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Minimum winter temperature reconstruction from average earlywood vessel area of European oak (*Quercus robur*) in N-Poland

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ABSTRACT

Tree-ring-based temperature reconstructions form a substantial part of the international proxy data base used to examine and model global climate variations of the last Millennium. However, most tree-ring-based reconstructions are derived from study sites in the high latitudes or high altitudes, paying very little attention to low elevation sites. Thus, a large gap in the geographical coverage of climate reconstructions from temperate low elevation sites in central Europe still exists. This motivated us to concentrate our efforts on the European oak (*Quercus robur*) in N-Poland. We developed a new robust tree-ring width chronology (TRW), as well as four wood anatomical chronologies (e.g. average vessel area and number of vessels) from *Q. robur* for the period 1810 to 2010. The chronologies were examined for their climatological responses. While TRW was found to have weak correlations with climate, the earlywood vessel parameters (EVP), especially average vessel area (AVA), revealed significant positive correlations to minimum winter temperatures. Based on stable climate–growth correlations, a reconstruction of minimum winter temperatures (29th November to 20th January) back to 1810 was performed for north Poland. The reconstruction indicates a promising potential to reveal low-frequency climate information. An additional extreme year analysis suggested that in cold winters, a cold–warm–cold pattern in the minimum temperatures was responsible for the relatively small earlywood vessels. Spatial field correlations imply that our reconstruction is more related to temperature variations towards the east of Europe. The reconstructed temperature compared well with two existing temperature reconstructions, especially during most of the 20th century, even though the temperature reconstructions differ spatially and temporally. Based on these findings, the relatively extensive resource of archeological oak material from this region may be useful to perform multicentennial climate reconstructions in the temperate climate zone.

1. Introduction

Climate reconstructions based on tree rings are mainly derived from sites with extreme climates at high latitudes or altitudes (Gagen et al., 2006). The closer a tree grows to its distribution limits, the stronger is the influence of one principal climate parameter mainly limiting growth (Fritts, 1966; Hughes, 2002). Dendroclimatology uses this strong relation between climate and tree rings to generate robust climate proxies. Since forests cover large parts of the continental earth surface, theoretically, dendroclimatological studies may facilitate climate reconstructions almost everywhere. However, in reality, the climate signal strengths implemented in tree-ring parameters such as tree-ring width (TRW) are often not strong enough for reconstructions at sites with less extreme climate conditions (Buckley et al., 1997), and thus most temperature reconstructions are from remote and sparsely populated regions where the climate–growth relations are less diffuse (Young et al., 2012).

In order to challenge this geographical imbalance concerning tree-ring-based climate reconstructions, new dendroclimatological parameters such as stable isotopes (Gagen et al., 2006; Treydte et al., 2007) and wood cell structures (Fonti et al., 2010) were established as new proxies in dendroclimatology studies. Recent studies revealed the large potential of stable isotopes and quantitative wood anatomy for high-quality dendrochronological reconstructions to overcome such geographical restrictions to extreme sites only (Fonti et al., 2010; Young et al., 2012). By analyzing conifers growing in the temperate lowland forests of southern Australia (Drew et al., 2011) and northeastern Germany

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(Liang et al., 2013) the existence of strong climate information in series of wood anatomical parameters was demonstrated, while the tree-ring widths did not correlate well with climate. Likewise, wood anatomical parameters of Siberian larch trees (*Larix cajanderi*) were used for the longest existing temperature reconstruction based on a tracheid dimensions series (Panyushkina et al., 2003).

Wood anatomical parameters of deciduous trees such as earlywood vessel size, however, were mostly used either for ecophysiological (Fonti and García-González, 2004) or hydrological studies (Eckstein et al., 1977; García-González and Eckstein, 2003; Fonti and García-González, 2008; Bryukhanova and Fonti, 2012). Nevertheless, a few studies also investigated the relation between temperature and xylem anatomy. Studies of vessel dimensions of oaks growing in Latvia (Matisons and Dauškane, 2009; Matisons and Brūmelis, 2012) and Canada (Tardif and Conciatori, 2006) revealed a close relation between the average earlywood vessel lumen areas and temperatures. Likewise, vessel lumen areas of trees growing in the Mediterranean demonstrated high sensitivities toward late-winter-to-early-spring temperatures (Fonti et al., 2007). Gea-Izquierdo et al. (2013) found a strong dependency between the earlywood vessel anatomy of the evergreen shrub *Erica arborea* and winter temperatures. Such correlation patterns with winter temperatures are under scientific debate, since during European winters many tree physiological processes are minimized in evergreen species or even dormant in deciduous species, and thus the correlations cannot readily be explained. The explanations proposed for this particular relation so far ranged from temperature influences on physiological processes determining vessel sizes to externally induced freezing embolisms in the vessels during colder winters (Fonti et al., 2007; Gea-Izquierdo et al., 2013).

Previous studies of wood anatomical parameters suggested little age-related trends in the mature sections of the series and it was demonstrated that climate reconstructions at less extreme sites will be feasible on the basis of wood anatomical parameters where tree-ring widths have failed so far (Liang et al., 2013; Pritzkow et al., 2014). Following the promising results of these pilot studies, the current study aims to (a) produce a long earlywood vessel chronology of lowland oaks in Northern Poland, (b) screen the chronology for its climate signals and, if possible, to (c) reconstruct a selected climate variable.

2. Materials and methods

2.1. Study site and wood material

In northern Poland, two cores per tree of 21 trees (*Quercus robur*) were collected at breast height with an increment corer (Ø 5 mm) in June 2011. The study site (53° 50′ N, 18° 17′ E, 120 m a.s.l.) belongs to the UNESCO biosphere reserve Tuchola Forest (supplementary S1). The forest consists largely of *Q. robur*, approximately 200 years old, mixed with *Pinus sylvestris*. The Tuchola Forest region was almost constantly under environmental protection during the 20th century which resulted in undisturbed tree growth. Northern Poland is influenced by a temperate and warm climate with high amounts of precipitation and fairly cool summers. In the eastern part, continental climate conditions are characterized by frosty winters and hot and dry summers. The coastal zones at the northern border to the Baltic Sea are mainly of maritime character. The study site is located in the intermediate climate between maritime and continental influences. The annual mean temperature is 8 °C, whereas the mean winter and summer temperatures are −0.6 °C and 16.8 °C, respectively. The highest temperature variability occurs naturally in the winter months (Kozuchowski and Degirmendzic, 2005). The annual precipitation amounts to about 650 mm. The average vegetative season on the western Polish Baltic Sea starts on 20th March and ends on 16th November (Tylkowski, 2015). The lowlands of Northern Poland were shaped by the Weichselian Late Glacial period resulting in soils which are dominated by nutrient-poor podsols or semipodsols (Miotk-Szpiganowicz, 1992; Roering, 1999).

