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ORIGINAL PAPER

Influence of climate on tree-ring and earlywood vessel formation in *Quercus robur* in Latvia

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Abstract We studied the effects of climatic factors on tree-ring width and vessel lumen area (VLA) in earlywood of English oak (*Quercus robur* L.) in Latvia. Cores were obtained from healthy canopy oaks in 40 stands located across Latvia. Tree-ring widths and VLA were measured. Principal component analysis was used to arrange the sites along gradients of response of tree-ring width and earlywood to environmental factors. Significant relationships of tree-ring width and mean VLA with climatic factors (mean monthly temperature and precipitation sum) were determined by correlation analysis. Relationships between tree-ring, early- and latewood widths were tested in three sampled stands. The patterns of response of VLA and tree-ring width to environmental factors differed in relation to a west–east gradient of increasing continentality. Three regions of Latvia (western, central and eastern) were distinguished along this gradient. Responses to climate differed between tree-ring width and mean VLA. Occurrence of significant correlations between climatic factors and the proxies differed between regions, likely due to regional differences in temperature and precipitation. Tree-ring width correlated with climatic factors (most commonly with March, May and June temperature and August precipitation of the current growing season and July–August temperatures of the previous growing season); VLA was more strongly related to climatic factors, particularly with temperature in winter and spring months. The proportion of significant correlation coefficients with climatic factors differed between the regions. Among sites, significant correlation of tree-ring width with temperature in spring and summer was more frequent in the western region, while correlation with winter temperature of the previous growing season and precipitation in August was more frequent in the eastern region. For VLA, the frequency of significant correlation coefficients with temperature in winter and spring was higher in the eastern region.

Keywords *Quercus robur* · Wood anatomy · Wood formation · Climatic gradient

Introduction

Climate change is causing shifts in the distribution ranges of many plants and animals (Carstens and Knowles 2007; Harrison et al. 2006; IPCC 2007; Sykes and Prentice 1996), which are most evident at their northern and southern distribution boundaries, and along altitudinal gradients (Bradshaw et al. 2000; IPCC 2007; Thuiller 2004; Walther et al. 2002). The expected shifts in species distribution can be forecasted, as long as knowledge of the limiting factors and dispersal abilities are available (Drobyshev et al. 2008; Guisan and Thuiller 2005; McKenney et al. 2007; Theurillat and Guisan 2001; Torres-Meza et al. 2009). Tree-ring series act as natural archives that store information on the past growth and environment (Fritts 2001; Schweingruber 1996; Speer 2010). The relationships between climate and dynamics of wood formation can thereby be used to determine if, and to what extent, the climatic factors are limiting growth of the respective tree species in different areas of their distribution ranges (Austin 2002; Drobyshev et al. 2008; Sykes and Prentice 1996; Walther et al. 2005). In the Northern Hemisphere, the northern distribution boundary of

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trees most often is limited by minimal temperatures (Fritts 2001).

Global climatic changes during the last 100 years have been most rapid after the 1970 (IPCC 2007). During the past ~40 years, European mean autumn to spring temperatures have risen by 0.9°C (Benestad 2005; IPCC 2007; Klavins and Rodinov 2010; Linderholm 2006; Morberg and Jones 2005), and the length of the growing season has increased by about 10 days (Kalvāne et al. 2009; Linderholm 2006; Menzel et al. 2006; Sparks and Menzel 2002). This warming might be expected to result in a northward shift of nemoral tree species, such as English oak (*Quercus robur* L.) (Drobyshev et al. 2008; Kullman 2008; Sykes and Prentice 1996). The northern distribution of oak extends up to Fennoscandia (EUFORGEN 2009; Jones 1959). If autumn to spring temperatures are limiting growth of oak at its northern distribution limit, then a range shift to the north might be forecasted.

Although oak can survive low temperatures in the dormant period, rapid decrease of temperature after strong thaws and during cold hardening and late spring frosts can significantly decrease wood increment (Jones 1959; Repo et al. 2008; Thomas et al. 2002; Wargo 1996). In central and southern Europe, tree-ring formation in oak can be limited by drought and high temperature in summer (Cedro 2007; Čufar et al. 2008; Fletcher 1974; Friedrichs et al. 2008; Garcia-Suarez et al. 2009; Kelly et al. 2002; van der Werf et al. 2007). In these regions, the predicted change in spring–summer precipitation amounts (IPCC 2007) might also lead to a range shift. However, in southern Sweden, where the climate is oceanic, summer precipitation and temperature, autumn temperature and temperature anomalies (i.e., arctic air masses) are the main climatic factors associated with tree-ring formation (Drobyshev et al. 2008).

Tree-ring width has been typically used to model the dynamics of wood formation in relation to climatic factors (Fritts 2001; Speer 2010). However, tree-ring width is affected by many environmental factors and also by the condition of the individual tree (Fritts 2001; Schweingruber 1996; Speer 2010). Since the 1970s with the progress of digital technologies and automation of measurements, the use of anatomical structures of wood has gained importance in dendrochronology (Eckstein and Frisse 1982; Fonti et al. 2009a, 2010; Woodcock 1989). Wood anatomical proxies, such as earlywood vessel (EV) parameters, can provide additional information about climatic factors, which are not evident in tree-ring width series (Fonti et al. 2009b, 2010; Matisons and Dauškane 2009).

In English oak, vessels are arranged in rings; the largest vessels are located in earlywood and the smallest in latewood (Jones 1959; Schweingruber 2007). The largest earlywood vessels are the main water conductive wood elements of ring-porous species (Carlquist 2001; Granier et al. 1994; Zimmermann 1964). Latewood vessels act as a backup water transport system in periods of drought (Leal et al. 2007). Compared to tree-ring width, variation in size of EV is considered to be more strictly related to environmental factors (less autoregressive) in the year of their formation (Campelo et al. 2010; Eckstein and Frisse 1982; Tardif and Conciatori 2006). Vessels (EV) in oak participate in water transport only in the year of their formation (Rozas et al. 2009). During the life of an oak, mean size of EV usually increases with tree age as a response to increased transport demand, while tree-ring width decreases (Funada et al. 2001; Leal et al. 2007; Tardif and Conciatori 2006). The size and density of EV have been shown to be related also with the physiological vigour of the tree (Fonti et al. 2009b; Thomas et al. 2002). An effect of environmental factors on EV before their formation has been observed for *Castanea sativa* (Fonti et al. 2007) and oak species (Campelo et al. 2010; Fonti et al. 2009b; Garcia-Gonzalez and Eckstein 2003; Tardif and Conciatori 2006). In the Mediterranean region, mean EV size was found to be better related to drought than tree-ring width (Campelo et al. 2010; Corcuera et al. 2004; George et al. 2002). However, in a study on *Quercus alba* and *Q. rubra* at their northern distribution limit in the USA, vessel lumen area of earlywood and tree-ring width showed similar relationships with climatic factors (Tardif and Conciatori 2006).

