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Climatic sensitivity of *Quercus robur* L. in floodplain near Kyiv under river regulation

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Abstract: Climate change has a significant impact on natural ecosystems, particularly on floodplain forests that are among the most transformed ecosystems in the world. The climate sensitivity of dominant species is likely to play a key role in determining the susceptibility of flooded forests to climate changes. Here, we use dendrochronological approaches and local climate records from 1880 to 2015 to assess the response in pedunculate oak (*Quercus robur* L.) trees growing in a floodplain of the Dnipro River near Kyiv to climatic variables. Correlation analysis reveals the strongest positive association of the *Q. robur* tree-ring width chronology with May–June precipitation, May–June temperature, and May self-calibrating Palmers drought severity indices (scPDSI). The moving-window correlation analysis points to positive association with the scPDSI after the 1950s, when local river regulation was implemented. The positive correlation with current March precipitation is the least expected change in the oak growth-to-climate relationship that occurred in the aftermath of human alterations in the local river and regional climate changes. This study discusses the probable ecological consequences and ecophysiological mechanisms of observable climate-to-growth relationships and their temporal stability.

Keywords: pedunculate oak, tree-ring width, riparian forest, dendroclimatology, moving correlation

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Introduction

Floodplain forests represent ecosystems that provide essential habitats and food resources for diverse plant and animal species (Gren et al., 1995; Bauer et al., 2010), reduce soil erosion, perform water regulation, improve water quality, supply material for wood products, and provide people with recreation (Gren et

al., 1995; Klimo, 1998). However, riparian and flooded ecosystems are likely to be highly vulnerable to climate change and human impact (Turner et al., 2004; Schnitzler et al., 2005; Kaminski et al., 2011; Capon et al., 2013) and thus need to be understood through their relationship with environmental variables.

As climate change manifested itself by warming and varying precipitation patterns, it exerts an influence

on riverine ecosystems, altering impact on rivers' hydrology (Middelkoop et al., 2001; Kundzewicz, 2008; Schneider et al., 2013) that directly affects floodplain ecosystems biota (Poff et al., 1997; Ström et al., 2011; Politti et al., 2014; Morid et al., 2016). An ecosystem's capacity to adjust to climate change largely depends on morphological and physiological plasticity of its components (Capon et al., 2013). The ability to cope with soil-water excess and root hypoxia, which enables persistence of trees under fluctuating soil-water level, differs among tree taxa. For instance, *Fagus sylvatica* L. and *Quercus petraea* Matt. Liebl. belong to a very low flooding tolerance class, whereas, *Alnus glutinosa* L. and *Salix alba* L. are among highly flood-tolerant species (Glenz et al., 2006). Pedunculate oak (*Quercus robur* L.), on the contrary to its congener species *Q. petraea*, is known to be tolerant to flooding and is able to withstand 50 days flooding in its juvenile stage and up to 100 days flooding as adult (Siebel et al., 1998; Kreuzwieser et al., 2004; Glenz et al., 2006).

Flood during the onset of earlywood growth is known to cause formation of anomalous anatomical structures, i.e. collapsed sickle-shaped vessels, but in both juvenile (Copini et al., 2016) and adult (Stuijzand et al., 2008) *Q. robur* trees this happens only in the submerged part of the stem and is attributed to hypoxia. Flood has a significant negative effect on the ring width only in juvenile oaks (Copini et al., 2016), but in contrary may result in wider tree rings in adult trees (Gričar et al., 2013). Oak growth is positively affected by May–June precipitations, particularly when hydrology is altered and floods occur in winter-spring at many flooded sites in Central Europe (Čater & Levanič, 2015; Goršić, 2014; Stojanović et al., 2015b; Hafner et al., 2015).

The oak radial growth response on temperature in the growing season is ambiguous, being negative at sites with regulated rivers (Goršić, 2014; Stojanović et al., 2015a; Stojanović et al., 2015b), and absent or positive where river regulation is not imposed (Čejková & Poláková, 2012; Scharnweber et al., 2013; Hafner et al., 2015; Tumajer & Treml, 2016). The high positive temperature signal in tree-ring chronology is possibly a consequence of sufficient water availability during wood formation (Tumajer & Treml, 2016). Moreover, the *Q. robur* decline and rise in its mortality rate are expected to be more common phenomena in the future, in the regions where global warming leads to an increase in annual precipitation and in frequency of extreme rainfall events (Rozas & García-González, 2012). The oak decline and decrease in wood production also happen in areas experiencing excess of water in winter-spring and drought events in summer during the growing season (Lévy et al., 1999; Vincke & Delvaux, 2005). This effect is in line with the finding that wet and warm conditions in spring can exacerbate the summer drought effect

by promoting the formation of large-sized earlywood vessels (Tumajer & Treml, 2016), as large vessels are able to transfer greater volumes of water while abundant, but vulnerable to cavitation and embolism under soil-water deficit (Sperry et al., 2008).