2.2. Chronology development

For the tree-ring widths (TRW) measurements, all samples were prepared according to dendrochronological procedures described by Stokes and Smiley (1968), Schweingruber (1983), Cook and Kairiukstis (1990). Afterwards, all samples were scanned on a flatbed scanner and the TRW were measured by WinDENDRO™. To ensure correct dating, the TRW were visually cross-dated and also statistically analyzed using the COFECHA program (Holmes, 1983). Age-related trends in the TRW were removed by a 66-year smoothing spline in ARSTAN (Cook and Kairiukstis, 1990) and the residual chronology was used for investigations.

The analysis of the anatomical measurements was performed for a subset of 14 cores from 7 trees which were found to be highly correlated with the mean TRW chronology. The surfaces of the cores were cut with a core microtome (Gärtner and Nievergelt, 2010). Tyloses and wood dust were removed from the vessels with blasts of high-pressure water. Finally, according to the suggestions of Fonti and García-González (2008), the wood surface was stained black with a permanent marker and the vessels were filled with white soft wax to increase the contrast between the vessels and the surrounding wood. Afterwards, the surfaces of the cores were scanned using a flatbed scanner and analyzed in WinCELL™. The enhanced contrast of the wood surface allowed for a semi-automatic detection of the vessel lumen areas. Several EVP were derived from the measurements and considered for this study: average vessel area (AVA), average radial vessel diameter (AVD), average tangential vessel width (AVW), and number of vessels (NV). Since no long-term trends were found in the EVP, detrending of the time series was omitted and raw values without any modification were used instead. The yearly values of each variable were averaged into individual chronologies. For each chronology, the following descriptive dendrochronological statistics were calculated: standard deviation (SD), mean sensitivity (MS), first-order autocorrelation (AC1), mean correlation between trees (r) and expressed population signal (EPS). In order to test the five EVP chronologies for possible similarities a principal component analysis (PCA) as well as a bootstrapped cross-correlation was conducted with the individual chronologies as input data. Significance of PCA axes was evaluated by a Monte Carlo test. All performed correlations were repeated 1000 times with a random process to derive robust correlation results (bootstrap method; Guiot, 1991). The PCA tested all chronologies against each other for the years of 1810–2010 by using SPSS v 22.0 software.

2.3. Climate–growth relations and extreme year analyses

The climate–growth relationships were examined with Pearson's correlation coefficients determined pairwise for the tree-ring variables and climate parameters. Equally to the performed cross-correlations also, the climate–growth correlations were bootstrapped (1000 times). For this, the daily weather data from the meteorological station Koscierzyna (54° 8′ N, 17° 58′ E) were averaged into monthly mean, minimum, and maximum temperatures and sums of precipitation for further analysis. The meteorological station runs since 1951 and is located approximately 30 km northwest of the study site.

Besides the monthly correlations, climate response analyses using daily climate data from the meteorological station Koscierzyna were also conducted. For this purpose, the computer program CLIMTREG allows investigation of the relation between the measured wood variables and climate data with a high temporal resolution rather than using the traditional monthly correlations. In the program, moving Pearson's correlations between climate and tree-ring data are calculated. Daily meteorological data are summarized by the program for a minimum period of 21 days and a maximum of 121 days. Correlations are first calculated between 21-day averages of the climate data and the selected tree-ring variables. For the next round of analysis, 1 day is added until the maximum window length of 121 days is reached. The moving correlation process starts on 1 July of the previous year and stops at 31 October of the current year, moving day by day along the calendar overall resulting in 42,218 correlations per analysis (Beck et al., 2013).

In addition, a closer examination of climate–growth correlations during extreme years promises to further enhance the comprehension of the relationship between tree growth and climate (Heinrich et al., 2008). Thus, an extreme year analysis was performed using the Cropper method (Cropper, 1979) to identify years with abrupt growth changes. After z-transforming the individual wood anatomical parameter series extreme years in the series were identified. If the threshold of ± 0.5 in minimum of four out of seven trees was exceeded, the year was defined as an extreme year. The two most extreme positive and negative years replicated by the largest number of trees were compared to daily temperature data to determine if climatic anomalies were associated with extreme growth anomalies. The long-term means were subtracted from the extracted climate data for the extreme years and the resulting residuals plotted as daily values starting in mid-November of the previous growing season to the end of February of the current period.

2.4. Climate reconstruction

The dominant climate factor exerting the strongest influence on tree growth within a time window of a specific number of days indicated by the examination of the climate–growth relations was selected for reconstruction purposes. Hereby, AVA as the most promising tree growth parameter was used to reconstruct the minimum temperature from 29th November to 20th January over the course of the last 200 years. The simple least square method was applied to find the best regression which was then used as transfer function (Fritts, 1976). The model validation was performed by using the split sample approach. By splitting the climate data into two independent periods, an independent evaluation for temporal stability can be performed (Meko, 1997). Therefore, the climate record of the Koscierzyna station was split into the calibration period, between 2010 and 1981 and the verification period from 1980 to 1951. The coefficient of determination (r^2) was calculated in order to measure the amount of variance explained by the model. Moreover, the Reduction of Error and the Coefficient of Efficiency (RE and CE; Cook et al., 1994) were computed to statistically estimate the ability of the tree-ring parameters to predict the climate. The theoretical limits for the RE and CE statistics range from 1 which indicates perfect agreement to minus infinity. A minus value indicates no agreement but any positive value can be considered as encouraging. For both periods, the mean squared error (MSE) was calculated to assess the quality of the reconstruction model, with smaller MSE values suggesting a better model. Finally, the statistically verified simple linear regression model was used to reconstruct climate (Fritts, 1976).

In a final step, it was also interesting to spatially correlate selected EVP with gridded minimum temperature data, in order to identify the geographic regions with significant correlations between temperature and our wood anatomical record. We used the KNMI Climate Explorer website (http://www.knmi.nl/; van Oldenborgh and Burgers, 2005) to generate correlation fields with seasonal December-to-January minimum temperatures.

2.5. Comparison with other reconstructions

For direct comparison, our reconstruction was compared to a collection of 92 regional, hemispherical, and global temperature reconstructions (Wahl et al., 2010). Wahl et al. (2010) described an integrated archive of high-resolution temperature reconstructions for the last 2000 years included in NOAA's National Climatic Data Center, from small regional to global scale. The 92 surface temperature records were downloaded from the PaleoClimate Network (PCN v. 2.0.0) at http://www.ncdc.noaa.gov/paleo/pubs/pcn/pcn.html. Most of the records reconstruct annual mean temperatures with annual resolution for the last Millennium (Wahl et al., 2010). The reconstructions were compared with our reconstruction by means of simple Pearson's correlation analysis and those correlating best with it were selected for further examination.