Further knowledge of the factors limiting growth of English oak at its northern distribution limit will aid in understanding forest adaptation to climate change. Considering that oak in Latvia occurs close to its northern distribution limit, where dormant season temperatures are harsher, we might expect that temperatures in winter and spring are the most important limiting factors. An effect of precipitation was hypothesised to be at best low, as a moisture deficit rarely occurs. In addition, considering that the climate in Latvia changes from maritime to continental in eastern direction we also thought that there might be regional differences in the limiting climatic factors. The aim of this study was to determine the effects of climatic factors on tree-ring width and EV area of English oak in different regions of Latvia.

Materials and methods

Study area and sampled stands

The study was carried out in Latvia, which is situated on the Eastern European plain in the temperate climate zone (Pūriņš 1975). Latvia is covered mostly by lowlands interspersed with low uplands. The maximum elevation is

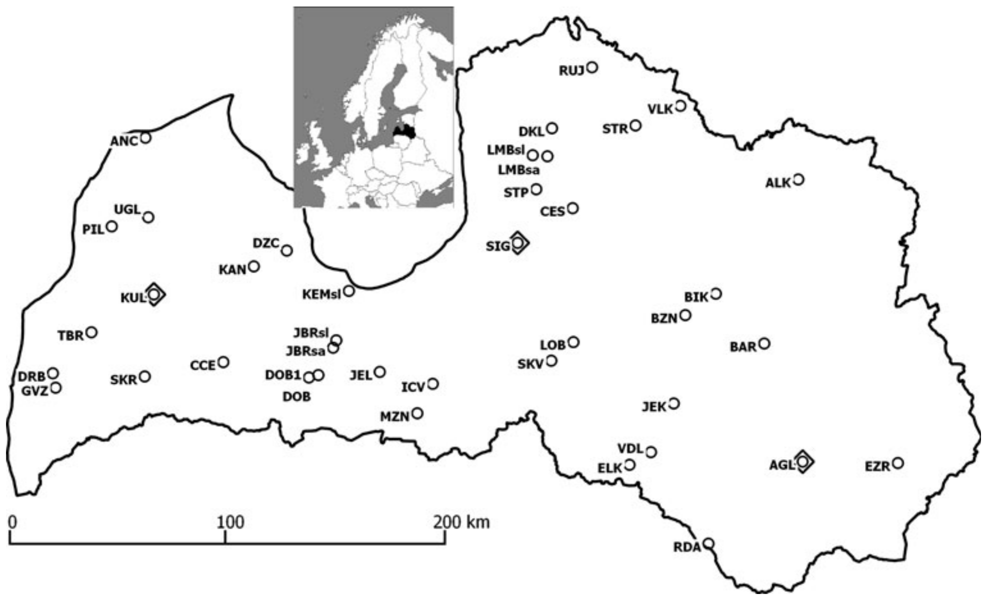

Fig. 1 Location of sampled stands (in stands indicated by *squares*; latewood, earlywood and ring width and VLA and earlywood width were compared)

312 m a.s.l. and the area above 200 m a.s.l. occupies only 2.5% of the total area of the country. The most common soil types in Latvia are podsols and gley soils (Nikodemus et al. 2008).

The climate in Latvia is mild due to moist air masses crossing from the Atlantic Ocean and the Baltic Sea. The climate changes from maritime to continental in the west to east direction. According to data from the Latvian Environment, Geology and Meteorology Agency, mean monthly temperature ranges from −3 to −7°C in January and from 16 to 17.5°C in July (from coastal to eastern regions); extreme temperatures were −43.2°C and +34.6°C in January (1956) and July (1943), respectively. The mean 120-year annual temperature is about 5°C. Annual precipitation is 550 mm in central regions and 850 mm in coastal and upland regions. The climate is rather moist and precipitation usually exceeds evapotranspiration. The vegetation period extends from mid April to mid October.

In Latvia, English oak is close to its northern distribution boundary; the northern distribution limit is approximately 500 km to the north (Estonia and southern Finland) (Jones 1959, Hytteborn et al. 2005). Oak is common in Latvia, but usually has low abundance in stands (Laiviņš et al. 2009). The relative area of oak-dominated stands is ∼0.3% of the total forest area and the mean size of an oak stand is about 1 ha (Latvia State Forest Service). English oak is considered as a species that occurs mostly on clay soils, but it also can occur on poor soils under a conifer overstorey and on dunes (den Ouden et al. 2007; Hytteborn et al. 2005). As Latvia is located in the hemiboreal forest zone, oak stands are often mixed with conifers and/or nemoral forest species (Hytteborn et al. 2005).

In this study, oak stands with an area of more than 1 ha and an age of more than 100 years were selected from the State Forest Service data base. A network of 40 stands (Fig. 1) located throughout the country was established. Characteristics of the sampled stands are shown in Table 1. Most of the studied stands occurred in dry habitats with flat relief. In almost all stands oak was mixed with other tree species. Stand ages (mean age of four oldest cores) ranged from 105 to 285 years.

Sample collection, preparation and measurement

In each sampled stand, healthy canopy oaks were cored with a 5-mm Pressler borer from opposite sides of the stem, ∼1.4 m above ground (Table 1); trees on slopes were cored on sides of the stem perpendicular to the slope. In addition, increment cores were obtained from other studies on the ecology of oak stands (stands BZN, DOB1, JEL, KAN, LOB and RDA). The number of sampled trees in these stands was higher, but in three stands (BZN, DOB1 and RDA) only one core had been taken from each tree. As the study aimed to test for regional differences within Latvia, it was aimed to obtain data from the largest number of stands possible, considering time and financial constraints on sample processing.

In the laboratory, the increment cores were glued into fixation planks and placed under pressure to dry. Fixed increment cores were gradually sanded (grain sizes from 80 to 400) using a vibration sander (Makita BO3700) until the cross-section surface of an increment core was uncovered. Dust from samples was removed with compressed air. Samples were rubbed with chalk to expose the earlywood vessels and to increase their contrast.

