess between-site homogeneity of high frequency variation of wood formation in Latvia, in relation to stand properties and age of individual trees,
5) establish regional chronologies of oak tree-ring proxies,
6) determine climatic factors affecting wood formation in oak (climatic signals) in Latvia,
7) characterize relationship between wood formation and large-scale atmospheric circulation,
8) determine temporal changes in climatic sensitivity of tree-ring proxies,

9) determine effect of climatic conditions on abrupt changes in wood formation (pointer years),
10) characterize changes in wood formation in oak during the past ~30 years (most rapid climate changes) and their relation with climatic factors.

Hypotheses:

A) High frequency variation of wood formation is homogeneous (common) in Latvia due to limitation by similar factors. Wood increment of pedunculate oak growing close to its northern distribution limit is strictly limited by low temperatures in the dormancy period.
B) Change (warming) of climate has significantly increased wood increment.
C) A shift in climatic factors affecting wood increment has occurred during the 20th century due to decreasing sensitivity to temperature and length of growing season.
D) Climatic factors affect wood anatomical features of pedunculate oak and the effect is clearer (compared to ring-widths) due to a shorter period of their formation. In Latvia factors affect wood increment and wood anatomical properties are similar.
E) Climatic extremes have forced abrupt changes in wood formation of pedunculate oak in Latvia. The effect of these extremes on tree-rings and wood anatomical properties extend for several years due to effect of previous growth.

Theses:

I. High frequency variation of wood formation and the contained climatic signals are affected by geographical location and continentality.
II. The main limiting climatic factor for wood formation in Latvia is temperature in the dormant period, spring and summer; effect of precipitation is increasing.
III. Effect of climatic factors on wood formation in oak has changed during the 20th century due to climate change (warming).
IV. Yearly variation of earlywood vessel size (lumen cross-section area) is more strongly related with dormancy period temperature than width of tree-rings in whole Latvia.

1 Literature review

1.1 Dendrochronology

Changes in environmental conditions to a certain extent are reflected in condition of trees, as assimilation and growth can be affected (Schweingruber, 1996; Speer, 2010). Growth of trees is seasonal and growth rings (tree-rings) form in perennial parts: stems branches and roots (Schweingruber, 2007, 1996). It was already observed in ancient Greece by Theophrastus that tree-rings form each year. During the Renaissance, Leonardo da Vinci noticed that tree-rings have different width, which he supposed to be caused by environmental conditions (climate). During the 19th century several authors, such as Carl Linnaeus, Theodor Hartig, Charles Babbage, Jacob Kuechler and Fyodor Shvedov have used tree-rings in their studies (Fritts, 2001; Schweingruber, 1996; Speer, 2010). Tree-ring science or dendrochronology, however, has evolved most rapidly only since the beginning of the 20th century with work of A.E Douglass, who is considered as the father of dendrochronology (Speer, 2010), as he and his students applied cross-dating (Douglass, 1941, 1920). A.E. Douglass, in the study of solar activity, found that trees respond to processes on the Sun via differences in tree-ring width (TRW) (Douglass, 1927; Speer, 2010). Dendrochronology has evolved rapidly and has become a multidisciplinary science with several sub-disciplines dealing with tree-rings. According to field of application and proxies used, sub-disciplines, such as dendroarchaeology, dendroclimatology, dendropyrology etc, are distinguished (Schweingruber, 1996). Different proxies along with width components of tree-ring such as concentrations of chemicals and stable isotopes, density (Helle and Schleser, 2004; McCarroll and Loader, 2004; McClenahen et al., 1989) and anatomical features in different parts of tree-rings have been used for various studies (Fonti et al., 2010; Wimmer, 2002; Zhang, 1997).

Trees are long-lived organisms and information about environmental conditions during the life of a tree is usually recorded in wood (Schweingruber, 2007, 1996). One of the keystones in dendrochronology is sensitivity of growth, which reflects changes of environmental factor in tree-rings (Speer, 2010). High sensitivity can be gained by selection of study sites with expressed limiting factor(s), where trees grow in severe conditions near their distribution limit. Limiting factors usually differ within distribution areas of species and a gradient can be observed (Drobyshev et al., 2008a; Garcia-Gonzalez and Eckstein, 2003; LeBlanc and Terrell, 2011; Lebourgeois et al., 2004; Neuwirth et al., 2007; Ruseckas, 2006). Northern distributions of temperate tree species are usually limited by minimal temperatures in the dormant period and length of growing season; while precipitation in the growing period is usually limiting at southern distributions (Fritts, 2001). Additional information on factors affecting growth can be obtained by analysis of wood anatomical proxies (Campelo et al., 2010; Fonti et al., 2010; Matisons and Dauškane, 2009; Wimmer, 2002).

1.2 Dendroclimatology

Dendroclimatology is a multidisciplinary science; it incorporates climatological studies (climate reconstructions) and ecological aspects (relation between growth and climate, forest dynamics) of tree growth (Fritts, 2001). As climate is one of the main factors determining distribution and growth of tree species (Fritts, 2001; Schweingruber, 1996; Speer, 2010), knowledge about the effect of climate is crucial for understanding of the past and predicting the future tree distribution and growth (Harrison et al., 2006; IPCC, 2007; Iverson and Prasad, 1998; Sykes et al., 1996; Walther et al., 2002). As limiting factors (i.e. climate) for tree-growth differ within the distribution area of a species (LeBlanc and Terrell, 2011), fine geographic resolution of data is needed for accurate estimates and forecasts (Fritts, 2001; McGregor, 1997). Reconstruction of past climate based on tree-ring records is one of the aspects of dendroclimatology (Fritts, 2001); information about past climate can be extended for several millennia by cross-dating (Friedrich et al., 2004; Helama et al., 2005; Mann et al., 2008). For such purposes knowledge about effect of climate on tree-growth and its temporal variability is necessary (Fritts, 2001; Helama et al., 2005; Mann et al., 2008). Use of instrumental data from the closest climate observation station is required to reduce bias (Rodriguez-Puebla et al., 1998; Speer, 2010). Knowledge about climate-growth relationships of living trees can help to better understand effect of climate change on forest ecosystems (Harrison et al., 2006).

Climatic factors vary each year and the exact date of formation for each tree-ring is important (Fritts, 2001; Speer, 2010). Therefore, a representative sample size (usually considered as 20 trees with at least two cores from tree) is necessary for cross-dating and reliable results (Douglass, 1941; Fritts, 2001; Tjarve, 2012). In this respect, ring-porous species are particularly suitable due to easy detection of tree-rings and rather easy cross-dating (few anomalous tree-rings, such as false and missing rings) (Bailie and Pilcher, 1973; Speer, 2010). Thus, even a lower number of trees (~10) in a stand can provide a reasonable chronology (Fonti et al., 2009a; Fritts, 2001; Garcia-Gonzalez and Fonti, 2008). For that reason, ring-porous hardwood species such as beech and oak are widely used in dendroclimatological studies in Western, Central and Southern Europe (Cedro, 2007; Čufar, 2007; Čufar et al., 2008a, 2008b; Eckstein and Pilcher, 1992; Friedrichs et al., 2008; Haneca et al., 2009; Jones, 1959; Kelly et al., 2002; Lebourgeois et al., 2004; Rozas, 2001; Rozas et al., 2009; Thomas et al., 2002; Wazny and Eckstein, 1991) and also in Northern America (Cook, 1992; Douglass, 1920; LeBlanc and Terrell, 2011; Speer et al., 2009; Tardif and Conciatori, 2006). In the Baltic States, where oak is situated close to its distribution limit and where sensitivity to climate should be high, only a few studies have been reported in this field (Karpavicius, 2001; Läänelaid et al., 2008; Ruseckas, 2006).

Variation of climatic factors and subordinately of tree-ring proxy records can be divided in long-term (decadal) and short-term (yearly) variation (Cook et al., 1992a; Esper et al., 2002; Fritts, 2001). Although climatic factors have an important role in determining tree growth (Fritts, 2001), tree age, competition within stand, pest activity etc. can significantly affect low frequency variation of growth (Schweingruber, 1996; Speer, 2010). When short-term (yearly) variation of tree-ring-climate interactions is analyzed, long-term variation must be removed from record series (Cook et al., 1992a). This is usually done by data standardization (detrending) and development of a chronology: a dimensionless time-series representing growth (Speer, 2010), usually with minimized individuality of tree growth (Cook et al., 1992b; Fritts, 2001). Tree-ring records usually show autocorrelation (AC) due to dependence on previous growth, which adds bias to the signal (Fritts, 2001; Speer, 2010). This is usually removed by autoregressive modelling during standardization (Cook and Holmes, 1986). The effect of climate on wood formation (climatic signal) classically is analyzed by correlation or response function analysis between a chronology and climatic data (i.e. monthly and seasonal precipitation and temperatures) (Biondi and Waikul, 2004; Blasing et al., 1984; Fritts and Wu, 1986). Reaction of tree growth to climatic factors can change during a year, i.e. temperature may have an opposite effect in the beginning and end of the growth period (Friedrichs et al., 2008; Garcia-Gonzalez and Eckstein, 2003; Läänelaid et al., 2008; Ruseckas, 2006). Difficulties in such analyses may be caused by several factors. Microclimate conditions of stands, which are rather hard to evaluate, can influence a part of trees in a stand (Lloyd and Fastie, 2002; Pilcher and Gray, 1982) or hinder development of regional chronologies (Cook et al., 1992b; Wigley et al., 1984). Climatic signals also can be affected by coactions of several influencing factors or non-linear response of growth (Friedrichs et al., 2008; Fritts, 2001). For example, effect of summer temperature may be limiting in years when summers are dry (Drobyshev et al., 2008a; Kelly et al., 2002), and winter temperatures may have stronger effect in cases of a thin snow layer (Hardy et al., 2001). Effect of environmental factors on growth also can change with age of tree. For example, seedlings often can tolerate shading, but mature trees require well–lit conditions (Mauriņš and Zvirgzds, 2006).

Rapid changes in wood formation can be caused also by short-term (up to several days or hours) environmental (weather) extremes (Drobyshev et al., 2008a; Neuwirth et al., 2004; Schweingruber et al., 1990). However, the effect of the extreme events may be underestimated if high frequency variation is analyzed, as the expression of extreme events may be decreased during standardization. Specific data processing i.e. pointer year analysis (Neuwirth et al., 2004; Schweingruber, 1992) can be used for determination of effect of climatic extreme events.

1.3 Pedunculate oak (*Quercus robur* L.)

1.3.1 General description

Pedunculate oak (*Quercus robur* L.) is a large (25-35 m in height) deciduous tree of the Fagaceae family (Mauriņš and Zvirgzds, 2006). It is long-lived and can reach age of ~700–800 years under favourable conditions (Drobyshev and Niklasson, 2010; Friedrich et al., 2004). However maximum age of oaks growing in stands is considered to be ~200–350 years (Drobyshev et al., 2008b; Ikauniece et al., 2012). Bud break occurs in May, later than for other deciduous tree species in Latvia. Flowering occurs during bud break. Acorns ripen in September-October. Flowering begins at age of ~55 years in forest stands and acorn production peaks occur every 4–7 years. During the first 10 years after establishment, development of oak is rather slow and it reaches a maximum at age of ~70 years. By the age of 120–200 years, height growth practically stops, but radial increment still may be remarkable (Mauriņš and Zvirgzds, 2006). Oak has rather high requirements for light, while oak seedlings can sustain shading (van Hees, 1997); shading of crowns of adult oaks may cause mortality (Jones, 1959). Oak favours fertile soils, but can grow also on poor soils together with conifers (spruce) and other broadleaved trees (Ikauniece et al., in press; Latvian Forest Service). Wind damage is rarely observed due to a strong root system and wood properties (Mauriņš and Zvirgzds, 2006; Menitskii et al., 2005).

Oak is a valuable commercial species due to its hard and dense wood (Johnson et al., 2009; Mauriņš and Zvirgzds, 2006; Zhang, 1995). The large dimensions of oak make it a good source of timber (Johnson et al., 2009). In Central and Western Europe oak is planted in commercial stands. However, in Latvia oak is not a major commercial species, as oak stands occupy a rather small area (according data from Latvian Forest Service) and establishment of plantations can be problematic (Liepiņš, 2004).

1.3.2 Distribution

Pedunculate oak is a nemoral tree species native to Europe. Its distribution area (Fig. 1) spreads in the West-East direction from the British Isles and northern Portugal to the Ural Mountains. The northern distribution border is southern Finland, southern Sweden and western Norway (coastal belt up to 63^{o} N). The southern distribution limit reaches central Italy, but it is uncertain as pedunculate oak there hybridizes with other oak species (Ellenberg, 1988; Jones, 1959). Distribution of oak is limited by mean temperatures, which range from 13–30 ^{o}C in July and -10– -15 ^{o}C in January (Huntley and Prentice, 1993).

Although situated close to its northern distribution limit, in Latvia oak occurs in most of the territory (Appendix 1); however its abundance usually is low and it occurs mostly as single individuals or small groups of trees (Gailis and Šmaukstelis, 1998; Laiviņš et al., 2009). In Latvia (hemiboreal zone), oak stands are often mixed (Hytteborn et al., 2005; Sjors, 1963), while pure oak stands are quite rare (Ikauniece et al., in press). Oak-dominated stands are scattered (Gailis and Šmaukstelis, 1998) and occupy 0.35% of the total forest area. According to Latvian Forest service data in 2011, mean stand area is ~1 ha, rarely exceeding several hectares. Distribution of oak-dominated stands in Latvia is uneven and decreases in the eastern direction (Fig. 2).

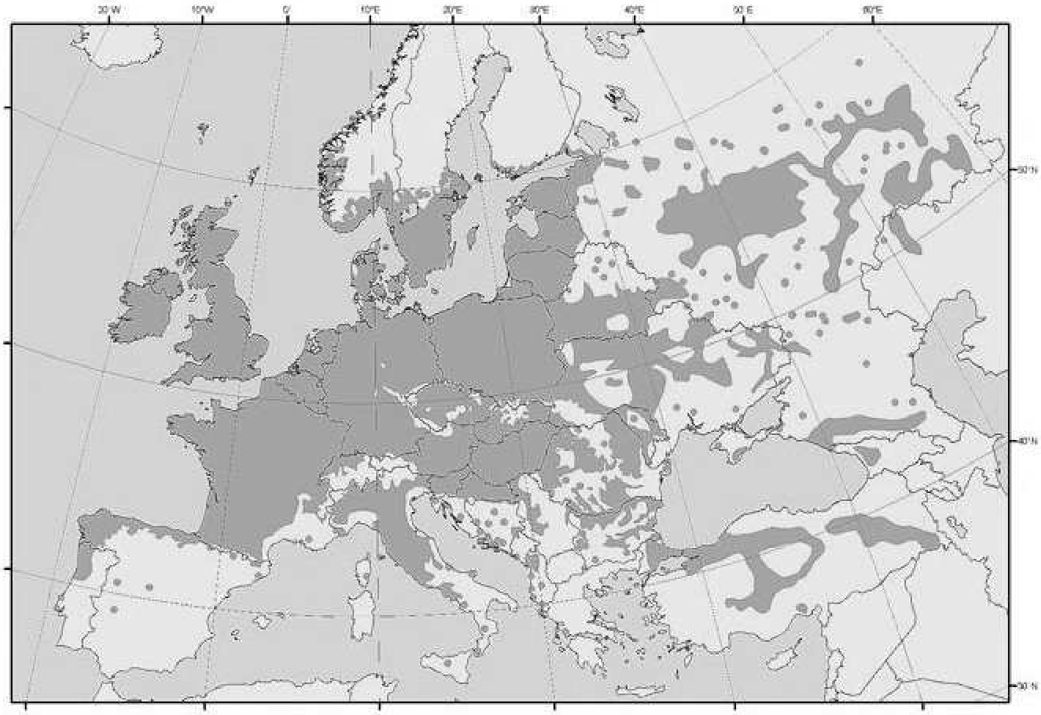

Fig. 1. Distribution area of pedunculate oak (*Quercus robur* L.) in Europe (EUFORGEN, 2009). http://www.euforgen.org/ fileadmin/www.euforgen.org/Documents/Maps/JPG/ Quercus_robur.jpg.

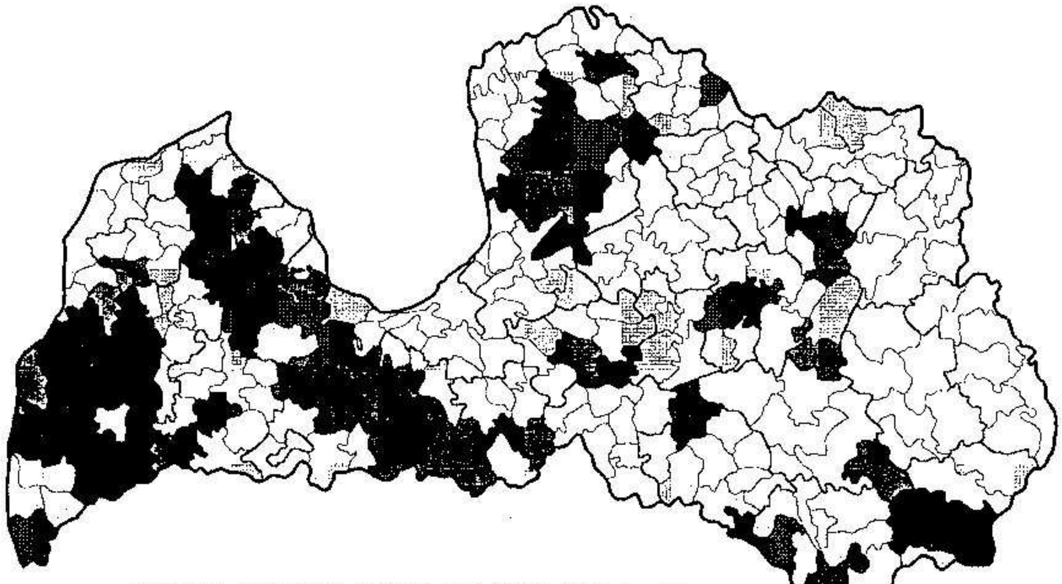

Fig. 2. Distribution of oak dominated stands in Latvia (percentage of total forest area) (Gailis and Šmaukstelis, 1998)).

Since the last glaciation, forest tree species distribution in Europe has changed according to changes in climate (Huntley and Prentice, 1993; Lindbladh and Foster, 2010). Oak has shifted its distribution several times during the past 10 000 years, re-colonizing central and Eastern Europe from Mediterranean regions. During most of the Holocene, the territory of Latvia was covered by mixed forests and broadleaved forests (including oak) were dominant during the Atlantic period around 6000 BP (Ellenberg, 1988; Suško, 1997). Later, with cooling of climate, the abundance of broadleaved trees decreased (Huntley and Prentice, 1993). In this regard, under climate warming, changes in distribution of broadleaves might occur (Harrison et al., 2006; Kullman, 2008; Sykes and Prentice, 1996). However, growth and re-establishment of oak have been problematic (den Ouden et al., 2005; Liepiņš, 2004; Palmer et al., 2004) and in the last 1000 years in Europe oak has been gradually replaced by other species (Harmer et al., 2005; Ikauniece et al., 2012; Lindbladh et al., 2007). Although climate might resist northern spread, in Southern Sweden attempts of restoration of oak forests have been applied (Löf et al., 2006; Okland et al., 2008).

1.4 Wood formation

Wood is a product of secondary growth of trees and is formed during division of cambium cells (Pallardy, 2008; Plomion et al., 2001). Cambium cells form mother cells which radially enlarge and differentiate into wood elements (vessels, tracheids, fibres and parenchyma); vessels, tracheids and fibres form secondary walls (Fukada, 1996; Larson, 2012). Wood formation is directly dependent on assimilated nutrients (carbohydrates) and “success of growth”; increment of wood can be used to characterize growth of trees during a season (Cannel, 1989; Pallardy, 2008). However, nutrient reserves can affect growth in the beginning of the season (particularly earlywood) (Barbaroux and Breda, 2002; Pallardy, 2008).

In the temperate climatic zone growth is strictly seasonal; growing periods shift with dormancy periods (Fritts, 2001; Schweingruber, 1996). The growing (vegetation) period in Latvia is considered to extend from April to October, when mean diurnal temperature is > 5 ^{o}C (Latvian Environment, Geology and Meteorology Centre (LEGMC); Grišule and Briede, 2007), but the period of growth varies between species (Ahas et al., 2000; Grišule and Briede, 2007; Kalvāne et al., 2009). Wood formed during one season is not uniform and at least two parts of a tree-ring can be distinguished (Schweingruber, 2007; Schweingruber et al., 2006). In the beginning of the season, earlywood (wood cells and vessels with large lumen and thin walls) with high water conductivity is formed to ensure water transport to shoots (Schweingruber, 1996). As the growing season advances, latewood, which has mechanic function, is produced (Plomion et al., 2001; Speer, 2010).

Environmental factors (i.e. light, soil characteristics, climate and anthropogenic influence) determine cambial activity, growth and wood increment (Cannel, 1989; Schweingruber, 1996; Wilson, 1984). Availability of nutrients and light generally determine growth (Plomion et al., 2001; Pallardy, 2008), but yearly variation of wood formation is often determined by climate (Fritts, 2001; Schweingruber, 1996). Formation of wood in ring-porous species (including oak) begins before bud break, with initiation of formation of vessels (Michelot et al., 2012; Sass-Klaassen et al., 2011). Although onset of cambial activity is controlled by inherited mechanisms, weather conditions can influence the onset dates (Ahas et al., 2000; Čufar et al., 2008c; Heide, 1993; Sass-Klaassen et al., 2011) and duration of cambial activity (Deslauriers et al., 2008; van der Werf et al., 2007).

Wood formation differs between parts of trees. Although wood with different architecture is formed in above and below ground parts of trees (Carlquist, 2001), wood formation can vary at different heights and sides of stem (Schweingruber, 2007, 1996). These differences may be controlled by various factors, such as physiological regulation, age, microclimate conditions, competition and mechanical impact (Fukada, 1996; Heinrich et al., 2007; Pallardy, 2008; Tyree and Ewers, 1991). For example smaller vessels may be formed in upper parts of stem (Aloni and Zimmermann, 1983; Pallardy, 2008). Wood increment also varies at different heights of stem due to competition within a stand and age (Schweingruber, 1996). In some years no wood can be formed in response to unfavourable conditions (i.e. spring frosts) in a part or in the entire stem (Lorimer et al., 1999; Speer, 2010), but such missing rings are rare for oaks (Speer, 2010). Samples for dendrochronological studies are taken at breast height (~1.3 –1.45 m height depending on height of the researcher/corer) due to lower occurrence of anomalous rings (Parent et al., 2002; Schweingruber, 1996) and convenience of sampling (Chhin and Wang, 2005).

With ageing of wood, in cross-sections of a stem of a mature tree, heartwood and sapwood can be distinguished by wood anatomy, colour and hardiness (Taylor et al., 2002). Heartwood is the oldest part of wood located closer to pith. In oak heartwood is formed when wood fibres are filled with tyloses (Zimmermann, 1979) and a variety of substances, including tannins, oils, gums, resins, and organic salts (Nonier et al., 2005), making heartwood more durable (Taylor et al., 2002). Sapwood is formed by outer tree-rings, which contain living parenchyma cells (Plomion et al., 2001). In oak it is lighter and softer, and is considered to participate in transport (Gartner and Meinzer, 2005) and storage of nutrients (carbohydrates) (Barbaroux and Breda, 2002). Wood water content in oak is higher in heartwood (Pallardy, 2008). The number of tree-rings in sapwood differs between species and is affected by environmental factors and location (Sohar et al., 2011); unhealthy trees (oaks) can have a lower number of tree-rings in sapwood (Pallardy, 2008). In Latvia sapwood is on average formed by the last 12 tree-rings (Sohar et al., 2011).

1.5 Temporal changes in wood formation

Wood formation is not constant; it varies depending on environmental factors, and genetic, physiological properties and age of tree (Plomion et al., 2001; Schweingruber, 1996). Cyclisity of wood formation can often be observed in tree-ring width, in response to Sun, atmospheric and biological cycles (i.e. peaks of seed production) (Douglass, 1927; Koenig and Knops, 1998; Macias et al., 2004; Speer, 2001) and due to effect of previous growth (Barbaroux and Breda, 2002). Increment of biomass of wood generally increases as a tree reaches maturity, after which production of biomass (wood) gradually decreases (Johnson et al., 2009; Wilson, 1984). When trees occur in favourable conditions, TRW usually has an explicit age trend. In the first years after seed germination tree-rings are narrow, followed by rapid growth and large TRW, which gradually decreases when trees have reached maturity (due to larger diameter of stem and decrease of biomass production) (Cook et al., 1992a; Tjarve, 2012). However, if growing conditions improve; wider tree-rings can also be produced in old trees (LaMarche et al., 1984; Robalte et al., 2012; Schweingruber, 1996).

Shot-term (high-frequency) variation usually is a result of annual differences in environmental factors such as climatic factors (Fritts, 2001; Schweingruber, 2007, 1996). The impact of conditions in one year can also extend for up to a few years (Fajvan et al., 2008; Speer, 2010), which varies depending on species, age and condition of tree (Helama et al., 2009; Rozas, 2005; Tardif et al., 2006). Oak is known to show rather high AC particularly in TRW (Barbaroux and Breda, 2002; Drobyshev et al., 2008a; Rozas, 2005).

Intra-annual (within season) wood formation is also variable between years (Deslauriers et al., 2008; Seo et al., 2011; van der Werf et al., 2007). Anatomical features of different parts of a tree-ring have been shown to be specifically related to short-term environmental conditions, which may not be visible in TRW (Fonti et al., 2010; Garcia-Gonzalez and Eckstein, 2003; Wimmer, 2002). Several studies have demonstrated that proxies such as lumen area of earlywood vessels (VLA) show low AC (Fonti and Garcia-Gonzalez, 2008, 2004; Garcia-Gonzalez and Eckstein, 2003; Tardif and Conciatori, 2006), which implies clearer signals. Understanding of intra-annual wood formation can help to better understand relationships between tree growth and the environment (Fonti et al., 2010; Wimmer, 2002).

1.6 Wood structure of oak

Wood of oak (Fig. 3) consists of fibres, vessels, tracheids, wood parenchyma and wood rays (Carlquist, 2001; Gasson, 1987). As oak is a ring-porous species, earlywood in oak is mainly occupied by the largest vessels, which are arranged in rows (rings) (Carlquist, 2001; Gasson, 1987). Width of the earlywood in oak is rather constant exhibiting little variation (Garcia-Gonzalez and Eckstein, 2003; van der Werf et al., 2007; Zhang, 1997), compared to coniferous species (Lebourgeois, 2000; Tuovinen, 2005). In mature oaks growing in optimal conditions, latewood occupies the largest proportion of tree-rings and exhibits rather wide yearly variation, but in cases of suppressed growth latewood may practically by absent (Zhang, 1997). Latewood is dense as it is formed by fibres and vessels with smaller lumen (Rao et al., 1997). Earlywood vessels (EVs) are large (even up to 0.4 mm in diameter) and are easily recognizable; latewood vessels are considerably smaller (Fig. 3; Gasson, 1987; Schweingruber et al., 2006); their total lumen area may be small (in case of extremely narrow tree-ring) (Badel et al., 2006; Rao et al., 1997). Within earlywood, EVs differ in size. The largest vessels are formed first and are located in the first row(s) (Garcia-Gonzalez and Fonti, 2006; Gasson, 1987). A gradual decrease of latewood vessel size can also be observed as the season proceeds (Garcia-Gonzalez and Fonti, 2006). Under some conditions there can be a gradual decrease of vessel size from early- to latewood (Schweingruber et al., 2006). In these cases, the border of early-latewood may not be clear (Garcia-Gonzalez and Fonti, 2006). However external mechanical influence such as stem tilting, burial and flooding alters (decreases) vessel size in the whole tree-ring; larger vessels may even be absent (den Ouden et al., 2007; George et al., 2002; Heinrich et al., 2007; Lei et al., 1996).