3. Results

3.1. Chronology characteristics

The TRW chronology contains a strong interseries correlation ($r = 0.57$; Table 1) and a stable population signal ($EPS = 0.95$; Supplementary S2). Analyses of the common year-to-year variation of wood anatomical chronologies indicated low similarities between the trees at the study site (see values of mean correlation between trees (r) and expressed population signal in Table 1). Compared to the TRW chronology, the wood anatomical chronologies reveal a weak mean sensitivity of less than 0.10 (Table 1, Supplementary S3) as well as a lower autocorrelation [AC (1) ~ 0.46]. The wood anatomical chronologies AVA, AVD, and AVW demonstrate similar statistical properties. However, the number of vessels (NV) has marginally higher MS and AC (1) statistics than the other wood anatomical chronologies. The results of the PCA indicate that the five chronologies cluster into two separate groups. The distribution along the first axis (54.6% of the variance) and the second axis (31.2% of the variance) suggest a clear distinction between NV and TRW on one side and the earlywood vessel parameters AVA, AVD, and AVW on the other side (Table 1 & Fig. 1). Small differences along the second axis somewhat separate the AVD from AVW while AVA is situated in the middle. Pearson's correlation coefficients suggest the same pairings (Table 2), since low correlations between NV and the other EVP are indicated.

3.2. Climate–growth relations

The general correlation patterns between monthly temperature and precipitation data from the meteorological station Koscierzyna and the tree-ring data (TRW and EVP) suggest stronger correlations with temperatures rather than with precipitation (Fig. 2; Supplementary S5). EVP correlates positively with minimum temperatures of previous December to current March, while weaker correlations are exhibited by TRW and NV (Fig. 2). The strongest correlations are evident between minimum temperatures of previous December and AVA and AVW ($r = 0.49$ and $r = 0.50$). These positive correlations suggest that higher minimum temperatures (warmer winter temperatures) tended to result in longer (AVD) and wider (AVW) earlywood vessels in the following growing season, which in consequence results in an increased earlywood vessel area (AVA).

Table 1
Descriptive statistics of the raw earlywood vessel parameter (EVP) and the residual TRW chronologies.

Parameter	AVA [μm^2]	AVD [μm]	AVW [μm]	NV	TRW [mm]
Trees/No. of samples	7/14	7/14	7/14	7/14	20/40
First year	1810	1810	1810	1810	1760
Last year	2010	2010	2010	2010	2010
Mean	59,766.2	318.6	241.1	14.9	1.9
SD	6805.3	20.8	15.5	2.7	1.0
MS	0.09	0.05	0.05	0.13	0.20
AC (1)	0.48	0.44	0.43	0.54	0.81
r	0.27	0.25	0.21	0.27	0.57
EPS	0.55	0.52	0.57	0.57	0.94

Note: Abbreviations of the descriptive dendrochronological statistics are according to description in the methods section. AVA—averaged vessel area; AVD—average radial vessel diameter; AVW—average tangential vessel width; NV—number of vessels; TRW—tree-ring width.

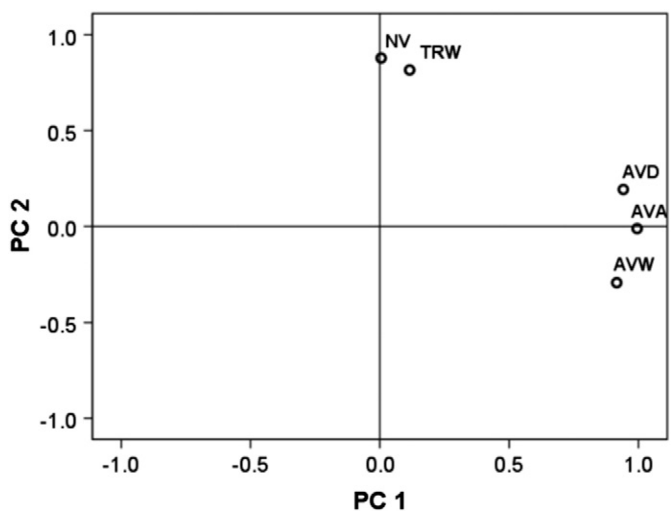

Fig. 1. Principal component analysis (PCA) for the EVP and TRW. PC1 explains 54.6% of the variance and the PC 2 explains 31.2% of the variance. AVA—average vessel area; AVD—average radial vessel diameter; AVW—average tangential vessel width; NV—number of vessels; TRW—tree-ring width.

3.3. Extreme year analysis of AVA

The extreme year analysis of AVA reveals 1979 and 1987 as the most extreme negative and 1961 and 1994 as the most extreme positive years. In both negative years, strong fluctuations of minimum temperatures (cold–warm–cold pattern) during the entire period of analysis between previous November and current February are illustrated (Fig. 3). Minimum temperatures dropped to less than −10 °C on the 29th November and stayed low until the 03th December. This phase, in the following described as first cold phase, is noteworthy because the long-term averages of the minimum temperatures were as high as −1.3 °C (SD ± 3.7 °C). The first cold phase is followed by a warm phase. Minimum temperatures increased during December and reached maxima of 5.1 °C in 1979 and 6.5 °C in 1987. The daily biological minimum temperature of 5 °C (according to Tylkowski, 2015), an indicator threshold value when an activation of physiological processes in the trees may take place in this region of Poland, was surpassed in both years. The second cold phase in both years started with a characteristic sharp temperature cooling at the beginning of January. Within 4 days, temperatures decreased by 28 °C from 4.1 °C on 31th December 1978 to −24 °C on 04th January 1979. This change was even more drastic in the year 1987 when the temperature fell by 34 °C within 13 days from 6.5 °C (26th December 1986) to −27 °C (08th January 1987). It is interesting to note that in both negative extreme years the December temperatures were above the freezing point (warm phase) whereas in late November (first cold phase) and early January (second cold phase), the temperatures were much lower. It is possible that due to the low temperatures of −25 °C for 1979 and −27 °C for 1987 freezing-induced embolism occurred which ultimately influenced the earlywood vessels of the following year.

In contrast to the negative extreme years, the positive extreme years were characterized by smaller temperature amplitudes, with temperatures mostly within the range of the long-term averages. It is also noteworthy that the cold–warm–cold phases observed for the negative extreme years were temporally shifted in positive extreme years. The first cold phase for the positive extreme years occurred during Decembers of 1960 and 1993 with daily minimum temperatures of −20 °C and −17 °C, respectively. In the following warm phase, the daily temperatures stayed mainly within one standard deviation of the long-term averages and did not exceed the 5 °C indicator threshold for an activation of physiological process (Tylkowski, 2015). The duration of the warm phases ranged from 17 days in 1961 to 29 days in 1994 and exhibited average minimum temperatures of −1.8 °C and −1.1 °C, respectively. Within the second cold phase in late January 1961 and mid-February 1994, minimum temperatures decreased to temperatures of approximately −15 to −20 °C.