Consistent patterns of relationships for floodplain *Q. robur* and climate variation are still mainly uncertain probably due to the various hydrological regimes over different sites coupled with the effect of regional climate trends. Even relatively short meteorological and hydrological recordings point out a recent climate trend effect on tree growth in flooded sites (Stella et al., 2013; Tumajer & Treml, 2016). Obviously, longer series of both the tree-ring and the climate variables are desirable to more comprehensively appreciate how climate controls oak growth in floodplains.

The objective of this study was to assess how climate variables governed *Q. robur* radial growth since 1880 in an extant old-growth floodplain forest near Kyiv, Ukraine. The long-term climatic records and ring-width chronology sampled from living trees growing in the Siverka River valley, which is a tributary of the Dnipro River, were used to compute the correlation function over the entire 136-yr interval and the 102 consecutive 35-yr intervals. Changes in the correlation function coefficients were compared with 35-yr level of smoothing, fitted to monthly climate records, with respect to the date of the river regulation onset. Our general expectation was that the regional warming trend coupled with river flow alteration enhanced a detrimental effect of water deficit and summer temperatures on oak growth in a floodplain. We also suggest that well documented historical floods had a negative effect on studied trees before the river regulation was implemented.

Material and Methods

Study site

The studied site is located in the southern part of Kyiv (50°17'40" N, 30°32'57" E) and pertains to the Lisnyky Reserve of the National Natural Park "Holosiivsky". The Lisnyky Reserve spans an area of 1110 ha with altitudes ranging from 93 to 115 m a.s.l. The eastern part of the Lisnyky forest is dominated by Scots pine (*Pinus sylvestris* L.) on poor sandy soils, and the western part, including the studied site, is represented by deciduous species on acidic sod-podzolic gley soil. The western portion of the reserve is situated between the Siverka River and its tributary the Petyl River. There is a low-lying site at 93 m a.s.l. that is abundant with sedge bogs, oxbows, and swampy alder-woods here. In more elevated locations (94–97 m a.s.l.) of the western portion, the dominant forest associations are the *Convallario*

majali-Quercetum roboris Shevchyk et V. Solomakha 1996 and the *Quercetea robori-petraeae*. The overstory here is dominated by *Q. robur* and the midstory is comprised by *Tilia cordata* Mill., *Fraxinus excelsior* Mill., *Acer platanoides* L., *A. campestre* L. and *A. tataricum* L. (Didukh & Aloskhina, 2012).

The studied site historically experienced flooding in spring before the river regulation was implemented (Vishnevsky, 2007). Following the 1950s channelization and channel straightening of the Siverka River, the deep natural flooding in the Lysnyky forest ceased. Since the 1976, when a levee downstream of

Kyiv was built, the river's water is backed up by the main stream, i.e. the Dnipro River. In the 2000s, the drainage construction was partially dismantled and filled in, causing flooding in spring. The Siverka River's rain-snow regime makes it full in April–May and nearly dried up in July–August (Vishnevsky, 2007).

Climatic data

The regional monthly temperature and precipitation records were obtained from the Central Geophysical Observatory CGO in Kyiv, 165 m a.s.l., and

