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Influence of climate on earlywood vessel formation of *Quercus robur* at its northern distribution range in central regions of Latvia

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Abstract

Annual variation in vessel cross-section area suggests that vessels as water transport tissues in plants can adjust size and numbers according to exogenous factors, such as climate. Earlywood vessels in ring-porous species such as oak *Quercus robur* are considered to contain climatic signals (climatic factors influence their formation). The aim of the study was to investigate the relationship between vessel cross-sectional area and climatic factors at its northern distribution range. Living oaks growing on dry forest sites in central parts of Latvia were cored. Cores were sanded and treated with chalk to expose vessels. Earlywood vessel cross-section areas were measured for each tree-ring. Relationship between climatic factors and vessel formation was examined using correlation analysis. Earlywood vessel formation depended on spring (March, April) and annual (previous year October to current year September) temperatures. Precipitation had low influence, which is not surprising considering location close to the northern limit of distribution, but precipitation was suggested as a non- limiting factor. Climatic factors of the current year were more important for vessel formation than previous year factors.

Key words: central Latvia; climatic signals; earlywood vessels; lumen area; *Quercus robur.*

Introduction

Many plants, including trees, can be used as bioindicators that respond to environmental changes over a long period of time. The past history of metabolic processes affected by the environment is reflected in wood structural features. Width, density and structure of the cells, tissues and organs, with their spatial relations and physiological states encode valuable annual information about climate, competition, predators, diseases, human impacts and radial growth of young and old trees grown on different soils (Wimmer 2002; García-González, Eckstein 2003; Schweingruber 2007).

Tree-ring width, earlywood and latewood width and density, and stable isotope composition in wood are the most widely used parameters in dendroscience. Genetic factors determine the basic structure of wood anatomy (Fritts 2001) but environmental factors such as climate during xylem development also can affect the anatomical characteristics of the woody cell, such as the size of tracheids in conifers and vessels in deciduous trees (Fonti et al. 2009).

Vessels are xylem elements involved in the transport of water (Rust et al. 2004; Thomas et al. 2006; Steppe, Lemeur 2007). Earlywood vessels usually are generated before budbreak and controlled by the overall physiological vigor of the tree that is preconditioned by environmental stress and growth rates of previous growing season (Zahner 1968; Thomas et al. 2006). Vessels vary in size and in the type of openings (perforations) at their ends. Earlywood vessels in ring porous woods such as oak (*Quercus* spp.), elm (*Ulmus* spp.) and ash (*Fraxinus* spp.) are markedly wider than those in the latewood and tend to be barrel-shaped and as wide as they are long. There is variation in the size and arrangement of the pits that connect one vessel element to another, as well as vessel element to parenchyma (Schweingruber et. al. 2006). In oaks of the northern temperate zones earlywood vessels are only functional in the year of their formation (Thomas et al. 2006).

Interest in intra-annual anatomical features as indicators is steadily increasing in ecology, e.g., to determine water transport and effects of defoliation and drought stress on biomass. The oak species respond differently to defoliation and drought stress but even a small reduction in vessel diameter may result in a distinct decrease of water transport in the tree (Thomas et.al. 2006). In Mediterranean region it was suggested that in drought conditions only earlywood with large vessels is produced in Portuguese oak (*Quercus faginea* Lamk.) rather than latewood to compensate water loss by improving transport (Corcuera et al. 2004a). Holm oak (*Q. ilex* L.) (Corcuera et al. 2004a) and English oak (*Q. robur* L.) showed decrease in vessel size caused by drought but in sessile oak [*Q. petrea* (Mattuscha) Liebl.] repeated defoliation led to a significant increase in the vessel area (Zahner 1968; Corcuera et al. 2004b). This different anatomical response can be explained by the fact that sessile oak has a lower demand for water and nutrients and is less susceptible to drought stress than English oak (Gieger, Thomas 2002; Thomas et al. 2006). Although tension can strongly affect formation of vessels in tension wood, especially in young trees, vessel size variables still can be a useful tool in dendroecological studies (Heinrich, Gärtner 2008).