Wood of oak is dense and hard with high mechanical strength (Markwardt and Wilson, 1935), which, however, depends on the proportion of latewood (Badel et al., 2006; Rao et al., 1997). Earlywood of oak is fragile due to high proportion of vessels, while latewood is harder (Carlquist, 2001; Rao et al., 1997). Thus, a higher proportion of latewood results in higher mechanical durability.

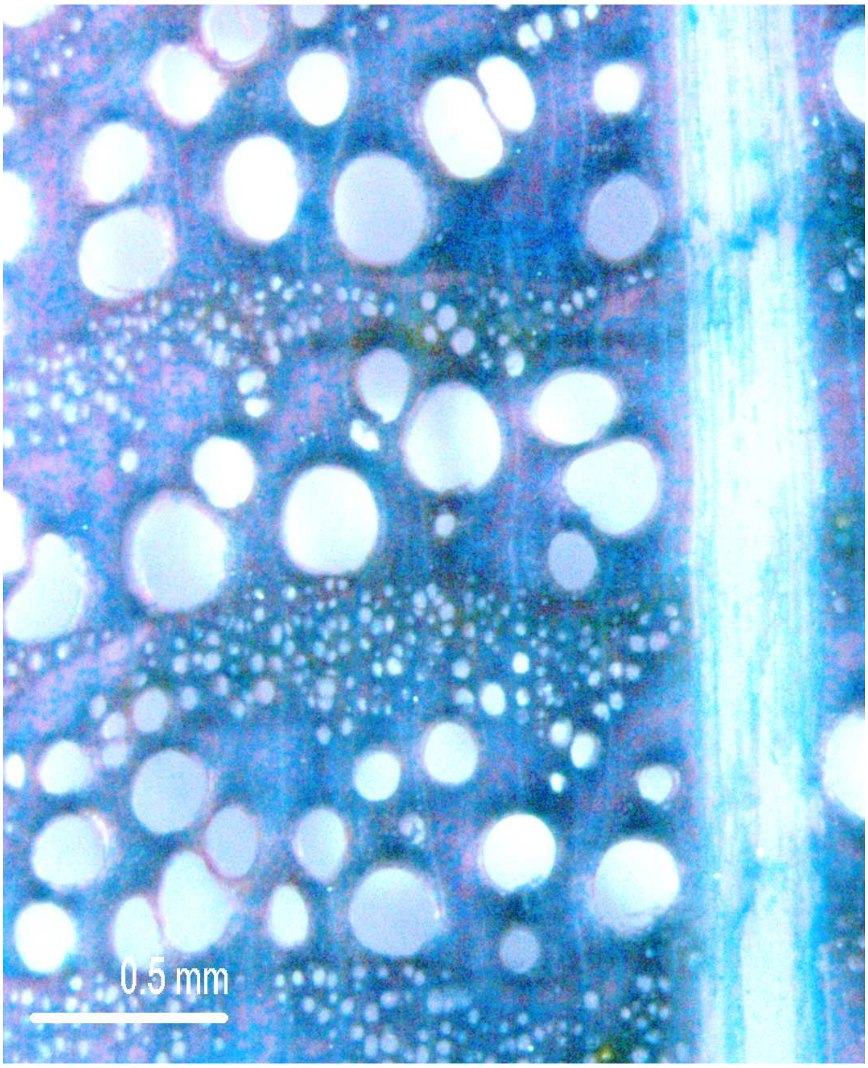

Fig. 3. Cross-section of oak wood. Several tree-rings and a wood ray are shown. Latewood is occupied by large vessels; the smallest vessels are located in latewood. A gradual decrease of vessel size can be observed in the oldest tree-ring.

1.7 Vessels and water transport in wood of oak

Transport of water (sap) is driven by turgour, capillary, osmotic and gravity pressure, which determine the water potential (Pallardy, 2008; Pickard and Melcher, 2005). Water potential is influenced by water availability, temperature of both – soil and air, moisture and rates of respiration and transpiration (Kramer and Boyer, 1995; Pallardy, 2008). Differences in water potential between parts of plant cause movement of sap (water). The highest velocity of sap flow occurs in the stem and the lowest in peripheral parts of a tree: leaves and fine roots (Aloni and Zimmermann, 1983; Pallardy, 2008). Wood architecture determines conductive properties of wood and specifics of water transport (Tyree and Ewers, 1991). In wood of ring-porous species water transport mainly occurs in specialized vessels (Carlquist, 2001; Sperry, 2003). The largest vessels (EVs) are the main water conduits (Granier et al., 1994; Tyree and Ewers, 1991). According to the Pouseuille equation, larger vessels result in higher conductance but capillary forces are weaker (Tyree and Zimmermann, 2002) increasing possibility of embolism: a rupture of the water column and appearance of air bubbles that plug vessels (Cochard and Tyree, 1990; Tyree and Sperry, 1989; Tyree and Zimmermann, 2002). Angiosperm woody plants have evolved a mechanism to protect their tissue from embolism i.e. by formation of tyloses (Zimmermann, 1979), which block vessels preventing further embolization (Cochard and Tyree, 1990; Pickard and Melcher, 2005). Although mechanisms of refilling embolized vessels have been observed in several angiosperm woody plants (Ameglio et al., 2004; Borghetti et al., 1991; Clearwater and Goldstein, 2005; Cochard et al., 2001; Salleo et al., 1996; Sperry et al., 1994, 1987), they have not been reported for pedunculate oak. When embolism (damage) of vessels occurs locally, water transport can be continued using “detour” paths around affected regions (Pallardy, 2008).

Embolism of vessels can occur in both the growing and dormant periods (Sperry et al., 1994; Tyree and Cochard, 1996). During the growing period, embolism occurs when water supply from roots is insufficient (i.e. drought) (Cochard et al., 1992, Tyree and Zimmermann, 2002). Occurrence of embolism also depends on the transpiration rate and air vapour pressure (Jones and Sutherland, 1991; Pallardy, 2008). Embolism in ring-porous species also occurs in winter, when temperature is below zero (Cavender-Bares and Holbrook, 2001; Tyree and Cochard, 1996). Air appears in vessels when water freezes and such embolization is facilitated by thaws, as air cannot be dissolved in ice in the same quantities as in liquid water (Sperry and Sullivan, 1992). In such cases, direct damage to vessels from ice crystals also can occur (Pearce, 2001; Zhu et al., 2000).

EV of oak (ring-porous species) in the temperate climate zone function particularly in the year of their formation (Copini et al., 2010; Umebayashi et al., 2008), as they generally are embolized during winter (Tyree and Cochard, 1996; Tyree and Sperry, 1989; Tyree and Zimmermann, 2002), and become completely blocked later in the season (Cochard and Tyree, 1990; Tyree and Cochard, 1996), thus new EVs are formed each year. To minimize effect of embolism, smaller EV can be produced (Campelo et al., 2010; Tyree and Zimmermann, 2002). Thus, as similar conductance can be gained by different combinations of vessel size and density (Tyree and Zimmermann, 2002), vessel size can be characterized as the balance between sufficient transport and risk of embolism. Vessels in latewood act as a backup transport system, which can also conduct water before new vessels are formed in spring (Copini et al., 2010; Leal et al., 2007; Umebayashi et al., 2008). Although EV size is determined by genetic and physiologic factors (Aloni and Zimmermann, 1983; Mather et al., 1993), environmental factors, such as availability of water, cause yearly variation (Fonti and Garcia-Gonzalez, 2008; Fonti et al., 2010; Wimmer, 2002).

Vessel size can be affected by ageing, however, in contrast to TRW, size of EV usually slightly increases as a tree ages (Fonti et al., 2009b; Tardif and Conciatori, 2006). This trend can be explained by changes of TRW. As a tree ages, TRW and increment of the stem surface decreases (Cook et al., 1992a), and therefore larger vessels need to be produced to maintain the necessary amounts of transport in narrower tree-ring (Ryan and Yoder, 1997; Tyree and Zimmermann, 2002). In cases of narrow tree-rings, there might be less space for more numerous, smaller vessels. This is also supported by a negative correlation between TRW and VLA (Tardif and Conciatori, 2006). Older oaks are more sensitive to drought (Rozas, 2005), which might also be related to increase of EV size.

1.8 Effect of climate on wood formation in oak

1.8.1 Effect of climate on TRW

Climate is one of the main environmental factors determining establishment, growth and mortality of trees (Sykes and Prentice, 1996). Variation of climatic factors usually is the cause of high-frequency variation of TRW in the temperate climate zone (Fritts, 2001; Schweingruber, 1996). As oak is a nemoral tree species, it generally favours a moderate and moist climate (Jones, 1959; Friedrichs et al., 2008; Garcia-Gonzalez and Eckstein, 2003). Oak is sensitive to water deficit (Epron and Dreyer, 1993; Jones, 1959) practically throughout its distribution range (Bronisz et al., 2012; Cedro, 2007; Čufar et al., 2008a; Friedrichs et al., 2008; Garcia-Gonzalez and Eckstein, 2003; Helama et al., 2009; Kelly et al., 2002; Lebourgeois et al., 2004; Rozas, 2005, 2001; Ruseckas, 2006; Satini et al., 1994). The effect of drought (water deficit) is the most expressed in the southern parts of the oak distribution range (i.e. Mediterranean region), where precipitation in summer strictly limits wood increment (Garcia-Gonzalez and Eckstein, 2003; Rozas, 2005, 2001; Satini et al., 1994). In these regions precipitation in summer has a positive effect, while summer temperature has a negative effect, as it intensifies evapotranspiration (Holdridge, 1959; Traykovic, 2005). High temperatures can cause heat stress, which reduces water uptake and assimilation (Haldimann and Feller, 2004; Pallardy, 2008). In regions where summers are mild and water deficit occurs seldomly (particularly in northern parts of the distribution area), spring-summer temperatures generally can have positive effect (Drobyshev et al., 2008a; Fletcher, 1974; Läänelaid et al., 2008; Ruseckas, 2006), through more intense assimilation (Jurik et al., 1988; Pallardy, 2008) and lower risk of late frosts (Avotniece et al., 2010; Scheifinger et al., 2003). Additionally, cool summers in northern and Eastern and Northern Europe are cloudy (Henderson-Seller, 1986), which decreases the amount of available light (Young et al., 2012).

In northern parts of the distribution area of oak, temperature generally has positive effect on TRW (Drobyshev et al., 2008a; Helama et al., 2009; Läänelaid et al., 2008; Repo et al., 2008; Ruseckas, 2006), except in cases when temperature is related with drought (Drobyshev et al., 2008a; Helama et al., 2009). Low temperatures can have effect on TRW (wood formation) in several ways. In spring after the dormancy period, low temperature can interrupt earlywood formation (formation of vessels) (Pearce, 2001; Rossi et al., 2008; Schweingruber et al., 2006), potentially resulting in reduced transport ability of wood later in the growing season (Tyree and Zimmermann, 2002). Cold in late spring (late frosts) (Scheifinger et al., 2003) can damage newly formed leaves, sometimes causing defoliation (Korstian, 1921; Thomas et al., 2002), thus reducing assimilation. Effect of temperature in summer is related with assimilation rates, which can be lower in case of cold summers (Fletcher, 1974; Jurik et al., 1988). Temperature in the end and in the beginning of the dormant period (spring and autumn) usually has positive effect on TRW (Cedro, 2007; Čufar et al., 2008b; Drobyshev et al., 2008a; Fletcher, 1974; Ruseckas, 2006), which is related to length of the vegetation period and assimilated amount (White et al., 1999). In autumn, cold hardening, which is affected by temperature (Morin et al., 2007; Repo et al., 2008), proceeds in oak, when the amount of water in tissues is decreased and concentration of soluble carbohydrates is increased to minimize risk of forming of ice crystals (Alden and Hermann, 1971; Essiamah and Eschrich, 1985). Effect of cold partially depends on success of cold hardening (Alden and Hermann, 1971; Repo et al., 2008). A rapid drop of temperature during cold hardening (especially in the beginning phase) can cause damage, due to incomplete acclimatization for low temperature and cold damage (Repo et al., 2008). Under a mild climate (warm years), cold hardening may proceed until December–January (Morin et al., 2007), when shifts of temperature in Latvia are common (LEGMC; Lizuma et al., 2007).

Extremely low temperatures in winter can damage cambium, resulting in suppressed growth in the next growing season (Alden and Hermann, 1971; Pearce, 2001). Also, severe cold in winter can cause frost shake and frost cracks (Butin and Shigo, 1981; Cinnoti, 1989; Pearce, 2001) in stems, potentially reducing vigour of the tree (Timbal and Aussenac, 1996). Freeze-thaw cycles promote embolization of vessels (Sperry and Sullivan, 1992; Utsumi et al., 1999), potentially decreasing water transport in spring. Temperature shifts in winter during strong thaws may also have a negative effect, as the dormancy period may be interrupted (Heide, 1993; Heide and Prestrud, 2005) and partial depletion of stored carbohydrates may occur (Essiamah and Eschrich, 1985; Ögren et al., 1997; Pilcher and Gray, 1982). In regions of the oak distribution with a mild oceanic climate, December and/or January temperatures can have negative effect, which has been explained by over usage of stored assimilates in response to raised (above zero) temperatures (Helama et al., 2009; Läänelaid et al., 2008; Pilcher and Gray, 1982; Rozas et al., 2009).

Climate in Central and Northern Europe is generally determined by large-scale atmospheric circulations, such as NAO (Trigo et al., 2002), which has a significant relationship with TRW (Bijak, 2009; Cook et al., 1998). However, different effect of climatic factors (climatic signals) on high-frequency variation of TRW can be found even at small geographic distances (Matisons and Dauškane, 2009; Merian et al., 2011; Pilcher and Gray, 1982), suggesting that habitat may influence growth-climate relationships (Fletcher, 1974; Merian et al., 2011; Pilcher and Gray, 1982). Condition of a tree (stand) may also influence sensitivity to climatic factors (i.e. dying oaks in Finland were sensitive to different factors than living ones) (Helama et al., 2009). Common changes in growth (TRW) of oak expressed in larger regions have been assigned to weather extremes (Drobyshev et al., 2008a; Kelly et al., 2002; Neuwirth et al., 2007). In Central Europe and Southern Sweden, negative signature years have been associated with inflow of arctic masses during winter and spring, and a positive effect when warm and moist air masses approached from the Atlantic (Drobyshev et al., 2008a; Kelly et al., 2002). Signature years have also been associated with moisture condition during the growing season, drought has caused negative and abundant moisture in summer caused positive signature years in TRW (Kelly et al., 2002; Neuwirth et al., 2007).

Effect of climatic factors on tree-rings is not constant during life of an oak. A study conducted in Spain showed that with age more climatic factors became significant; TRW in young oaks was less influenced by precipitation and temperature, likely due to higher capability of assimilation (Rozas, 2005). The effect of climatic factors also changes over time (Läänelaid et al., 2008; Merian et al., 2011; Reynolds-Henne et al., 2007; Rozas, 2005). A loss of climatic signals can be observed in tree-rings of trees growing in northern parts of their distribution (Briffa et al., 1998; Jones, 1959), which is called the divergence problem (D'Arrigo et al., 2008; Lloyd and Fastie, 2002). In cases when low temperatures have been the main limiting factor, under climate warming they begin to lose their significance (Briffa et al., 1998). A shift of limiting climatic factors has been also observed in northern parts of the distribution of tree species, where summer precipitation has become more significant or negative effect of temperature has appeared (Lloyd and Fastie, 2002; Wilmking et al., 2004).

1.8.2 Effect of climate on EV

TRW is a popular and widely used proxy when climate-growth interaction is studied, but wood anatomical proxies, such as EV, also contain climatic signals (Garcia-Gonzalez and Eckstein, 2003; Garcia-Gonzalez and Fonti, 2006; Fonti and Garcia-Gonzalez, 2008, 2004; Tardif and Conciatori, 2006; Wimmer, 2002). Previously, EV has not been widely used in dendroclimatological studies due to difficulties in measurement (Fonti et al., 2010; Tardif and Conciatori, 2006). However, with advance of image analysis this proxy is getting wider attention (Fonti et al., 2010, 2009a). Although earlywood width has rather low variation (Garcia-Gonzalez and Eckstein, 2003; van der Werf et al., 2007; Zhang, 1997), range and variation of EV size is higher (Garcia-Gonzalez and Eckstein, 2003; Tardif and Conciatori, 2006), suggesting stronger effect of environmental factors (signals). Size of EV has been shown to contain even stronger climatic signals than TRW (Campelo et al., 2010). EV in pedunculate oak form in a shorter time ~35–40 days (Sass-Klaassen et al., 2011) compared to whole tree-rings and thus information stored in EV is more specific as it is affected by less environmental factors (Campelo et al., 2010; Fonti and Garcia-Gonzalez, 2008; Garcia-Gonzalez and Eckstein, 2003). Although weather conditions during vessel formation show the strongest influence (Campelo et al., 2010; Garcia-Gonzalez and Eckstein, 2003), vessel size also contains information about environmental conditions during the dormant period (Fonti and Garcia-Gonzalez, 2008; Fonti et al., 2007; Tardif and Conciatori, 2006).

Variation of vessel size in relation to climate has been studied for several species (Fonti et al., 2010), but these studies provide fragmentary geographic information for each species. EV size of oaks (*Quercus rubra* and *Q. alba*) growing on their northern limit in Canada showed positive effect of temperature in spring and summer, positive effect of soil moisture during summer and negative effect of summer precipitation of the previous year, and these relationships were quite similar as those found in TRW (Tardif and Conciatori, 2006). EV size in oaks (*Q. ilex, petraea, faginea*) growing close to their southern distribution limit was strongly influenced by climatic factors related with drought (Campelo et al., 2010; Corcuera et al., 2004; Fonti et al., 2009b). In the Swiss Alps, vessel size of *Q. petraea* was affected by April-May precipitation and April temperature (Fonti et al., 2009b; Garcia-Gonzalez and Fonti, 2008). In maritime areas in Spain, EV size in pedunculate oak was limited by moisture in winter–spring (positive response to spring precipitation and negative to temperature) (Garcia-Gonzalez and Eckstein, 2003; Leal et al., 2008). In Germany vessel size was correlated with winter and yearly temperature (positively) and spring precipitation (Eckstein and Frisse, 1982 after Fonti et al., 2010), and in France additionally also with spring precipitation (positively) and yearly maximal temperatures (Huber, 1993). Although there can be cases when EV and TRW both contain similar climatic signals (Campelo et al., 2010; Tardif and Conciatori, 2006), nevertheless EV can provide additional climatological information due to a difference in timing of their formation (den Ouden et al., 2007; Fonti and Garcia-Gonzalez, 2004; George et al., 2002; Matisons and Dauškane, 2009; Wimmer, 2002). Knowledge about vessels-climate relationships can be useful for development of chronologies, for accuracy of reconstructions and can help to better understand response of trees (Fonti et al., 2010; Wimmer, 2002).

1.9 Oak decline and climate

Oak decline has been reported for pedunculate oak in Europe during the 20th century (Brassier et al., 1993; Führer, 1998; Haavik et al., 2011; Helama et al., 2009; Sonesson, 1999; Sonesson and Drobyshev, 2010; Thomas et al., 2002; Wazny et al., 1991), with higher intensity since around 1980 (Sonesson, 1999; Sonesson and Drobyshev, 2010). Declining oaks show several symptoms, such as crown loss and decrease of wood production and vitality, which can result in tree death (Drobyshev et al., 2007a, 2007b; Helama et al., 2009; Wargo et al., 1983). Time between first symptom of decline and tree mortality is variable, depending on location and habitat (Drobyshev et al., 2007b; Helama et al., 2009; Thomas et al., 2002).

On the northern distribution limit of oak in southern Finland, a decrease in TRW for about 20 years and lack of wood formation in the last 3–6 years of life of oaks showing decline has been observed (Helama et al., 2009). The cause of this phenomenon is not completely clear, but is considered to be a result of a complex of environmental factors (Helama et al., 2009; Thomas et al., 2002), such as unfavourable temperature and moisture regimes in combination with pest activity (Führer, 1998; Helama et al., 2009, Thomas et al., 2002; Wargo et al., 1983). In Europe, the *Phytophthora* fungus, which can invade oaks, is considered as one of main causes of oak decline (Blaschke, 2007; Brassier et al., 1993). Change of climate has also been attributed to decline of oak (Brassier, 1996; Siwecki and Ufnalski, 1998), as a warmer climate is more favourable for fungal activity (Coakley et al., 1999; Robin et al., 1994; Zentmeyer et al., 1976) along with increased frequency of drought (climatic extremes) (IPCC, 2007), which can weaken the trees (Epron and Dreyer, 1993; van der Werf et al., 2007). In Fennoscandia, oak was more susceptible to decline on thin soils (low water capacity), where the effect of drought was observed in the growing season (Drobyshev and Sonesson, 2010; Helama et al., 2009). Susceptibility of oaks also increases with age (Sonesson, 1999). The proportion of oaks showing decline in southern Sweden has increased dramatically during the last 30 years, reaching 59% of all oaks damaged in 1999 (Drobyshev and Sonesson, 2010). This decline was related with infection by different fungus and pests, and triggered by unfavourable weather conditions, such as extremely low temperatures and water deficit (Drobyshev and Sonesson, 2010; Sonesson, 1999). However, in south-eastern Sweden improvement of crown condition and vitality of oaks has been observed during the last 10 years (Drobyshev and Sonesson, 2010).

2 Material and Methods

2.1 Study area

2.1.1 Geographic characteristics

The study was carried throughout Latvia, which is situated in the western part of the Eastern European Plain. The land relief was formed during the last glaciation and is dominantly flat with small hills in upland areas (Ramans, 1975). Latvia is a low lying country, with maximal elevation of 312 m a.s.l. in the Vidzeme Upland. The land area above 200 m a.s.l. occupies 2.5 % of the territory. Elevation increases in the West-East direction. Territories with low elevation (<50 m a.s.l.) are situated along the coast of the Baltic Sea and Riga Gulf and in the central part of country south from the southern coast of the Riga Gulf to the border with Lithuania (Jaunputniņš, 1975). Soils are dominantly clayey and sandy. The most fertile soils are found in lowlands of the central part of the country (Āva, 1975). Latvia is situated in the hemiboreal forest zone (Hytteborn et al., 2005; Sjors, 1963), where boreal and nemoral tree species occur together. Approximately 50 % of the land area in Latvia is covered by forests. Pine, spruce and birch are the dominant forest tree species, and the proportion of broadleaved stands is rather low (data from Latvian Forest Service).

2.1.2 Climate

The climate of Latvia is mild oceanic due to dominant western winds that bring warm and moist air masses from the Atlantic and the Baltic Sea (Temņikova, 1975). Variability of climate is partially determined by Atlantic oscillation of air masses (AMO, NAO) (Lockwood and Pfister, 2011). NAO particularly affects weather conditions in Latvia during the dormant period in November–April (Rodwell et al., 1999). However north-south circulations have effect on weather conditions particularly in summer (Draveniece, 2006; Klavins and Rodinov, 2010). According to data from the Latvian Environment, Geology and Meteorology Centre (LEGMC), mean annual temperature is about 5 ^{o}C. The warmest month is July (16.5 ^{o}C) and the coldest is January (-5 ^{o}C). The vegetation period extends from mid-April until mid-October. The continentality of climate increases in the eastern direction with increasing distance from the sea (Fig. 4). Climate in western Latvia is milder with cooler summers (mean temperature in July 16 ^{o}C) and warmer winters (mean January

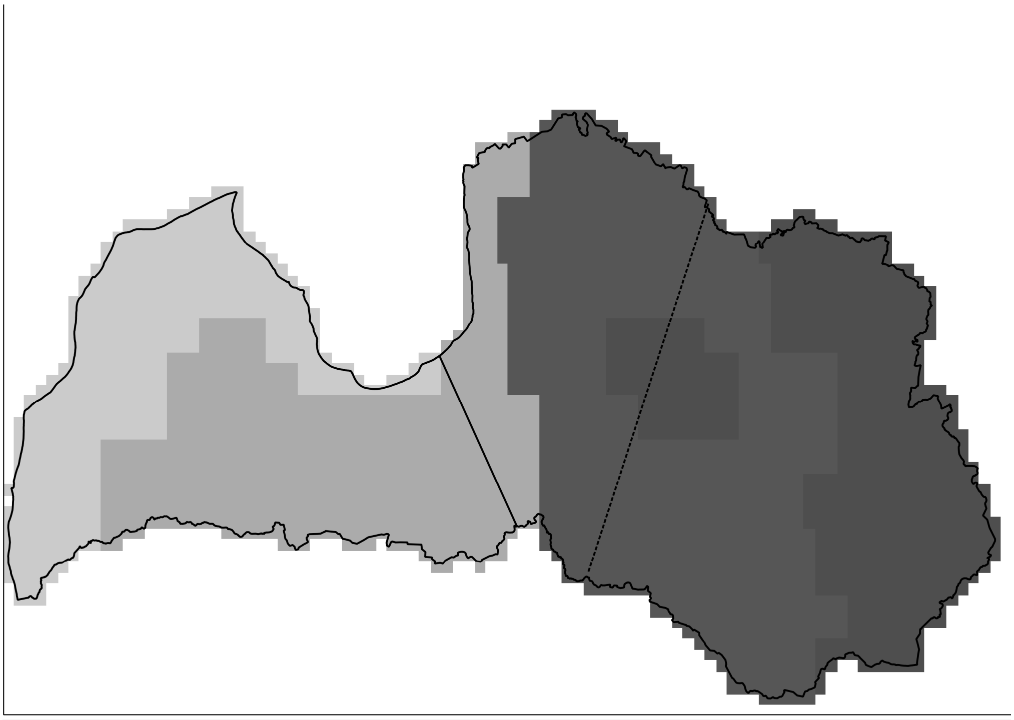

Fig. 4. Increase of extent of continentality of climate (colour intensity) in Latvia. Two sub-regions with low (west of broken line) and high continentality (east of solid line) can be distinguished. Additionally, a transition region can be distinguished between these.

temperature is ~ -3 °C) with frequent thaws. In eastern regions of Latvia the climate is harsher with higher amplitudes of temperatures: summers are warm (mean temperature in July is 17.5 °C) and winters are cold (mean temperature in January is -7 °C), and thaws are less frequent and weaker than in western Latvia. Mean monthly temperatures and precipitation sums for western, central and eastern regions of Latvia are shown in Table 1. The largest difference in temperature between regions occurs in winter, when temperature is about 2.9 °C lower in eastern than in western Latvia. Temperature in summer is lower in western Latvia, by about 0.5 °C compared to central and eastern Latvia. Mean temperature in spring and autumn is similar in all regions. Absolute registered temperature extremes occurred in Daugavpils (Eastern Latvia) in August (36.4 °C) of 1992 and in February (-43.2 °C) of 1956. Years with highest mean temperature (7.65 °C, 7.60 °C and 7.54 °C) occurred in 1989, 2008 and 2000, respectively. The higher yearly temperatures in those years were caused by warm winters. The coldest recorded year (yearly temperature 3.1 °C) occurred in 1941 (coldest recorded winter). Extreme temperature events are related with anticyclone activity: low temperatures in winter are caused by inflow of air masses from the Arctic and in summer by inflow from southern regions (Mediterranean).