Table 1 Information on stands: geographic coordinates, soil moisture, relief, estimated stand age, tree species composition of stands and number of cored trees

Stand	Coordinates	Soil moisture	Relief	Stand age	Mixed stands	Number of cored trees
AGL	26°54′5E, 56°12′41N	Dry	Flat	206	No	10
ALK	26°57′37E, 57°22′54N	Dry	Slight slope	115	Yes	10
ANC	21°56′5E, 57°34′23N	Dry	Flat	215	Yes	10
BAR	26°38′59E, 56°42′30N	Moist	Flat	165	Yes	12
BIK	26°17′51E, 56°55′19N	Dry	Flat	160	Yes	10
BZN	26°3′41E, 56°50′11N	Dry	Flat	118	Yes	23
CCE	22°34′18E, 56°39′1N	Dry	Flat	176	Yes	10
CES	25°13′24E, 57°17′30N	Dry	Slight slope	252	Yes	10
DKL	25°4′35E, 57°37′28N	Dry	Flat	186	Yes	10
DOB	23°17′24E, 56°36′9N	Dry	Slight slope	184	Yes	10
DOB1	23°13′10E, 56°35′34N	Dry	Slight slope	192	Yes	18
DRB	21°17′42E, 56°35′0N	Dry	Flat	212	Yes	10
DZC	23°2′17E, 57°7′5N	Dry	Flat	227	Yes	10
ELK	25°36′45E, 56°13′19N	Dry	Flat	118	Yes	11
EZR	27°36′28E, 56°11′15N	Dry	Flat	202	No	10
GVZ	21°19′5E, 56°31′26N	Moist	Flat	230	Yes	10
ICV	24°8′56E, 56°34′9N	Dry	Flat	148	No	10
JBRsa	23°23′57E, 56°43′0N	Dry	Flat	237	No	8
JBRsl	23°25′22E, 56°44′51N	Moist	Flat	176	Yes	7
JEK	25°57′16E, 56°28′17N	Dry	Slope	180	Yes	10
JEL	23°45′0E, 56°37′4N	Dry	Flat	225	Yes	18
KAN	22°47′27E, 57°3′0N	Dry	Flat	201	Yes	22
KEMsl	23°30′52E, 56°57′9N	Moist	Flat	285	Yes	15
KUL	22°2′6E, 56°55′26N	Dry	Flat	118	Yes	11
LMBsa	24°55′26E, 57°30′52N	Dry	Flat	184	Yes	10
LMBsl	25°2′11E, 57°30′33N	Moist	Flat	220	Yes	10
LOB	25°12′42E, 56°44′12N	Dry	Flat	193	Yes	16
MZN	24°1′58E, 56°26′47N	Dry	Flat	223	Yes	10
PIL	21°41′53E, 57°12′5N	Dry	Flat	197	Yes	12
RDA	26°10′57E, 55°53′11N	Dry	Slight slope	180	Yes	14
RUJ	25°23′40E, 57°52′26N	Moist	Flat	114	No	10
SIG	24°48′2E, 57°9′5N	Dry	Slope	219	Yes	12
SKR	21°59′7E, 56°34′58N	Dry	Slight slope	173	Yes	10
SKV	25°2′33E, 56°39′38N	Dry	Flat	117	No	10
STP	24°56′45E, 57°22′21N	Dry	Slight slope	180	No	10
STR	25°43′19E, 57°37′44N	Dry	Slight slope	176	Yes	10
TBR	21°34′23E, 56°45′32N	Dry	Flat	167	Yes	12
UGL	21°58′31E, 57°14′35N	Dry	Flat	223	Yes	14
VDL	25°46′31E, 56°16′21N	Dry	Flat	173	Yes	10
VLK	26°4′18E, 57°42′21N	Dry	Slight slope	149	Yes	7

Then, they were scanned at 1,200 dpi resolution and 24-bit colour depth using an Epson GT-15000 scanner. Tree-ring, earlywood and latewood widths were measured using the program LignoVision v.1.36 (RinnTECH) with a precision of 0.01 mm. Tree-ring borders were set manually. For determination of mean vessel lumen area in earlywood (VLA), separate images of single tree-ring earlywood were cut from scanned core images using Paint

Table 2 Statistics of mean time series of tree-ring width and earlywood vessel area