The use of time series of earlywood and latewood vessel features is becoming more popular also in dendroclimatology. Time series of vessels lumen area display little autocorrelation and show a greater stability through time compared to tree-ring width series, i.e., they provide more detailed information about seasonal climatic variability (García-González, Eckstein 2003).

Vessels such as the water-conducting elements (Rust et al. 2004; Steppe, Lemeur 2007) have been shown to reflect past rainfall regime in various ring-porous tree species, e.g., sweet chestnut (*Castanea sativa* Mill.) (Fonti, García-González 2004; García-González, Fonti 2006; García-González, Fonti 2008), beech (*Fagus sylvatica* L.) and oaks (Sass, Eckstein 1995; van der Werf et al. 2007). There have been a few studies on the influence of climate on the vessel size of ring-porous oaks in Switzerland (Eilmann et al. 2006; Fonti, García-González 2008; Fonti et al. 2009), at their northern distribution limit in Canada (St. George, Nielsen 2003; Tardif, Conciatori 2006) and in an oceanic climate (García-González, Eckstein 2003), and it was recommended to use vessels as a proxy for dendroclimatic reconstruction. Little is known about climate controls on vessel features in English oak and, considering climatic change, such studies would be particularly important at the northern distribution border.

The aim of the study was to assess the effect of climate on earlywood vessel formation in stem of English oak in dry habitats in Latvia and to evaluate of earlywood vessel cross-section area climatic signals as a potential proxy for climate.

Materials and methods

Study area

Five sampling plots were established in northwestern and central Latvia (Fig. 1), of which four were located in the eastern part of Kurland at Kandava, Sēme, Dzirciems and Tukums, and one in southern part of Vidzeme near Lobe. LKS-92 TM coordinates of sampling plats are shown in Table 1. All sites were located in dry habitats on clayey soils, covered with oak or mixed broadleaved managed forests. The relief in sampling plots was flat or with flat hills.

Sample collection, preparation and measurements

Samples were taken using a Pressler increment corer from living oaks at ~1.4 m height above tree base (breast height). Two cores were taken from each tree on opposite sides of the stem. Trees growing on relatively slight slopes were cored on sides of the stem perpendicular to the slope. Trees growing on steep slopes were not cored to avoid tension wood effect on vessel development. Samples were taken in autumn 2008.

In the laboratory samples (increment cores) were dried, glued into fixation planks and placed under pressure to dry. It was ensured that the direction of wood fiber and vessel cavity was perpendicular to surface of fixation plank. Fixed increment cores were gradually sanded (grain sizes from 80 to 400) using a vibration sander (Makita BO3700) until the radial plane of increment was uncovered. Dust from samples was removed with compressed air. Samples were rubbed with chalk to expose wood vessels and to increase their contrast. Quality checking was performed and only continuous cores with no rot present (breaking continuity) where all vessels were filled with chalk (in some samples vessels were filled with glue during fixation) were processed for scanning.

Chalked samples were scanned with 1200 dpi resolution and 24-bit colors using an

Fig. 1. Location of sampling plots in Latvia.

Table 1. Coordinates of sampling plots (LKS92 TM coordinate system)

Sampling plot	X coordinate	Y coordinate
Kandava	426640	6324050
Sēme	448460	6318850
Dzirciems	441840	6330950
Tukums	451180	6314740
Lobe	573940	6288760

Table 2. Numbers of cored trees, suitable samples and reference periods from sampling plots

Sampling plot	Number of trees cored	Number of suitable samples	Reference period (years)
Kandava	11	16	1906 - 2008
Sēme	10	15	1905 - 2008
Dzirciems	10	19	1900 - 2008
Tukums	10	15	1941 - 2008
Lobe	12	19	1900 - 2008
Total	53	84	

Epson GT-15000 scanner. Sample images were cut in sections along tree-ring borders and saved as separate tree-ring images for further analysis (wood vessels placed in central part of images). The youngest 100 to 110 tree-rings (where possible) were used.

Earlywood vessels were measured using the program WinCELL pro v.2007a (Regent Instruments). Tree-ring images were used as input data. Average lumen area in "H&W" mode of tree-ring earlywood vessels was measured using gray level pixel classification (values 220 - 235). Filters were used to avoid noise from chalk debris and sample surface defects. Batch function was applied to obtain data from tree-ring image groups (samples). Before starting batch function several randomly selected earlywood vessel images were manually checked to adjust measuring and filter parameters and to ensure measurement quality. Global data for each tree-ring image analysis was calculated for further analysis.