Table 1

Mean yearly temperature and precipitation sums for western, central and eastern regions of Latvia. Data is calculated for the Liepāja, Rīga and Rēzekne meteorological stations for the period from 1950–2009 (LEGMC).

	Region		
	Western	Central	Eastern
	Temperature (°C)		
Oct	6.3	6.1	5.3
Nov	2.0	1.1	0.0
Dec	-1.3	-3.0	-4.2
Jan	-3.3	-5.3	-6.5
Feb	-3.6	-5.4	-6.4
Mar	-0.9	-1.7	-2.5
Apr	4.2	4.9	4.6
May	9.3	11.2	11.1
Jun	12.8	15.1	14.9
Jul	15.0	17.3	16.9
Aug	14.4	16.1	15.6
Sep	10.6	11.3	10.6
	Precipitation sum (mm)		
Oct	60.3	65.1	61.0
Nov	52.6	55.4	52.2
Dec	42.3	42.4	43.1
Jan	36.0	35.3	36.7
Feb	27.1	28.1	31.0
Mar	27.6	29.1	31.8
Apr	31.6	36.0	37.8
May	39.5	49.7	56.0
Jun	51.7	65.8	73.6
Jul	67.4	86.1	86.7
Aug	65.9	78.8	80.1
Sep	60.3	68.6	66.3

According to data from LEGMC, mean annual precipitation is about 680 mm. Highest precipitation falls in July and most of the precipitation falls during summer. Distribution of precipitation is spatially heterogeneous (annual precipitation range is 480–850 mm) and determined by dominant winds and relief (Appendix 2). Highest amounts of precipitation fall in west-facing coastal areas and uplands that intercept air masses. Lowest amounts of precipitation fall in the lowland area of central Latvia. Precipitation usually exceeds evapotranspiration, causing excess moisture that forms river runoff and causes paludification of relief depressions (Krams and Ziverts, 1993; Temņikova, 1975).

Global climate changes in northern Europe and in Latvia are particularly reflected by increase of autumn, winter and spring temperatures, particularly in April (IPCC, 2007; Lizuma et al., 2007) and increase of growing period (Ahas et al., 2000; Menzel and Fabian, 1999). Although yearly precipitation has slightly increased in Latvia due to global change, the effect is regional: a decreasing tendency (insignificant decrease) of summer precipitation has been observed during the last 100 years, while distribution of summer precipitation is becoming more variable (Briede and Lizuma, 2007; IPCC, 2007). Along with a rise of temperature extreme cold events are becoming less frequent, while hot days and days with heavy precipitation are getting more frequent (Avotniece et al., 2010). Trends in winter temperature (December – February) and summer (June – August) precipitation at meteorological stations of western (Liepāja), central (Rīga) and eastern (Rēzekne) regions of Latvia for period from 1900–2000 are shown in Fig. 5. Annual and winter temperatures have increased during the whole period and have visibly increased in variability since 1990. Mean temperatures between regions are well correlated (mean Pearson correlation coefficient between meteorological stations is high r=0.98), which implies similar yearly variation. Summer precipitation has slightly decreased during the whole period. Correlation of annual variation of summer precipitation data between eastern and western Latvia is lower (mean Pearson correlation coefficient r=0.54) than for temperature.

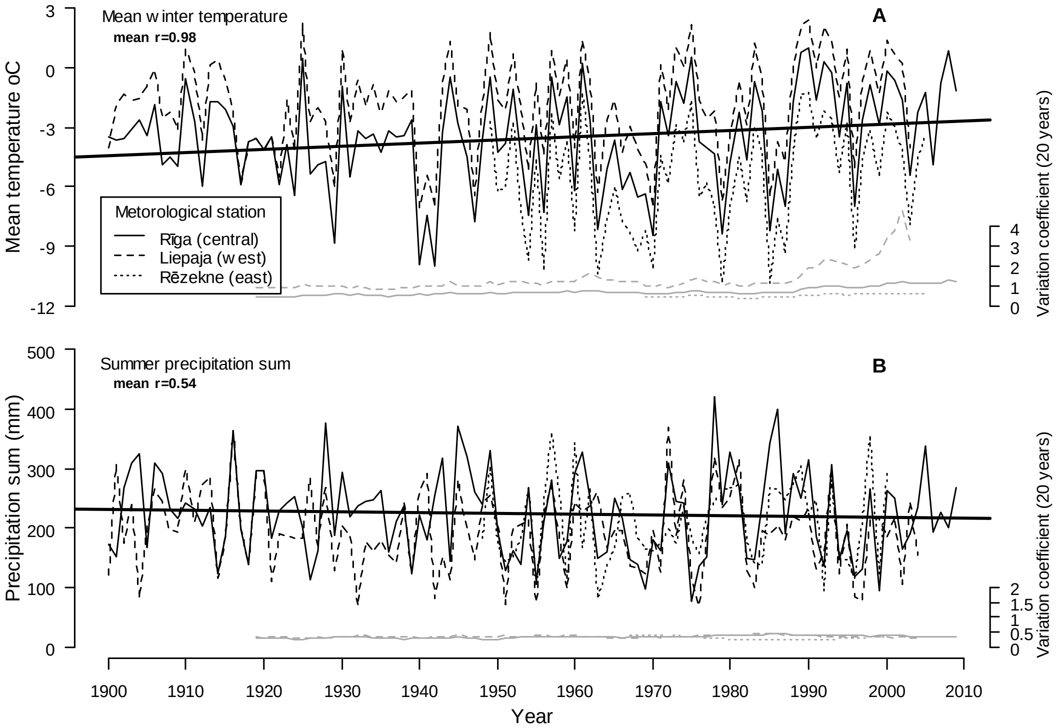

Fig. 5. Mean winter (Dec–Feb) temperature (A) and summer (Jun–Aug) precipitation sums (B) for Liepāja, Rīga and Rēzekne meteorological stations and their variation (coefficients calculated for moving 20-year periods). Data obtained from LEGMC. r- Pearson correlation between stations.

2.2 Study material

2.2.1 Sample collection

Most of the material was collected during 2008–2010. A network of 43 sampling plots across the territory of Latvia was established (Fig. 6). Stands were selected from the Latvian Forest Service forest inventory database based on criteria of oak dominated stands with age > 100 years and area more than 1 ha. Most of the selected stands were located on flat relief and on dry soils (Table 2). More detailed description of sampling sites is given in Table 2. In each site it was planned to obtain cores from 10–14 oaks, but the number of cored oaks was lower in some sites due to lack of suitable trees. Visually healthy, dominant canopy oaks were cored with a Suunto 5 mm Pressler increment corer (Garcia-Gonzalez and Fonti, 2008) from opposite sides of stem at breast height (~1.4 m). Oaks growing on slopes were cored from stem sides that were perpendicular to the slope, to avoid reaction wood (Speer, 2010). Additional increment cores were obtained from other studies related with oak forest ecology (sites DOB1, MOR, RDA and BZN); in these studies only one core per tree was collected, but the number of sampled trees was higher.

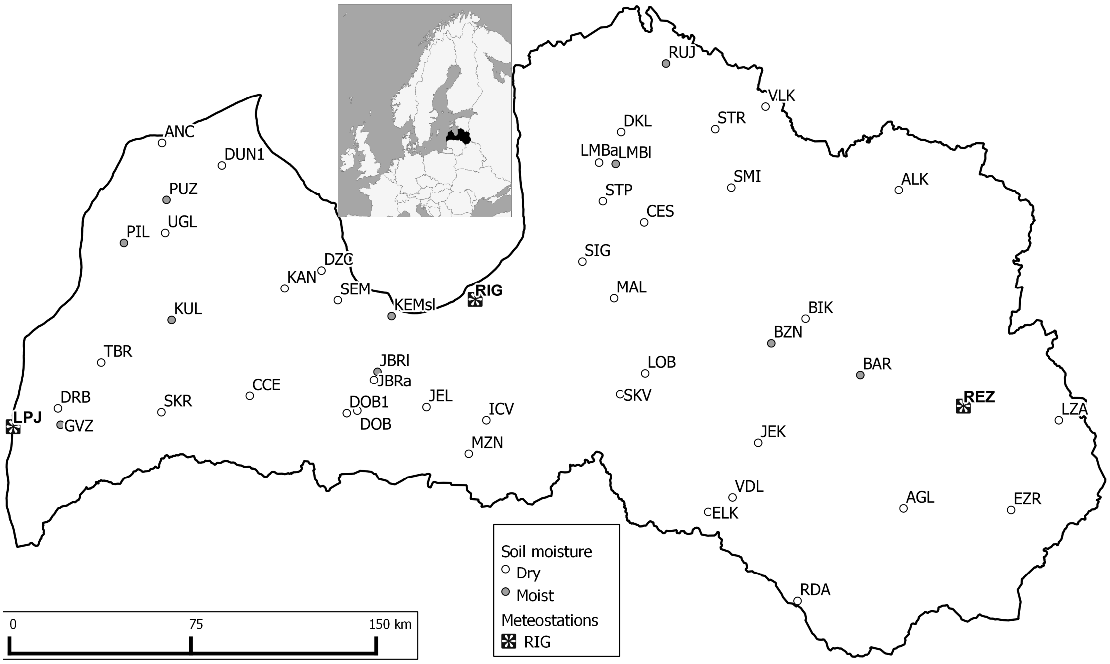

Fig. 6. Location of sampling plots (sampled stands) and used meteorological station and moisture regime of sampled stands.

Table 2

Coordinates, moisture regime, relief, mean age (mean age of five oldest cored oaks), stand composition (cleared or mixed) of sampling plots and number of cored trees.

Code	Coordinates	Habitat moisture	Relief	Mean age	Mixed stands	Number of cored trees
Western Latvia						
ANC	21º56'5E, 57º34'23N	Dry	Flat	215	Yes	10
CCE	22º34'18E, 56º39'1N	Dry	Flat	176	Yes	10
DOB	23º17'24E, 56º36'9N	Dry	Slight slope	184	Yes	10
DOB1	23º13'10E, 56º35'34N	Dry	Slight slope	192	Yes	18
DRB	21º17'42E, 56º35'0N	Dry	Flat	212	Yes	10
DUN	22º20'52E, 57º29'47N	Dry	Flat	157	No	10
DZC	23º2'17E, 57º7'5N	Dry	Flat	227	Yes	10
GVZ	21º19'5E, 56º31'26N	Moist	Flat	230	Yes	10
ICV	24º8'56E, 56º34'9N	Dry	Flat	148	No	10
JBRsa	23º23'57E, 56º43'0N	Dry	Flat	237	No	8
JBRsl	23º25'22E, 56º44'51N	Moist	Flat	176	Yes	7
JEL	23º45'0E, 56º37'4N	Dry	Flat	225	Yes	18
KAN	22º47'27E, 57º3'0N	Dry	Flat	201	Yes	22
KEMsl	23º30'52E, 56º57'9N	Moist	Flat	285	Yes	15
KUL	22º2'6E, 56º55'26N	Dry	Flat	118	Yes	11
MOR	22º9'16E, 57º11'46N	Dry	Flat	219	Yes	37
MZN	24º1'58E, 56º26'47N	Dry	Flat	223	Yes	10
PIL	21º41'53E, 57º12'5N	Dry	Flat	197	Yes	12
SKR	21º59'7E, 56º34'58N	Dry	Slight slope	173	Yes	10
TBR	21º34'23E, 56º45'32N	Dry	Flat	167	Yes	12
UGL	21º58'31E, 57º14'35N	Dry	Flat	223	Yes	14
Eastern Latvia						
AGL	26º54'5E, 56º12'41N	Dry	Flat	206	No	10
ALK	26º57'37E, 57º22'54N	Dry	Slight slope	115	Yes	10
BAR	26º38'59E, 56º42'30N	Moist	Flat	165	Yes	12
BIK	26º17'51E, 56º55'19N	Dry	Flat	160	Yes	10
BZN	26º3'41E, 56º50'11N	Dry	Flat	118	Yes	23
CES	25º13'24E, 57º17'30N	Dry	Slight slope	252	Yes	10
DKL	25º4'35E, 57º37'28N	Dry	Flat	186	Yes	10
ELK	25º36'45E, 56º13'19N	Dry	Flat	118	Yes	11
EZR	27º36'28E, 56º11'15N	Dry	Flat	202	No	10
JEK	25º57'16E, 56º28'17N	Dry	Slope	180	Yes	10
LMBsa	24º55'26E, 57º30'52N	Dry	Flat	184	Yes	10
LMBsl	25º2'11E, 57º30'33N	Moist	Flat	220	Yes	10
LOB	25º12'42E, 56º44'12N	Dry	Flat	193	Yes	16
LZA	27º57'22E, 56º30'23N	Dry	Flat	167	Yes	5
RDA	26º10'57E, 55º53'11N	Dry	Slight slope	180	Yes	14
RUJ	25º23'40E, 57º52'26N	Moist	Flat	114	No	10
SIG	24º48'2E, 57º9'5N	Dry	Slope	219	Yes	12
SKV	25º2'33E, 56º39'38N	Dry	Flat	117	No	10
STP	24º56'45E, 57º22'21N	Dry	Slight slope	180	No	10
STR	25º43'19E, 57º37'44N	Dry	Slight slope	176	Yes	10
VDL	25º46'31E, 56º16'21N	Dry	Flat	173	Yes	10
VLK	26º4'18E, 57º42'21N	Dry	Slight slope	149	Yes	7

2.2.2 Sample preparation and measurements

In the laboratory, as soon as possible after collection, increment cores were glued into fixation planks with water solvent wood glue (PVA) and placed under pressure to dry for at least a week. When dry, samples were sanded with a vibration sanding machine Makita BO 3700 until the widest cross-section (diametric plane) of core was uncovered. To gain a smooth surface of cores, sandpaper of four different roughness grits (120, 240, 320 and 500) was gradually applied. It was ensured that cores were prepared properly and that no scratches had remained on the sanded surface. After sanding, dust was removed by compressed air (~ 4 bars) ensuring removal from vessel lumens. Cores were gently rubbed with white chalk to enhance contrast between earlywood and latewood and to highlight vessels, visually ensuring that chalk remained only in vessels and that the surface of cores was not smeared.

Core images were made with an EPSON GT15000 scanner with resolution 1200 dpi using 24-bit colour depth (Fonti et al., 2009a). Images of each core were kept as separate files. For measurement of VLA core images were cut into earlywood images containing the large vessels in earlywood of the first 2–3 rows of each tree-ring (Fig. 7), which contain the strongest signals (Garcia-Gonzalez and Fonti, 2006). In each core earlywood images were cut from each tree-ring from the year 1899 or up to the oldest ring with five consequent tree-rings that were very narrow and skewed (earlywood image contained less than 10 EV).

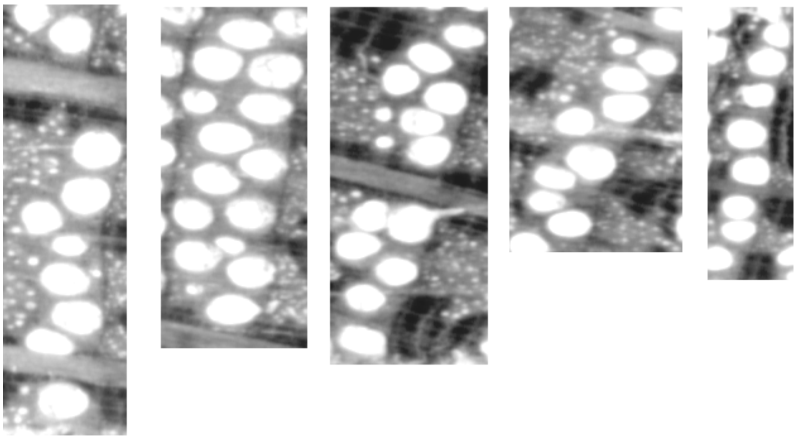

Fig. 7. Samples of prepared (manually cut) earlywood images for measurement of VLA. Samples (cores) rubbed with white chalk.

Tree-ring, earlywood and latewood widths were measured using the program LignoVision v.1.36 (RinnTECH). Tree-ring borders were set manually. Earlywood and latewood borders were detected automatically based on greyscale level with threshold value 50. VLA, area of earlywood images and number of vessels per image were measured with the program WinCELL2007a (Regent Instruments). Gray level pixel classification with threshold values from 185 to 235 was used. A data filter (VLA 6500–120000 μm^2) was applied to exclude any remaining chalk debris and the smallest (in some cases latewood) vessels from the image analysis. Batch function was used for automation of measurements for each core. Quality of material (images) was checked before measuring material from each site. Correct recognition of EV was ensured by visual inspection of measurements of al least 30–40 earlywood images and adjustments in measurement parameters were made if necessary.

2.2.3 Climate data

Climate data was obtained from LEGMC. Data from the Riga meteorological station was used for analysis of growth of oaks and climate as it had the longest record series (continuous records for the period 1880-2000, fragmented records of temperature up to 1795 and precipitation from 1848). Data from Liepāja and Rēzekne were used for description of climatic conditions between western and eastern Latvia. These stations, however, had too short data series for dendroclimatological analysis. Effect of climatic factors on the proxies was considered for climatic data (mean temperature and precipitation sum) from October of the year prior to tree-ring formation (p.t.f.) to September of the current year. Climatic data was also divided into seasons: winter (December–February), spring (March–May), summer (June–August) and autumn (September–November). Data for whole growing season was also used. A list of climate extremes for the 20th century was used for analysis of extreme changes in wood formation. Monthly extremes were characterized as the difference from past 110-year mean values. Data for the monthly self-calibrating Palmer Drought Severity Index (scPDSI) (van der Schrier et al., 2006) and North Atlantic Oscillation (NAO) index (Trigo et al., 2002) were obtained from the Climatic Research Unit for a point closest to the Riga meteorological station for 1901–2002.

2.3 Data Analysis

2.3.1 Cross-dating, quality check and statistics of time series

Cross-dating of time-series of tree-ring proxy (TRW and VLA) measurements at stand and regional levels was done by graphical inspection and statistical evaluation using the program COFECHA (Grissino-Mayer, 2001). Most input parameters in the program COFECHA were set as the program default, but segment length and lags were changed for TRW and VLA to gain maximal precision. For TRW, 40 year periods with lag 10 years and for VLA 55 year periods with lag 5 years were used. Characteristics of time series were described by first order AC coefficients (AC), interseries correlations (IC), mean sensitivity (SENS) (Speer, 2010), calculated in COFECHA (Grissino-Mayer, 2001) and expressed population signal (EPS) (Wigley et al., 1984), calculated based on standardized (detrended) measurement series in program R v .2.10.1 using library dplR (Bunn, 2008).

2.3.2 Comparison of tree-ring proxies

For three sites (KUL, SIG and AGL), which were located in western, central and eastern Latvia, respectively (Fig. 6), several tree-ring proxies (TRW, latewood, earlywood width, VLA, vessel density and potential conductivity) were compared using Pearson correlation analysis (Sokal and Rohlf, 1995). Vessel density was calculated for each earlywood image by dividing the number of measured vessels with the area of the earlywood image and expressed as number of EV per mm^2. Potential conductivity was calculated according to the Pouseuille equation (Tyree and Zimmermann, 2002) for each earlywood image as $F = \frac{\sum r^4}{S}$, where r – vessel radius, S – area of earlywood image. Proxy data from each site were cross-dated and their quality was checked using COFECFA (Grissino-Mayer, 2001).

2.3.3 Detrending and standardization of time-series

For the analysis of yearly variation of wood formation and climate, residual chronologies of TRW and VLA were established for sites and regions with the program ARSTAN (Cook and Holmes, 1986). Double detrending using a negative exponential curve method with wavelength 128 years and 50% cut-off and autoregressive modelling was used (ARSTAN defaults).

Pointer year indices were calculated according to Neuwirth et al. (2004) for TRW and VLA time-series for sampling sites and for regions. The calculation was based on a modified skeleton plot method. Relative differences $\Delta i = (x_i - \overline{x}_{i-5..i-1}) / \overline{x}_{i-5..i-1}$ in TRW or VLA (x) were calculated for each year (i), with respect to the mean of the previous 5-year period. The relative differences were expressed as scores, ranging from -5 to 5 (except 0) in 20% steps. A score of -5 corresponded to a relative difference of <-80%, and a score of 5 to a value of > 80%. A pointer year index for a group of trees was calculated as $I = \frac{100}{kn}\sum_{j=1}^{k} h_j s_j$, where k = 10 (number of possible score values, n– number of trees included in the calculation, h– number of trees with each score, s– frequency of score). Pointer years with an absolute index value exceeding 0.25 were considered as a result of extremes affecting a large number of tress.

2.3.4 Effect of site characteristics on wood formation

Principal component analysis (PCA) was used to assess similarity of wood formation between sites (stands) and to test which site characteristics (geographic location, moisture, fertility, tree species composition, stand (mean) age and steepness of slope) had effect on wood formation. The PCA used sites as samples and the variables were years. Standardized time-series of proxies (residual chronologies and pointer year index values) for sites served as input data. The analysis was conducted using PC-ORD v.5.0 (McCune and Mefford, 1999). A randomization (Monte-Carlo) test (999 iterations) was used to assess significance of principal components. Correlation (Pearson) of PCA components with site characteristics was determined. Grouping of sites by region for development of regional chronologies was based on the PCA results.

2.3.5 Effect of climatic factors on wood formation

Data from 40 sites (Appendix 3) were used to determine effect of climatic factors (mean monthly temperatures and precipitation sums) on yearly variation of TRW and VLA represented in residual chronologies of sites. Pearson correlation coefficients were calculated for climatic factors with TRW and VLA using the program DendroClim2002 (Biondi and Waikul, 2004) for each site. Data for period 1899–2010 was used. Significance of correlations was tested with a bootstrap method. For each group of sites distinguished by PCA, the proportion of sites (stands) showing significant correlations to each climatic factor was calculated.

2.3.6 Regional chronologies and analysis of temporal changes in climatic signals

Data from 40 sites (Appendix 4) showed good agreement between measurement time-series and were used for construction of regional chronologies and assessment of temporal changes in climatic signals of TRW and VLA. Relations between wood formation and site characteristics were assessed by PCA using residual chronologies of sites. Two groups (regions) of sampling plots were established based on the PCA division. For each group (region) a residual chronology was established based on time-series of all cross-dated trees within the region. Correlations of regional chronologies with climatic factors (mean monthly temperatures and precipitation sums for April p.t.f. to September of year of tree-ring formation) for the whole period and by mowing intervals of 50 years were determined. Also, the effect of scPDSI was tested. Significance of Pearson correlation and response function coefficients was assessed by bootstrap method using DendroClim2002 (Biondi and Waikul, 2004).

2.3.7 Influence of NAO on wood formation

The effect of NAO on wood formation was assessed by Pearson correlation analysis (Sokal and Rohlf, 1995). Regional residual chronologies (produced by pooling time series of trees within regions according to results of PCA) of TRW for periods of 1806–1900 and 1901–2000 and of VLA for the period of 1900–2000 were tested for significant correlation with NAO indices for months (October of year p.t.f– September of current year) and seasons (winter, spring, summer, autumn and entire growing season). Significance of correlation coefficients was determined by Student criteria (Sokal and Rohlf, 1995).

2.3.8 Relationship of pointer years and climate and weather extremes

Data from 40 sites (Appendix 4) was used to determine pointer years and to assess their relation with climatic factors. As the analysis focuses on abrupt changes in wood formation, after cross-dating it was additionally ensured (graphical inspection) that signature years matched. Also, sites where chosen to contain a similar sampling depth during the period 1908–2008 (≥7 trees). For each site pointer year index series were calculated for TRW and VLA. PCA was performed based on site index series to assess differences among sites and to test if site characteristics had effect. For each group of sites (distinguished by PCA) regional pointer years were calculated based on all cross-dated trees within the group. Influence of climatic factors (mean temperatures and precipitation sums for months, seasons and years) on extreme changes in wood formation (pointer years) was evaluated by Pearson correlation analysis using DendroClim2002 (Biondi and Waikul, 2004). To test for significant differences in correlation coefficients between groups of plots for a climatic factor, a randomization test was conducted using the program R v.2.13.1 (R Development Core Team, 2009). Pointer year indexes and their correlation with each climatic factor were calculated for groups containing randomly selected plots, repeated 999 times. Group sizes were maintained as in the original classification (division). Differences in correlation coefficients obtained between groups identified by the PCA analysis were considered to be significant if larger differences in correlations between groups containing randomly selected plots were obtained in ≤5% of randomized iterations. Relation of climate (weather) extremes to the expressed pointer years (absolute index value ≥0.25) was assessed.

2.3.9 Age dependent climatic signals in TRW

The analysis was performed using material collected in site MOR (western Latvia), for which data from oaks with different age (only TRW) was available. Cross-dated data were divided into two groups according to age of oaks; one group represented oaks with age from 90–130 (data from 12 oaks) and 180–210 years (data from 13 oaks). For each group residual chronologies were produced. Climatic signals were assessed by Pearson correlation and response function analysis for the period from 1900–2007. Significance of relationships was determined by bootstrap method using DendroClim2002 (Biondi and Waikul, 2004). Effect of mean monthly temperature and precipitation sums from April of the year p.t.f. to September of current year was tested.

2.3.10 Changes in wood formation during the past 30 years

To test for differences in wood formation in recent decades, mean regional time-series of TRW and VLA were calculated from mean time-series of sites within western and eastern regions of Latvia, distinguished according to results of PCA. Mean TRW and VLA was compared between periods of 1950–1980 and 1981–2009 using a t-test in program R v.2.13.1 (R Development Core Team, 2009). Trends were compared using ANCOVA (Sokal and Rohlf, 1995). Sensitivity of regional time series for these periods was also calculated in program R v.2.13.1 using the package “dplR” and function “sens2”, which calculates sensitivity in time series with a trend (Bunn, 2008).