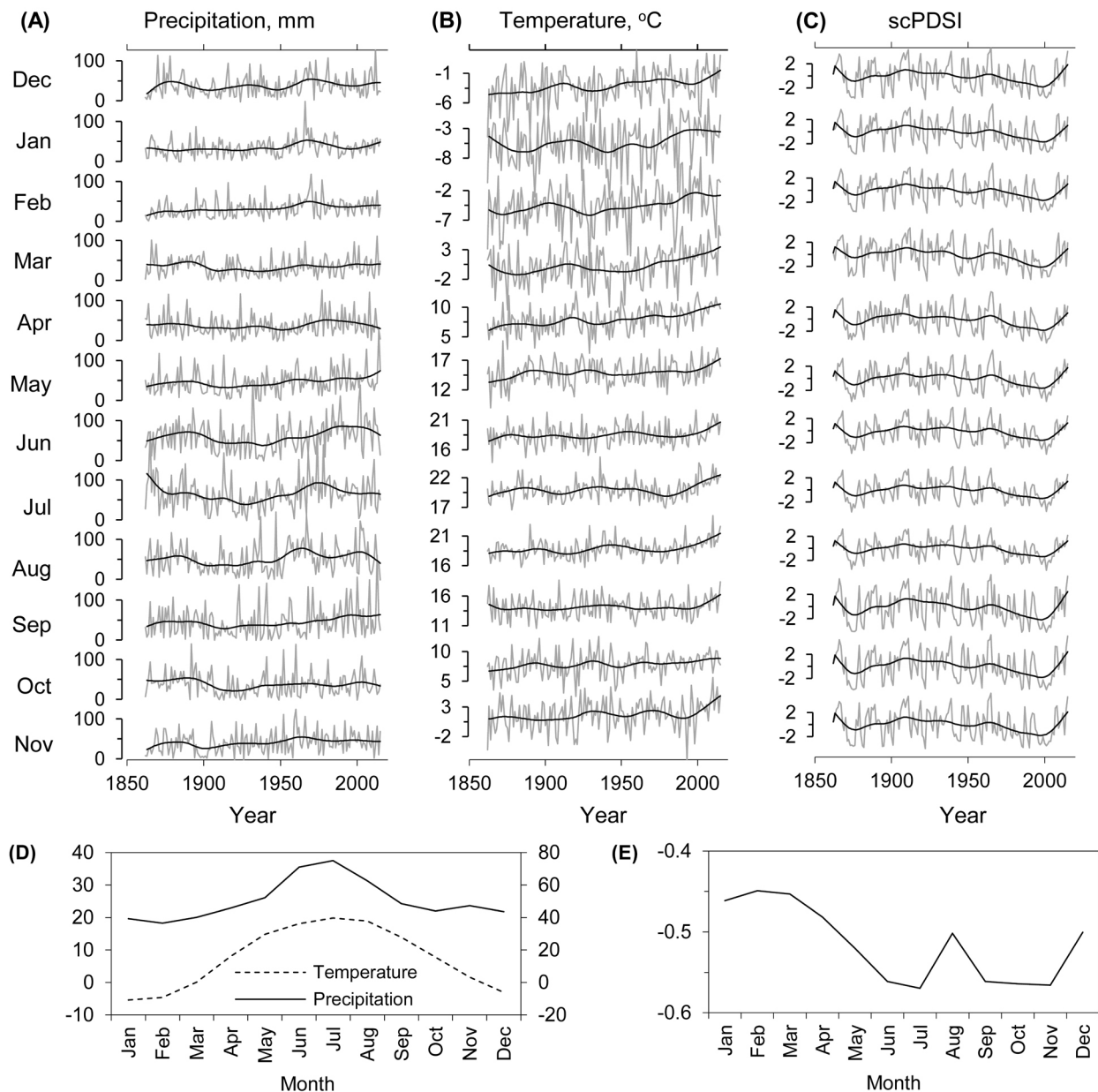


Fig. 1. Inter-annual variations in precipitation (A), temperature (B), and self-calibrating Palmer Drought Severity Index (C); the composed residual chronology of ring-width indices RWI (D), and the number of trees (E). The black lines in panels (A–C) represent the 15-yr spline smoothing. The panels D and E refer to the period 1880–2015

10.5 km north-west of the study site. The self-calibrating Palmer Drought Severity Indices (scPDSI) were derived from climatic data, and the available soil-water storage capacity was extracted from Global Soil Texture and Derived Water-Holding Capacities (Webb et al., 2000). The scPDSI calculation was performed using Zang's R-codes that are available online (<https://github.com/cszang>).

The climate records indicate a known warming trend in temperature, but no long-term change in precipitation in Kyiv during the past 150 years (Fig. 1 A, B). The one and a half century of scPDSI variation shows several periods 1865–1900, 1940–1960, and 1970–2010, during which a short-term increase in the soil-water deficit occurs (see gray line in Fig. 1 C). The records show that the maximal precipitation value of 75 mm occurs in July and the lowest value of 37 mm occurs in February (Fig 1. D). Since 1863 the average total annual precipitation value is 606 mm. The monthly mean temperature ranges from -5.4°C in January to 19.8°C in July (Fig. 1 D), while the annual temperature averages 7.5°C . The obtained scPDSI monthly mean values were below 0 during the year indicating an overall soil-water deficit in Kyiv (Fig. 1 E).

Field sampling and data analysis

We selected 40 old dominant trees that did not show any visual evidence of stem damage and decay to take wood samples. The studied trees grew in a site with the area of about 42 ha and with an altitude differential of about 4 m. The age of studied trees was from 86 to 163 years, while the age of 83 percent of the trees ranged from 121 to 158 years. The studied trees were located at distances of 35–180 m from the river or oxbows.

During spring-summer 2016, we extracted at least two cores per tree at breast height, using an increment borer. Each core was air-dried, glued onto wooden supports and surfaced. Then, the cores were scanned at a resolution of 3200 dpi using an Epson V33 scanner. The tree-ring widths were measured employing AxioVision (Carl Zeiss) software to the nearest 0.001 mm. To identify false rings, cores were thoroughly investigated under conventional microscopes (MBS-1 and Ulab XY-B2T LED).