Stand	Tree-ring width								Vessel lumen area in earlywood							
	Period	Min–max (10^{-2} mm)	Mean (10^{-2} mm)	AC	SENS	IC	EPS	ICs	Period	Min–max (10^{-4} mm^2)	Mean (10^{-4} mm^2)	AC	SENS	IC	EPS	ICs
AGL	1805–2010	69–385	163	0.59	0.20	0.71	0.90	0.47	1899–2010	217–646	414	0.55	0.15	0.60	0.91	0.80
ALK	1896–2010	104–590	294	0.77	0.19	0.57	0.87	0.49	1899–2010	123–605	319	0.72	0.17	0.57	0.95	0.59
ANC	1697–2009	52–318	145	0.74	0.18	0.46	0.85	0.61	1899–2009	101–411	241	0.31	0.24	0.33	0.55	0.50
BAR	1845–2009	51–399	154	0.72	0.24	0.70	0.93	0.36	1899–2009	89–419	241	0.47	0.22	0.55	0.89	0.68
BIK	1851–2010	69–423	149	0.62	0.18	0.74	0.91	0.78	1899–2010	223–737	452	0.31	0.16	0.58	0.81	0.74
BZN	1892–2009	39–546	192	0.76	0.30	0.69	0.94	0.65	1899–2009	76–544	270	0.60	0.24	0.37	0.95	0.65
CCE	1834–2009	54–237	112	0.75	0.16	0.65	0.86	0.60	1899–2009	111–422	230	0.32	0.23	0.30	0.70	0.55
CES	1759–2010	61–322	152	0.69	0.18	0.59	0.87	0.75	1899–2010	230–643	402	0.52	0.15	0.41	0.87	0.70
DKL	1825–2010	59–334	144	0.60	0.26	0.67	0.92	0.61	1899–2010	143–612	305	0.52	0.20	0.47	0.86	0.70
DOB	1826–2009	35–240	120	0.84	0.17	0.60	0.88	0.51	1899–2009	114–439	244	0.46	0.20	0.32	0.76	0.71
DOB1	1818–2009	53–268	131	0.59	0.22	0.58	0.88	0.72	1899–2009	178–581	363	0.30	0.20	0.29	0.66	0.75
DRB	1798–2009	57–319	152	0.67	0.21	0.61	0.89	0.53	1899–2010	115–439	244	0.43	0.21	0.26	0.70	0.41
DZC	1782–2008	46–217	113	0.63	0.19	0.55	0.85	0.56	1900–2008	198–514	327	0.31	0.15	0.31	0.70	0.58
ELK	1894–2010	82–486	217	0.81	0.19	0.69	0.89	0.57	1899–2010	142–626	325	0.67	0.17	0.44	0.94	0.81
EZR	1809–2010	49–228	109	0.54	0.21	0.71	0.86	0.52	1899–2010	167–582	324	0.53	0.17	0.55	0.90	0.77
GVZ	1780–2009	49–321	148	0.71	0.21	0.66	0.85	0.39	1899–2009	146–454	275	0.27	0.19	0.35	0.59	0.59
ICV	1862–2009	59–458	208	0.80	0.21	0.70	0.92	0.59	1899–2009	119–552	277	0.45	0.23	0.31	0.81	0.65
JBRsa	1773–2009	60–293	126	0.73	0.17	0.52	0.91	0.49	1899–2009	128–384	226	0.37	0.22	0.28	0.49	0.62
JBRsl	1834–2009	64–381	187	0.69	0.22	0.73	0.89	0.52	1899–2009	124–408	251	0.37	0.20	0.34	0.71	0.56
JEK	1831–2010	86–465	234	0.76	0.18	0.64	0.83	0.61	1899–2010	127–606	293	0.73	0.17	0.36	0.93	0.67
JEL	1785–2009	52–372	170	0.73	0.21	0.59	0.93	0.70	1899–2009	123–479	246	0.44	0.18	0.35	0.88	0.76
KAN	1809–2008	59–249	135	0.62	0.18	0.51	0.87	0.65	1906–2008	179–530	297	0.31	0.17	0.12	0.44	0.48
KEMsl	1754–2007	78–404	200	0.66	0.21	0.67	0.91	0.57	1906–2007	146–390	255	0.28	0.17	0.22	0.52	0.48
KUL	1892–2009	43–411	184	0.78	0.24	0.76	0.92	0.54	1899–2009	84–324	194	0.39	0.22	0.31	0.75	0.58
LMBsa	1826–2009	74–359	176	0.63	0.21	0.68	0.91	0.62	1899–2009	150–505	292	0.43	0.20	0.47	0.81	0.67
LMBsl	1710–2009	53–356	160	0.65	0.26	0.69	0.91	0.72	1899–2009	135–480	303	0.28	0.23	0.38	0.69	0.77
LOB	1816–2008	46–281	125	0.63	0.23	0.62	0.92	0.56	1900–2008	142–676	310	0.51	0.19	0.34	0.86	0.37
MZN	1777–2009	46–261	130	0.47	0.25	0.63	0.85	0.53	1899–2009	159–620	378	0.39	0.21	0.26	0.54	0.54
PIL	1813–2009	58–241	121	0.68	0.18	0.65	0.89	0.62	1899–2009	77–331	204	0.38	0.20	0.25	0.67	0.57
RDA	1830–2009	25–309	126	0.70	0.27	0.61	0.90	0.60	1899–2009	150–547	335	0.27	0.22	0.35	0.71	0.70
RUJ	1897–2010	41–483	172	0.83	0.21	0.70	0.94	0.54	1903–2010	93–540	249	0.73	0.18	0.44	0.95	0.65
SIG	1792–2010	42–270	117	0.66	0.23	0.68	0.90	0.71	1899–2010	176–563	324	0.59	0.16	0.57	0.91	0.84
SKR	1837–2009	63–262	127	0.68	0.17	0.62	0.82	0.58	1899–2009	144–500	288	0.42	0.19	0.39	0.78	0.60

Table 2 continued

Stand	Tree-ring width								Vessel lumen area in earlywood							
	Period	Min–max (10^{-2} mm)	Mean (10^{-2} mm)	AC	SENS	IC	EPS	ICs	Period	Min–max (10^{-4} mm^2)	Mean (10^{-4} mm^2)	AC	SENS	IC	EPS	ICs
SKV	1894–2010	71–619	253	0.83	0.20	0.74	0.93	0.72	1903–2010	94–650	309	0.74	0.19	0.48	0.96	0.79
STP	1831–2010	61–321	159	0.71	0.20	0.68	0.93	0.73	1899–2010	112–453	247	0.55	0.18	0.34	0.88	0.66
STR	1835–2010	46–294	126	0.67	0.21	0.58	0.85	0.67	1899–2010	138–494	282	0.55	0.17	0.39	0.85	0.71
TBR	1843–2009	75–292	164	0.64	0.17	0.57	0.87	0.49	1899–2009	141–580	315	0.32	0.24	0.21	0.73	0.34
UGL	1787–2009	54–255	122	0.72	0.18	0.63	0.90	0.61	1899–2009	139–493	293	0.31	0.22	0.26	0.72	0.58
VDL	1838–2010	59–424	195	0.79	0.20	0.68	0.93	0.67	1899–2010	109–476	261	0.64	0.18	0.50	0.93	0.78
VLK	1862–2010	65–456	193	0.68	0.23	0.59	0.76	0.66	1899–2010	66–393	235	0.66	0.20	0.53	0.90	0.68

Autocorrelation (AC), mean sensitivity (SENS), interseries correlation within stands (IC), expressed population signal (EPS) for stands and interseries correlation of mean site time series of a stand with a master series for all stands (ICs) were calculated for the period of 1908–2008

Shop Pro4 (JASC Inc.). Effort was made to include the maximum number of EV as far as possible. EV images were obtained for tree-rings formed from 1900 to 2008, except in cases where the oaks were younger. In total ~88,000 images were produced. The image area and number of EV in each image varied because tree-ring widths differed and because tree-rings were sometimes orientated diagonal to the axis of the core image. In cases of narrow and skewed tree-rings the numbers of EV per image were lower than in wide rings. If tree-rings were very narrow and skewed and earlywood images contained <8 vessels, core images was not cut, decreasing the sampling depth for the stand in the respective years. The proportion of skewed trees rings with number of EV >8, and which were used in the analysis, was <0.5%. For each earlywood image, VLA was measured using the program WinCell2007a (Regent Instruments). The analysis parameters in WinCell2007a were set to omit vessels crossing image boundaries. To exclude chalk debris from analysis, a filter was used to measure vessels with area from 65 to 1,200 × 10^{-4} mm^2. Grey level pixel classification (threshold ~215) for vessel recognition was adjusted manually. A batch function was applied to obtain data from vessel image groups (samples). Correct recognition of vessels was ensured by visual inspection of vessel detection of 30 randomly selected vessel images from different cores and dates before launching the batch function.

Data analysis

All tree-ring width and VLA series were crossdated visually and using COFECHA (Grissino-Mayer 2001). Data for the period from 1908 to 2008 were used. Mean time series of tree-ring width and mean VLA were derived for each tree and stand. Mean autocorrelation (AC), sensitivity (SENS), mean interseries correlation (IC) of trees within stands, and interseries correlation between mean time series of each stand with the master series calculated from the time series of all stands (ICs) were calculated using COFECHA (Grissino-Mayer 2001). Quality of VLA measurement was also verified by visually matching event years (pointer years). The expressed population signal (EPS) was calculated using the R program (Wigley et al. 1986). To eliminate autocorrelation, residual chronologies of tree-ring width and VLA were produced for each stand using ARSTAN (Cook and Holmes 1996).