Data analysis

Mean yearly vessel lumen area (VLA) for individual trees was calculated, and used to estimate yearly mean VLA sites. To characterize influence of climatic factors on VLA correlation analysis was performed with DENDROCLIM 2002 program (Biondi, Waikul 2004). Climatic factors used were average monthly and seasonal (autumn, winter, spring, summer, and yearly – previous year October to current year September) temperature and precipitation sums of current and previous year on vessel formation.

Climatic data was obtained from the Latvian Environment, Geology and Meteorology Agency for the Riga meteorological station (missing data replaced by modeled). Annual mean VLA was compared with mean monthly temperature, monthly precipitation sum, and mean temperature and precipitation sum in season (i.e., from October of the preceding year to September of the growth year), as well as average temperature and precipitation sums in autumn (September - November previous year), winter (December - February), spring (March - May) and summer (June - August).

Results

During the study 106 samples were taken from 53 living oaks. Number of cored trees, suitable samples and reference periods from sampling plots are shown in Table 2. In most cases rejection of suitable samples was caused by glue that filled the vessels or decay of parts of the samples. The Tukums plot had the shortest reference period due to relatively small tree age.

Mean vessel lumen areas for sampling plots are shown in Fig. 2. The formation of vessels among sampling places was rather similar, but there were some periods when quite large differences were visible (1900 - 1930, 1996 - 2008). Also a slight increase of VLA during the whole reference period could be suggested.

Significant correlations with climatic factors are shown in Table 3. In total 73 positive and four negative significant correlations were identified for 68 climatic factors. The highest absolute correlation value was 0.53 (with spring average temperature), lowest –0.16 (previous year March temperature). Significant monthly precipitation and temperatures correlation coefficients differed among the territories even in sampling plots from the same part of Latvia (Kandava, Sēme, Dzirciems and Tukums). Vessel lumen areas in all territories showed high correlation with winter, spring and yearly mean temperature. The highest correlation coefficients were observed with spring temperature, both seasonal and monthly. March, April and season mean temperatures overall showed highest correlation in most of sites.

Precipitation correlated with vessel formation in a few months, mostly positively. There were more correlations with current than with previous year climatic factors. Current year April precipitation showed a negative correlation only in one sampling plot, previous August precipitation showed three negative correlations. Overall only a few significant correlation coefficients were observed with current year summer precipitation data, correlation with previous year data was even less abundant.

Discussion

In the present study fluctuation and variability of VLA in English oak (Fig. 2) was similar to tree ring width fluctuations, suggesting that not only endogenous but also environmental factors had an influence on VLA formation (Fritts, Swetnam 1989; Wimmer 2002; Tardif, Conciatori 2006). The observed slight gradual increase of VLA during the reference period could be due to an ageing effect or changes in environmental factors (Fritts, Swetnam 1989; Schweingruber 1996). The most visible increasing trends of vessel formation occurred in periods of 1900 - 1930 and 1996 - 2008, which might be related with rising minimal temperatures under climate change (Walther et al. 2002), as previously observed in growth and establishment of Scots pine (*Pinus sylvestris*) (Brumelis et al. 2005).

Vessel formation more depended on current season climatic factors compared to previous season (Table 3). Influence of the previous season ending temperature on vessel formation in some regions might be related to local phenology of wood formation and microhabitat conditions (Menzel et al. 2001; Brüger et al. 2003). Although vessel formation

Table 3. Significant (a = 0.05) correlations (r) of mean vessel lumen area of *Quercus robur* with monthly and seasonal mean temperature and precipitation sum