The series from each individual tree were averaged to yield the individual ring-width chronologies. To reduce non-climatic effects on growth we fitted a cubic-smoothing spline and autoregressive model to each tree series. In order to build the mean residual chronology the individual series were averaged using a bi-weight robust mean. The tree-ring series were crossdated, standardized, and checked for errors using the COFECHA program, Version 6.06p (Holmes, 1983) and “dplR” package (Bunn, 2010) in R (R Core Team, 2016).

Dendro-climatological analyses

The relationship between annual variations in the oak residual chronology, and the monthly climatic variables, was investigated using the stationary and moving time-window correlation functions (Zang & Biondi, 2015). The stationary correlation function spanned the climatic window from May of the previous growth season to October of the current growth season in the period 1880–2015 and two 66-year intervals before and during the Siverka River regulation that was implemented since 1950. The 16-months (for precipitation and temperature) window covers two successive growing seasons with intermittent dormant period. In order to respect the equality between the total number of climatic predictors and the time interval in the moving window correlation function, we considered temperature and precipitation data set only from prior-June to current August. The scPDSI data used in both versions of correlation function spans period from May to August of the only current growth period. Thus, the total number of climatic variables was 34 (15 for precipitation, 15 for temperature, and 4 for scPDSI) and 40 (18 for precipitation, 18 for temperature, and 4 for scPDSI) in the moving and stationary version, respectively. The interval to perform moving correlation analysis was 35 years. We used Gershunov's test (Gershunov et al., 2001) to decide whether the obtained correlations between growth and climatic variables are temporarily stable.

The superposed epoch analysis was performed to test the significance of a mean tree ring response to severe or extreme drought events that occurred over the interval from prior-September to current August. The raw tree-ring series were scaled, but not detrended or prewhitened in this analysis. The drought events expressed in the scPDSI were classified using Palmer's original categories of the PDSI (Palmer, 1965; Wells et al., 2004).

There were no records of ground-water level for the studied forest or the Siverka River hydrology information was available. We thus used the dates of well-documented, extreme flood events as well as the construction of dams and channel straightening (1950s) as possible reference points to interpret the growth-climate relationship stability. The superposed epoch analysis was performed to quantify the changes in tree ring width after flood events and to decide whether these changes were more pronounced in young trees. The superposed epoch analysis was applied to 4 flood events in the period before river flow regulation and to 3 events that happened in the period when more than 50% of studied trees were younger than 50 years.

All statistical calculations were performed using the “bootRes” and “treeclim” packages (Zang & Biondi, 2013) in R software environment (R Core Team, 2016).

Results

Tree growth and chronology statistics

The *Q. robur* in the Lisnyky forest showed age-related growth trend, i.e. a decrease in the mean ring width with the tree age (Fig. 2 A). The mean ring width reduced from 3.3 ± 1.9 mm to 1.8 ± 0.8 mm, as the mean cambial age increased from 20 to 160 years,

averaging 2.5 ± 1.4 mm over the entire dataset (Fig. 2 B). The mean and the residual versions of the tree-ring width chronology spanned 160 and 159 years, respectively, ranging from 1866 to 2015 and from 1867 to 2015 (Fig. 2 C, D), and were obtained from 82 individual series of 40 trees (Fig. 2 E). The trees < 20, 30, 40 and 50 years of cambial age represented more than 50 percent of the entire group until 1885, 1886, 1908, and 1919, respectively (Fig. 2 F).