To determine the main gradients in patterns of high-frequency variation (due to climatic variation) in tree-ring width and VLA, Principal Component Analysis (PCA) was conducted on residual chronologies of tree-ring width and of VLA using PC-ORD v.5.0 (McCune and Mefford 1999). Significance of PCA axes was evaluated by a Monte-Carlo test. The relationships of PCA axes with projected geographical coordinates of stands, habitat fertility (Latvia State Forest Service), age and proportion of oaks in stands were determined by Pearson correlation analysis. For three sites (AGL, SIG and KUL), Pearson correlation analysis was performed to test for significant relationships between time series of tree-ring, earlywood and latewood width and between earlywood width and VLA.

Climatic data recorded at the Riga Meteorological Station were obtained from the Latvian Environment, Geology and Meteorology Agency. The climatic factors used were mean monthly temperatures and precipitation sums from October$_{(t-1)}$ to September$_{(t)}$ and from October$_{(t-2)}$ to September$_{(t-1)}$ of wood formation. For comparing the climatic conditions between regions in Latvia, mean monthly temperatures and precipitation sums from Liepāja (western region), Rīga (central region) and Rēzekne (eastern region) were used. Relationships between climatic factors and tree-ring width and VLA chronologies were tested for the period 1908–2000 by Pearson correlation analysis using DENDROCLIM2002 (Biondi and Waikul 2004); the significance was determined using the bootstrap method.

Results

Mean width of tree-rings ranged from 1.09 to 2.94 mm and mean tree VLA ranged from 194 to 452 × 10^{-4} mm^2. Autocorrelation and EPS were lower for VLA than for tree-ring width. The sensitivity for both VLA and ring-width series was in the range from 0.15 to 0.24, except for three stand ring-width series with higher values. Tree-ring width showed higher interseries correlation than VLA (mean IC 0.64 ± 0.01 and 0.38 ± 0.02, respectively) for trees within stands. However, among sites, the mean interseries correlation (ICs) in tree-ring width mean series was lower than for VLA (mean ICs = 0.595 ± 0.015 and 0.64 ± 0.02, respectively) (Table 2).

Mean tree-ring width in stands showed a slight to strong decreasing trend with age, resulting in less spread of values at older tree ages (Fig. 2a). In contrast, mean annual VLA in stands increased and there seemed to be an evident increase in spread of values during the last 20 years (Fig. 2c). Also, the amplitude of tree-ring width and tree-ring width indexes in stands were higher than for VLA (Fig. 2b, c). Sampling

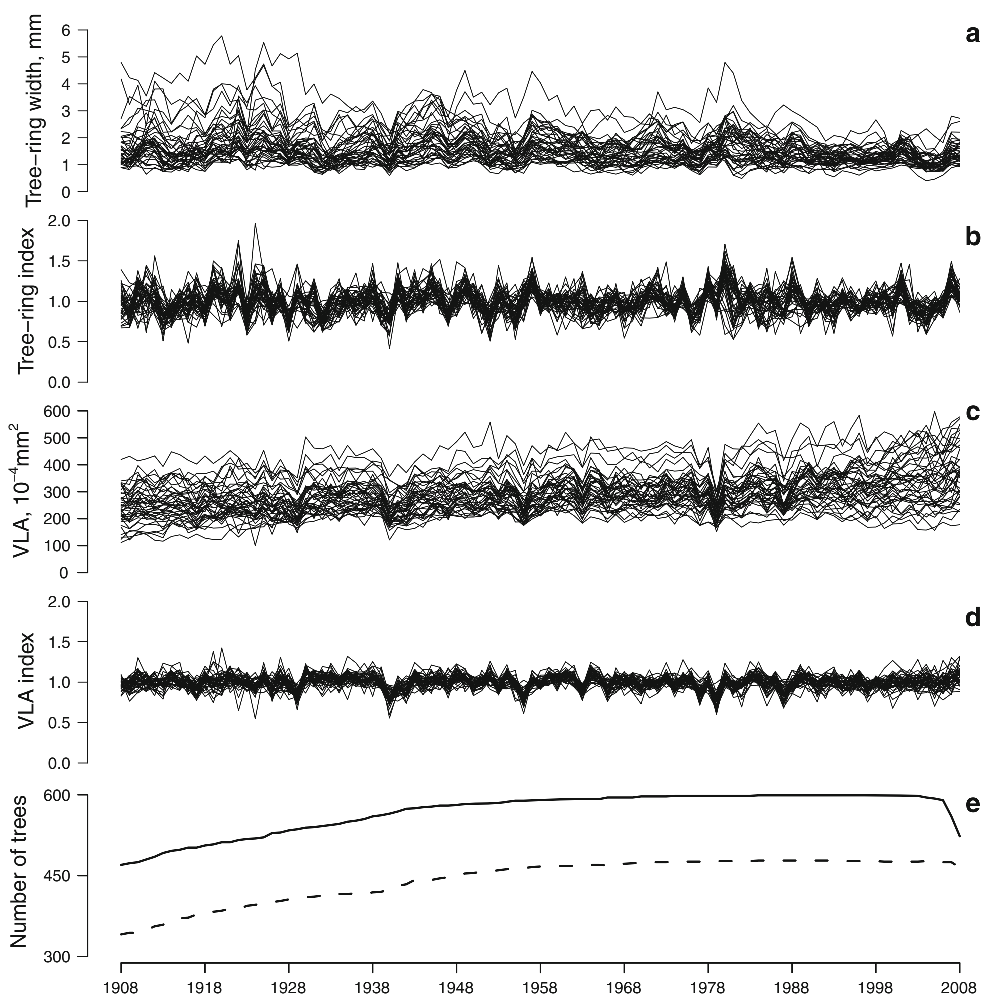

Fig. 2 Mean time series, residual chronologies and sampling depth of sampled stands. **a** Tree-ring width, **b** residual chronologies of tree-ring width, **c** earlywood vessel cross-section area (VLA), **d** residual chronologies VLA, **e** sampling depth (number of trees; *solid line* tree-ring data, *dashed line* VLA)