3 Results

3.1 Measurements and cross-dating

In total data from 43 sites (stands) were used. About 130000 tree-rings from 490 trees were measured. For ~95000 tree-rings from 460 trees, core images representing earlywood were prepared, measured and checked. Cross-dating was successful, as only ~10% of measured series for TRW and ~15% for VLA were excluded during quality checking. Statistics of site time-series are shown in Table 3, Appendix 5. Both TRW and VLA showed rather high mean sensitivity. Autocorrelation was lower for VLA. EPS values calculated for trees in sites were above 0.85 (mean between all sites 0.88) in most sites for TRW, but for VLA in about half of the sites EPS was below 0.85. Interseries correlation (IC) calculated between trees in a site was also lower for VLA than for TRW, but interseries correlation (ICs) between mean site time-series was higher for VLA, indicating that high frequency variation of VLA is similar in the studied sites, despite lover agreement (EPS and IC) between trees in a site. VLA time series also showed higher GLK (Gleichläufigkeit, synchrony) compared to TRW, indicating that VLA time-series of sites are more synchronous between sites. Mean site time-series of TRW and VLA are shown in Fig. 8. TRW records extend from 1697–2010. However replication for the 130 years up to 1827 was rather low. Vessel measurements are time-consuming, and considering the time limits imposed, VLA was measured for the period from 1899–2010. As VLA was measured for the last 110 years, replication is high in whole analyzed period. However, it is lower than for TRW, as more measurement series were excluded during quality checking. Amplitude of TRW among studied sites increased during most of the analyzed period, but a decrease in TRW and its range is visible since the late 1980s. VLA showed a slight increase during the whole period. However the spread between sites in VLA occurred at approximately the same time when TRW showed decrease of amplitude. Common signatures are visible in time-series of both TRW and VLA, but they are only partly synchronous between proxies. Common signatures (strong decreases or increases) are visible in several years (i.e. 1827, 1881, 1940 and 1977) for TRW and VLA time-series (i.e. 1928, 1940, 1956 and 1979).

Table 3

Mean statistics for all measurement time series: range of measurements (10^{-2} mm for TRW and 100 µm^2 for VLA), mean autocorrelation (AC) calculated for trees in a site, mean sensitivity (SENS), mean EPS (calculated for trees in a site), mean interseries correlation (IC, calculated between trees in site; ICs calculated between mean time-series of sites) and mean GLK indices.

	Min	Max	Mean	AC	SENS	EPS	IC	ICs	GLK
TRW whole period	58	472	254	0.77	0.22	0.87	0.6	0.49	0.61
TRW 1899–2010	65	404	220	0.72	0.21	0.88	0.62	0.54	0.62
VLA whole period	132	512	323	0.49	0.2	0.78	0.35	0.65	0.63

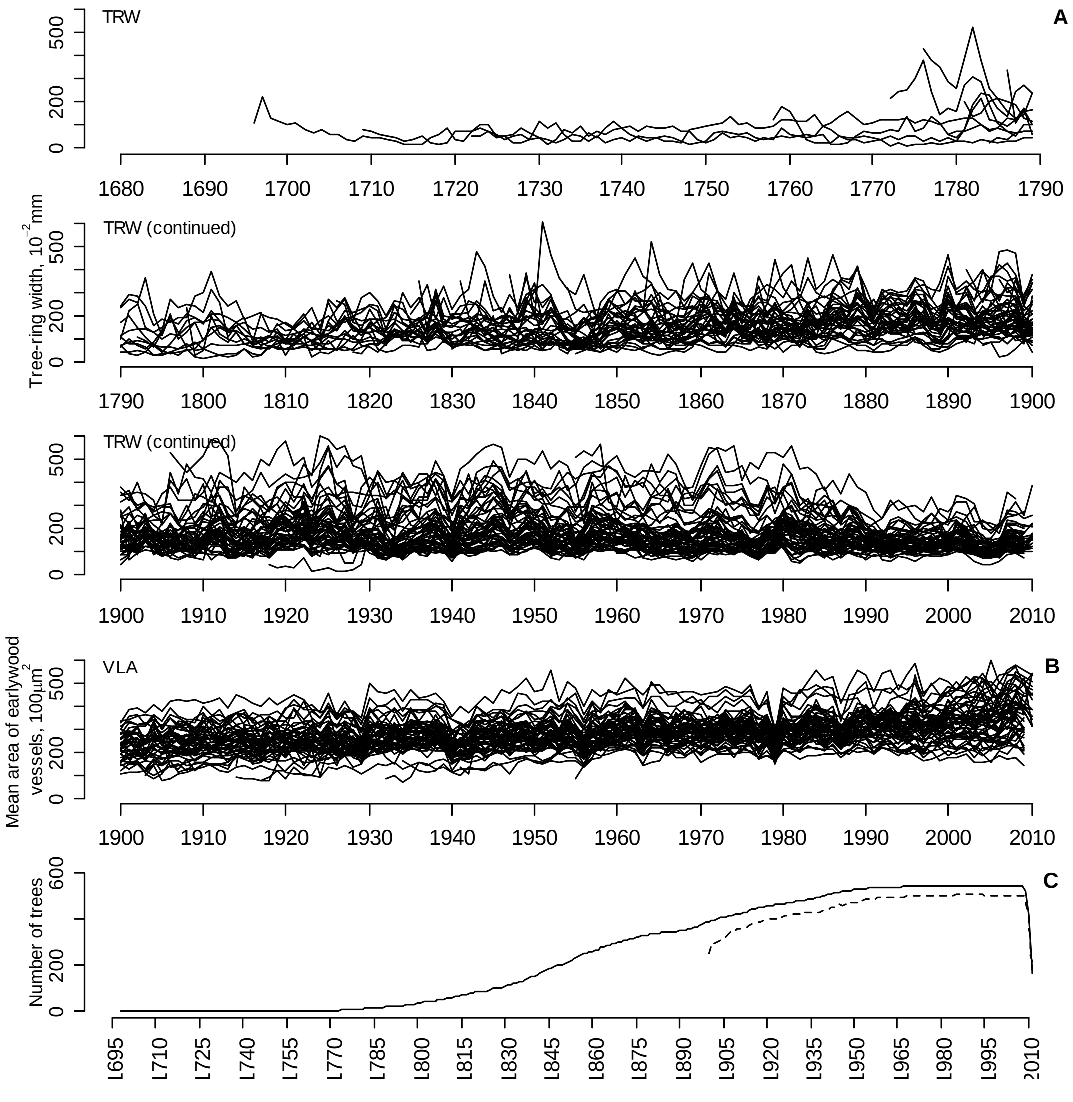

Fig. 8. Mean site time-series of TRW (A) and VLA (B) measurements and their sample depth (replication, number of trees, TRW – solid line, VLA – broken line) (C).

3.2 Comparison of wood proxies

Significant Pearson correlation coefficients were found between three TRW proxies (trees-ring, earlywood and latewood width) and between EV proxies (VLA, potential conductivity and vessel density) in three sites (Table 4). Correlation coefficients (r) ranged from 0.11 to 0.96. TRW was significantly correlated with earlywood and latewood width in all tested sites. TRW and latewood width correlated tightly (r= 0.94–0.96), thus showing similar variation. Earlywood and latewood width showed the weakest correlation (r=0.24–0.36). Correlations between vessel proxies generally differed between the tested sites. VLA was significantly correlated with potential conductivity in all tested sites and the correlation was stronger in the site in the eastern region of Latvia (AGL) than in western site (KUL). There was a significant correlation between vessel density and potential conductivity only in the site in the western region of Latvia (KUL), while vessel density and VLA were significantly correlated in sites from central and eastern regions of Latvia (SIG and AGL). There was no significant correlation between earlywood width and vessel parameters (correlation coefficients were low, r ≤ 0.05).

Table 4

Comparison of tree-ring proxies. Correlations between TRW, early- and latewood widths and VLA, potential conductivity and EV density.

AGL			SIG			KUL		
	Early wood width	Late wood width		Early wood width	Late wood width		Early wood width	Late wood width
TRW	0.64*	0.95*	TRW	0.60*	0.96*	TRW	0.58*	0.94*
Earlywood width		0.36*	Earlywood width		0.35*	Earlywood width		0.26*
	Vessel density	VLA		Vessel density	VLA		Vessel density	VLA
Potential conductivity	-0.11	0.79*	Potential conductivity	-0.17	0.75*	Potential conductivity	0.35*	0.45*
Vessel density		-0.54*	Vessel density		-0.45*	Vessel density		-0.10

3.3 Effect of site characteristics on oak wood formation in Latvia

A PCA was performed to identify common trends of wood formation between the studied sites using site residual chronologies and pointer year indices of TRW and VLA. The PCA was conducted using data from 40 sites showing good agreement between trees. Residual chronologies and pointer year indices of TRW and VLA showed similar patterns (Fig. 9). A continuous gradient with no obvious grouping was evident, with some outlier plots, mainly from the eastern region of Latvia (i.e. BAR, AGL and ALK). In all cases PCA component I (ordination axis I) was significant (Table 5), but the explained variation was rather low (8.7–13.8 %) (Økland, 1999). Among the site properties, longitude coordinate of sampling plot (representing distance from the Baltic Sea) was significantly correlated with PCA axis 1, indicating that high frequency variation of wood formation (both TRW and VLA) in oak differed along a West-East gradient. High frequency variation of TRW showed stronger correlation with longitude coordinate than VLA. The amount of variation in pointer year indices explained by PCA component 1 was slightly higher than for residual chronologies. PCA scores overlain on their geographic locations (Appendix

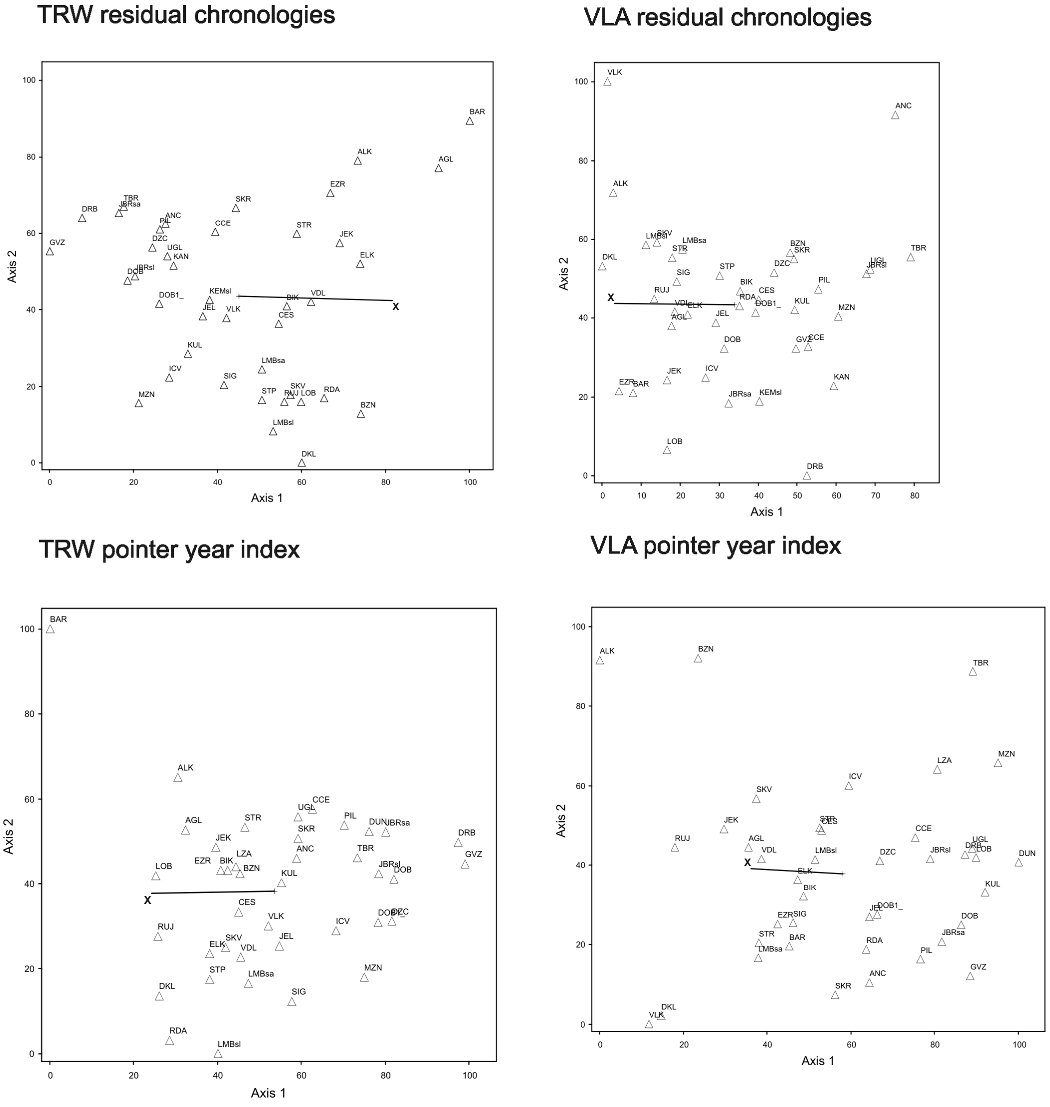

Fig. 9. PCA ordination biplots of site residual chronology and pointer year index time-series. Axis I was significant in all cases, X – projected latitude coordinate (LKS92 TM) of sapling plots.

6) showed that sampling plot scores had a rather expressed gradient in the West-East direction, confirmed by significant correlation with longitude (Table 5). The geographic gradient of PCA scores was clearer for TRW, which showed positive scores in the western region of Latvia and negative scores in the eastern region (when residual chronologies were used). Although VLA also showed a geographic gradient, it was slightly less expressed. Nevertheless, two regions of Latvia (western and eastern) based on PCA scores for pointer years could easily be arbitrarily distinguished (Appendix 6, solid line). Based on the PCA of residual chronologies, an additional central region of Latvia with intermediate PCA scores (Appendix 6, between solid and broken lines), could be distinguished.

Table 5

Statistics of PCA analysis of residual chronologies and pointer year index time-series of TRW and VLA. X – longitude coordinate of sampling sites.

	TRW residual	VLA residual	TRW pointer years	VLA pointer years
Significance of axis, p-value	0.001	0.001	0.001	0.001
Explained variation (%) by axis 1	12.1	8.7	13.8	10.2
Pearson correlation coefficients between axis 1 scores and site properties	X (r=0.86)	X (r=0.78)	X (r=0.76)	X (r=0.66)

3.4 Effect of climatic factors on wood formation

3.4.1 Effect of climatic factors on wood formation at site level

Local chronologies from 40 sites (19 sites in the western region, 11 in the central and 10 in the eastern region (Appendix 6), distinguished by solid and dashed lines) showed different climatic factors and proportions of stands with significant correlations (Table 6) to climatic factors. The proportions of stands showing significant correlation with a specific climatic factor were overall lower for TRW (only several factors showed significant correlations in more than 30% of sites) than for VLA (up to 80% and 100% for TRW and VLA, respectively). TRW showed more frequent correlations to climatic factors during summer (except in the eastern region), while VLA was significantly correlated with temperature in the dormant period and spring in all regions. Significant correlations with spring and summer temperatures were more frequent in the western region, while correlations with July, August and October temperature of the year prior to tree-ring formation (p.t.f.) and August precipitation were more common in the eastern region. Proportions of stands showing significant correlations between VLA and climatic factors were higher in the eastern region. Weather conditions in the period from May in the year p.t.f. until September of year of tree-ring formation had the highest proportions of significant correlation with VLA. Temperature showed more frequent correlations among sites than precipitation sums.

There were no single climatic factors significantly correlated with TRW in all sites within a region (Table 6). However, several climatic factors were significant in more than 30% of sites within a region. In the western region of Latvia, March and June temperatures showed highest occurrence of positive significant correlations, while July temperature of year p.t.f. showed the most frequent negative correlations. Precipitation was significant in several sites and overall had low effect (November of year p.t.f. precipitation was significant in 26% of sites). In the eastern region October of year p.t.f. temperature showed positive significant correlation in 30% of the studied sites and July and August of year p.t.f. had negative effect in half of the sites. August precipitation in the eastern region showed the most frequent significant effect (80% of sites) among climatic factors affecting formation of TRW. A negative effect of February of year p.t.f. was observed in 50% of sites. A gradual shift of climatic factors and proportion of sites showing significant correlations was apparent in the west to east direction. Significant climatic factors shifted from summer month temperatures in the western region to autumn temperatures and August precipitation in the eastern region. In the central region of Latvia, significant climatic factors and proportions of sites showing significant correlations were intermediate between western and eastern regions. However, there was a stronger negative effect of July of year p.t.f. temperature in the central region.

Temperature in the dormant period (December–March) and in April was significantly (positively) correlated with VLA in a high proportion of sites in all three regions, increasing in proportion in the eastern direction (Table 6). Of these months, temperature in January and April temperature showed the most frequent correlation (74% and 84% of sites, respectively, in the western region and 100% of sites in the eastern region). Also, in most sites the highest coefficient values (ranging r= 0.40–0.54, not shown) were observed for these factors. Temperatures in June and September of year p.t.f. showed frequent significant correlations (positive). Precipitation had minimal effect on VLA compared to temperature. Only several precipitation factors in the eastern region were significantly correlated with VLA in ≥30% of sites (precipitation in January and June in year of tree-ring formation and January in year p.t.f.). Nevertheless precipitation of January of the year p.t.f. was significantly correlated with VLA in 70% of sites.

Table 6

Proportion of sites showing significant correlation between residual chronologies of TRW and VLA and climatic factors in western, central and eastern regions of Latvia.

	Tree-ring width residual chronology						VLA residual chronology					
	Region						Region					
	Western		Central		Eastern		Western		Central		Eastern	
	+	-	+	-	+	-	+	-	+	-	+	-
Current growing season												
Temperature												
Oct	11		45		30		21				30	
Nov							5					
Dec							79		64		90	
Jan							74		100		100	
Feb	5		9				68		91		100	
Mar	37		18		10		32		18		50	
Apr						10	84		100		100	
May	21						16					
Jun	42		27				5			27		20
Jul	16		27		10				18			
Aug	21						5					
Sep	11		18					5	9			
Precipitation												
Oct	5							11				
Nov	5	26			10		5		9			
Dec		11					5					
Jan		11		9		10	26		9		70	
Feb						10						
Mar	5		9									
Apr	16									9		
May												
Jun	5		18		20		16		9		30	
Jul	11				10		5					
Aug	5		36		80		11				10	
Sep				27						9		
Previous growing season												
Temperature												
Oct			9			10		5				
Nov												
Dec		5				10						
Jan	5			27		20		11		18		20
Feb				36		50						
Mar	11					10	5		9			
Apr							11		9			
May							42		9		60	
Jun							26		64		30	
Jul		37		73		50	5		18			
Aug		26		36		50	16					
Sep							63		82		90	
Precipitation												
Oct		11		9		10	11					
Nov												
Dec			9									
Jan								5		27		30
Feb				9								
Mar		5					5					
Apr		11				20	11				10	
May												
Jun												
Jul	16		27		20							
Aug		5						21		9		10
Sep	11				20					9		

3.4.2 Regional chronologies and their relation with climatic factors

The PCA analysis indicated that sites could also be grouped into two regions: western (18 sampling plots) and eastern (22 sampling plots) Appendix 6, solid line). Regional chronologies of TRW and VLA were built by pooling of time-series of trees within each region (Fig. 10). Interseries correlations of site time series of TRW within regions were similar, but they were significantly higher (p-value < 0.05) within each region than between regions, indicating differences of wood formation between the regions. TRW showed higher amplitude and variation of index values compared to VLA. Both TRW and VLA proxies also showed higher amplitude and variability (Table 7) and also higher index values (Fig. 10) in the eastern region of Latvia. A decrease in amplitude after about 1980 is visible for both proxies, which is clearer for the VLA chronologies. Common signatures occurred between regional chronologies of TRW (extreme values in 1940, 1957, 1980 and 2008) and between chronologies of VLA (extreme values in 1940, 1956, 1979 and 1987), and a few common extreme values were visible for the proxies (e.g. in 1940). TRW had both expressed common negative and positive extreme index values in both regions, while VLA had only expressed common negative extreme index values. Statistics for the chronologies are shown in Table 7. EPS and GLK were high (>0.96 and >0.53, respectively) for all of the chronologies (for both TRW and VLA), indicating that the datasets contained expressed common signals and that the chronologies were reasonable, despite low agreement between time-series of trees in several sites (Appendix 5). However, agreement of time-series was slightly higher in the eastern region. Autocorrelation and mean sensitivity of the chronologies were higher for TRW compared with VLA, and there were only slight differences between western and eastern regions of Latvia for these estimates.

Generally, high-frequency variation in regional chronologies of TRW was more influenced by climatic factors during summer, while the effect of temperature in the dormant period had stronger effect on VLA. Of the tested 19 monthly temperature and 19 monthly precipitation parameters, 13 and 6, respectively, were significantly correlated with TRW and/or VLA (Fig. 11) and eight temperature factors and two precipitation factors showed significant response functions (Fig. 12) with these proxies in one or both regions. Regarding TRW, July and August temperature of the year p.t.f. had significant negative effect (both correlation and response) in eastern

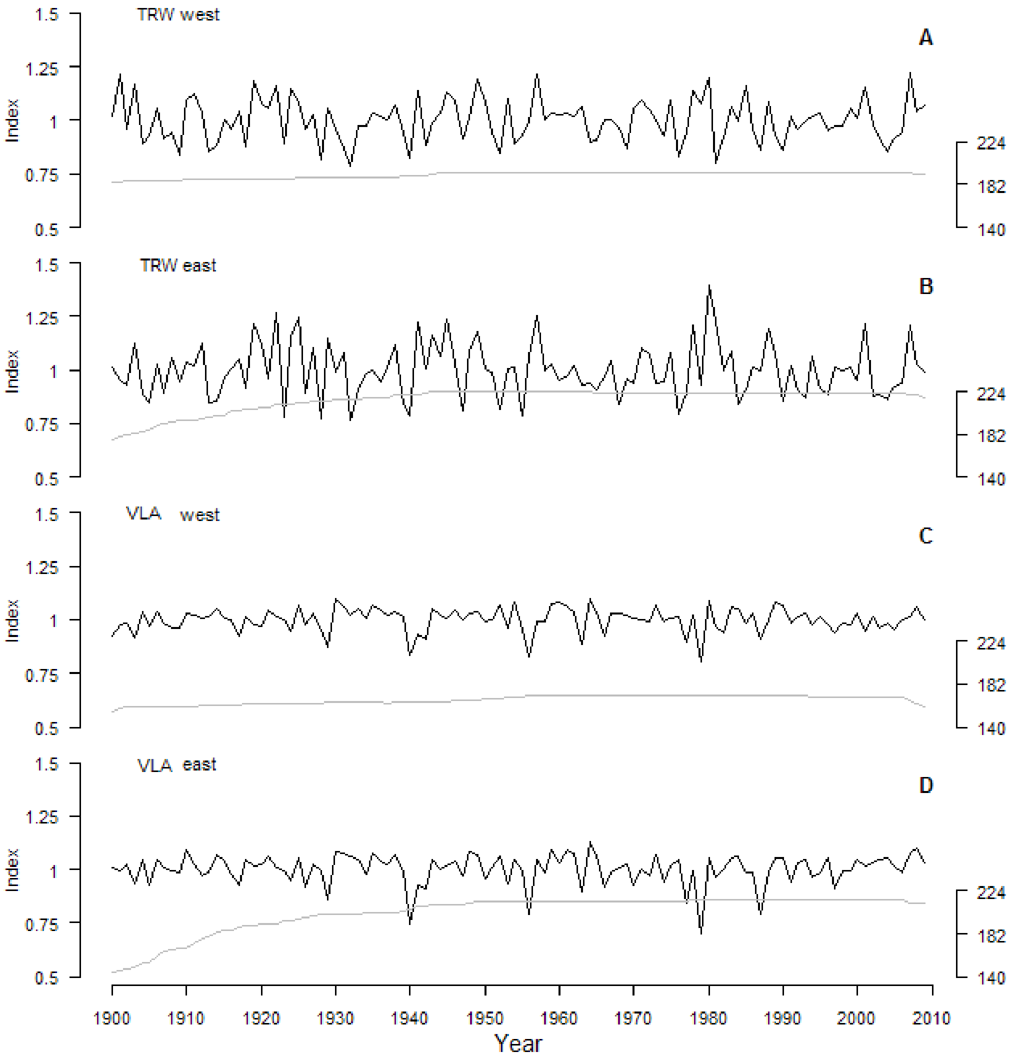

Fig. 10. Regional residual chronologies of TRW (A and B) and VLA (C and D) for western and eastern regions of Latvia. Time-series of trees within region were pooled. Grey line indicates sample depth (replication).

Table 7

Statistics of data (time-series) pooled within regional chronologies of TRW and VLA for eastern and western regions of Latvia.

	TRW		VLA	
	West	East	West	East
Number of trees	192	224	167	214
Interseries correlation	0.443	0.481	0.34	0.468
Mean sensitivity	0.218	0.233	0.207	0.192
Autocorrelation (first order)	0.761	0.761	0.373	0.546
EPS	0.975	0.987	0.968	0.992
GLK	0.577	0.59	0.536	0.563
Min	155	167	272	309
Max	912	982	849	891
SD	69	78	64	83

and western regions. Current year March and June temperatures had positive correlation only in the western region and July temperature showed significant correlation only in the eastern region, but the response function values for these factors were insignificant. In the eastern region, precipitation in July of the year p.t.f. and August of the current year showed positive correlation, and the latter also showed significant response in TRW. In contrast, in the western region, November of year p.t.f. precipitation had a negative correlation and spring (April) precipitation had positive correlation with TRW, but neither of those showed significant response function values. October temperature showed significant correlation only in the eastern region, but response to this factor was significant in both regions. There was no significant effect of drought (scPDSI) observed neither for TRW nor VLA.

Compared to TRW, VLA had a greater number of significant correlations with monthly temperature, and the correlation coefficients were higher (Fig. 11), indicating stronger relationship. The climatic factors correlated with regional chronologies were rather similar to those identified at site level (Table 6). Winter and spring temperature (December–April) in the current year, as well as May–June and September temperature in year p.t.f., were significantly correlated with VLA in both regions. Precipitation had weaker effect than temperature: a significant effect was evident only for January of the year of tree-ring formation in both regions, and also for June of current year in the eastern region. VLA showed positive response to December and April temperatures in both regions, and in the eastern region additionally to September of year p.t.f, January and June temperature (Fig. 12). In the eastern region also a significant negative response to December precipitation was observed, which was not evident in the correlation analysis.