		Current year					Previous year				
		Kandava	**Sēme**	**Dzirciems**	**Lobe**	**Tukums**	**Kandava**	**Sēme**	**Dzirciems**	**Lobe**	**Tukums**
Temperatures	Oct	0.29									
	Nov										
	Dec	0.23		0.34	0.21						
	Jan	0.27		0.23	0.30	0.29					
	Feb				0.30	0.27					
	Mar		0.24	0.23	0.25	0.49				0.16	
	Apr	0.26	0.32	0.42	0.40					0.27	
	May					0.30	0.28	0.24			0.26
	Jun		0.32			0.28		0.20		0.22	
	Jul										
	Aug		0.28		0.25			0.25	0.23	0.26	
	Sep										
Precipitation sum	Oct									0.25	
	Nov										
	Dec										
	Jan	0.25									
	Feb										
	Mar										
	Apr				-0.21						
	May	0.26	0.19								
	Jun	0.19					0.27				
	Jul										
	Aug							-0.17	-0.24	-0.29	
	Sep		0.17								
Temperatures	Autumn	0.24	0.30								
	Winter	0.27	0.22	0.35	0.37	0.28					
	Spring	0.24	0.35	0.34	0.34	0.53		0.27		0.26	0.28
	Summer		0.33		0.22			0.26		0.25	0.24
	Season	0.29	0.41	0.40	0.43	0.44		0.30		0.28	0.27
Precipitation sum	Autumn		0.20					0.22			
	Winter										
	Spring										
	Summer	0.20									
	Season	0.30					0.32				

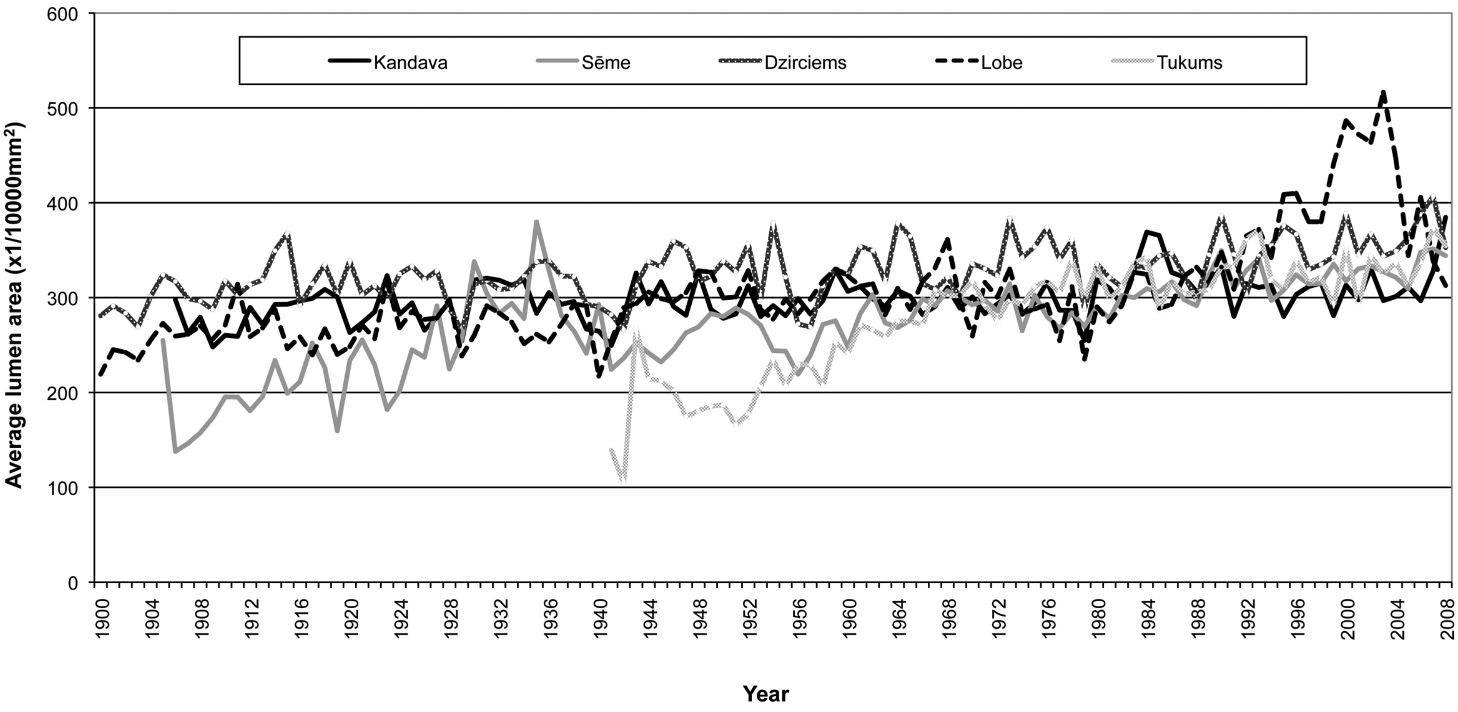

Fig. 2. Yearly fluctuation of vessel lumen area of *Quercus robur* at different sites.

depended on climate, site characteristics also had an influence; correlations with monthly temperature factors were not alike in all sites, even situated at short geographic distances from each other.