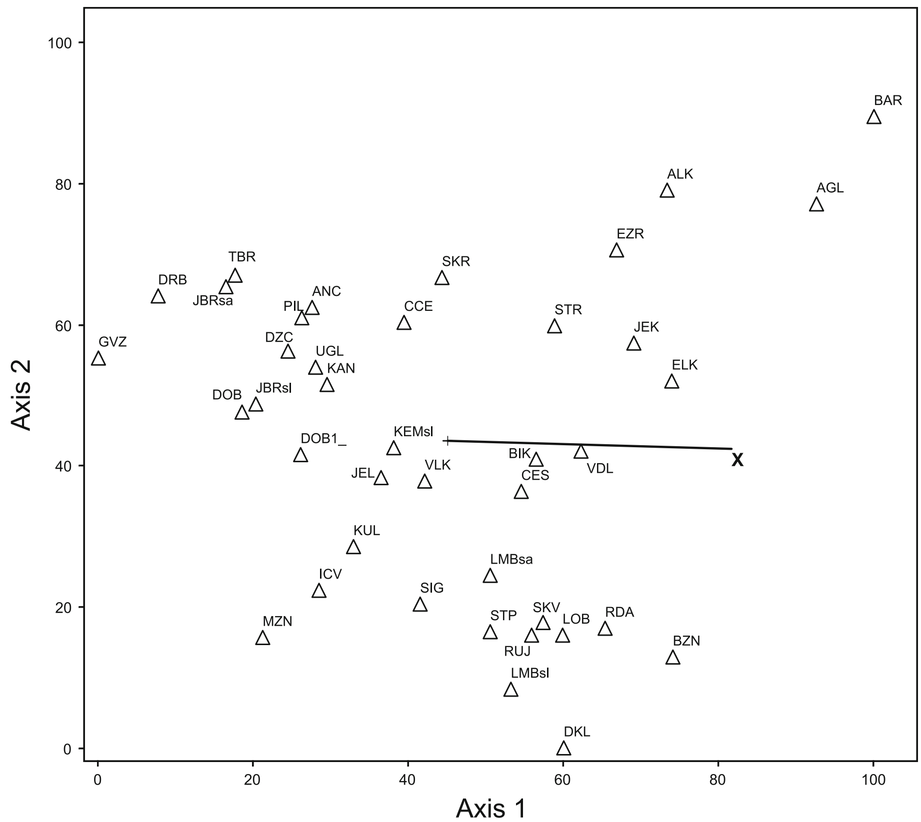

Fig. 3 PCA ordination of sampled stands using residual chronologies of tree-ring width as variables (vector X, relation of gradient to longitude coordinate of sampled stand)

depth of VLA series was lower, as more time series were rejected during quality checking (Fig. 2e).

The first axis of a PCA ordination of stands (Fig. 3), generated using annual index values of tree-ring residual chronologies as variables, was significant (p value = 0.001) and explained 12.1% of the total variation. PCA axis 1 was significantly related ($r = 0.86$) to the stand longitudinal coordinate, which also represents the distance from the Baltic Sea in the east to west direction. Similarly, PCA axis 1 of an ordination generated using annual VLA as variables (data not shown) was significant (p value = 0.001) and explained 8.6% of the total variation. This axis was also related to distance from the sea ($r = 0.78$). Based on the ordination scores for tree-ring width, stands were arbitrarily divided into three groups representing western, central and eastern regions of Latvia (Fig. 4).

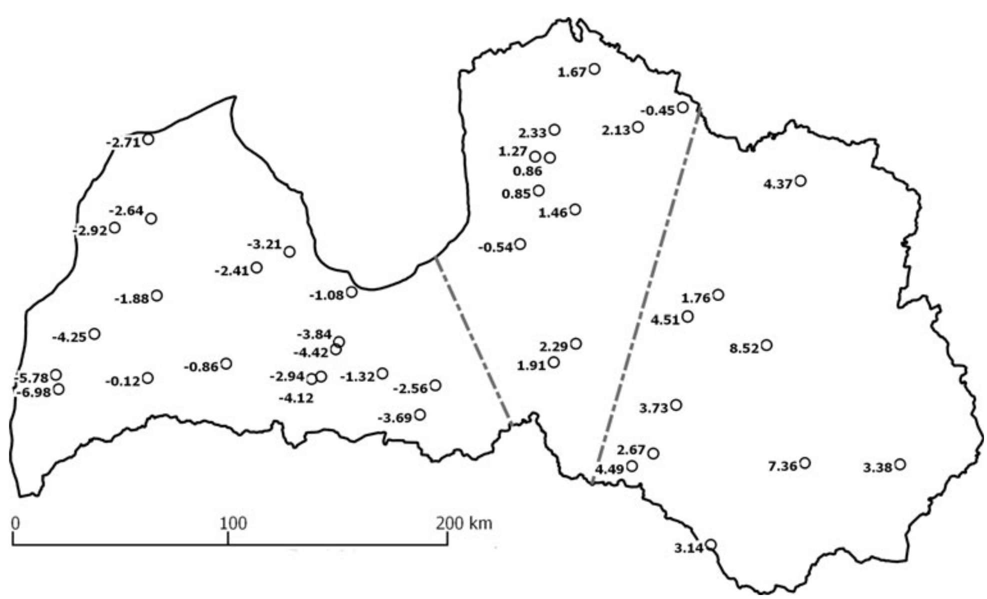

Fig. 4 PCA component I scores of sampled stands overlain on their geographic locations. Three regions were distinguished based on the PCA component I scores

Table 3 Pearson correlation coefficients between tree-ring width, earlywood width and latewood width

Stand	AGL (eastern region)		SIG (central region)		KUL (western region)	
	Early wood width	Late wood width	Early wood width	Late wood width	Early wood width	Late wood width
Tree-ring width	0.64*	0.95*	0.60*	0.96*	0.58*	0.94*
Earlywood width		0.36*		0.35*		0.26*

* Significant correlation, $p \leq 0.05$ for the period 1908–2008

Correlation coefficients between tree-ring, earlywood and latewood widths were similar in the three selected stands (Table 3). Correlation was higher between tree-ring width and latewood width than between tree-ring width and earlywood width. Correlation was low, but significant, between earlywood and latewood width. No significant correlation was found between earlywood width and VLA ($r = -0.01$ to 0.03) in the three tested stands.

The mean monthly temperatures and precipitation sums (Table 4) recorded in the respective meteorological stations differed between the three regions distinguished by patterns of tree-ring width response. The western area, which was closer to the Baltic Sea, had milder temperature in winter and cooler in summer, compared to the eastern area. For example, mean February temperature was −3.6°C in the western region and −6.4°C in the eastern region. The respective July temperatures in the western and eastern regions were 15.0 and 16.9°C. The central area had intermediate February and July temperatures. Autumn and spring temperatures were rather similar among the three areas. Mean monthly precipitation in the period from May to September was higher in the eastern region. In June and July the mean monthly precipitation was higher by about 20 mm in the east.