Table 2
Bootstrapped cross-correlations between the earlywood vessel parameters (1810–2010) and tree-ring width; significant levels: 95% * ($p < 0.05$); 99% ** ($p < 0.01$); 99.9% *** ($p < 0.001$).

	AVA		AVD		AVW		NV	
AVL	0.94	***						
AVW	0.90	***	0.74	***				
NV	0.02		0.20	**	−0.27	***		
TRW	0.08		0.19	**	−0.07		0.46	***

Note: Pearson's correlation results are based on 1000 repetitions (bootstrap method). AVA—average vessel area; AVD—average vessel diameter; AVW—average vessel width; NV—number of vessels; TRW—tree-ring width.

3.4. Spatial correlation

The spatial field correlations indicate that the new AVA record correlates best with minimum temperatures of previous December and current January in central and northern Europe, but particularly well in Eastern Europe (Fig. 4). The strongest correlation in longitudinal direction covers an area from north Poland via Belarus to west Russia and in latitudinal direction from Estonia in the north to Ukraine in the south. In contrast, minimum temperatures of the Mediterranean as well as the British islands do not correlate well. Thus, it seems that the strength of the spatial correlation signal is increasing from southwest to northeast.

3.5. Climate reconstruction

In order to optimize the climate–growth-response model, the program CLIMTREG was used to identify the season with the strongest impact on tree growth based on a daily accuracy. The most significant result CLIMTREG obtained for the period 29th November to 20th January, when 31% of the variance of AVA was explained by the minimum temperatures. The regression analysis determined the linear relationship $y = 2.22 \times -4.19$. This relationship was utilized for a 200-year reconstruction of the minimum temperatures for the period of late November of the previous year to late January of the current year (Fig. 5). The reconstruction statistics are all significant and thus indicate that the reconstruction is of good quality (Table 3). The correlation $r = 0.51$ ($p < 0.001$) is highly significant for the calibration period (1981–2010) and also for the verification period (1951–1980) ($r = 0.58$; $p < 0.001$). The reconstruction is stable in time and exhibits a good statistical quality confirmed by the reduction of error (RE = 0.37) and coefficient of efficiency (CE = 0.27). The overall coefficient of determination of $r^2 = 0.31$ demonstrates a moderate explanatory power of the reconstruction, explaining almost a third of the variance in the minimum November-to-January temperatures. The most notable features of the reconstruction are the multidecadal fluctuations of warm and cold periods (Fig. 5). The coldest period over the last 200 years is centered on AD 1820 whereas the warmest period with yearly average minimum temperatures of +0.79 °C is centered on AD 1837. It is notable that the reconstruction indicates the periods around AD 1837 as well as AD 1932 as having been warmer than the late 20th century. The reconstruction suggests a constant increase in average minimum temperatures over the last two centuries, showing a warming in the winter minimum temperatures from −7 °C in 1810 to −4 °C in 2010. In several years (1837, 1847, 1851, 1887, 1948, 1961, and 1994) the study area experienced relatively high minimum winter temperatures. In contrast, extremely cold years occurred in 1820, 1841, 1845, 1867, 1877, 1888, 1917, 1922, 1940, and 1987. Interestingly, except for AD 1987, no extreme

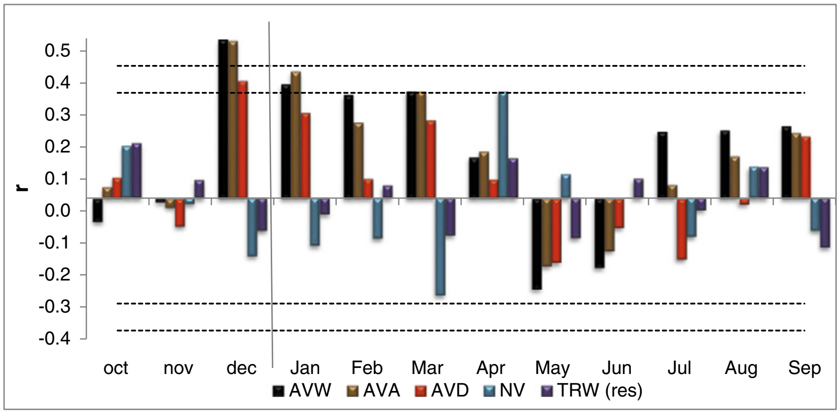

Fig. 2. Bootstrapped climate response plot for the earlywood vessel parameters and tree-ring width (TRW) with monthly minimum temperatures (1951–2010). Correlation results are based on 1000 repetitions (bootstrap method). The dashed lines represent the 95% ($p < 0.05$) and 99% ($p < 0.01$) significance levels.

cold winters are reconstructed for the last 70 years. It seems that in some instances the regression model used for the reconstruction underestimated extreme values recorded in the measured series, e.g., cold spells in 1963, 1970, 1997, and 2004, as well as warm events in 1998, 2002, and 2006.

3.6. Comparison with other reconstructions

The comparison of our Polish temperature reconstruction with the collection of 92 regional, hemispherical, and global temperature reconstructions (Wahl et al., 2010) by means of simple Pearson's correlation analysis resulted in the selection of two reconstructions. The new minimum winter temperature reconstruction was compared to a regional mean winter temperature reconstruction (Luterbacher et al., 2010) and a hemispherical mean annual temperature reconstruction (Moberg et al., 2005), both based on multiproxy approaches. The regional temperature reconstruction was derived from the grid box 53.25 to 53.75 °N and 18.25 to 19.25 °E (http://www.cru.uea.ac.uk/cru/projects/soap/data/recon/#luter04; Luterbacher et al., 2010). The data of Moberg et al. (2005) represent a large-scale reconstruction of mean temperature anomalies in the Northern Hemisphere (NH) (https://www.ncdc.noaa.gov/paleo/pubs/moberg2005/moberg2005.html).

The reconstruction of minimum winter temperatures correlates well ($r = 0.39$; $p < 0.001$) with the reconstruction of Luterbacher et al. (2010) for the common period 1810–2010. Both reconstructions share a common long-term trend (Fig. 6). However, our reconstruction exhibits somewhat stronger low-frequency trends, as indicated by the larger amplitude (Fig. 6, middle panel). During the second half of the 19th century, the early 20th century, the late 1950s and the late 1980s, the running correlation falls below the significance level. On the other hand, some strong increases are shown for the periods