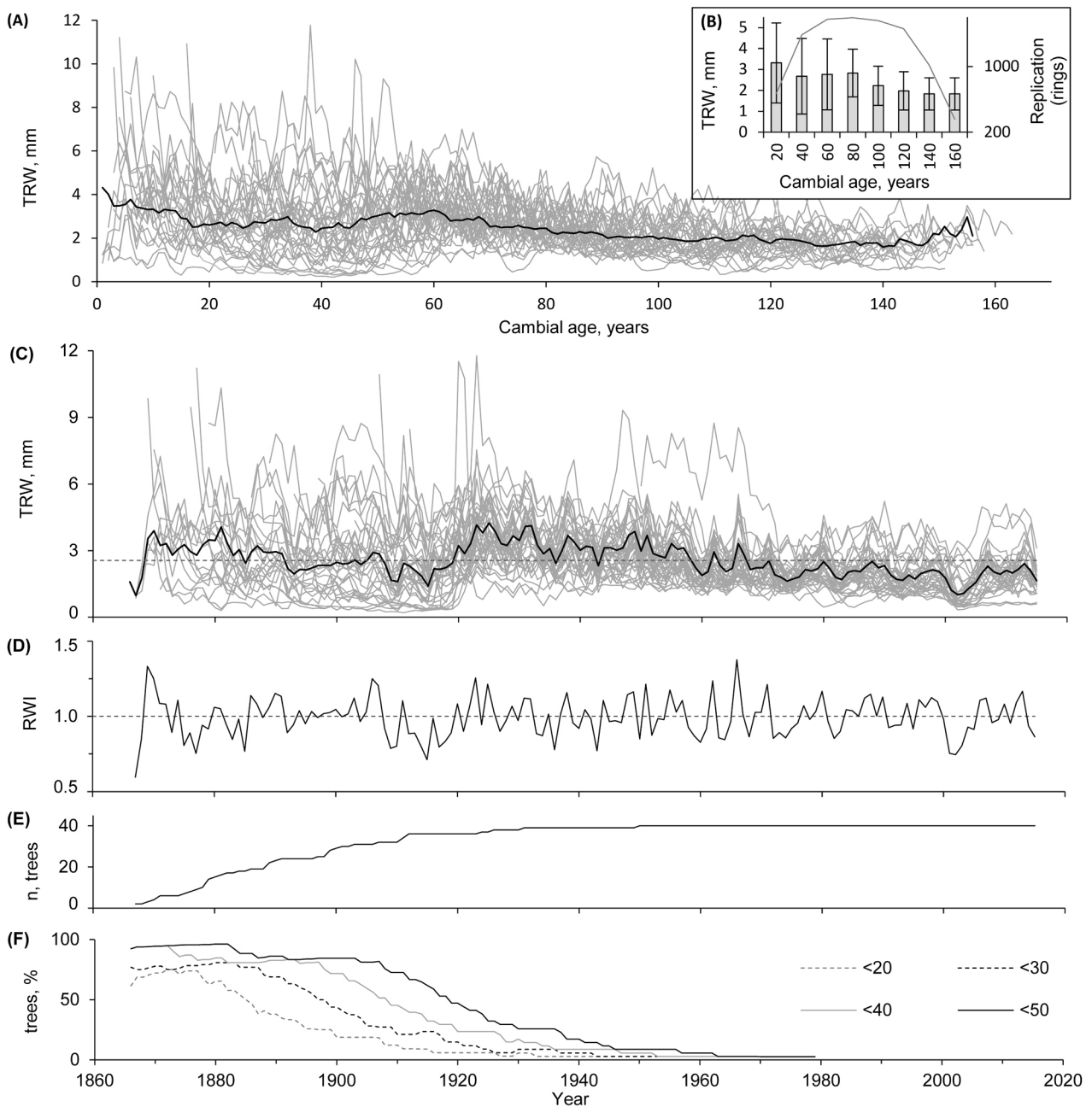


Fig. 2. (A) *Quercus robur* tree-ring width TRW (individual (gray lines) and mean (black line)) aligned by cambial age. (B) TRW (bars) distributed by age-classes and replication (line). (C) Raw chronologies of the tree-ring width (individual (gray lines) and the mean (black line)). (D) The composed residual chronology of ring-width indices RWI. (E) The number of trees. (F) Percentage of trees < 20, 30, 40, and 50 years of age. Horizontal dotted lines in plots (C) and (E) denote average values

Table 1. Descriptive statistics of the ring width chronology of *Quercus robur*

Time-span	cores	trees	r_{bt}	r_{eff}	EPS	SNR
1880–1914	62	34	0.20	0.23	0.88	7.2
1895–1929	75	38	0.29	0.35	0.95	17
1910–1944	80	39	0.34	0.38	0.96	22.4
1925–1959	82	40	0.32	0.38	0.96	23.5
1940–1974	82	40	0.38	0.46	0.97	33.2
1955–1989	82	40	0.35	0.42	0.97	28.3
1970–2004	82	40	0.29	0.36	0.96	22.5
1880–2015	87	40	0.30	0.38	0.95	21.1

Note: r_{bt} – correlation between trees, r_{eff} – effective chronology signal.

EPS – expressed population signal, SNR – signal-to-noise ratio.

The between-tree correlation (r_{bt}) and the effective chronology signal (r_{eff}) calculated over the total chronology length were 0.30 and 0.38, respectively, indicating a moderate strength of the common statistical signal (Table 1). The expressed population signal (EPS) exceeded 0.85 over the first 35-yr interval starting in 1880, suggesting an acceptable confidence level (Table 1). The signal-to-noise ratio (SNR), considered as a measure of chronology's quality, has reached a value above 20 in 1910.

Radial growth-climate relationships

The correlation function revealed that oak ring width significantly correlated with 5 out of 34 climatic variables over the 1880–2015 interval (Fig. 3 A). In particular, the chronology was significantly ($p < 0.05$) positively correlated with current March ($r = 0.22$) and prior-August ($r = 0.19$) precipitation, current May ($r = 0.21$) and prior-June ($r = 0.19$) temperature, and current May ($r = 0.19$) scPDSI. Correlations computed for the pre-1950 interval (Fig. 3 B) showed that growth before the Siverka River regulation was positively affected by May temperature, prior-November and current June precipitation, but was negatively affected with June temperature. Growth-climate relationships since 1950 (Fig. 3 C) had a clear shift toward stronger positive effect of precipitation in March and soil-water availability in May compared to earlier relationships, although precipitation in current October and temperature in previous August exerted a detrimental effect on *Q. robur* growth.