The proportions of stands with significant correlations between residual chronologies and climatic factors (Table 5) were determined for each of the three areas. The proportions of stands with significant correlation of tree-ring width and VLA with mean monthly temperatures were higher than with monthly precipitation sums, for both current and previous growing seasons. Much lower proportions of stands had significant correlation between climatic factors and tree-ring width, compared to VLA, particularly for monthly precipitation.

The proportions of stands with significant correlation between tree-ring width and March, May and June temperatures of the current growing season were higher in the western region and very low or zero in the eastern region (Table 5). A negative effect of previous season temperature in January and February on tree-ring width was evident in 36–50% of stands in the central and eastern regions, but generally lacking in the western region. A negative effect of previous growing season temperature in July and August on ring width was also observed, but there was no clear difference between the regions in proportion of stands showing this effect. The only clear difference between regions in proportion of stands with correlation between monthly precipitation and ring width was for August precipitation in the current year, which was higher in the eastern region.

An effect of temperature on VLA was more common among stands than the effect on tree-ring width. The

Table 4 Mean monthly temperature and precipitation in western, central and eastern regions (sampled stand groups) for the period 1908–2000

	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

Table 5 Proportions (%) of significant correlations (between residual chronologies of tree-ring width and VLA and climatic factors; "+" positive correlations, "−" negative correlations) in three regions for the period 1908–2000

	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												

Table 5 continued

	Tree-ring width residual chronology						VLA residual chronology					
	Region						Region					
	Western		Central		Eastern		Western		Central		Eastern	
	+	−	+	−	+	−	+	−	+	−	+	−
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		

proportions of significant correlations (Table 5) between VLA and temperature were highest in winter to spring months (December–April) of the current year and September of the previous year. Precipitation did not significantly affect VLA in more than 30% of stands in any of the areas, except for current year January in the eastern area.

Discussion

Trends in tree-ring width series differed from vessel area proxies. The decrease of tree-ring width and its amplitude (Fig. 2a) most likely is related to tree ageing, as often found in tree-ring width time series (Speer 2010). This trend is likely related with a decrease of latewood width (Zhang1997). The increase of VLA during the whole period might be explained by a need to compensate increasing demand of water transport resulting from a decrease of the increment of surface area of the stem as a tree ages (Leal et al. 2007; Ryan and Yoder 1997). This increase of VLA was associated with a recent (last 20 years) clearly evident wider variation of VLA among sites (Fig. 2c). It is interesting to consider whether this effect was due to global warming. To test this, correlation analysis needs to be conducted, splitting the time series in different periods of time. Despite the recently increased spread of VLA among stands, the yearly amplitude of VLA was lower than that of tree-ring width (Fig. 2b, d), likely due to greater genetic and physiological constraints on VLA formation (Garcia-Gonzalez and Eckstein 2003; Mather et al. 1993; Zakrzewski 1983).

Estimates of autocorrelation of site time series (Table 2) also suggested that tree-ring width, in comparison to VLA, is more dependent on environmental factors in the previous season, as shown previously (Campelo et al. 2010; Tardif and Conciatori 2006). However, EPS among trees at the studied sites was higher for tree-ring series than for VLA (Table 2). Three of 40 sites (8%) had EPS values below 0.85 (0.76–0.83) for tree-ring width. EPS values depend on sample size of time series and agreement between them (Wigley et al. 1986). Possible reasons for these low values are low number of sampled trees in those stands (such as in stand VLK), low yearly variation of tree-ring width (as in stands JEK and SKR), and low agreement between sampled trees. Nevertheless, IC and ICs values (Table 2) indicate that tree-rings series in those stands show reasonable agreement within stands and very good agreement with the time series of other stands. The number of stands with EPS values below 0.85 was higher for VLA (17 of 40 of stands), which was likely due to measurement errors caused by difficulties in earlywood image preparation and sampling technique. A single increment core of diameter 5 mm probably was not sufficient to be representative for the whole population of earlywood vessels in a tree-ring. Also, as for the tree-ring width, low EPS values for VLA time series most likely were partly due to the low number of sampled trees in some stands, particularly as more of them were excluded during quality checking than for tree-ring series. Nevertheless, site chronologies for VLA were considered as informative as they showed high inter-site correlations (0.64 ± 0.02, compared to 0.38 ± 0.02 for within site series), despite several low EPS values. Therefore, we consider that the agreement between time series for stands was sufficient to include them in the analysis. Also, preliminary analysis showed that the correlations with climatic factors did not differ when 45 stands were analysed, compared to the presented results based on the analysis of 40 stands, after five stands were omitted during preliminary quality control. This indicates that the results obtained are not due to an artefact created by low sample size of cores in stands.

For a limited number of stands, earlywood and latewood width were tested. Latewood width was well correlated ($r \geq 0.94$) with tree-ring width (Table 3), suggesting that additional information would not be obtained, as previously shown by van der Werf et al. (2007) and Zhang (1997). Earlywood width was also significantly correlated with tree-ring width, but the lower correlation coefficient ($r = 0.58$–0.64) between them suggests different sources of variation. Earlywood width has been shown to contain weaker climatic signals than latewood and tree-ring width (Eckstein and Schmidt 1974; Rozas et al. 2009; Zhang1997). The lower correlation may be due to an indistinct border between earlywood and latewood in the scanned images, particularly in cases when vessel size gradually decreased in size in successive rows within a tree-ring and rather large vessels were present in latewood (Schweingruber 2007). This might also explain the lack of significant correlation with VLA.

Vessel parameters, which can be used as proxies for climatic and other environmental factors (Berges et al. 2008; Garcia-Gonzalez and Eckstein 2003), are directly related to water transport in tree stems (Tyree and Ewers 1991). Water conduction in a tree-ring depends on the size and number of vessels; the same rate of conducted water can be attained through different combinations of vessel size and numbers (Tyree and Ewers 1991). Although larger vessels conduct more water, there is a higher risk that, in case of low water availability, embolism can occur, as capillary forces in larger vessels are weaker (Cochard et al. 1992; Tyree and Cochard 1996). Thereby, the EV size represents a balance between sustaining optimal water supply to leaves and avoiding drought embolism (Abrams 1990; Corcuera et al. 2004; Garcia-Gonzalez and Eckstein 2003). In response to flooding or extremely low winter and/or spring temperatures, smaller, but more numerous EV can be formed (George et al. 2002; Lei et al. 1996). Thus, vessel area and density can respond differently to climatic factors, and potential conductivity might serve as a better proxy of climate than size and density of EV. However, cores with a larger diameter or cut tree-ring discs would be needed to provide larger sample sizes of EV this type of analysis.