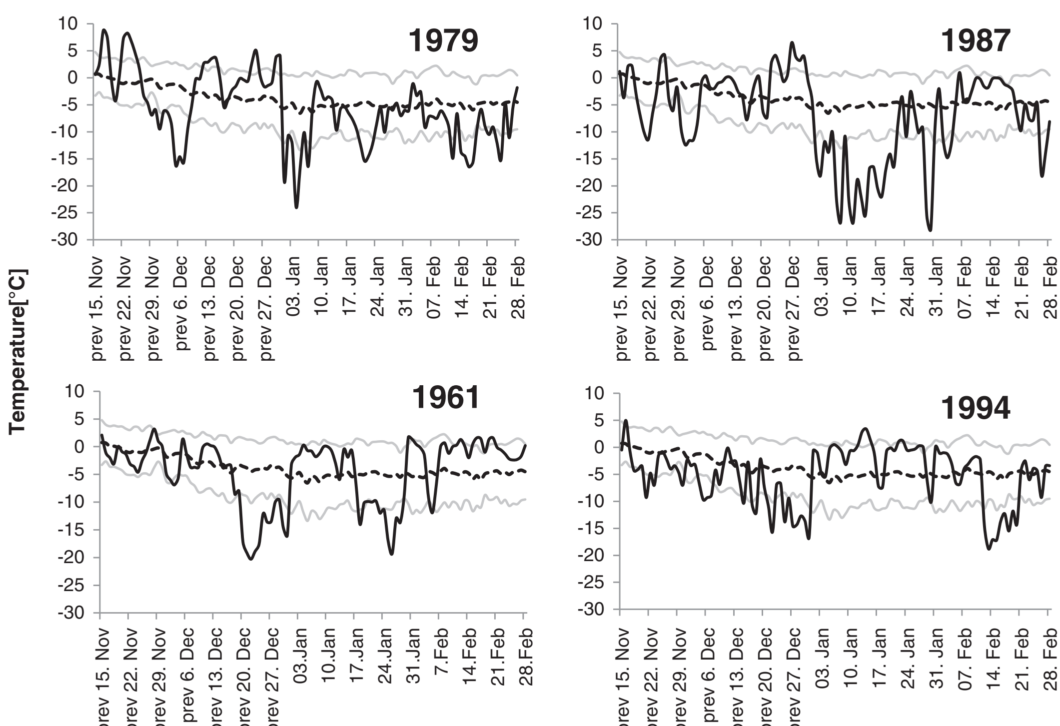

Fig. 3. Daily minimum temperature variations (black) for the two strongest negative (1979 and 1987) and positive (1961 and 1994) extreme years in comparison to the long-term averages (dashed black line) of the meteorological station Koscierzyna. Upper and lower standard deviations of the long-term averages are in gray.

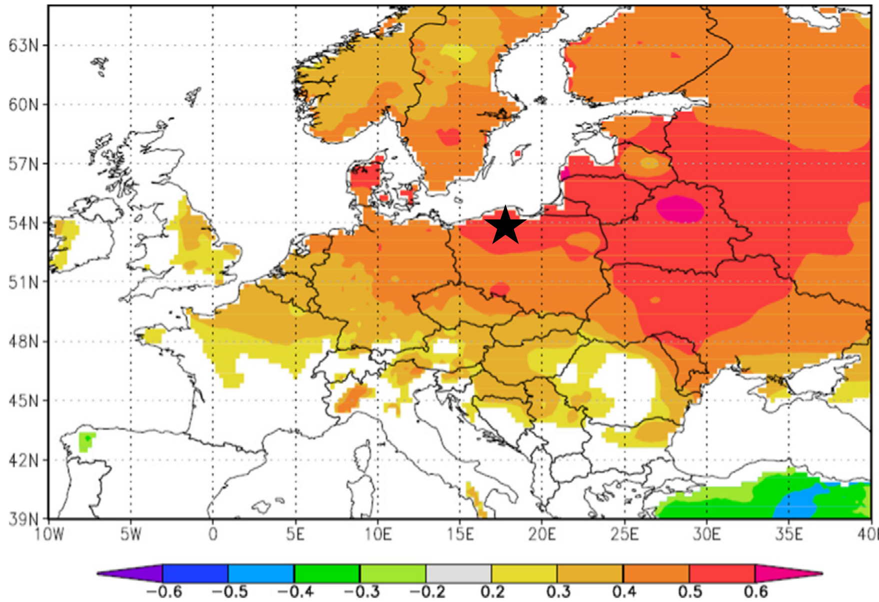

Fig. 4. Spatial field correlations (Trouet and Van Oldenborgh, 2013) between minimum temperatures of the previous December to January (0.25° E-OBS) and AVA (1950–2010); black star indicates location of the study site.

1930–1950 and 1965–1980. For the common period 1810–2010, our reconstruction correlates significantly ($r = 0.37$; $p < 0.001$) with the mean annual NH temperature anomalies reconstructed by Moberg et al. (2005). However, the relationship is also unstable in time, that is, while the correlations are positive around 1820, from 1850 to 1870, and 1890 to 1920, they are negative from 1825 to 1845, in the 1870s and 80s and from 1930 to 1970.

Generally, the correlations are less significant due to the small degrees of freedom as a result of the 21-year moving correlations. Interestingly, only during two periods, that is, 1850–1870 and 1888–1916, the moving correlation patterns are similar (Fig. 6, lower panel), but during the other times, the correlation patterns are reversed.

4. Discussion

4.1. Statistical quality of the chronologies

The results of the statistical analysis suggest that TRW and NV possess better qualities for dendroclimatological investigations than the wood anatomical chronologies presented here. The strength of the common signal (r) and year-to-year variability (MS) are highest in TRW and NV. In contrast, relatively low values of AC (1), MS and r are observed in the EVP, especially for AVW. Similar results have also been noted previously by Fonti and García-González (2004); Tardif and Conciatori (2006). However, Fonti and García-González (2008) demonstrated that higher chronology quality did not necessarily guarantee a better climatic signal in cell measurement variables.

By comparing the chronologies with each other and performing a PCA we revealed a grouping within the parameters which was also confirmed by similar climate–growth relationships of the chronologies within each group. The findings are corroborated by previous work on earlywood anatomical chronologies (Fonti and García-González, 2004, 2008; González-González et al., 2014) which also demonstrated a dipole behavior where the EVP were found in one PC and the NV and TRW in the other PC. The first group comprised the vessel size chronologies AVA, AVD, and AVW, indicating that all chronologies were derived from the same wood anatomical component, that is, the earlywood vessel characteristics. The second group contained TRW and NV