The correlation function with a 35-yr sliding window revealed that 12 out of 15 monthly precipitation variables significantly correlated with oak growth during one or more 35-yr intervals (Fig. 4). The positive correlation with current March (1934–1999),

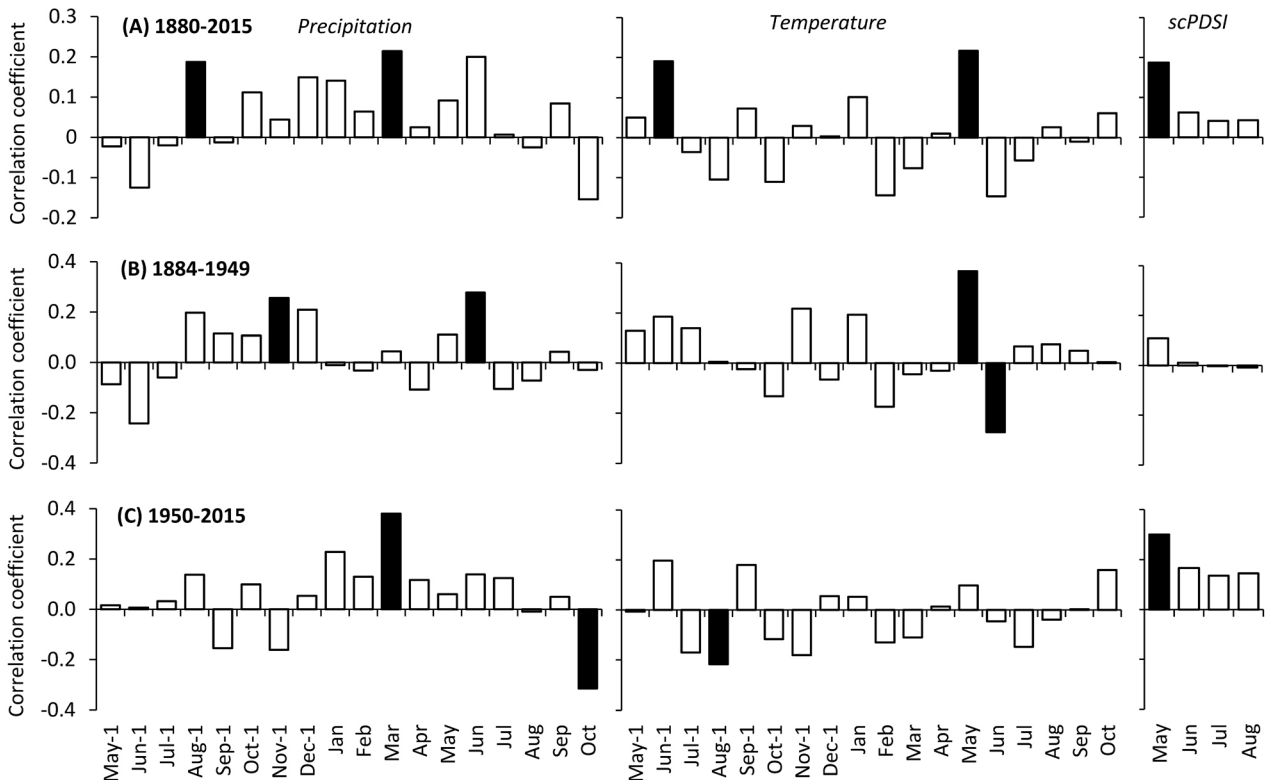


Fig. 3. Correlation between the residual ring-width chronology and the monthly series of precipitation, temperature and the self-calibrating Palmer Drought Severity Indices (scPDSI) for the entire reference period 1880–2015 (A), the 66-year interval (1884–1949) prior to the river regulation (B), and 66-year interval over the period (1950–2015) of the river regulation (C). Filled bars denote significant correlation coefficient ($p < 0.05$)