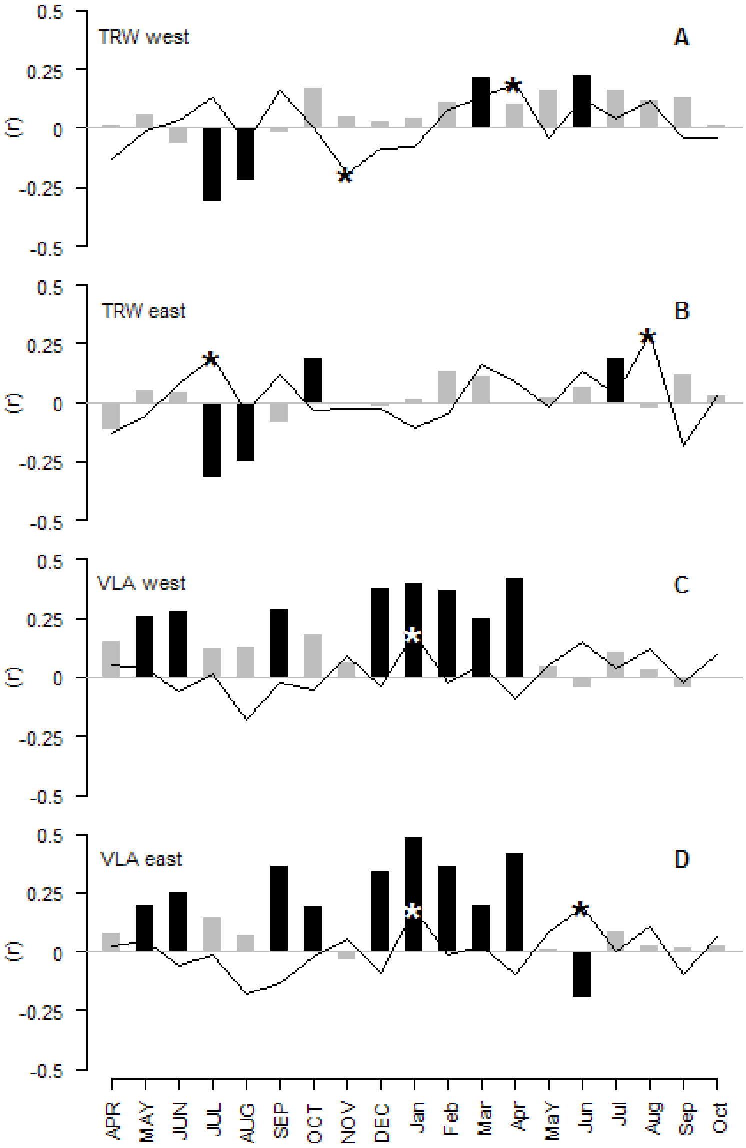

Fig. 11. Pearson correlation coefficients between residual chronologies of TRW (A and B) and VLA (C and D) and mean monthly temperature (bars) and monthly precipitation sums (lines) for western and eastern regions of Latvia, respectively. Significant correlations are shown by black bars and * (precipitation). Months in uppercase refer to the previous calendar year.

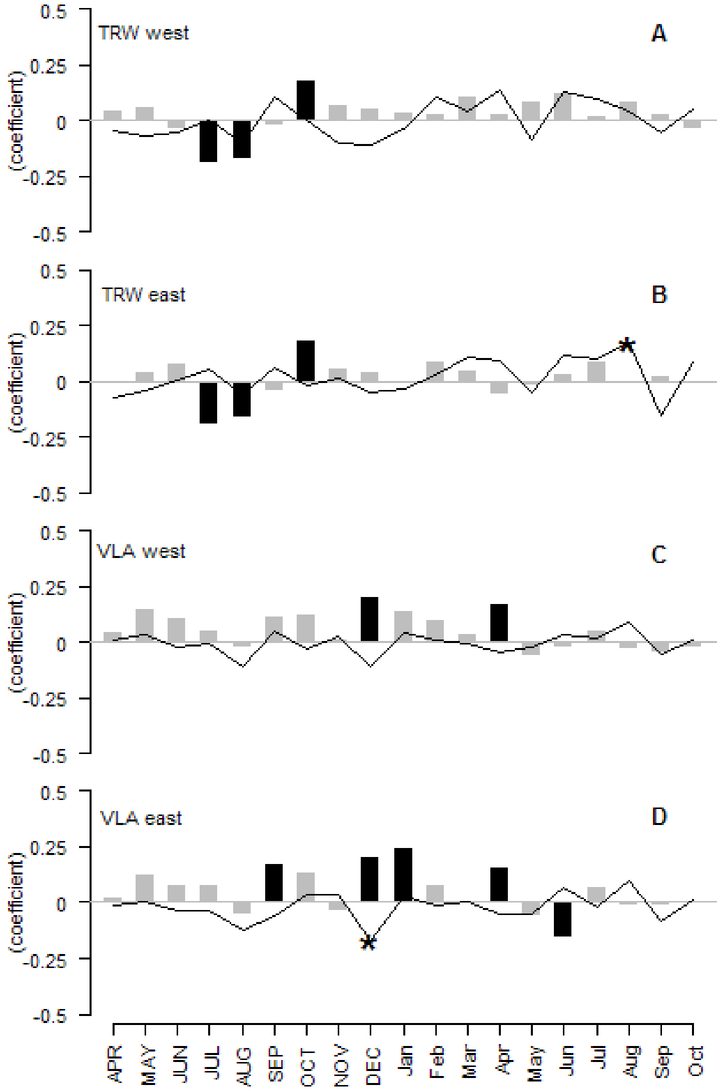

Fig. 12. Response function coefficients between residual chronologies of TRW (A and B) and VLA (C and D) and mean monthly temperature (bars) and monthly precipitation sums (lines) for western and eastern regions of Latvia, respectively. Significant coefficients are shown by black bars and * (precipitation). Months in uppercase refer to the previous calendar year.

3.4.3 Effect of NAO on yearly variation of wood formation

The effect of NAO (monthly and seasonal) was more expressed (showed higher correlation coefficients) on VLA than on TRW (Table 8). For the period from 1900–2002, VLA showed highest correlation with NAO indices in January, which was similar between regions. Correlation between VLA and seasonal NAO indices was also significant, but correlation was stronger in the western region. Weaker but significant correlations were found between VLA and April NAO indices in both regions, but June NAO had significant effect only in the western region. TRW showed weaker effect (lower correlation coefficients) of NAO and only three of the tested NAO factors showed significant correlation in the analyzed periods (1806–1900 and 1901–2002) (Table 8). In the period from 1900–2002 only the NAO index in April showed similar significant negative correlation in both regions of Latvia, which was opposite of that found for VLA (a positive effect). In the 19th century (period from 1806–1900), the seasonal NAO index in both regions and February NAO in western region had a significant effect. In the period from 1900–2002, effect of seasonal NAO on TRW was not apparent, but an effect of the seasonal NAO index was observed for VLA.

Table 8

Significant Pearson correlation coefficients between residual chronologies of TRW and VLA for western and eastern regions of Latvia, respectively. TRW analyzed for periods 1806 – 1900 and 1901 –2002. October –December corresponds to previous calendar year. p-values: *<0.05, **<0.01, ***<0.001.

	1806-1900		1901-2002		1901-2002	
NAO index	TRW west	TRW east	TRW west	TRW east	VLA west	VLA east
October						
November						
December						
January					0.36***	0.39***
February	0.25*					
March						
April			-0.22*	-0.22*	0.23*	0.21*
May						
June					0.29**	
July						
August						
September						
Autumn						
Winter					0.39***	0.37***
Spring						
Sumer						
Season	0.21*	0.21*			0.33***	0.23*

3.4.4 Changes in effect of climatic factors on wood formation of oak

During the period 1900–2009 changes occurred in the relationship between high frequency variation of wood formation (TRW and VLA) and climatic factors, shown by both Pearson correlation analysis (Fig. 13) and response function analysis (Fig. 14) of 50-year moving intervals. The temperature-VLA relationship for January and February clearly appears to have weakened after the late 1960–1970s, as the correlation and response coefficients in moving intervals after about 1927–1977 were lower than in previous intervals or they disappeared. The correlations between March temperature of the current year, and in particular October of year p.t.f., and VLA in moving intervals after 1927–1977 mostly disappeared. However there were only several short intervals with significant response to October of the year p.t.f. temperature in the first half of the analyzed period. The correlation with December temperature increased after intervals of 1928–1978 in both regions. In the eastern region response values become significant only in the last few intervals, while in the western region response was not significant in the first intervals of analyzed period. Although correlations with April temperatures were strong and present in all intervals within the analyzed period, response analysis showed that this effect weakened during the last 10 intervals, particularly in the western region. However, response to April temperature was also non-significant in the first periods and showed highest values in mid-intervals. Although May temperature of year p.t.f. was positively correlated with VLA in the first half of the analyzed period, only several intervals with significant response occurred in the eastern region. In the western region, a significant positive correlation between June precipitation of the current year and VLA appeared in moving intervals after 1924–1974, which extended to the interval 1955–2005. In the eastern region, this effect was evident only in mid-intervals of the study period. Significant response to June precipitation was evident only in a few mid intervals of the analyzed period in both regions. In the later part of the investigated period, in the western region, the effect of June temperature of the year p.t.f. strengthened (correlation coefficients and response increased and became significant). In the eastern region this effect was apparent earlier, as there were two periods of intervals with significant correlation coefficients, but neither extending to the start or end of the study period. However, significant response was evident only for about 1910–1967. A significant negative effect (both correlation and response) of August precipitation of the year p.t.f. occurred in a few moving 50-year intervals after 1938–1988. Drought (scPDSI) did not show periods of significant effect neither on TRW, nor VLA.

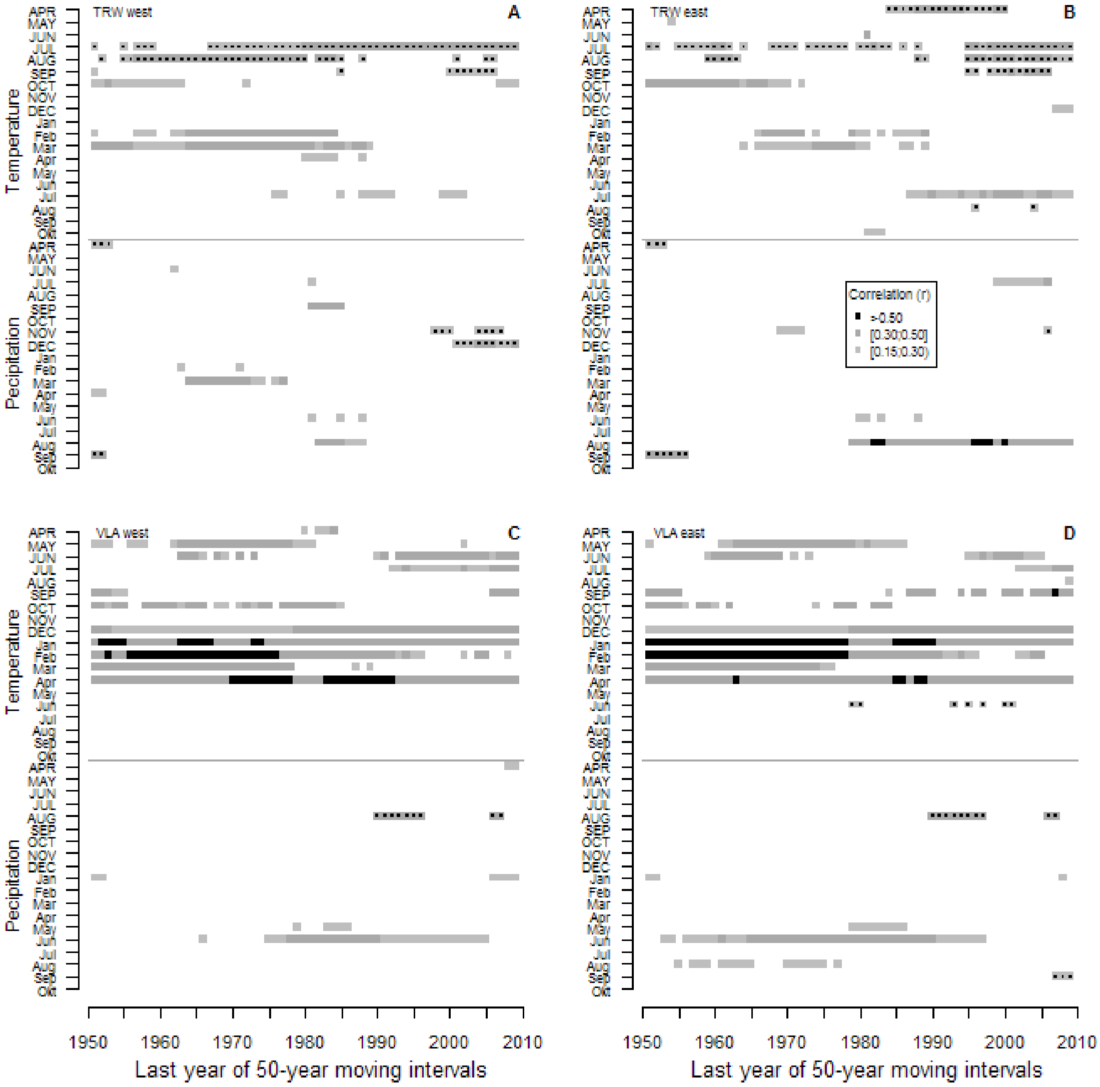

Fig. 13. Significant Pearson correlation coefficients between mean monthly temperature and monthly precipitation sums from April of the year previous to tree-ring formation to October of year of growth and residual chronologies of TRW (A western region and B eastern region) and VLA (C western region and D eastern region) for 50-year moving intervals in the period 1900–2009. Dots represent negative correlation. In uppercase –climatic factors in the year prior to tree-ring formation.

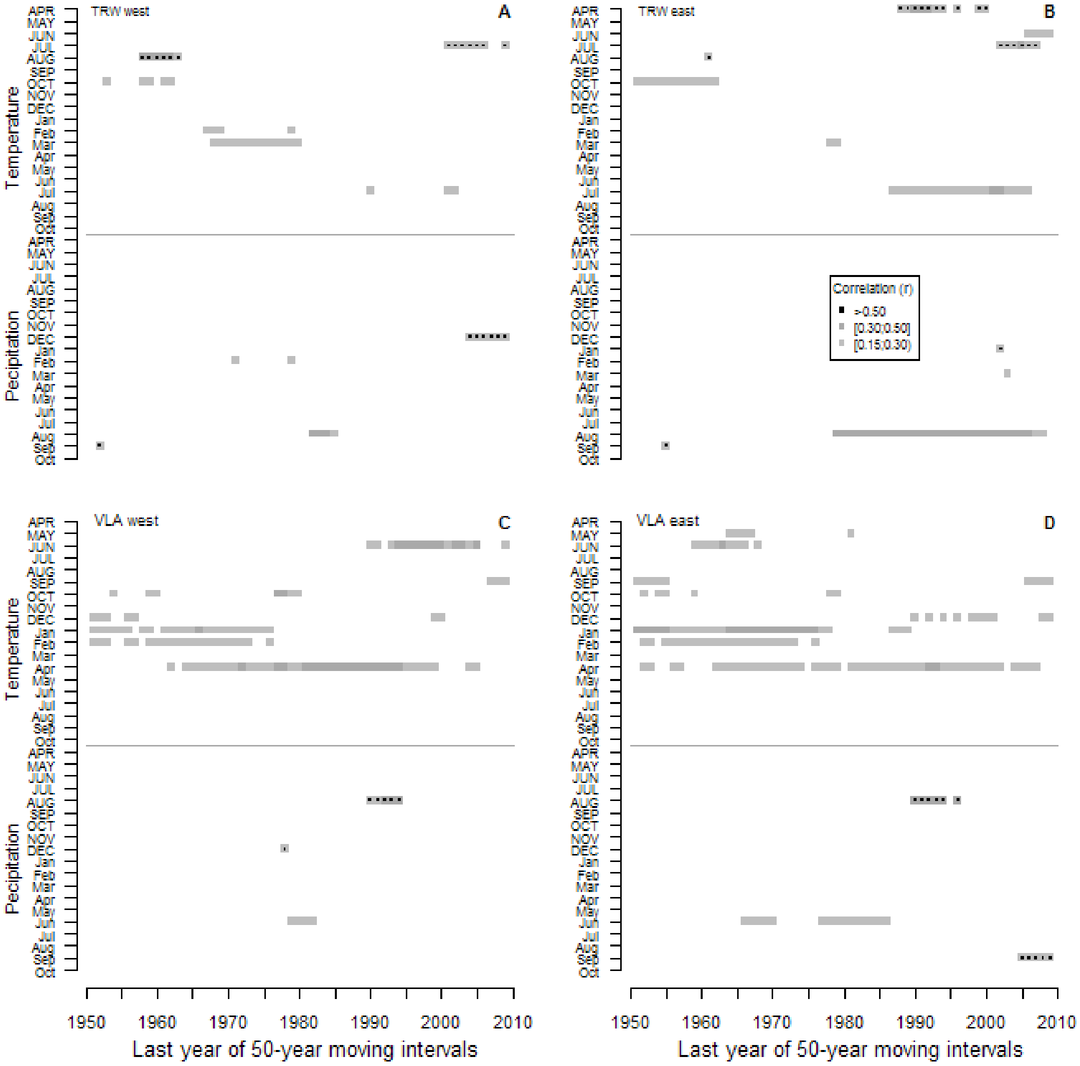

Fig. 14. Significant response function coefficients between mean monthly temperature (T) and monthly precipitation sums (P) from April of the year previous to tree-ring formation to October of year of growth and residual chronologies of TRW (A western region and B eastern region) and VLA (C western region and D eastern region) for 50-year moving intervals in the period 1900–2009. Dots represent negative correlation. In uppercase –climatic factors in the year prior to tree-ring formation.

TRW showed less stable correlation with climatic factors, as there were no single climatic factors showing significant effect during the whole study period, in contrast to VLA (Fig. 13), and periods of significant response were even shorter (Fig. 14). There were 17 climatic factors that showed significant effect with TRW in less than five 50-year moving intervals of the study period. Nevertheless, significant correlations with October of year p.t.f. temperature only occurred in moving intervals before 1963 and 1971 in the western and eastern regions, respectively, and significant response also occurred around that time in the western region. The correlation with current year February and March temperature was significant in intervals before 1980s in the western region. In the eastern region this effect was significant only in mid intervals of the analyzed interval. July and August temperature of year p.t.f. showed significant correlation with TRW during most of the analyzed period, but response function analysis suggested that the negative effect of July of year p.t.f was more expressed and become significant only in later intervals of the analyzed period. Significant response of TRW to August temperature of year p.t.f occurred, but this was apparent in only a few intervals in the earlier part of the analyzed period. Positive significant correlation and response to current year July was evident in the later part of the analyzed interval. This effect was continuous and more expressed in the eastern region. In the eastern region, effect of current August precipitation was significant for both correlation and response function analysis in moving intervals after 1929–1979. Precipitation in September of the current year and November and December of the year p.t.f. had significant effect on TRW in only a few moving intervals, but the former was evident only at the start and at the end of the study period.

3.4.5 Relationship of TRW and VLA pointer years with climatic factors

Pointer year indices, calculated for western and eastern regions for the period 1908–2008, generally were low and did not exceed ±0.50 (Fig. 15). Although the temporal fluctuation of pointer year indices was rather similar between regions for each proxy, major differences occurred between the proxies. Pointer years with an absolute index value ≥0.25 were more frequent for TRW than VLA and more frequent in the eastern compared to the western region. A decrease of pointer year indices during the last 20 years was visible for VLA. In the western region, there were 20 years with pointer year index absolute values ≥0.25 for TRW time series. Of these, 11 were positive and 9 were negative. In contrast, only 3 years were identified as significant pointer years (negative) for VLA time series. In the eastern part of Latvia pointer years with absolute index values ≥0.25 were more frequent: 31 pointer years (17 positive and 14 negative) for TRW and 6 (2 positive and 4 negative) for VLA were identified.

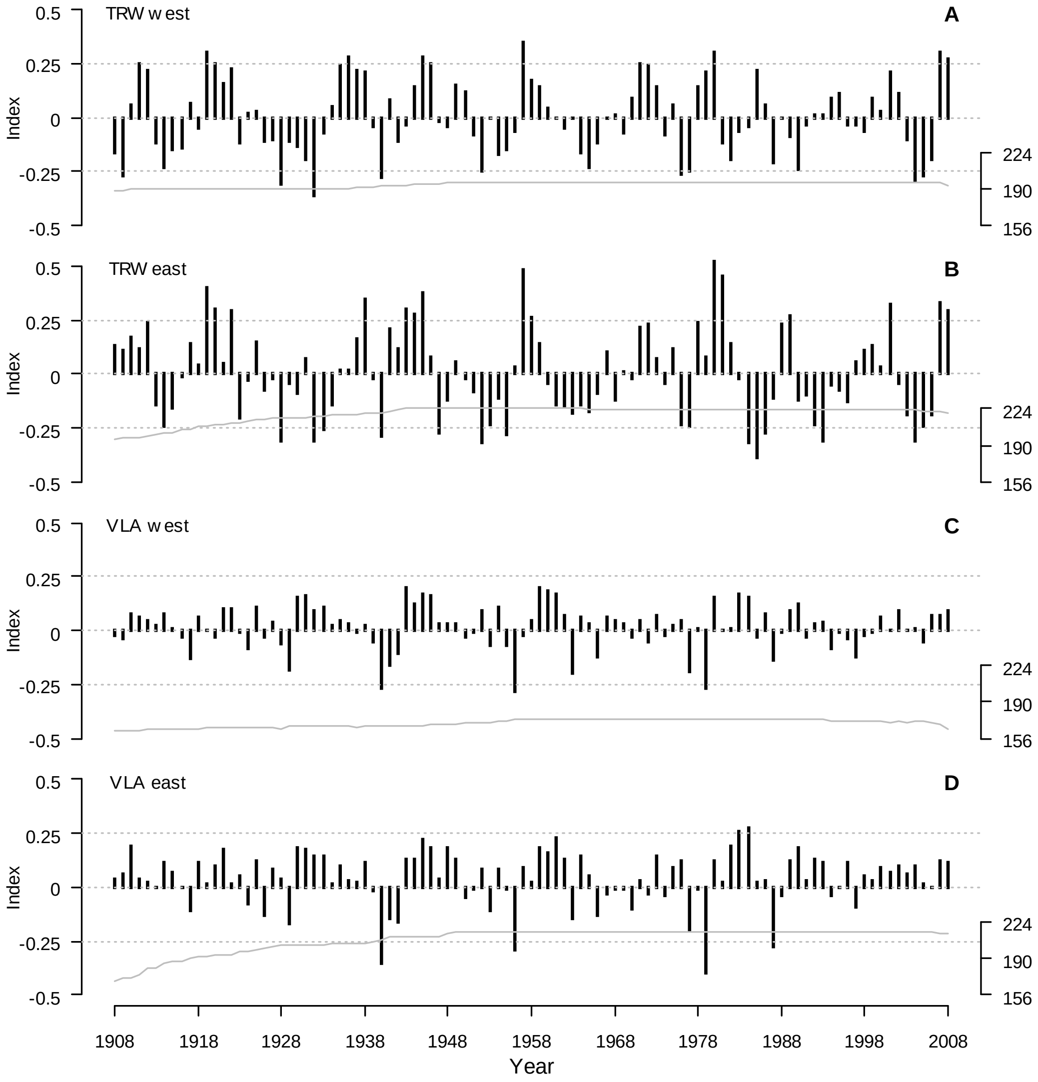

Fig. 15. Pointer year indices and sampling depths (number of trees) for A- tree-ring width in western Latvia, B- tree-ring width in eastern Latvia, C- VLA in western Latvia, D- VLA in eastern Latvia.

Years with high pointer year values could be associated with climate extremes (Table 9). The strongest pointer years (≥0.25) for TRW mostly were common for both regions, except 1985, when a negative pointer year occurred in the eastern region and positive pointer year (with value 0.23) in the western region. VLA also showed common pointer years associated with climate extremes for both regions. Positive pointer years appeared for VLA during the last 20 years. A strong negative pointer year for TRW and VLA occurred in 1940, which was associated with an extremely cold winter when the minimum winter temperature fell below -40 ^{o}C and winter temperatures were about 8 ^{o}C below 100-year mean. Warm winters associated with positive pointer years for TRW time series occurred in 1944, 1945 and 1983, when January temperatures were more than 2.5 ^{o}C above the 100-year mean value. Positive pointer years of VLA were associated with raised temperatures in winter and spring and increased precipitation in May. Raised precipitation in summer (July and August) and warm winters might be associated with positive pointer years of TRW (in 1919, 1945, 1957 and 1980).

Table 9

Extreme pointer years (absolute index value ≥ 0.25) of TRW and related climatic (weather) extremes. Numbers in brackets indicate differences from 100-year mean values.

Year	TRW	VLA	Weather anomalies (differences from 100 year mean)
1919	P		Cold end of March (-5.4 ^{o}C), high precipitation in August (+58 mm)
1928	N		Cold second decade of April (-5.2 ^{o}C), end of July (-4.0 ^{o}C) and beginning of August (-4.0 ^{o}C), high precipitation in June (+84 mm)
1932	N		Cold March (-5.3 ^{o}C)
1940	N	N	Extremely cold January (-8.7 ^{o}C) and February (-9,3 ^{o}C)
1944	P		Warm January (+4.3 ^{o}C), high precipitation in May (+61 mm) and low in July (-46 mm)
1945	P		Warm beginning of January (+2.5 ^{o}C), warm July (+2.8 ^{o}C), high precipitation in July (+168 mm)
1956		N	Extremely cold end of January (-6.3 ^{o}C), February (-7.8 ^{o}C), August (-2.9 ^{o}C)
1957	P		Warm January (+3.4 ^{o}C) and February (+4.4 ^{o}C), high precipitation in August (+75 mm) and September (+76 mm)
1979		N	Extremely cold December of 1978 (-8.3 ^{o}C)
1980	P		Cold May (-2.9 ^{o}C), warm June (+2.3) and moist August (+81 mm)
1983		P(east)	Warm January (+5.7 ^{o}C) and May (+2.9 ^{o}C); high precipitation in May (+75 mm) and the end of November (+35 mm)
1984		P(east)	Low precipitation in April (-33 mm)
1985	N(east)		Cold January (-6.3 ^{o}C) and February (-8.1 ^{o}C), especially in eastern region
1987		N(east)	Extremely cold January (-10.0 ^{o}C) and beginning of March (-9.6 ^{o}C), cold August (-1.6 ^{o}C), high precipitation in May (+50 mm)
2004	N		Warm beginning (+6.7 ^{o}C) and cold end (-3.7 ^{o}C) of May and cold June (-1.4 ^{o}C)

Pointer year indices of TRW and VLA were significantly correlated with 19 climatic factors (Table 10). The sets of significant correlations between climatic factors and pointer year indices for TRW time series completely differed between eastern and western parts of Latvia. In the western region, spring, summer, and seasonal temperatures were significantly correlated with pointer year index values and a negative correlation with November precipitation was observed. In the eastern region significant correlation coefficients between pointer year indices and climatic variables were found for current year February temperature (positive), previous-year December temperature (negative) and current year September precipitation (negative). In all cases of significant correlations for only one of the two regions, randomization tests showed that these significant correlations did not occur by chance (Table 10), confirming division of sites into regional subsets.

Table 10

Pearson correlation coefficients between pointer year index (TRW and VLA) and climatic factors in western and eastern regions of Latvia. Significant correlations are shown in bold, p-values for correlation coefficients are shown as: * < 0.05, ** < 0.01, *** < 0.001. In addition, randomization test p-values estimate the proportion of iterations in which a greater difference in pairs of correlation coefficients was obtained. A p-value ≤ 0.05 was considered as a significant difference between correlation coefficients of regions.