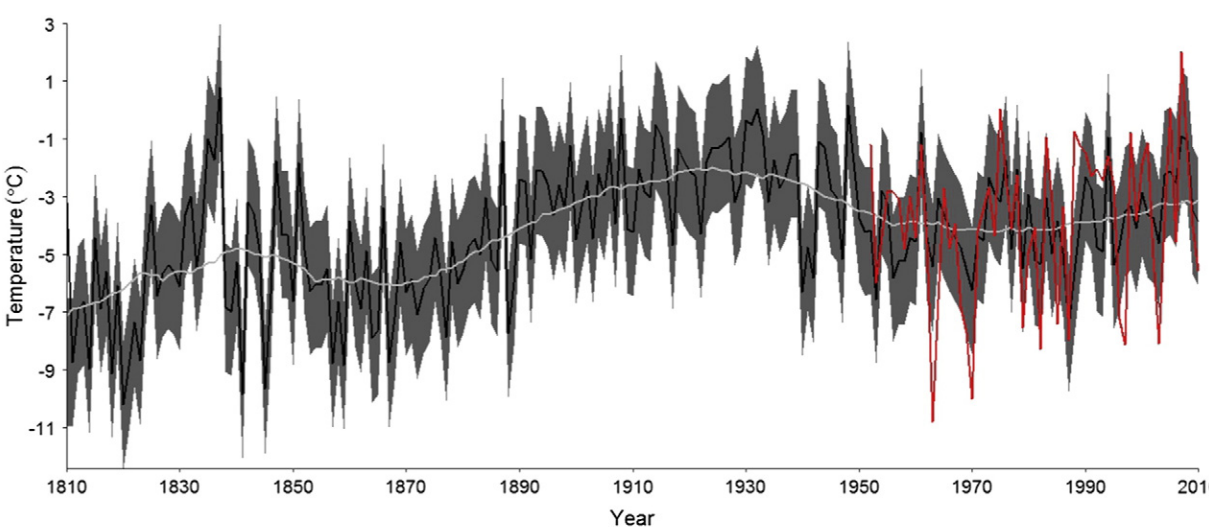

Fig. 5. Reconstruction (black line) of minimum winter temperatures (29th November to 20th January) based on AVA with standard deviation (dark gray shading); 31-year mean (light gray line) and original temperature data (red line).

Table 3
Calibration and verification statistics of reconstruction based on AVA.

	29. Nov. to 20. Jan
Cal r^2 (1981–2010)	0.26
Ver r^2 (1952–1980)	0.34
MSE Cal	5.38
MSE Ver	4.35
RE	0.37
CE	0.27
Full r^2 (1951–2010)	0.31

Note: Cal r^2—Pearson coefficient of determination for calibration period; Ver r^2—Pearson coefficient of determination for verification period; MSE Cal—mean squared error for calibration period; MSE Ver—mean squared error for verification period; RE—reduction of error; CE—coefficient of efficiency; Full r^2—Pearson coefficient of determination for complete period.

characterized by a strong positive correlation to each other. The positive correlation demonstrates that a higher number of earlywood vessels often results in larger tree rings. Overall, the results confirm the concept of additional information contained in the EVP in contrast to measuring only TRW, as was also recently suggested by González-González et al. (2014) and Kniesel et al. (2015).

4.2. Climate–growth relations

Despite the low qualities in the commonly used dendrochronological descriptive statistics of the wood anatomical chronologies, the climate–growth relationships were stronger for the EVP, thus indicating that valuable climatic information describing the climatic conditions at the site are well implemented (Fonti and García-González, 2004). The monthly and daily climatic signals recorded in the earlywood chronologies are stronger and different from those in the TRW and NV chronologies. The climate–growth relationships of TRW and NV are mostly weak and non-significant.

In contrast, the earlywood vessel size chronologies (AVA, AVD, and AVW) demonstrate strong responses toward winter temperatures, especially minimum winter temperature. This relationship may seem doubtful because one may argue that deciduous trees are usually dormant during winter months and thus may not be affected by the conditions in winter at all. However, already from the perspective of the meteorological data, it is more likely to achieve strong climate–growth relations with winter than with summer temperatures because the standard deviation of the minimum temperatures in winter is more than two times higher than in summer (data not shown) and thus more variable (Kozuchowski and Degirmendzic, 2005). This larger variability, or in other words sensitivity, is likely to facilitate a better responsiveness of the winter climate data toward the changes of the EVP.

Besides this suitability from a statistical point of view, previous studies of the same genera or at the same study region support the possibility of climate–growth relationships between winter climate and earlywood parameters. Recent work on *Pinus sylvestris* (Knorr, 2013) identified a strong correlation between tracheid lumen parameters and January-to-February temperatures in N-Poland. Similarly, significant positive correlations between winter temperatures and mean vessel areas of *Quercus robur* growing in central Latvia (Matisons and Dauškane, 2009) and of *Quercus petraea* in the Swiss Alps (Fonti and García-González, 2008) were identified. While Von Lührte (1991) discovered repeated growth reductions in *Quercus robur* and *Quercus petraea* due to cold winters near Berlin, Pederson et al. (2004) demonstrated for TRW of *Quercus alba* from the Hudson River Valley strong positive correlations with January temperatures.

Various potential explanations for the winter temperature-to-growth relationship ranging from xylem damage during harsh winters to hormone release have been put forward. In contrast to conifers,

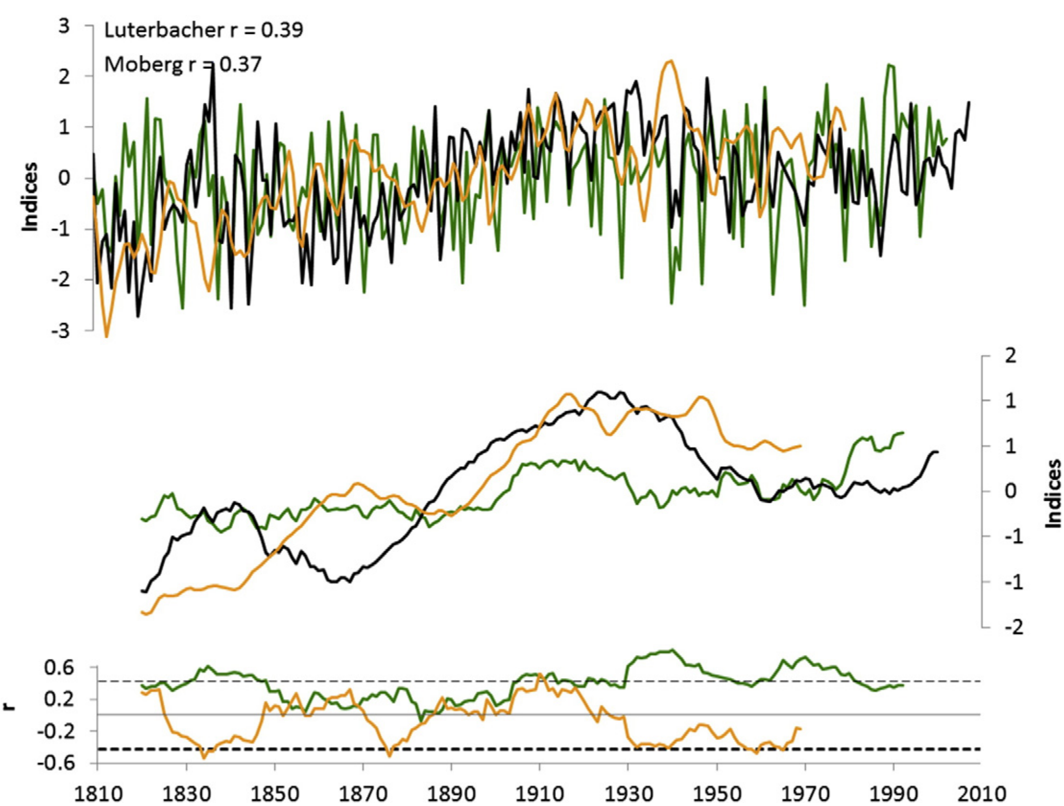

Fig. 6. Comparison of the minimum temperature reconstruction (29th November to 20th January) (current study, black line) with similar reconstructions: Dec. to Jan. mean temperatures in Poland (Luterbacher et al. (2010, green line) and northern hemisphere annual mean temperature anomalies (Moberg et al., 2005, orange line) (upper panel); 21-year running means (middle panel, same color coding as top panel); 21-year moving correlations between the minimum temperature reconstruction and Luterbacher et al. (green) and Moberg et al. (orange) (95% confidence levels are indicated).