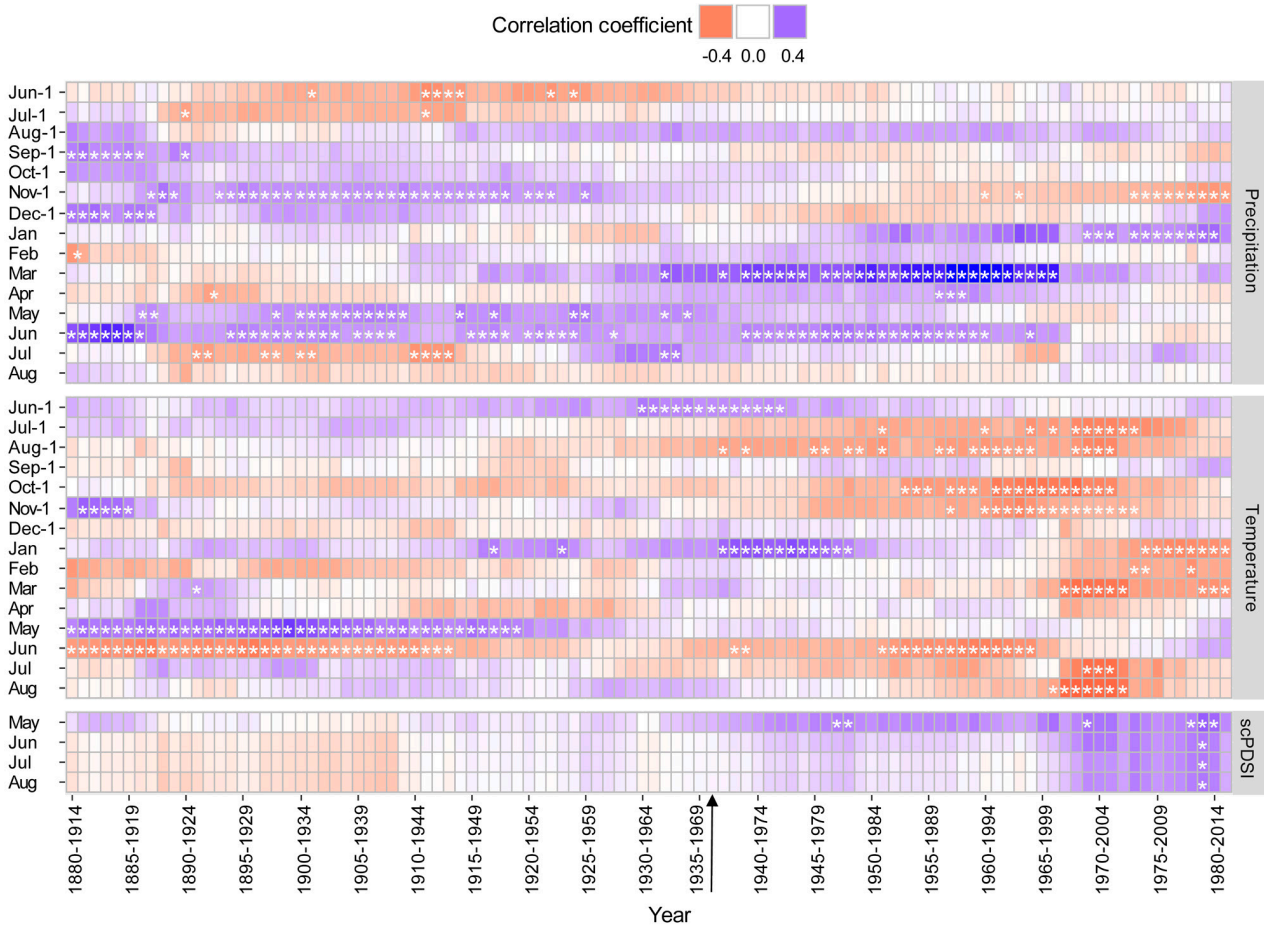


Fig. 4. Thirty-five-year moving correlation analysis between the residual ring-width chronology and the monthly climatic variables from the previous growing season (–1) June to the current growing season August. Statistically significant ($p < 0.05$) values are marked by the asterisk (*). The vertical arrow denotes the interval when the river regulation was implemented

current May (1886–1934), and current June (1880–1991) precipitation was the most prominent relationship between the oak radial growth and precipitation, although it was not stable over the entire interval. Prior-June precipitation negatively correlated with oak growth in the period from the early 1900s to the mid-1950s. Precipitation in previous autumn–winter (prior-September to prior-December) positively correlated with oak growth during the pre-1960 period, although prior-November effect shifted to being significantly negative after the 1960s. The moving correlation analysis indicated that the correlation between the growth and current February, current April, and current July precipitation reversed during the studied interval. In the recent decades, the only precipitation variables significantly correlated with oak growth were prior-November and current January.

The moving correlation analysis identified that relationships with 13 out of 15 monthly temperature variables were significant during some of the 35-yr intervals (Fig. 4). Only prior-June temperature had a significant positive correlation during the entire interval achieving highest values in the period 1929–1976.