The responses of tree-ring width and VLA to climatic factors widely differed between sites (stands), which might be partly explained by climatic differences between regions (Table 4). A PCA ordination sorted stands along a gradient tree-ring width indexes that was superimposed on a geographic east to west gradient (Figs. 3, 4). This indicates that years in which tree-ring increment was higher or lower in stands in western Latvia did not correspond to the years when tree-ring width was higher or lower in eastern Latvia. A similar gradient was also derived using VLA in different years as variables. Thus, the limiting climatic factors differ between the regions, due to a shift from a maritime to a more continental climate in eastern direction. As hypothesised, in Latvia temperature has a greater effect on wood formation than precipitation (Table 5). In Latvia, moisture is usually not limiting tree growth (Elferts 2007), as precipitation is generally higher than evapotranspiration (Krams and Ziverts 1993). However, in the eastern region, the correlation of tree-ring width in 20 and 80% of stands with June and August precipitation, respectively, suggests that the continental climate may create drought conditions in some years. This is supported by a positive correlation of VLA in 30% of stands with June precipitation and a negative correlation of VLA with June temperature in 20% of stands.

In the more maritime western region, where spring and summer temperatures are lower (Table 4), significant effect of March, May and June temperatures of the current growing season on tree-ring width was evident in greater proportions of stands. In western Latvia, snow melt can begin already in March, and years with a warmer March are usually associated with a longer growing season (DeForest et al. 2006; Jones 1959; Kalvāne et al. 2009) and an increased production of wood. A warmer October also can prolong the vegetation period (Drobyshev et al. 2008; Xu and Griffin 2006). In Latvia, May is the usual time of oak bud break (Ģērmanis 2005) and the highest rate of physiological activity of oak occurs in June (Morecroft and Roberts 1999). Apparently, May and June temperatures are not limiting in the eastern region, where phenological phases are delayed and spring and summer are warmer (Pūriņš 1975). A negative effect of July and August temperature in the previous year was observed in all regions, and particularly in the central region. This might be explained by a decrease of assimilation (photosynthesis) rate in response to high temperature (Haldimann and Feller 2004), which would decrease the amount of stored reserves (Xu and Griffin 2006), resulting in a narrower tree-ring in the next year. Negative correlation with October precipitation of the previous growing season might be explained by excessive soil moisture, which decreases root functioning (Larson and Whitmore 1970).

A high proportion of stands showing a significant correlation of VLA to temperature from December to April of the current year, particularly in the eastern region, suggests that temperatures in winter to spring months are limiting. EV formation is known to be affected by climatic factors in the months before their formation (Fonti et al. 2007). Severe cold in the dormant period causes frost damage and embolism (Zhu et al. 2000), which results in a decrease of physiological vigour of oak (Helama et al. 2009) and a decrease in size of EV (Fonti et al. 2010). The positive effect of January precipitation (Table 4) on VLA (70% of stands in the eastern region) suggests that a snow layer (winter precipitation) may mitigate the effect of cold winters, by acting as an insulator (Hardy et al. 2001), protecting the root system from freezing and from rapid shifts of temperature. Low soil temperature may damage fine roots or increase their mortality (Fonti et al. 2004; Tierney et al. 2001) decreasing water resorption in early spring. In these conditions, smaller EV are formed to minimise risk of embolism under decreased water uptake (Tyree and Cochard 1996), which can explain the effect of temperature in winter on VLA. The effect of temperature in winter might also be related with starch dissolution and sap availability and characteristics in spring (Essiamah and Eschrich 1985). In response to low temperature more starch may be dissolved to protect tree tissues from freezing (Ameglio et al. 2004), which can reduce the amounts of stored carbohydrates. Also, low temperature before the active growth period is associated with reduced sap ascent (Zimmermann 1964), which may delay growth and wood formation. EV in English oak begin to form in early spring before bud break (Rozas et al. 2009), and thus this process is dependent on stored assimilates (Tardif and Conciatori 2006). April is the most crucial period, when the larger part of EV is formed and sap flow increases through new-formed vessels (Granier et al. 1994; Zimmermann 1964). April in Latvia is characterised by rapid change of weather conditions: warm periods may change with frosts and snowfall; weather in May overall is more stable and temperatures are above zero, except for rare night frosts (Latvian Environment, Geology and Meteorology Agency). This can explain why May temperature had a minimal effect on VLA. Significant correlations with climatic factors after June of the current growing season are most likely coincidental, as oak has begun to produce latewood (Sass-Klaassen et al. 2011).

There was a significant positive effect of September temperature in the previous year on VLA, which was observed in larger proportions of stands in the central and eastern regions than in the western region. A similar, but less obvious effect was observed for October temperature of the current season. Most likely, this effect of autumn temperature can be explained by a longer vegetation season in the previous year, enabling additional storage of assimilates (Drobyshev et al. 2008; Xu and Griffin 2006). Probably, the previous September and October months should be included as months of the current year of tree-ring growth, and not the previous year, but we lack information on when the period of latewood formation ends in Latvia.

While it is known that VLA are most affected by environmental factors in the current year (Campelo et al. 2010; Tardif and Conciatori 2006), in the present study we observed a positive effect of May and June temperature of the previous growing season in 23–54% of stands in the three regions. This might be explained by a general effect of increased tree vigour due to greater accumulation of assimilates during a longer grower season. In some stands, there was a negative effect of the previous year's January temperature on VLA and of previous year's January and February temperature on tree-ring width. This might be associated with over-usage of stored reserves (Pilcher and Gray 1982) or increased activity of pathogens (Ayres and Lombardero 2000; Wargo 1996). It is more difficult to explain the negative effect of previous season's January precipitation on VLA, observed in 30% of stands in the eastern region. This effect, and others observed in small proportions of stands might be coincidental.

Although Latvia is a small country with a flat relief, regional differences in response to climatic factors were observed. Greater proportions of stands had significant correlations of climatic factors with VLA, than for tree-ring width. December–April temperatures were the main limiting factors for VLA formation, particularly in the eastern, more continental region. Summer temperature had a greater effect on tree-ring width in the maritime western region. Under global warming scenarios (IPCC 2007), winter temperatures are expected to increase. Therefore, the observed differences between maritime and continental regions of Latvia in proportions of stands with significant correlation of VLA with winter temperatures indicate that winter temperature will become less limiting, possibly leading to increased growth and a northern shift of the distribution limit. However, the correlation of tree-ring width with August precipitation in the eastern region of Latvia suggests that moisture can be limiting. An increased frequency of drought periods may lead to a change in the main limiting factors from winter temperature to summer precipitation. Analysis of correlations for different periods of time is needed to determine if changes in the limiting factors have occurred in the recent period of rapid global warming. The recent increase in spread in VLA among sites suggests that changes in limiting factors might already have occurred.

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