	TRW			VLA		
	Western	Eastern	p-values	Western	Eastern	p-values
			Current growing season			
Temperature						
October				**0.22***	**0.22***	0.208
December				**0.34*****	**0.35*****	0.160
January				**0.40*****	**0.55*****	**0.001**
February	0.12	**0.26***	**<0.001**	**0.40*****	**0.42*****	0.224
March	**0.24***	0.13	**<0.001**	**0.29****	**0.31****	0.202
April				**0.41*****	**0.43*****	0.228
June	**0.24***	0.11	**<0.001**			
August	**0.22***	0.06	**<0.001**			
WINTER				**0.51*****	**0.60*****	**0.050**
SPRING	**0.25***	0.03	**<0.001**	**0.36*****	**0.39*****	0.230
SUMMER	**0.31****	0.18	**0.002**			
SEASON	**0.24***	0.15	**<0.001**	**0.46*****	**0.51*****	0.175
Precipitation						
November	**-0.25***	-0.02	**0.004**			
January				**0.22***	**0.24***	0.199
June				0.18	**0.22***	**0.047**
September	-0.09	**-0.35*****	**<0.001**			
SUMMER				**0.21***	0.18	**0.037**
			Previous growing season			
Temperature						
December	-0.04	**-0.21***	**0.001**			
September				**0.21***	**0.31****	0.113

In contrast to TRW, the sets of significant correlations between pointer year index values calculated for VLA and climatic factors (Table 10) were quite similar in both regions of Latvia. Temperature factors showed higher correlation with VLA than with TRW, and precipitation showed lower coefficient values. In both parts of Latvia, winter and spring temperatures for months and seasons, as well as mean temperature of entire season (growth year), were significantly correlated with VLA pointer years. January, winter and growth year mean temperatures showed the highest correlations, of which January and winter temperature were significantly higher in the eastern region. Precipitation showed weaker effect, as correlation coefficients were lower compared to temperature factors. January precipitation was significantly correlated with VLA pointer year value and had similar effect in both regions. June precipitation showed a significant correlation only in the eastern region and summer precipitation only in the western region. Randomization tests showed that both of these correlations significantly differed between regions (Table 10).

3.4.6 Age-climate-growth relationship

TRW chronologies built for oaks with age 90–130 and 180–210 (Fig. 16) showed rather similar patterns of variation (r=0.66, GLK=0.74), but the range of TRW indices was higher in younger trees. EPS of both datasets exceeded 0.85, but sensitivity and EPS were higher for younger oaks and AC and interseries correlation was higher in older oaks (Table 11). Factors showing significant correlation and response with TRW differed between oaks of different age (Fig. 17); coefficient values were higher for older oaks, suggesting stronger effect of climatic factors. Younger oaks showed significant (positive) correlation only to temperature of September of the current and p.t.f. year and of current year June, and TRW significantly responded to September temperature. Older oaks showed significant correlation and response to both temperature and precipitation factors. Although positive correlations with October, March and April temperatures were observed, TRW of older oaks significantly responded to May temperature of the year p.t.f. TRW of older oaks also showed significant negative correlation with November temperature of the year p.t.f. and May precipitation and positive correlation with August precipitation. Significant response was found for the latter two precipitation factors.

Table 11

Statistics of measurement series of oaks of different age: mean sensitivity (SENS), autocorrelation (AC), interseries correlation (IC) and EPS for period 1900–2007.

	age 80–130	age 180–210
mean	162	100
max	495	440
SD	77	48
SENS	0.272	0.227
AC	0.713	0.771
IC	0.532	0.569
EPS	0.906	0.880

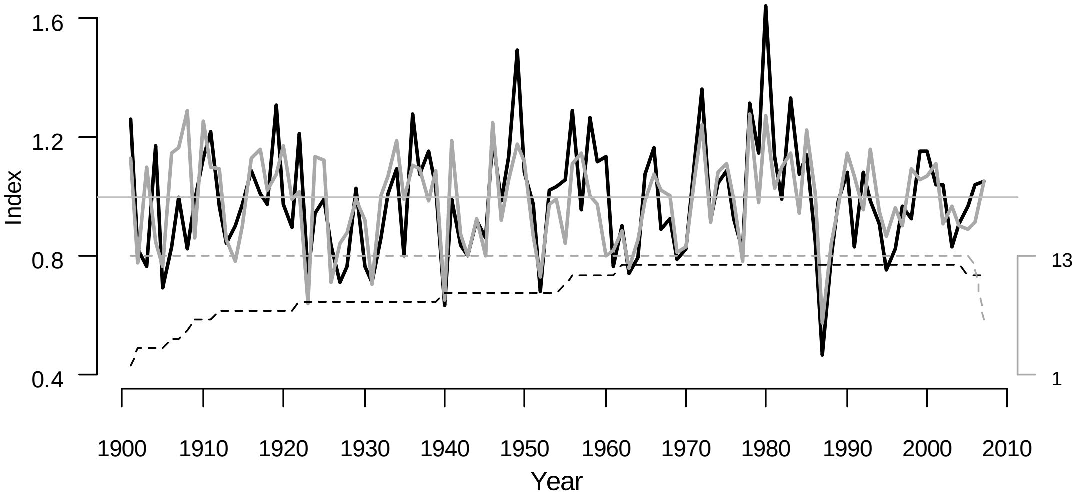

Fig. 16. Residual chronologies (solid line) and sample depth (broken line) of TRW for oak with age 90–130 (black line) and 180 –210 years (gray lines) for site MOR.

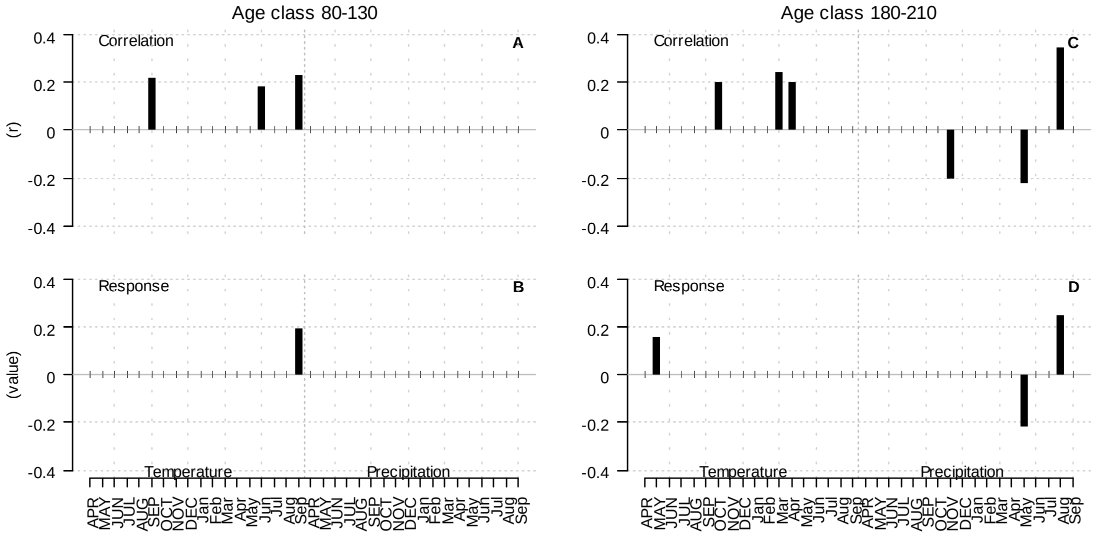

Fig. 17. Significant Pearson correlation and response function coefficients between climatic factors and residual chronologies of TRW of oaks with age 80–130 (A and B) and 180–210 years (C and D) from site MOR. Months in uppercase correspond to previous calendar year.

3.5 Changes in wood formation during recent decades

Regarding age trends and low frequency variation, during the period from 1800 to 1980s, both TRW and VLA (since 1899) showed rather similar variation and spread between time-series of sites (Fig. 8). Although mean TRW and VLA differed between sites, yearly range of TRW and VLA between sites was rather similar, and time-series showed yearly variation around mean values of sites even after the strongest pointer years (Fig. 15). During the last 30 years, the changes in TRW and VLA occurred synchronously. TRW showed reduced variation and spread of series between sites, while VLA series showed increasing spread between series with a tendency to increase. Changes in wood formation during the last 30 years compared to the previous 30 years are obvious in mean regional time-series of both TRW and VLA (Fig. 18, Table 12). A significant decrease of TRW occurred in both western and eastern regions of Latvia. The decrease of TRW in the eastern region was clearer. Along with decrease of TRW, year-to-year variation also decreased (lower SD), resulting in lower (slightly) sensitivity of measurement series in the last 30 years (Table 12), compared to the previous 30 years.

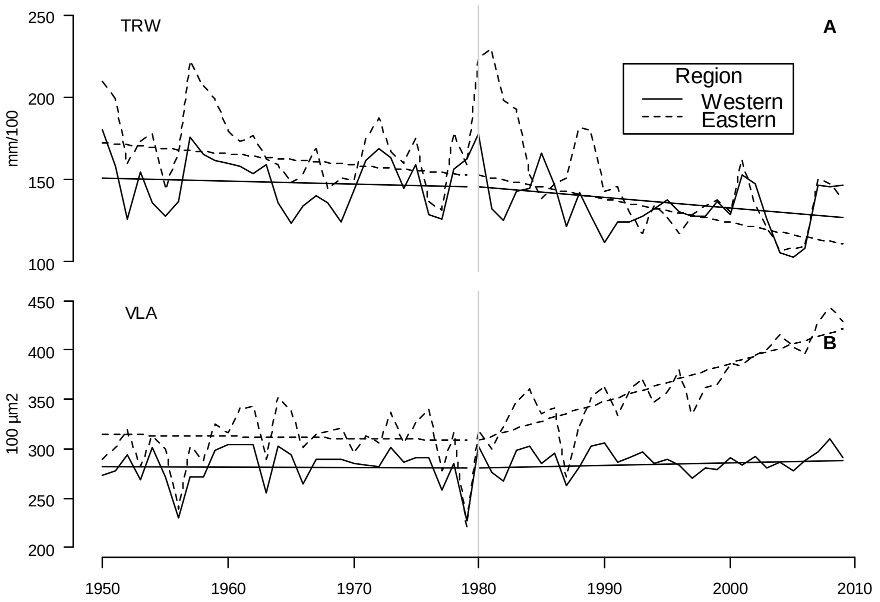

Fig. 18. Mean TRW (A) and VLA (B) in western and eastern regions of Latvia during 1950 – 2010 and their linear trend lines.

Table 12

Statistics and comparison of TRW and VLA in western and eastern regions of Latvia for 1950–1979 and 1980–2010 (SD–standard deviation, AC–autocorrelation, IC interseries correlation).

	TRW western region	TRW eastern region	VLA western region	VLA eastern region
		1950–1979		
Mean	148.75	169.95	281.61	307.86
SD	16.44	21.92	19.84	28.42
AC	0.49	0.46	0.13	0.10
IC	0.59	0.59	0.72	0.85
Sensitivity	0.11	0.12	0.06	0.10
		1980–2009		
Mean	134.02	147.42	288.19	364.21
SD	16.43	31.53	11.43	39.56
AC	0.54	0.70	0.36	0.59
IC	0.51	0.60	0.36	0.66
Sensitivity	0.08	0.08	0.04	0.05
Difference between means for periods, p-value of t-test	0.012	0.001	0.140	0.001
Differences of regression line slopes between periods, p-value	0.501	0.050	0.767	<0.001

Before 1980, VLA was higher in the eastern region compared to the western region, and in the last 30 years a significant increase of VLA occurred in the eastern region. VLA in sites in the western region showed no significant change. Regional differences in EV formation resulted in a spread of site time-series of VLA (Fig. 8). The increase of VLA in the eastern region seems to have occurred after 1979, when negative pointer years for VLA occurred in both regions and VLA reached minimal values of the past 60 years, immediately after an extremely cold December in 1978 (Table 9). Although VLA increased or remained at the previous level (in eastern and western regions, respectively), nevertheless, sensitivity of VLA time-series decreased in both regions of Latvia, similarly as observed for TRW (Table 12).

4 Discussion

4.1 Quality control of measurement time-series

Time-series of measured TRW in Latvia showed rather high agreement between trees in a site (Appendix 5), and only several time-series from each site were excluded during quality checking and cross-dating. In this study only some missing rings were found (not shown). Tree-rings in ring-porous species are easy to identify, as earlywood with large vessels is formed each year, and the occurrence of missing and false rings is low (Bailie and Pilcher, 1973; Speer, 2010). However, anomalies in wood formation have been related with dying oaks during the last years of their life (Drobyshev et al., 2007b; Helama et al., 2009), which, however, were not studied. Relatively easy cross-dating and good agreement of TRW series of oak is one of reasons for wide use of oak in dendrochronological investigations (Speer, 2010). Agreement between time-series is crucial for development of chronologies and extraction of environmental signals (information) (Wigley et al., 1984). Lower agreement (EPS below 0.85 suggests a weak common signal) of time-series within a few sites (Appendix 5) most likely was caused by lower numbers of sampled trees (Wigley et al., 1984), as EPS was high for regional subsets of data (Table 7). However, variation of TRW in oak is known to exhibit different patterns of high and low frequency variation between sites even at rather small distances (Matisons and Dauškane, 2009; Merian et al., 2011; Pilcher and Gray, 1982), explaining lower agreement between mean TRW time-series of sites (Table 3). TRW showed a decreasing trend (Fig. 8), which can be explained by ageing of trees (Speer, 2010) and a gradual decrease of the proportion of latewood in tree-rings (Zhang, 1997). However, the decrease of TRW during recent decades seems to stand out on top of the ageing trend, suggesting a recent change in the environment.

Cross-dating of VLA time-series of trees within a site was more difficult compared to TRW. The cross-dating of VLA time-series was conducted using both statistical and visual (graphical) techniques, paying high attention to years with common decreases (signatures). Although the quality checking was rather sufficient, agreement of VLA time-series at site (stand) level was lower compared to TRW. Low values of EPS (<0.85) in half of the sites (Appendix 5) can be explained by a low number of sampled trees (cross-dated time-series) (Wigley et al., 1984). This was also confirmed when regional chronologies were built, as regional data subsets had high EPS values (> 0.85, Table 7). EV size is more strictly determined than TRW (Aloni and Zimmermann, 1983; Mather et al., 1993; Zakrzewski, 1983; Savidge, 1996) resulting in lower range and variation of VLA (Fig. 10), which also might have caused lower values of EPS and IC (Wigley et al., 1984). Although EV size is determined by inherited and environmental factors (Fonti et al., 2010; Wimmer, 2002) before and during their formation (Fonti et al., 2007; Garcia-Gonzalez and Eckstein, 2003), there is certain variability of EV size within a tree-ring (Garcia-Gonzalez and Fonti, 2008, 2006). Sampling technique thus can have influence on measurements of VLA. Although a 5-mm increment borer width has been described as a minimum sufficient width (Garcia-Gonzalez and Fonti, 2008), it might not be truly representative of the variability of EV size in a tree-ring. Additionally, skewed and narrow tree-rings caused difficulty in preparation of earlywood images, but these were quite rare. Although agreement of VLA series between trees in site was rather low, the good agreement between sites was observed (ICs, Table 3). The agreement of VLA mean time-series of sites was higher than for trees within a site and higher compared with TRW, suggesting that similar factors influenced variation of VLA in Latvia. An increasing trend was visible in time-series of VLA with age and a spread of site time-series occurred during recent decades in contrast to TRW (Fig. 8). Although differences in trends (low frequency variation) of TRW and VLA rather synchronously occurred after 1980, differences of high frequency variation patterns of TRW and VLA suggest that different informative signals could be extracted from each proxy.

4.2 Comparison of tree-ring proxies

Due to differences in timing of earlywood and latewood formation (Sass-Klaassen et al., 2011; van der Werf et al., 2007), the effects of different factors can be distinguished for each part of the tree-ring, which might not be visible in TRW (Fonti et al., 2010; Wimmer, 2002). Analysis of early- and latewood widths is usually conducted for coniferous trees, due to rather high variation of both earlywood and latewood width (Lebourgeois, 2000; Tuovinen, 2005). However, in ring-porous species such as pedunculate oak, separate measurement of earlywood and latewood may not be informative due to lower yearly variation in earlywood similar variation of latewood and ring widths (Zhang, 1997). This was confirmed by a tight correlation between latewood width and TRW ($r \geq 0.94$, Table 4), which suggested that additional information would not be obtained. The lower correlation coefficients (r= 0.58–0.64, p- value <0.05)) between earlywood and TRW (Table 4) might be related to different sources of variation or measurement errors. In scanned images, the early- and latewood border, in cases when vessels gradually decrease in size in successive rows in a tree-ring, can be indistinct (Schweingruber, 2007). This might also explain the lack of significant correlation with VLA. Earlywood width has also been shown to contain weaker climatic signals than latewood and TRW (Eckstein and Schmidt, 1974; Garcia-Gonzalez and Eckstein, 2003; Rozas et al., 2009). Due to lower variation, difficulties in measuring earlywood width and high correlation between latewood width and TRW, further analysis of wood increment were based on TRW.

Wood architecture has a major role in water flow from roots to leaves and shoots (Tyree and Ewers, 1991; Tyree and Zimmermann, 2002), and thus analysis of various vessel characteristics can be useful for understanding of ecophysiological responses of trees (Fonti et al., 2010; Wimmer, 2002). Along with measurement of VLA, vessel density and potential conductivity have been used in ecophysiological studies (Fonti et al., 2010; Leal et al., 2008, 2007). The use of potential conductivity and vessel density was tested, but VLA was used in further analysis since it was the simplest proxy to estimate. Although VLA was significantly correlated with potential conductivity in all three tested sites (Table 4), the fairly high correlation coefficients suggested that little additional information might be gained. This was expected, as potential conductivity was expressed as the sum of the fourth power of EV radii. As earlywood width is rather constant (Garcia-Gonzalez and Eckstein, 2003; Zhang, 1997) it can contain a lower number of larger vessels or vice versa, explaining negative correlation between VLA and vessel density (Table 4). Use of manual cutting of EV images for estimation of vessel density (and also potential conductivity) was associated with rather large errors due to difficult-to-cut images that contained exclusively EV of a tree-ring, especially in cases when tree-rings were skewed. Most likely these errors caused low correlation between potential conductivity and vessel density.

4.3 Patterns of high frequency variation of TRW and VLA

High frequency variation of TRW is known to be specific for regions, due to influence of local factors (Cook et al., 1992b; Fritts, 2001). Lloyd and Fastie (2002) and Merian et al. (2011) showed that climatic signals can differ even at small distances. According to Lloyd and Fastie (2002), with warming of climate inverse reaction to climate can occur. Although residual chronologies of sites showed rather high agreement (Table 3) in Latvia, high frequency variation of wood formation (TRW, VLA) of oak differed regionally along a continuous gradient from west to east along a maximum distance of ~410 km (Fig. 9, Appendix 6). PCA axis 1 exhibited significant relation with distance from Baltic Sea (projected longitude coordinate) (Table 5), indicating an effect of continentality (Fig. 4) as observed in Finland (Linderholm et al., 2003). Thus the effect of limiting factors can be expected to be strongest in a continental climate, where winter conditions are colder and summers are hotter. As wood formation in oak is affected by many environmental factors (Friedrichs et al., 2008), which may co-act and/or change over time (Merian et al., 2011), the amount of variation explained by PCA component 1 (8.7–13.8%) was low (Table 5) (Økland, 1999), indicating also other sources of variation, i.e. stand microclimate.

Continentality, which represents yearly thermal variability and to some degree moisture availability in summer (Brubaker et al., 1993; Temņikova, 1975), is known to limit tree species distribution (Giesecke et al., 2008; Lindner et al., 1996). Under a continental climate, higher amplitude of temperatures and higher possibility of drought (weather extremes) (Brubaker et al., 1993) may result in physiological stress (Pallardy, 2008) that limits establishment and development of trees (Giesecke et al., 2008; Lindner et al., 1996). The occurrence of stands with different PCA scores at small distances (Appendix 6) might also imply that local (micro)climatic differences, due to perhaps topography, can affect wood formation in species near their northern distribution range (Lloyd and Fastie, 2002; Wilmking et al., 2004). Coverage of instrumental climatological data for Latvia, however, is too coarse (New et al., 2000; van der Schrier et al., 2006) to directly investigate effect of local climate.

The relationship with W-E location was slightly less expressed in VLA, suggesting weaker effect of continentality and more similar climatic signals (Appendix 6). A slight north-south gradient of PCA component 1 scores for VLA data can be observed, presumably suggesting higher sensitivity of VLA to temperature, which also exhibited a north-south gradient (LEGMC; Temņikova, 1975). However, the West-East gradient, which was the most expressed, was further used for discussing differences in climate-growth relationships.

4.4 Climatic factors and wood formation in oak

4.4.1 Effect of climatic factors on oak wood formation in stands in Latvia

One of the assumptions in dendroclimatology is that tree growth on the northern distribution limit of the species is limited by low temperature (Fritts, 2001; Speer, 2010). However, studies near the treeline in Alaska showed that an inverse reaction of warming can occur, as competition and availability of water can be altered resulting in heterogeneity of tree response (Lloyd and Fastie, 2002; Wilmking et al., 2004). Variable climate-TRW relationships were found in Latvia, particularly in the western region, where single climatic factors were significant in only up to 42% of stands (i.e. June temperature) (Table 6). However, also in central regions of the oak distribution area, where climatic conditions can be considered to be optimal for growth (Fritts, 2001; Speer, 2010), climate-TRW relationships vary locally and other environmental factors affect variation of TRW (Fletcher, 1974; Merian et al., 2011; Pilcher and Gray, 1982). Effect of climatic factors can also be modified by stand properties, such as moisture regime, exposure and microclimate (Fletcher, 1974; Karpavicius, 2001; Merian et al., 2011; Rozas, 2005, 2001; Ruseckas, 2006). In the continental eastern region of Latvia, significant effect of a single climatic factor was more expressed, i.e., August precipitation was significant in 80 % of investigated stands (Table 6) suggesting effect of water deficit. In the central region of Latvia, the proportion of stands showing significant correlations was intermediate between the western and eastern region, but July temperature of year p.t.f. was significant in 73% of stands, probably due to stands located in more continental upland areas (Fig. 4). In several stands oaks even showed no significant correlation with climatic factors (not shown), suggesting effect of other factors on TRW, as observed close to the northern distribution limit (Tardif and Conciatori, 2006). Considering the proportions of stands showing significant relationships with climatic factors, it can be suggested that the maritime western region might be more favourable for oak growth, due to less expressed limitation by climate, than more continental central and eastern regions.

In contrast to TRW, VLA was more clearly related to specific climatic factors that were significant in a higher proportion of sites throughout Latvia (Table 6). Even in the maritime western region of Latvia, 84% of stands showed significant correlations with April temperature. Although VLA was limited by specific climatic factors (temperature in winter and spring), there were climatic factors significant for VLA in relatively low proportions (<30%) (e.g., October temperature of year p.t.f. and April precipitation). This implies that effect of these climatic factors is weaker; probably determined by stand properties (i.e. microclimate). While the expected limitation of low temperature on TRW (Fritts, 2001; Sykes and Prentice, 1996) was not clearly evident, winter-spring temperatures clearly showed a limiting effect on VLA (Table 6), suggesting that the northern distribution of oak might be determined by water conducting capacity of wood. Proportions of stands showing significant correlation between VLA and climatic factors gradually increased from west to east, suggesting that the limiting effect of temperature on VLA increases with increasing continentality and yearly amplitude of temperature. As the eastern border of the European oak population (according to data from EUFORGEN, Fig. 1) lies near the eastern border of Latvia, it also might be determined by water transport capability of wood. Regarding similar climatic signals and agreement between site time-series, VLA has high potential for use in dendrochronology and dendroclimatology.

In the western region, where spring and summer temperatures are lower (Table 1), significant effect of March, May and June temperatures of the current growing season on TRW occurred in high proportions of stands. In western Latvia, snow melt can begin in March, and years with a warm March may be associated with a longer growing season (DeForest et al., 2006; Kalvāne et al., 2009; Menzel and Fabian, 1999). A warm October also can prolong the vegetation period (Kalvāne et al., 2009) and increase production of wood (van der Werf et al., 2007, White et al., 1999). May is the usual time of oak bud break (Ahas et al., 2000; Ģērmanis, 2005; Sass-Klaassen et al., 2011) and the highest physiological activity (assimilation) of oak occurs in June (Morecroft and Roberts, 1999; Xu and Baldocci, 2003; Xu and Griffin, 2006). Apparently, May and June temperatures are not limiting TRW in the eastern region, where phenological phases are delayed (Kalvāne et al., 2009; Temņikova, 1975) and temperature during the beginning of the growing season (late spring and early summer) is warmer (Table 1). A negative effect of July and August temperature in the previous year was most frequent in the central region, where August is warmest (Table 1). This might be explained by occasional water deficit (Rozas, 2005) and decreased assimilation in response to higher temperature (Epron and Dreyer, 1993; Haldimann and Feller, 2004; Xu and Baldocci, 2003). Temperature in June, July and August has been shown to have significant effect on increment of oak also in several studies (Cedro, 2007; Čufar et al., 2008a; Drobyshev et al., 2008a; Fletcher, 1974; Läänelaid et al., 2008; Rozas, 2005; Ruseckas, 2006; Tardif and Conciatori, 2006).

The frequent significant correlation of VLA with temperature from December to April (Table 6) suggests limiting effect of temperature, especially in the eastern region. Severe cold and thaws in the dormant period cause frost damage and embolism (Pearce, 2001; Sperry and Sullivan, 1992; Tyree and Cochard, 1996; Zhu et al., 2000), which may decrease physiological vigour of oak (Drobyshev et al., 2008a; Helama et al., 2009; Repo et al., 2008) and be reflected in size of EV (Fonti et al., 2010, 2009b). Chill damage apparently can cause decreased early cambial activity and hence EV size (Deslauriers et al., 2008; Lebourgeois et al., 2004; Waring, 1951). Low temperatures may also affect the concentration of auxin in spring, thus altering vessel differentiation (Pallardy, 2008). Correlation with January precipitation (observed in 70% of stands in the eastern region) suggests effect of temperature on root systems Winter temperature and snow depth affect temperature of soil layers and depth of soil freeze, as snow layer acts as an insulator stabilizing soil temperature and decreasing frost depth (Hardy et al., 2001). In cases of strong thaws in winter, the insulating snow layer can melt. Low soil temperature may damage fine roots or increase their mortality (Fahey and Hughes, 1994; Ponti et al., 2004; Tierney et al., 2001), decreasing water uptake in the beginning of spring (Pallardy, 2008; Steudle, 2000). Under such conditions, smaller EV must be formed to minimize risk of embolism under decreased water uptake (Garcia-Gonzalez and Eckstein, 2003; Tyree and Cochard, 1996; Tyree and Zimmermann, 2002). This can also explain the effect of temperature in winter on VLA. EV in oak begin to form before bud break (Sass-Klaassen et al., 2011; Waring, 1951), and thus this process is dependent on stored assimilates (Barbaroux and Breda, 2002; Pallardy, 2008). Winter temperatures alter starch dissolution and sap characteristics in spring (Essiamah and Eschrich, 1985). In cold winters more starch may be dissolved to protect tree tissues from freezing (Essiamah and Eschrich, 1985; Morin et al., 2007), potentially reducing the amounts of stored carbohydrates. Also, low temperature before the bud break may reduce sap ascent (Tyree and Zimmermann, 2002; Zimmermann, 1964), altering earlywood formation. April is a crucial period, when wood formation initiates in oak (Ģērmanis, 2005; Kalvāne et al., 2009; Sass-Klaassen et al., 2011) and the larger part of EVs must be formed to support sap flow to shoots (Granier et al., 1994; Sass-Klaassen et al., 2011, Waring, 1951). Weather conditions in Latvia in April may change drastically: warm periods may change with frosts and snowfall (LEGMC). Temperature directly influences cambial activity and cell differentiation (Deslauriers et al., 2008; Pallardy, 2008; Rossi et al., 2008; van der Werf et al., 2007) and rapid shifts of weather increase risk of chill damage to cambium (Gu et al., 2008; Pearce, 2001). Weather in May overall is more stable and temperatures are above zero, except for rare night frosts (LEGMC). More stable weather conditions in May can explain the lower effect on VLA, but an alternative explanation may be related with formation of subsequent rows of EV (Copini et al., 2010; Garcia-Gonzalez and Fonti, 2006; Sass-Klaassen et al., 2011), which were not present in all tree-rings. Significant correlations with climatic factors after June are most likely coincidental, considering the local phenology (Ahas et al., 2000; Kalvāne et al., 2009) and timing of vessel formation (Sass-Klaassen et al., 2011), as oak should have begun to produce latewood (Michelot et al., 2012; van der Werf et al., 2007). However in the eastern region, the negative effect of June temperature and positive effect of June precipitation suggest that formation of EV might be delayed compared with the western region, and that water deficit might occur in the beginning of summer. Positive effect of September temperature in the previous year on VLA and effect of October temperature of the current season can be explained by a longer vegetation season (White et al., 1999) when more assimilates are produced and stored (Barbaroux and Breda, 2002; Xu and Griffin, 2006). Probably, the previous year September should be included as a month of the current season of tree-ring formation, but the information on timing of wood formation in Latvia is insufficient.