many deciduous trees produce the cambium initials for the next season already at the end of the last growing season (Carlquist, 1988). In temperate climates, these cells are inactive during the winter dormancy and are then activated in spring of the following year (Frankenstein et al., 2005). One likely explanation for the positive correlations between minimum winter temperatures and EVP is the negative influence of harsh winter conditions on the cambium cell initials, resulting in a reduction of the earlywood vessel size characteristics (AVA, AVD, and AVW). As described in Aloni (2015), typical environmental influences of unusually cold winters will exert stress on plants, mediated by hormone releases regulating the vascular differentiation. In response to these environmental stresses, trees respond by synthesizing the plant hormone ethylene gas which was found to promote reduced vessel sizes (Aloni, 2015). Another possibility for the positive correlations might be embolism as a result of cavitation induced by freezing. Freezing induced by harsh winter conditions could destroy parts of the already existing vessel system during winter dormancy (Davis et al., 1999). A switch toward smaller earlywood vessels, as an adaptation to the new environmental conditions, could be the response in spring to such a situation of environmental stress in winter.

4.3. Extreme year analysis of AVA

The results of the climate–growth analyses suggested significant correlations and thus confirmed the ability of the species to implement climate information in their wood characteristics. In a second step, focusing on two positive and two negative extreme years only, detailed analyses of the correlations between AVA and daily minimum temperatures revealed particular daily temperature patterns influencing the extreme AVA values.

Strong temperature fluctuations in negative extreme years are likely to induce freeze–thaw embolisms within the existing sapwood xylem. Such temperature fluctuations between cold temperatures of −15 °C and warm temperatures of above 5 °C in a relatively short period can lead to a release of gas from the xylem water (Tyree and Zimmermann, 2002). The resulting embolisms cause losses of hydrological conductivity (Hacke and Sperry, 2001; Gea-Izquierdo et al., 2013), which lead to a decline of the xylem function. Still under scientific debate is the potential refilling of embolized vessels (Tyree et al., 1999; Améglio et al., 2002; Urli et al., 2013). Nevertheless, the negative effect of cold winter temperatures would also remain if refilling occurred. In this regard, Pederson et al. (2004) described the growth-reducing influences of cold January temperatures on TRW of *Quercus alba* in eastern North America as a result of sharing the available energy. Instead of using all energy to build only new wood cells, the energy would be split between the refilling of embolized vessels and investment in new cells, leaving only fewer resources for the formation of new vessels in spring.

Previously, it has also been stated that small vessels are built after harsh winters to reduce the likelihood of hydraulic failure. The production of small but more vessels would suggest a shift to a hydrologically safer wood structure (Zanne et al., 2010). Moreover, the sensitivity and vulnerability of trees for embolism due to freezing were found to be related to vessel diameters (Sperry and Sullivan, 1992; Davis et al., 1999). In our study, the trees exhibited a large mean AVD of 318.6 μm (Table 1) and therefore would be extremely sensitive toward freezing embolisms. The larger the vessels (higher volume), the more gases can dissolve from the sap and build bigger air bubbles that induced cavitation at lower tensions (Sperry and Sullivan, 1992). However, a certain resistance to freezing-induced embolism has been described for various oak species (Morin et al., 2007). It was demonstrated that depending on the growth environment, species which often have to cope with below zero temperatures develop a strong cold hardiness. These species harden over the course of the winter and reduce their freezing-induced embolism risk by avoidance of intracellular ice formation and tolerance of extracellular ice formation and consequent cellular dehydration (Levitt, 1978).

As another possible explanation, the mobilization of carbon needed for the formation of the earlywood vessels has been found to be temperature dependent (Loescher, 1990). Unusually low temperatures can affect the reserves in the root system and thus may delay the release of carbohydrates. The active transport of the carbohydrates from the roots into the stem is also temperature dependent (Loescher, 1990). Thus, small xylem vessels built after cold winters may also partially be the result of a delayed activation and transportation of the carbohydrate reserves.

During positive extreme years, minimum temperatures in January were almost constantly above the freezing point which in our study might have led to an earlier start of tree physiological processes (Kozlowski et al., 1962). Growth hormones, such as auxin, regulate the cambial growth (Aloni, 1987; Kozlowski and Pallardy, 1997), but their carriers (PAT genes) have been demonstrated to be deactivated during dormancy (Schrader et al., 2004) and re-established again between January and March (Lachaud, 1989). This could mean that warm winters with high minimum temperatures would trigger the re-establishment of the auxin carriers faster than normal (Schrader et al., 2003). However, an earlier start would not necessarily lead to increased vessel sizes. For this, in addition, the trees would need to be without any stress because then little or no amounts of the stress hormone ethylene gas would have been produced and thus larger vessels be formed (Aloni, 2015).

4.4. Spatial correlation

The analysis of the spatial correlation fields suggest that the EVP pattern can explain approximately 20%–30% of the variance in the minimum winter temperatures of large parts of Central and Eastern Europe. The results corroborate findings from Latvia (Matisons and Dauškane, 2009; 2012) suggesting significant correlations of oak vessel chronologies with winter temperatures especially in the east of Latvia. On the other hand, in our study, significant spatial field correlations were missing with most regions in Southern Europe. The results are in line with the findings of Alla and Camarero (2012) which revealed that in increasingly colder environments an intensification of the winter signal contained in the EVP could be observed. Since the spatial field correlations indicate the strongest values for the regions to the east of the study site, additional study sites in Eastern Europe would be desirable to reveal a possible continental west-to-east change of the climate–vessel growth relationships in Europe. One of the possible results of such a spatial analysis might be the understanding that winter temperature reconstructions based on vessel lumen variations of oaks from the temperate lowlands might be most promising in Eastern Europe.