Correlation analysis showed that temperature has been a more important factor affecting vessel formation than precipitation. Current year winter and spring monthly mean temperatures (except February and May) had the most important role in vessel formation among temperature factors, showing the highest correlation coefficients and occurring in most sites. English oak is known to require a higher temperature in the beginning of the growth season (Jones 1959), and this is likely to be more evident close to its northern border of distribution area, i.e., in Latvia. Thus March-April mean temperature can be considered to be an important factor influencing vessel formation at the study sites, as they showed the highest correlation coefficients were detected. Early wood begins development in early spring or in some occasions even in end of winter before bud burst (Thomas et al. 2006; Fonti et al. 2009). Correlation with current season climatic factors after August most likely can be explained as coincidental, as early wood formation should have ended at that time (Jones 1959; Menzel et al. 2001). Correlation with previous year mean temperatures in May, June and August at several sites might be explained by nutrient reserve formation for next season affecting vessel formation (Zahner 1968; Larcher 2003; Tardif, Conciatori 2006; Thomas et al. 2006). VLA showed a lower dependence on previous than current season climatic factors; but still autocorrelation was suggested, but probably lower than observed in tree ring widths (Eckstein 1990; Fritts 2001; García-González, Eckstein 2003). Correlation with mean seasonal temperatures showed the summed effect of spring and winter temperatures on vessel formation.

Precipitation showed a minimal effect compared with temperature (significant correlation coefficients scattered between sites, low values) on vessel formation despite the fact that oaks were growing on dry forest habitats. This suggests non-limiting availability of water resources from groundwater and relatively low evaporation from clayey soil. Typically precipitation is a limiting factor for growth of oak in central Europe (Fonti et al. 2009). However, in Latvia a negative correlation with spring precipitation was observed only in one sampling plot [Lobe, (April, $r = -0.21$)]. Negative correlation with previous August precipitation (observed in three plots) might be related with water abundance in soil at the end of growing season causing stress and vessel size (area) reduction in the next season. Seasonal precipitation sums in general also had a low influence; correlation coefficients were relatively low and scattered among sites, suggesting precipitation as a non-limiting factor for vessel formation.

Climatic signals in vessels in Latvia compared with the Mediterranean region differed: importance of precipitation was much higher in Spain, and temperature was suggested to have secondary influence; showing different limiting factors. Still negative correlation with previous year August precipitation was observed (García-González, Eckstein 2003). Garcia-Gonzalez and Fonti (2006) indicated that vessel area of sweet chestnut showed negative correlation with spring and a positive relation (in some sites) with summer temperatures. Also they found a climate effect on vessel size (area) in different parts of tree-ring (early wood and latewood).

Climatic signals contained in vessel sizes can also be identified in central Latvia. Consequently, VLA can be applied for dendroclimatology. The climatic signals were stronger and more homogeneous compared to tree-ring climatic signals (Matisons, unpublished results). Studies in Spain and Switzerland (with *Q. petrea*) suggest that VLA can be used in dendroclimatology and dendrochronology (Garcia-Gonzalez, Eckstein 2003; Fonti et al. 2009). Despite the extended time needed for material preparation and measurement, vessel size estimation is superior to tree-ring width for climatic reconstruction, as vessels provide more selective information (Wimmer 2002; Garcia-Gonzales, Eckstein 2003; Tardif, Conciatori 2006). VLA is well related to spring temperatures in the study sites (central parts of Latvia), but correlation with precipitation (as a non limiting factor) is poor. Tree-ring widths nevertheless are a good proxy to characterize ring-porous tree growth.

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