Although previous studies have shown that VLA is mainly affected by environmental factors in the current growing season (Campelo et al., 2010; Fonti and Garcia-Gonzalez, 2008; Fonti et al., 2009a, 2009b; Garcia-Gonzalez and Eckstein, 2003; Tardif and Conciatori, 2006), in the present study we observed a positive effect of May and June temperature of the previous growing season in 23–64 % of stands in the three regions (Table 6). This might be explained by increased tree vigour due to previous favourable conditions (Pallardy, 2008). It is difficult to explain the negative effect of previous-season January temperature and precipitation on VLA. This effect, and other effects observed in small proportions of stands might also be coincidental.

For chronologies (high-frequency variation) of TRW and VLA developed for each stand in western and central regions, temperature had a greater effect than precipitation (Table 6). In Latvia, moisture usually does not limit tree growth (Elferts, 2007; Maurinš and Zvirgzds, 2006), as precipitation is mostly higher than evapotranspiration (Klavins et al., 2002; Krams and Ziverts, 1993; Lauva et al., 2012; Temņikova, 1975). However, in the eastern region, the correlations of TRW with June and August precipitation suggest that the continental climate may create drought conditions. This is also supported by positive correlation of VLA with June precipitation and negative correlation with June temperature in the eastern region.

4.4.2 Climatic forcing of regional chronologies

Although climatic signals, particularly in TRW, exhibited effect of site properties, agreement of site time-series suggest that common tendencies in wood formation (Table 3) do exist. Regional chronologies for western and eastern regions of Latvia were established (Appendix 6, solid line). As previous analysis showed that wood formation generally differed between these regions, stands from the central region of Latvia were included in the eastern region, due to more similar climatic signals (Table 6) and to ensure similar sizes of pooled data (18 and 22 sites in western and eastern regions, respectively), thus decreasing the effect of individual stands. Validity of dividing plots into the defined regions is also supported by higher agreement (by about 5%) of time series within than between regions and a randomization test of pointer year indices (Table 10). The EPS values (0.975–0.992) obtained for regions (Table 7) indicated that the datasets contained a strong common environmental signal (Wigley et al., 1984), especially in eastern region where range of chronology indices was higher (Fig. 10).

Climatic signals of regional chronologies of TRW (Figs. 11, 12) were similar to those observed in analysis of individual stands (Table 6). Response function analysis (Fig. 12), however, showed that high-frequency variation of TRW was mainly related with climatic factors in year p.t.f. Active assimilation occurs also in July and August (Michelot et al., 2012; Morecroft and Roberts, 1999; Xu and Baldocci, 2003; Xu and Griffin, 2006), when availability of water is crucial for photosynthesis (Pallardy, 2008). As summer advances, water availability often decreases (Burt et al., 2002; Lauva et al., 2012); increased temperature then may cause (facilitate) water deficit (Holdridge, 1959; Traykovic, 2005) and affect photosynthesis (Epron and Dreyer, 1993; Haldimann and Feller, 2004) and growth (Xu and Baldocci, 2003). Significance of August precipitation of current year and effect of drought in the eastern region (Figs. 11, 12) was indicated by a significant response function. However this effect appears to be occasional and presumably not lasting, as August monthly scPDSI showed no significant effect on regional chronologies. Length of the growing period, which at present is 190 and 175 days in the western and eastern regions, respectively, had an influence on TRW, shown by a significant response function with October temperature (Figs. 11, 12). This confirms the role of additional assimilates in improvement of oak growth (Epron and Dreyer, 1993; Fritts, 2001; Morin et al., 2007; White et al., 1999) in Latvia.

Regional chronologies of VLA also revealed significant correlations (Fig. 11) with the factors identified during analysis of individual sites (Table 6). Response function analysis (Fig. 12) showed a higher number of significant factors in the eastern region in a more continental climate, but December and April temperatures had significant effect in both regions. In Latvia December is the beginning of winter, when temperature normally drops below zero (LEGMC) and cold hardening is terminating (Alden and Hermann, 1971; Essiamah and Eschrich, 1985; Morin et al., 2007). A sudden drop of temperature during cold hardening may reduce vigour of trees (Alden and Hermann, 1971; Ögren et al., 1997; Repo et al., 2008). However it may also rain in the beginning in December during warm years (LEGMC), increasing soil water content (Lauva et al., 2012). Moist soil can negatively influence growth and survival of roots (Kramer, 1951; Larson and Whitmore, 1970; Simard et al., 2007) by decreasing soil air and root respiration (Kramer, 1951; Pallardy, 2008), resulting in lower water uptake and smaller EV in spring. In the maritime western region, where the possibility of rainy Decembers is higher (LEGMC), oaks may have adapted to such conditions, explaining absence of a significant effect. Although VLA was correlated with January temperature in both regions (Fig. 11), significant response was observed only in the eastern region (Fig. 12), where winters are cooler (Table 1). Lack of a significant response function for January precipitation suggests that effect of a snow layer (Hardy et al., 2001) is occasional, presumably in years with a delayed winter or strong thaws. Importance of April temperature on VLA was indicated by a significant response function. Significant response function with June temperature suggests that EV can form until June in the eastern region. Apparently length of growing season has stronger effect in eastern region indicated by significant response function with September temperature of the year p.t.f.

4.4.3 Effect of NAO on high frequency variation of wood formation

NAO determines strength of western winds in Europe, which bring moisture from the Atlantic, particularly during November–April (Klavins and Rodinov, 2010) in the period of tree-dormancy (Ģērmanis, 2005; Kalvāne et al., 2009). The effect of NAO on TRW and VLA differs and has apparently changed during the past two centuries, particularly for TRW (Table 8). During the 19th century when climate was cooler (Lizuma et al., 2007), positive effect of NAO (February and seasonal) on TRW might be explained by reduced cold damage in mild winters, as observed previously for Scots pine (Elferts, 2008). In the 20th century, a negative effect of April NAO appeared, likely due to climate warming, as earlier onset of cambial activity might subject oak to damage due to weather shifts (Pearce, 2001).

As VLA is affected by winter temperature in Latvia, NAO in winter months showed significant correlation (Table 8). Air temperatures and precipitation have been linked with NAO (Klavins and Rodinov, 2010; Rodwell et al., 1999), explaining relationship between VLA and the winter and yearly NAO indices. The correlation with winter yearly (seasonal) NAO was higher in the maritime western region, which is more subjected to air masses from west (Draveniece, 2006; Temņikova, 1975). A higher NAO index indicates milder climate and also higher temperature in spring (April) (Klavins and Rodinov, 2010), which is important for EV formation (Fig. 11), explaining correlation between VLA and the April NAO index. As previous results suggested, EV formation ends earlier in the western region and correlation with June NAO most likely is coincidental.

4.4.4 Climate forcing of pointer years in TRW and VLA

The patterns of pointer years differed for TRW and VLA (Fig. 15). TRW showed more positive pointer years (values ≥ 0.25) than negative, as in favourable conditions wide tree-rings can be produced, even when trees are old (Becker et al., 1994; Jacoby and D’Arrigo, 1995; Robalte et al., 2012). VLA mainly showed negative pointer years (values ≥ 0.25), due to stricter physiological determination of maximal size of EV (Aloni and Zimmermann, 1983; Mather et al., 1993; Tyree and Zimmermann, 2002). Pointer years of VLA were discrete (index values changed abruptly), which can be explained by greater forcing of environmental factors (Campelo et al., 2010; Fonti and Garcia-Gonzalez, 2008) and lower effect of previous growth (AC) compared to TRW (Table 3; Fonti and Garcia-Gonzalez, 2008, 2004). Also, the correlation between pointer year indices for TRW and climatic factors was weaker than for VLA (Table 10), suggesting lower effect of the tested factors on TRW.

The relationships between VLA pointer year index values and climatic factors (Table 10) were similar to those observed for high frequency variation (Fig. 11, Table 6). However, harsher conditions under a continental climate (Giesecke et al., 2008; Lindner et al., 1996) in the eastern region (lower winter temperatures (Table 1)) resulted in significantly stronger effect of January and winter temperature. The effect of precipitation on VLA was weak, compared to temperature, as previously shown for high frequency variation (Fig. 11, Table 6). The effect of summer precipitation in the western region likely was coincidental, as suggested by previous analysis.

The climatic factors affecting pointer years of TRW significantly differed between regions (Table 10) and were generally similar to those observed for high frequency variation (Fig. 11). However, several other relationships were visible in pointer year indices. Positive effect of August temperature on TRW pointer years in western Latvia, where summers are cooler (LEGMC), can be explained by more intense assimilation under higher temperature (Jurik et al., 1988; Pallardy, 2008). Apparently, in years with warm August temperature, more latewood can be produced. In the continental eastern region temperature in the coldest month February (Table 1) showed an effect, likely due to cold damage (Pearce, 2001) when the cold tolerance of oak might had been exceeded (Drobyshev et al., 2008a; Repo et al., 2008). Over-moisture of soil can negatively influence vitality of oak (Alaoui-Sosse et al., 2005; Cinnoti, 1989; Kramer, 1951; Larson and Whitmore, 1970), explaining negative correlation with September precipitation.

Extremely low temperatures in winter and spring had a role in forcing of strong negative pointer years of TRW (≥ 0.25) (Table 9), but the strongest positive pointer years could be associated with several events, as many factors influence wood increment in oak (Friedrichs et al., 2008). Some of the extreme pointer years were associated with high or low precipitation in particular months. Most of these years also had extremely high or low temperatures, suggesting effect of a complex of factors. However, most of the positive TRW pointer years were associated with high precipitation in the second part of summer, in cases when the beginning of vegetation season was warm, as in 1919, 1945, 1957 and 1980. Apparently, drought in summer has not caused negative TRW pointer years, in contrast to central and southern Europe (Friedrichs et al., 2008; Kelly et al., 2002; Lebourgeois et al., 2004; Rozas, 2001), but abundant precipitation has increased (late)wood increment when summers are warm.

The strongest pointer years of VLA during the 20th century also can be explained by occurrence of temperature (cold) extremes in the dormant period and spring (Table 9) and this is supported by results reported above (Table 10). Apparently, a single extreme cold event can cause a distinct negative pointer year in VLA due to high temperature sensitivity of the proxy, in contrast to TRW. In 1984, a positive pointer year occurred for VLA when precipitation in April was very low. However, the lack of a significant correlation between VLA pointer year indices and April precipitation (Table 10) suggests an effect of a presently undermined factor on VLA formation in this year.

The identified pointer years for TRW (Fig. 15) coincide with some large scale pointer years detected in Southern Sweden and central Europe (Drobyshev et al., 2008a; Kelly et al., 2002), which can be explained by the influence of NAO and inflow of arctic air masses (Drobyshev et al., 2008a; Klavins and Rodinov, 2010; Kelly et al., 2002). For example, the winter in 1939/1940 was a cold winter throughout Northern Europe (Drobyshev et al., 2008a; Kelly et al., 2002), and has been recognized also in other studies (Wiles et al., 1998). The effect of a cold winter in 1955/1956 was reported from Southern Sweden and central Europe (Drobyshev et al., 2008a; Kelly et al., 2002; Neuwirth et al., 2007), which was evident as a pointer year for VLA (not for TRW) in Latvia (Fig. 15), probably due to lower effect of previous growth.

4.4.5 Changes of climatic signals during 1900–2010

During the 20th century, a change in climatic signals (climate growth relationships) was observed for TRW and VLA of oak in Latvia, as observed for other tree species near borders of their distribution areas (Carrer and Urbinati, 2006; D’Arrigo et al., 2008; Jacoby and D’Arrigo, 1995; Lloyd and Fastie, 2002; Oberhuber et al., 2008; Wilmking et al., 2004; Zhang et al., 2008). The loss of effect of October temperature of the year p.t.f. after the 1960-ies and loss of correlation with March temperature (Figs. 13, 14) can be associated with a longer growing season due to climate warming (Menzel and Fabian, 1999). The temperature in these months at present might be considered as non-limiting for wood increment. Milder winters in recent decades (Avotniece et al., 2010; Lizuma et al., 2007) can explain loss of significant correlation with February temperature. In the eastern region, where winters are harsher, this effect, however, was observed only in the mid part of the 20th century, when warming was slower (Lizuma et al., 2007). The negative correlation of April temperature of the year p.t.f. with TRW in the eastern region during 1934–2000 (Fig. 13) might be explained by unstable weather conditions which can damage cambium and reduce growth (Gu et al., 2008). A negative effect of current year April temperature on TRW was also observed on Saaremaa Island (Läänelaid et al., 2008), where the climate is oceanic.

Climatic factors that can be attributed to occurrence of water deficit (drought) have appeared to be limiting for TRW. Correlation and response function analysis (Figs. 13, 14) suggest that a drought effect (negative p.t.f. July temperature and positive current year August precipitation) has increased, by increasing effect of previous summer assimilation (Barbaroux and Breda, 2002; Xu and Griffin, 2006), as previously widely observed in central and southern regions of the distribution of oak (Campelo et al., 2010; Cedro, 2007; Friedrichs et al., 2008; Pilcher and Gray, 1982; Rozas, 2005, 2001). However, a positive effect of current year July temperature on TRW (Figs. 13, 14) in the eastern region in the later part of analyzed period, contradicts the idea of water deficit. This might be explained by increased frequency of periods with both high temperature and high precipitation (Avotniece et al., 2010). In some years, in periods with low precipitation the available moisture can be decreased (water deficit), while in years with abundant precipitation, temperature promotes assimilation (Epron and Dreyer, 1993; Jurik et al., 1988; Pallardy, 2008; Stokes et al., 2010). Precipitation in August at present appears as the main limiting factor for TRW in the eastern region, showing highest response function coefficient values (Fig. 14). The effect of water deficit in August might also be facilitated by increased frequency of days with minimum temperature >20 °C in July (Avotniece et al., 2010; Lizuma et al., 2007). As shown by pointer year analysis, abundant precipitation apparently might be increasing wood production. However, the observed possible effect of drought water deficit might partially reflect age-related increase of maintenance costs (Rust and Roloff, 2002; Ryan, 1990) and climatic sensitivity (Rozas, 2005).

Climatic signals of VLA have changed during the 20th century (Figs. 11, 12) and these changes are more expressed than for TRW, likely due to stronger relationship with temperature during dormancy (Figs. 11, 14). Sensitivity of VLA to temperature in January–March has decreased after about 1925–1975 (Fig. 13), which can be explained by warmer winters (Briffa et al., 1998; Lizuma et al., 2007) and reduced cold damage to cambium (Pearce, 2001; Zhu et al., 2000) and amounts of stored assimilates used to decrease damage caused by low temperature (Essiamah and Eschrich, 1985; Morin et al., 2007). Previous analysis has shown significance of April temperature, which can explain both correlation and response function throughout the study period (Figs. 13, 14). However the effect of April temperature might potentially weaken in the future due to climate warming (IPCC, 2007; Lizuma et al., 2007), suggested by loss of response function in recent intervals (Fig. 14). The response was insignificant also in the beginning of the 20th century, particularly in the western region, hence the effect of April temperature has not always been strictly limiting. June precipitation appeared to be significant for VLA in the middle of analyzed period (Fig. 13, 14) when the warming trend was less expressed (Lizuma et al., 2007), probably due to later springs. Increased temperature in December might prolong cold hardening (Morin et al., 2007, Repo et al., 2008), subjecting oak to more rapid temperature in later part of December, which can do damage (Gu et al., 2008), thus explaining increasing correlation with December temperature.

Positive effect of temperature in May–October of the year p.t.f. on VLA associated with amounts of stored assimilates (Barbaroux and Breda, 2002; White et al., 1999; Xu and Griffin, 2006), have weakened, likely due to warmer climate (Lloyd and Fastie, 2002; Merian et al., 2011). Positive effect of June temperatures of the year p.t.f. has become significant particularly in the cooler western region (Fig. 13), probably assimilation is higher in years with a warmer June (Jurik et al., 1988; Morecroft and Roberts, 1999). The positive effect of July temperature of the year p.t.f. on VLA observed in the later part of the analyzed period (Fig. 13) (which contradicts the effect of water deficit as observed for TRW) can be explained by negative relation between TRW and VLA (Tardif and Conciatori, 2006). Possibly under raised temperatures (and water deficit), more assimilates can be stored for next year, as wood increment is decreased (Slot et al., 2012).

4.4.6 Age dependency of climate-growth (TRW) relationship

In the studied site (MOR), high-frequency variation of TRW was similar between younger and older trees, as expected for oaks in one stand. However, the amplitude of index values was higher in younger trees (Fig. 16). This can be explained by an age-related decrease of TRW (Cook et al., 1992a; Speer, 2010), resulting in a higher range of TRW in younger oaks (Table 11), leading to higher sensitivity and EPS values (Wigley et al., 1984). However higher interseries correlation suggested that high-frequency variation was more similar between older trees, presumably due to higher sensitivity to abiotic factors (Rozas, 2005). With age, maintenance costs rise, increasing the importance of stored reserves for growth (Rust and Roloff, 2002; Ryan, 1990) and causing higher AC of TRW in older oaks (Table 11).

A higher number of tested climatic factors showing significant effect (correlation and response function) and higher coefficient values for older oaks (Fig. 17), confirming age-dependent increase of sensitivity (Rozas, 2005). Younger and older oaks showed significant effect to temperature in autumn and hence length of growing season, (White et al., 1999). However, significant response to September temperature suggests that this effect was stronger for younger trees, presumably furthered by competition in the stand. Older oaks showed significant correlation with spring temperatures, which might be explained by increasing susceptibility to frost damage under decreasing assimilation (Alden and Hermann, 1971; Morin et al., 2007). Monthly precipitation sum was significant only for older oaks (Fig. 17) that can be explained by age-related increase of VLA (Fig. 8) and susceptibility to embolism (Tyree and Zimmermann, 2002). Embolization thus can affect formation of latewood in July–August (Morecroft and Roberts, 1999; van der Werf et al., 2007) due to physiological water stress and decreased assimilation (Pallardy, 2008). Although such an effect was observed for TRW in the eastern region, apparently it might be significant for older oaks also in the western region. Negative correlation with November precipitation might be explained by excess soil moisture as discussed above. Negative effect of precipitation in May (significant correlation and response) might be explained by formation of larger vessels in response to high precipitation (Campelo et al., 2010; Fonti and Garcia-Gonzalez, 2008; Garcia-Gonzalez and Eckstein, 2003) thus increasing susceptibility to embolism later in the season

(Cochard et al., 1992; Tyree and Cochard, 1996; Tyree and Zimmermann, 2002). Significant response to temperature in May of the year p.t.f. might be related with higher effect of previous growth in older oaks. Only TRW data was obtained from other studies, thus VLA was not measured.

4.5 Recent changes in wood formation

4.5.1 TRW

TRW exhibits an age related reduction (Cook et al., 1992a; Speer, 2010). However, on top of this, during the recent 30 years TRW has rapidly reduced below the expected trend with decreasing spread between sites (Figs. 8, 14). This reduction of TRW and its sensitivity, likely due to growth suppression during the last 30 years (Fig. 18, Table 12), was observed throughout Latvia. Occurrence of abrupt and synchronous reduction of TRW suggests that this has been caused by large-scale environmental factors (Drobyshev et al., 2008a; Kelly et al., 2002), such as climate. The decrease of TRW during the recent 30 years was stronger in the more continental eastern region (Fig. 18, Table 12), thus confirming relation with climatic factor. Decrease of TRW (decline) is considered to be caused by a complex of environmental factors and climate (weather) can have triggering effect (Führer, 1998; Helama et al., 2009; Siwecki and Ufnalski, 1998; Thomas et al., 2002; Wargo et al., 1983). TRW reduction in Latvia might have been triggered by an extremely cold December and July of 1978 and 1979 (Table 9), which might have caused cold damage (Pearce, 2001; Repo et al., 2008) and reduced assimilation in summer (Wargo, 1996). Effect of cold damage can be enhanced by rapid changes of weather. In 1978, November was warm (4–5 ^{o}C above average), but in the second decade of December the temperature suddenly dropped (reaching -43 ^{o}C in eastern Latvia) and temperature during the second part of December remained 16–18 ^{o}C below average (LEGMC). Considering that cold hardening was delayed in response to a warm November (Alden and Hermann, 1971; Morin et al., 2007), the cold effect (a rapid drop of temperature) was likely strong for the insufficiently cold-hardened oaks. However tree-rings of 1979 were not extremely narrow (Fig. 18) likely due to effect of previous growth (AC, Appendix 5), but the reduction of TRW might be considered as a subsequent effect. As variation of TRW generally depends on latewood width (Zhang, 1997), the observed decrease might be promoted by conditions in summer (i.e. water deficit), as shown by effect of summer precipitation and temperature, particularly in the eastern region (Figs. 13, 14). Although lasting reduction of TRW is considered as one of the symptoms of oak decline (Drobyshev et al., 2007b; Helama et al., 2009; Wargo et al., 1983), the decline in Latvia is disputable, as during sampling the oaks appeared visually healthy without obvious reduction of crowns.

It can take a up to several decades for oak to recover after intense stress (Epron and Dreyer, 1993; Sonesson and Drobyshev, 2010; Wazny et al., 1991), and the growth of oaks might have improved in recent years, as a slight increase of TRW in several sites occurred in 2008–2010 (Fig. 8). In Southern Sweden (which is near the northern distribution limit of oak), widespread reduction of oak increment has also been reported during the second half of the 20th century, but growth improvement (recovery) of previously suppressed oaks was observed during the last decade (Sonesson and Drobyshev, 2010). Although decreased TRW near the treeline in Alaska was observed during 1950–2000 in response to warming (increased competition and water deficit), a recovery was also observed in the last decade of the 20th century (Lloyd and Fastie, 2002; Wilmking et al., 2004). Wazny et al. (1991) also showed gradual improvement of growth in Poland after decrease caused by water deficit.

4.5.2 VLA

Increased spread between site time-series of VLA can be observed during the recent 30 years (Fig. 8), which stands out against the slight increase during 1900–1979. However, in contrast to decreasing TRW, VLA showed a significant increase only in the eastern region, while VLA remained at the previous level in the western region (Fig. 18, Table 12). The onset of change and spread of VLA co-occurred with changes in TRW, which again might be related to extreme cold in December 1978 (Table 9). As AC in VLA is lower compared with TRW (Table 3), EV in the tree-ring of 1979 were extremely small (exhibiting a strong negative pointer year (Fig. 15).

Variation of EV size (VLA) has been related with availability of water in the previous and current year (Table 6; Fig. 11; Campelo et al., 2010; Fonti and Garcia-Gonzalez, 2008; Garcia-Gonzalez and Eckstein, 2003). As shown above, under a continental climate, occurrence of water deficit is more probable (Figs. 13, 14), thus, EV would be expected to be smaller, to avoid embolism (Cochard et al., 1992; Tyree and Cochard, 1996; Tyree and Zimmermann, 2002). However, VLA in the eastern region was larger than in western region in the period 1950–1980 and increased during the last three decades, increasing susceptibility to embolism. Larger VLA in the eastern region during 1950–1980 might be explained by higher amplitude of diurnal temperature in the second part of April (LEGMC), where the moderating effect of Baltic Sea is weaker (Temņikova, 1975), resulting in larger vessels due to slower differentiation (Aloni and Zimmermann, 1983; Pallardy, 2008; Zakrzewski, 1983). As VLA showed a significant relationship with winter and spring temperatures (Figs. 13, 14), increase of VLA during the past three decades also might be facilitated by warming (Lizuma et al., 2007). An increase of VLA occurred only in the eastern region. In the western region, under milder climate, VLA might be less subjected to warming. Under a maritime climate, where spring starts earlier and temperatures are more stable (LEGMC), differentiation of cambial cells can be faster, resulting in smaller EV (Aloni and Zimmermann, 1983; Pallardy, 2008; Zakrzewski, 1983). Another explanation for increase of VLA in the eastern region (Fig. 18) might be attributed to inverse relationship between VLA and TRW (Tardif and Conciatori, 2006). In the western region, the necessary transported amount of water is lower in the milder climate (Friedrichs et al., 2008; Pallardy, 2008), and thus larger EVs may not be formed.

VLA also decreased in sensitivity (Table 12), which can be explained by greater physiological regulation of EV under decreased TRW. In narrower rings there is less space for different combinations of EV of different size, and thus EV with size close to the “forced” optimum are formed, decreasing variation. Although Fonti et al. (2009b) related (positively) long-term variation of VLA with vigour of the tree, apparently, under suppressed growth, the opposite effect might be observed. The increase of VLA during the past 30 years seems to be steeper than the tree-vigour related increase described by Fonti et al. (2009b). Decreased sensitivity can also be explained by increase of winter temperature (Fig. 5). Apparently winter temperatures are becoming less significant for wood formation (Figs. 13, 14), and thus the variation of VLA related with these factors is smaller. For greater understanding of the VLA increase, precise estimates of vessel density (from large diameter cores) are needed.

5 Conclusions

I VLA, as a proxy for climatological studies of pedunculate oak in Latvia (close to oaks northern distribution limit), showed stronger and spatially and temporally more stable climatic signals in Latvia than did TRW. A 5-mm increment core can be used to obtain representative samples, but wider cores would ease measurement and quality control and decrease bias at the stand level. From the tested tree-ring proxies, TRW and VLA were the most sufficient.

II TRW and VLA showed weak relationship, suggesting different sources of variation, and thus can be used to obtain additional information from the same material.