4.5. Climate reconstruction and comparison with other reconstructions

The analysis of the EVP in oaks growing in Poland yielded some interesting facts: although the chronology statistics such as EPS and interseries correlations were lower than for tree-ring widths, the correlations with climate were most significant for EVP. It has to be taken onto account that the EPS for the EVP remains below the 0.85 threshold, above which a chronology is generally regarded as satisfactory. Therefore, our reconstruction possibly is not covering the full potential of the climate signal for the population at this site. Nevertheless, our study as well as the research of González-González et al. (2014) demonstrated temporally stable climate–growth relationships embedded in the EVP, which could be used to reconstruct climate. As far as we know, it is the second temperature reconstruction based on wood anatomical parameters in general and the first based on wood anatomical parameters of broadleaf trees in particular. The first was established by Panyushkina et al. (2003) which reconstructed Siberian summer temperatures using tracheid dimensions and cell numbers of *Larix cajanderi*. Since our temperature reconstruction is the first using oak vessel measurements, additional studies are needed to explore the ability of this method to capture climate signals. The study of EVP in oak also needs to focus on longer chronologies to facilitate the analysis of different frequency domains.

Despite the fact that we have been able to produce a statistically sound reconstruction based on highly significant climate–growth correlations, it is still not perfectly clear how winter temperatures can have such a strong impact on the dimensions of vessels growing in the months afterwards. We have presented concepts to explain this correlation but certainly additional tree physiological research would be needed to identify which of the mechanisms is responsible for this response of the oaks towards variations of the winter temperatures. Especially long-term comprehensive monitoring of oak growth seems to be an important tool to shed more light on this challenging subject (Bens et al., 2012). Based on stable climate–growth relationships, this first winter temperature reconstruction based on oak vessel dimensions explains 31% of the temperature variances between 1810 and 2010. It is remarkable that oak vessels are able to capture a stronger temperature signal within the temperate lowlands than what has been demonstrated by tree-ring width chronologies so far due to the diffuse climate–growth relations at sites with less extreme climate conditions (Buckley et al., 1997).

The course of the reconstructed temperature indicates variations with decadal to multidecadal trends. The coldest period is indicated for the early 19th century. It is possible that the low temperatures indicated for 1810 to 1820 were induced by changes in the solar activity of the sun, namely, during the Dalton Minimum which occurred during this time (Eddy, 1977) and most likely influenced tree growth negatively in Poland and elsewhere (Büntgen et al., 2005; Trouet and Taylor, 2010). Besides this early 19th century cooling, a second and third cooling phase took place during the 1860s to 1870s and somewhat weaker between 1955 and 1975. The constant increase in winter temperatures since 1970 is in line with the modern warming trend indicated by tree-ring research from remote sites where the climate–growth relations are more extreme (Young et al., 2012). A general decrease of extremely cold winter temperatures as indicated for Northern Poland might be a symptom of the regional effects of global warming in Poland, as suggested previously (Kozuchowski and Degirmendzic, 2005).

The comparison between the new minimum winter temperature reconstruction and the regional mean winter temperature reconstruction by Luterbacher et al. (2010) and the hemispherical mean annual temperature reconstruction (Moberg et al., 2005) showed significant overall correlations; however, with temporal instabilities. Some of the discrepancies between the three reconstructions might be explained by the differences regarding the temperature targets, ranging from annual mean temperatures of the Northern Hemisphere (Moberg et al., 2005), regional mean winter temperatures (Luterbacher et al., 2010) to local minimum November-to-January temperatures. It is still interesting to see that the correlations are highly significant. On the other hand, the patterns of the moving correlations between our reconstruction and the other two are only rarely similar, that is, 1850–1870 and 1888–1916 (Fig. 6, lower panel). During the other times, the temporal correlation patterns work in opposite directions, that is, when the correlations between our reconstruction and the temperature reconstruction by Luterbacher et al. (2010) were negative the correlations between our reconstruction and the NH temperature reconstruction by Moberg et al. (2005) were significantly positive and vice versa. This phenomenon is most obvious between 1930 and 2010 when the correlation with Luterbacher et al. (2010) are highly positive and with Moberg et al. (2005) moderately negative but also during the 19th century long periods of opposite behavior can be detected. Since the reconstructions are based on diverse proxies from different geographical regions, it seems possible that temporally varying climate dynamics may occur influencing the correlation patterns of the reconstructions in different ways. The results substantiate expectations for the climate in Northern Poland situated in a transitional zone between the temperate zone of Central Europe affected by westerly flows and the more continental Eastern Europe with its cold fronts from Siberia (Heinrich et al., 2013). Moreover, methodological differences, that is, unlike the current study Luterbacher et al. (2010) applied a multiproxy approach comprising tree-ring data from Scandinavia and the Alps as well as long series of meteorological data and documentary information from selected locations in Europe. Moberg et al. (2005) also combined low-resolution proxies such as lake sediments with tree-ring widths, using a wavelet transform technique. While in the current study, raw values of the earlywood vessel parameter AVA were used, the other two studies needed to detrend the tree-ring width series, because tree-ring width always contain unwanted age-related trends. Unfortunately, during the detrending procedure, low-frequency components both related and unrelated to climate might be removed. Therefore, some of the differences concerning the low-frequency behavior of the series and their temporal discrepancies might be explained by the different detrending approaches.

5. Conclusions

In this study, a new reconstruction of minimum winter temperatures (1810–2010 AD) based on average earlywood vessel areas of *Quercus robur* from northern Poland was presented. It is the first time that oak vessel measurements were used in the temperate lowlands of Europe for such a reconstruction over 200 years. The EVP, especially average vessel area (AVA), revealed significant positive correlations to the minimum winter temperatures (29th November to 20th January). We discussed possible explanations how minimum winter temperatures during dormancy may have shaped the wood anatomical vessel parameter of *Q. robur* growing in north Poland. While low winter temperatures may be responsible for damages to the root system, it is also likely that externally induced freezing embolisms may occur which will finally lead to smaller vessels being formed in spring. The tree responses to stressful environmental winter conditions are usually mediated via changing hormone levels which also have their impacts on the vessel characteristics. The extreme year analysis further indicated a close relation between a cold–warm–cold pattern visible in the minimum winter temperatures of selected years and relatively small earlywood vessels.

The reconstruction demonstrated a stable climate–growth relation, comprised high- and low-frequency components, and spatial correlation fields suggested that the reconstruction correlated with a large range of territories in Central Europe, in particular in Eastern Europe. Besides, the reconstructed winter temperature data compared well with two existing temperature reconstructions, especially during most of the 20th century. Interestingly, the moving correlations since the 1930s were negative with one reconstruction and positive with the other, indicating temporally varying climate dynamics which may influence the correlation patterns of the reconstructions in different ways. Further investigations focusing on sampling sites in Eastern Europe would be desirable. Site chronologies of earlywood vessel measurements are suggested as novel proxies for new temperature reconstructions for regions in the temperate lowlands where traditional dendrochronological parameters such as tree-ring widths have failed so far.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.palaeo.2016.02.046.

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