III A continuous gradient of high-frequency variation of wood formation, related with continentality of climate (distance from the sea) is evident in Latvia. Two regions (western and eastern part of Latvia) of differing wood formation and climatic signals can be distinguished. Significant differences in climatic signals can be observed over a distance of ~ 150 km. Although effect of climatic factors is stronger in more continental eastern Latvia, climatic signals in TRW also largely depends on habitat, presumably microclimatic conditions.

IV TRW in the western region is affected mainly by temperature in early spring and early summer, while August precipitation and temperature in previous season’s summer (July and August) limits TRW in the eastern region of Latvia. VLA is controlled by temperature during the dormant period and spring (April) and precipitation has minimal effect.

V Regional chronologies for western and eastern parts of Latvia have been established. Temperature of previous year July and August, and August precipitation (eastern region of Latvia) showed the strongest signals in regional chronologies. December and April temperature showed strongest effect on VLA regional chronologies. Winter and spring NAO has stronger effect on VLA than TRW.

VI Climatic signals significant for wood formation have changed during the 20th century. TRW has lost sensitivity to winter (February–March) temperature and has increased in sensitivity to previous year July temperature. Increasing sensitivity of TRW to August precipitation in the eastern region suggests increasing effect of water deficit (drought). VLA showed common changes in both regions: loss of sensitivity to February–March temperature and an increase of sensitivity to December temperature.

VII Occurrence of pointer years in TRW is related with spring and summer temperatures in the western region and February temperature in the eastern region of Latvia. The strongest negative pointer years in TRW are caused by extremely low temperatures in the dormant period. The strongest positive pointer years are associated with warm and moist summers. Pointer years in VLA are caused by extreme cold events during the dormant period. The strongest pointer years in VLA are more discrete than in TRW.

VIII Climate-growth (TRW) relationships are affected by age of oaks. With age, the effect of precipitation intensifies, presumably due to increase of VLA or increasing maintenance coasts.

IX Although wood increment (TRW) is not directly and strongly linked with temperature in the dormant period, VLA high-frequency variation indicates limitation of growth and northern distribution of pedunculate oak by temperature in the dormant period via conductive properties of wood.

X TRW and VLA have synchronously changed during the past 30 years, particularly in eastern region of Latvia. TRW show a significant decreasing trend and VLA an increasing trend while loosing sensitivity. Increasing VLA suggests increasing susceptibility for water deficit. These changes seem to have been triggered by a drastic weather shift in winter of 1978/1979.

XI Considering high dependence of VLA on climatic factors and low dependence on previous growth (AC), this proxy is appropriate and valuable for further climatological studies (reconstruction), despite time consuming measurement process.

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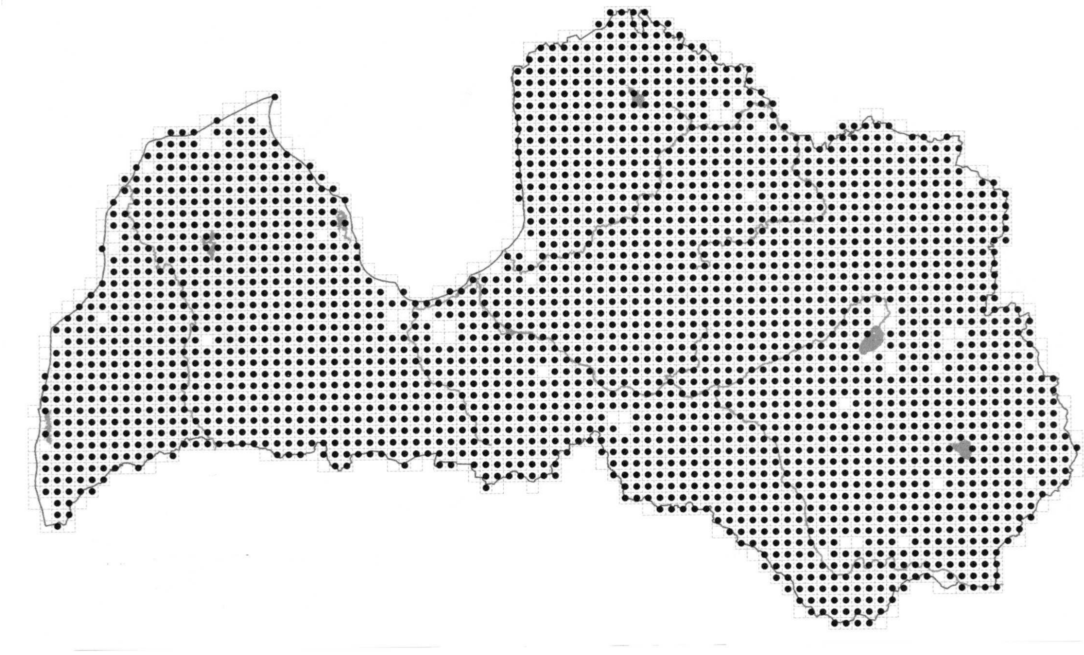
Appendix

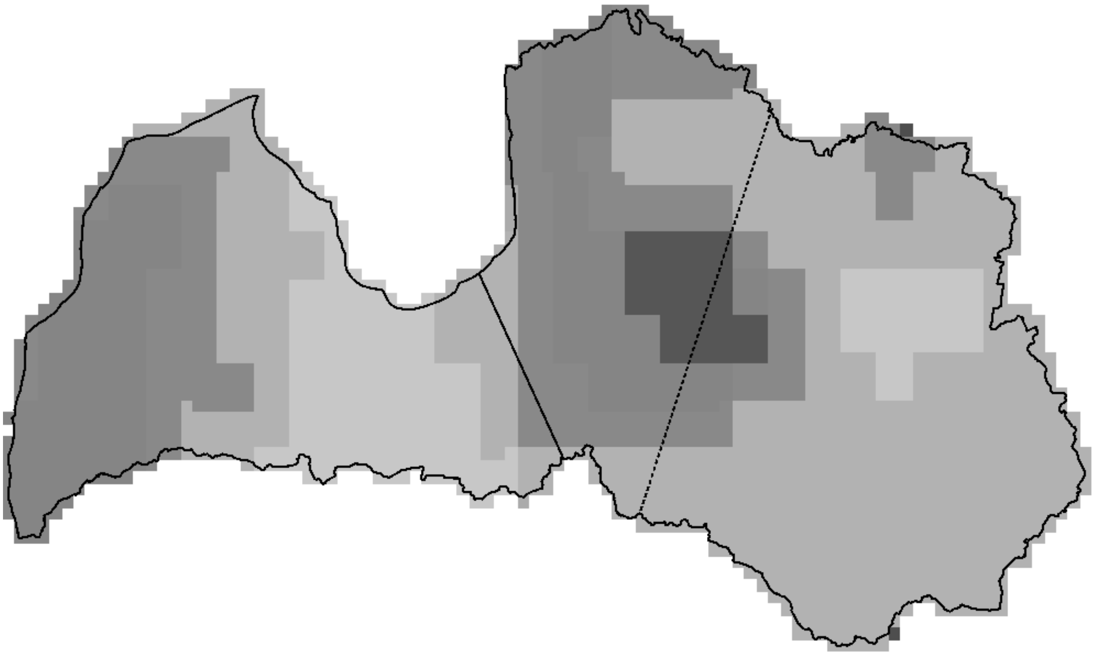
Appendix 1

Distribution of pedunculate oak in Latvia (grid 5x5 km) (Laiviņš et al., 2009).



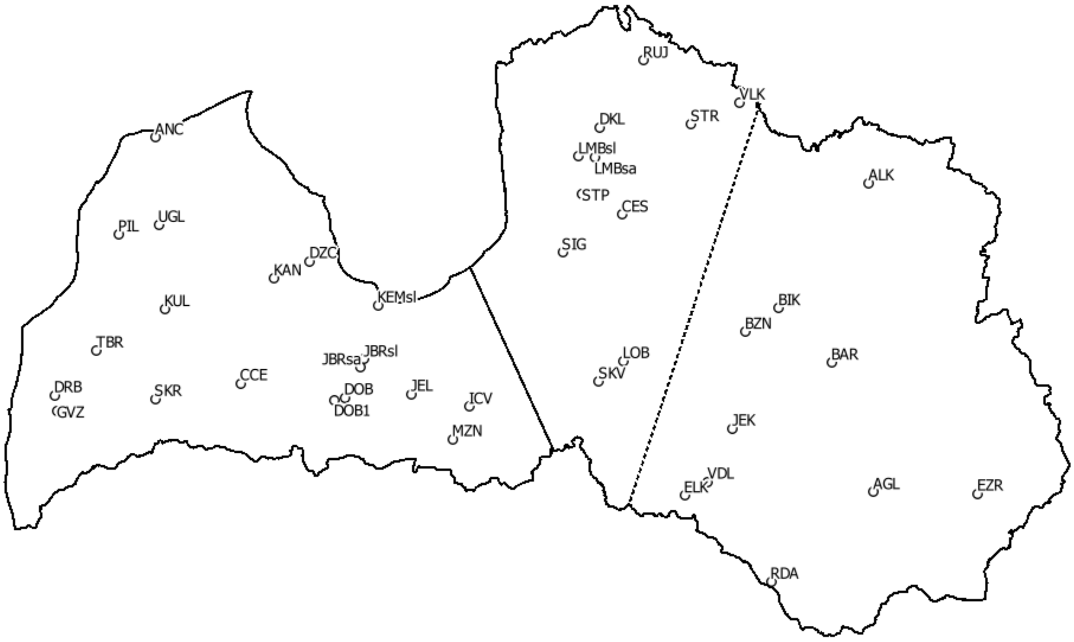
Appendix 2

Distribution of precipitation in Latvia (colour intensity). Lines represent sub-regions of continentality.



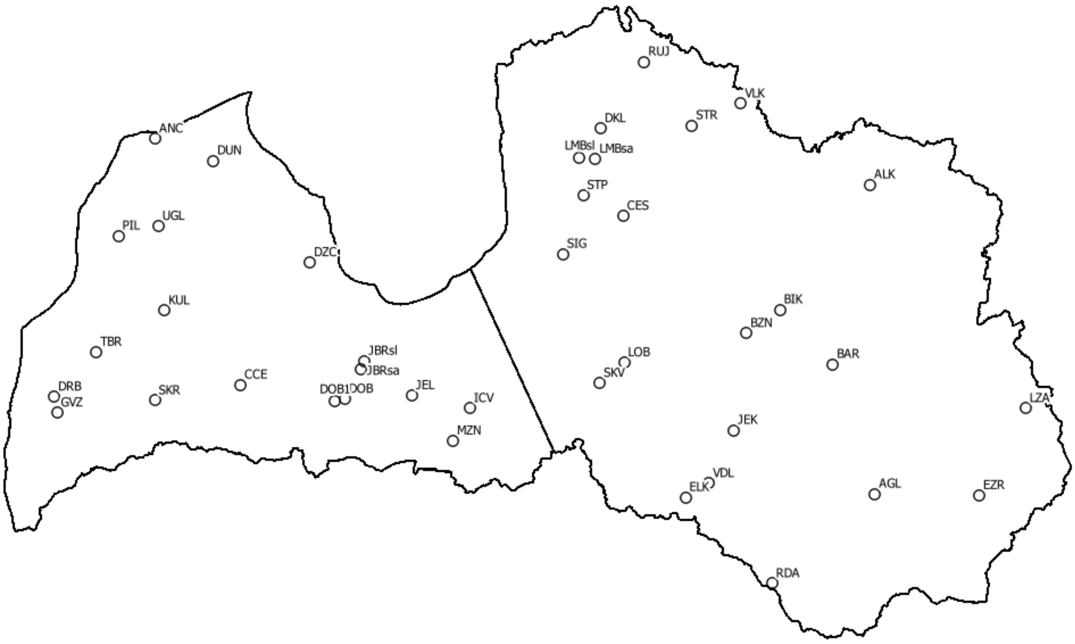
Appendix 3

Location of sampling spots (stands) used for determination of regional differences in high frequency variation of wood formation (TRW and VLA).



Appendix 4

Location of sampling plots (stands) used for construction of regional chronologies of TRW and VLA. Regional chronologies were built from data from 22 and 18 stands respectively.



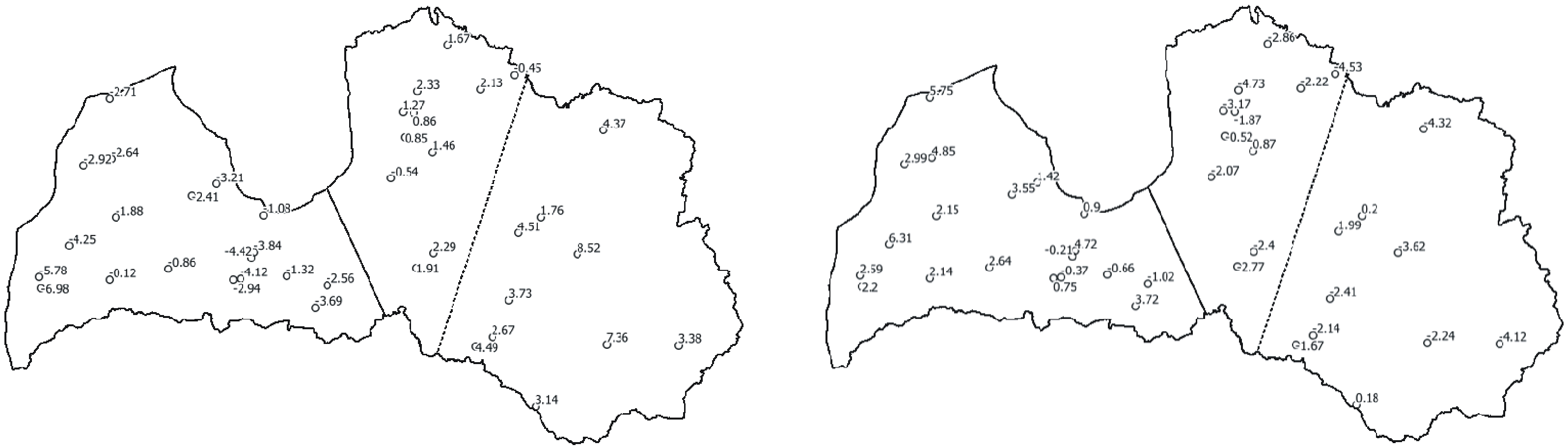
Appendix 5

Statistics of measurement time-series for TRW and VLA for whole and common periods. Range of measurements (10^{-2} mm for TRW and 100 μm^2 for VLA), mean autocorrelation (AC) calculated for trees in a site, mean sensitivity (SENS), mean EPS (calculate for trees in a site), mean interseries correlation (IC, calculated between trees in site; ICs calculated between mean time-series of sites).

	TRW																	VLA								
	Whole period									1899–2010																
Site	Period	Min	Max	Mean	AC	SENS	EPS	IC	ICs	Min	Max	Mean	AC	SENS	EPS	IC	ICs	Period	Min	Max	Mean	AC	SENS	EPS	IC	ICs
AGL	1805–2010	28	436	163	0.76	0.25	0.94	0.67	0.43	69	385	141	0.60	0.21	0.91	0.71	0.47	1899–2010	217	646	414	0.55	0.15	0.91	0.60	0.60
ALK	1896–2010	104	590	294	0.77	0.19	0.88	0.57	0.48	104	590	269	0.77	0.19	0.88	0.58	0.41	1899–2010	123	605	319	0.73	0.18	0.96	0.58	0.58
ANC	1697–2009	46	405	145	0.80	0.22	0.79	0.45	0.30	52	318	130	0.75	0.19	0.84	0.46	0.51	1899–2009	101	411	241	0.31	0.24	0.55	0.34	0.34
BAR	1845–2009	50	465	154	0.73	0.26	0.93	0.69	0.31	51	399	128	0.73	0.24	0.94	0.71	0.29	1899–2009	89	419	241	0.47	0.22	0.90	0.56	0.56
BIK	1851–2010	70	526	149	0.76	0.20	0.92	0.74	0.64	69	422	126	0.63	0.18	0.92	0.75	0.71	1899–2010	223	737	452	0.32	0.17	0.81	0.58	0.58
BZN	1892–2009	38	546	192	0.77	0.30	0.94	0.69	0.60	39	546	189	0.77	0.30	0.95	0.69	0.65	1899–2009	76	544	270	0.61	0.24	0.96	0.38	0.38
CCE	1834–2009	48	418	112	0.85	0.19	0.79	0.61	0.57	54	237	94	0.75	0.17	0.86	0.66	0.55	1899–2009	111	422	230	0.32	0.24	0.71	0.31	0.31
CES	1759–2010	38	435	152	0.80	0.20	0.87	0.56	0.58	61	322	142	0.69	0.18	0.88	0.60	0.68	1899–2010	230	643	402	0.52	0.16	0.88	0.42	0.42
DKL	1825–2010	50	480	144	0.75	0.26	0.93	0.66	0.44	59	334	123	0.60	0.26	0.93	0.68	0.51	1899–2010	143	612	305	0.53	0.21	0.87	0.47	0.47
DOB	1826–2009	53	510	120	0.84	0.19	0.85	0.49	0.56	35	240	111	0.84	0.18	0.88	0.61	0.56	1899–2009	114	439	244	0.47	0.20	0.76	0.33	0.33
DOB1	1818–2009	44	416	131	0.78	0.23	0.85	0.60	0.68	53	268	125	0.60	0.22	0.88	0.58	0.73	1899–2009	178	581	363	0.31	0.20	0.67	0.30	0.30
DRB	1798–2009	37	331	152	0.73	0.24	0.89	0.62	0.41	57	319	143	0.68	0.22	0.89	0.62	0.50	1899–2010	115	439	244	0.44	0.21	0.70	0.27	0.27
DUN	1852–2008	60	491	143	0.82	0.18	0.78	0.54	0.59	67	398	125	0.79	0.18	0.81	0.55	0.60	1899–2008	154	561	284	0.41	0.21	0.65	0.09	0.09
DZC	1782–2008	38	364	113	0.71	0.23	0.87	0.59	0.52	46	217	113	0.63	0.19	0.86	0.56	0.57	1900–2008	198	514	327	0.31	0.16	0.70	0.32	0.32
ELK	1894–2010	82	563	217	0.81	0.19	0.90	0.70	0.61	82	486	178	0.82	0.19	0.90	0.70	0.60	1899–2010	142	626	325	0.68	0.18	0.94	0.45	0.45
EZR	1809–2010	42	374	109	0.72	0.24	0.89	0.69	0.43	49	228	88	0.55	0.22	0.86	0.71	0.53	1899–2010	167	582	324	0.53	0.18	0.90	0.56	0.56
GVZ	1780–2009	37	421	148	0.79	0.23	0.81	0.62	0.43	49	321	140	0.72	0.22	0.86	0.67	0.39	1899–2009	146	454	275	0.28	0.19	0.60	0.36	0.36
ICV	1862–2009	59	466	208	0.79	0.22	0.93	0.64	0.52	59	458	193	0.80	0.22	0.93	0.70	0.60	1899–2009	119	552	277	0.46	0.23	0.81	0.32	0.32
JBRsa	1773–2009	56	454	126	0.75	0.20	0.90	0.54	0.49	60	293	102	0.73	0.18	0.92	0.52	0.44	1899–2009	128	384	226	0.38	0.22	0.50	0.29	0.29
JBRsl	1834–2009	30	388	187	0.74	0.25	0.89	0.73	0.46	64	381	153	0.70	0.22	0.90	0.74	0.42	1899–2009	124	408	251	0.37	0.20	0.72	0.35	0.35
JEK	1831–2010	86	469	234	0.74	0.19	0.83	0.63	0.56	86	465	212	0.77	0.19	0.83	0.64	0.69	1899–2010	127	606	293	0.74	0.18	0.94	0.36	0.36
JEL	1785–2009	46	392	170	0.75	0.23	0.93	0.56	0.53	52	372	138	0.73	0.22	0.93	0.60	0.66	1899–2009	123	479	246	0.45	0.19	0.88	0.36	0.36
KAN	1809–2008	50	376	135	0.78	0.20	0.83	0.48	0.56	59	249	108	0.63	0.18	0.87	0.52	0.65	1906–2008	179	530	297	0.31	0.18	0.45	0.13	0.13
KEMsl	1754–2007	61	427	200	0.76	0.25	0.97	0.56	0.43	78	404	170	0.66	0.22	0.91	0.67	0.58	1906–2007	146	390	255	0.28	0.18	0.06	0.22	0.22
KUL	1892–2009	43	465	184	0.80	0.24	0.93	0.75	0.57	43	411	160	0.78	0.24	0.93	0.77	0.58	1899–2009	84	324	194	0.40	0.23	0.75	0.31	0.31
LMBsa	1826–2009	50	435	176	0.73	0.22	0.92	0.66	0.39	74	358	161	0.64	0.21	0.91	0.68	0.68	1899–2009	150	505	292	0.43	0.20	0.81	0.48	0.48
LMBsl	1710–2009	40	404	160	0.75	0.27	0.89	0.65	0.61	53	356	138	0.66	0.26	0.91	0.69	0.63	1899–2009	135	480	303	0.29	0.24	0.70	0.39	0.39
LOB	1816–2008	45	358	125	0.70	0.24	0.95	0.61	0.49	46	281	101	0.63	0.24	0.93	0.63	0.57	1900–2008	142	676	310	0.51	0.19	0.87	0.34	0.34
MOR	1789-2009	37	370	161	0.76	0.26	0.90	0.56	0.50	34	326	145	0.77	0.25	0.90	0.55	0.53	-	-	-		-	-	-	-	-
LZA	1844–2010	79	655	122	0.76	0.19	0.54	0.35	0.34	79	625	102	0.85	0.19	0.51	0.35	0.34	1899–2010	143	569	361	0.64	0.18	0.69	0.18	0.18
MZN	1777–2009	39	499	130	0.69	0.27	0.88	0.64	0.51	46	261	118	0.47	0.25	0.86	0.63	0.60	1899–2009	159	620	378	0.39	0.22	0.54	0.26	0.26
PIL	1813–2009	43	350	121	0.74	0.21	0.92	0.63	0.45	58	241	108	0.68	0.18	0.90	0.65	0.53	1899–2009	77	331	204	0.39	0.21	0.67	0.26	0.26
RDA	1830–2009	23	438	126	0.77	0.29	0.94	0.56	0.37	25	309	123	0.71	0.27	0.90	0.62	0.51	1899–2009	150	547	335	0.27	0.23	0.72	0.35	0.35
RUJ	1897–2010	41	483	172	0.83	0.22	0.94	0.70	0.48	41	483	143	0.84	0.21	0.94	0.70	0.46	1903–2010	93	540	249	0.73	0.19	0.95	0.44	0.44
SIG	1792–2010	30	358	117	0.73	0.25	0.91	0.68	0.58	42	270	98	0.66	0.24	0.90	0.69	0.69	1899–2010	176	563	324	0.60	0.16	0.91	0.57	0.57
SKR	1837–2009	55	440	127	0.76	0.19	0.78	0.59	0.52	63	262	110	0.68	0.17	0.83	0.62	0.55	1899–2009	144	500	288	0.42	0.19	0.79	0.40	0.40
SKV	1894–2010	68	619	253	0.84	0.21	0.93	0.74	0.64	71	619	226	0.84	0.21	0.93	0.74	0.67	1903–2010	94	650	309	0.75	0.20	0.97	0.49	0.49
STP	1831–2010	53	447	159	0.81	0.21	0.93	0.66	0.64	61	321	138	0.71	0.20	0.93	0.68	0.66	1899–2010	112	453	247	0.56	0.19	0.88	0.35	0.35
STR	1835–2010	41	354	126	0.73	0.22	0.84	0.61	0.53	46	294	106	0.67	0.21	0.85	0.59	0.53	1899–2010	138	494	282	0.55	0.17	0.86	0.39	0.39
TBR	1843–2009	52	332	164	0.67	0.20	0.88	0.60	0.56	75	292	133	0.65	0.18	0.87	0.57	0.55	1899–2009	141	580	315	0.33	0.24	0.73	0.22	0.22
UGL	1787–2009	40	399	122	0.79	0.21	0.90	0.62	0.49	54	255	121	0.73	0.18	0.91	0.64	0.52	1899–2009	139	493	293	0.31	0.22	0.73	0.27	0.27
VDL	1838–2010	44	424	195	0.82	0.21	0.94	0.64	0.57	59	424	177	0.79	0.20	0.93	0.68	0.66	1899–2010	109	476	261	0.64	0.18	0.93	0.50	0.50
VLK	1862–2010	60	485	193	0.71	0.24	0.72	0.56	0.50	65	456	162	0.68	0.23	0.76	0.60	0.55	1899–2010	66	393	235	0.66	0.20	0.91	0.54	0.54

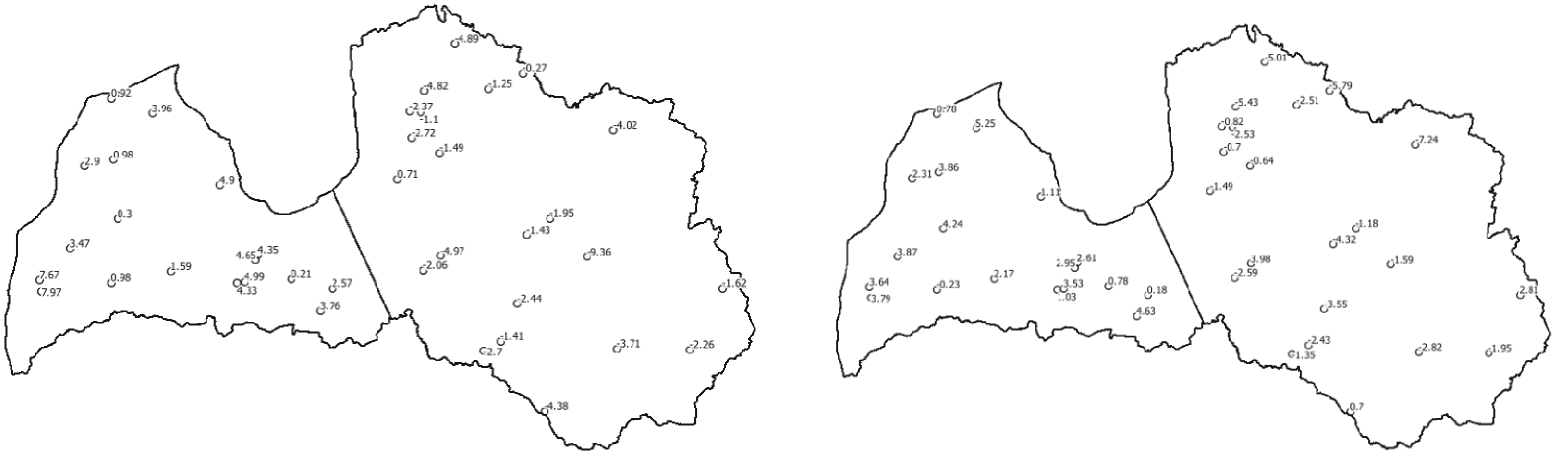
Appendix 6

PCA scores of sampling plots overlain on their geographic locations. Two or three regions of Latvia can be arbitrarily distinguished based on PCA scores.



TRW residual

VLA residual



TRW pointer year

VLA pointer year