Current May (positive) and current June (negative) temperature had a tendency to become less significant after the 1960s and after the 2000s, respectively. The significant negative relationships with temperature in the previous radial growth season (prior-July, prior-August), intermittent “dormant” season (prior-October, prior-November, January–March), and in the current radial growth season (July–August) developed mainly after the 1950s. Several of the growth-temperature patterns reversed during this period. In particular, prior-November temperature had a positive correlation from 1881 to 1918, and a negative correlation from 1954 to 2005. The effect of January temperature on oak growth was positive in the 35-yr sequences from 1916–1950 to 1948–1982, and became negative in 1975–2009 and thereafter. The sign of the correlation between current March temperature and growth reversed twice, i.e. from negative (1880–1914) to positive (1891–1925) and later again to negative (1967–2015).

None of the monthly drought variables showed a sustained significant influence on oak growth in the Lisnyky forest (Fig. 4), but the current May scPDSI

had a strong correlation during three intervals (1946–1982, 1969–2003, and 1979–2014). ScPDSI over the entire oak radial growing season had a significant correlation during the 1979–2013 interval.

The results of Gershunov's test indicated that changes in the correlation with only prior-November and current March precipitation cannot be considered as spurious fluctuations.

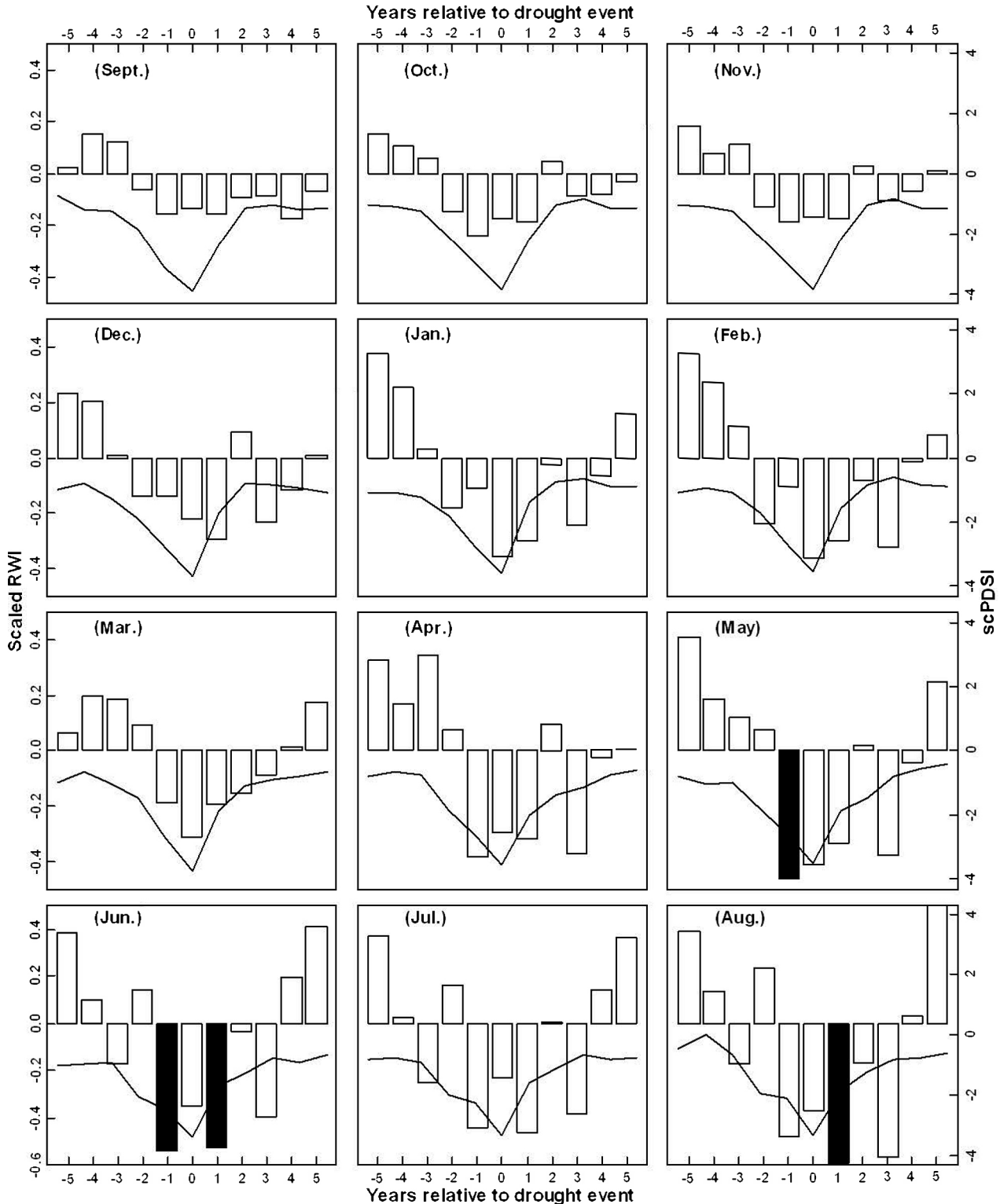


Fig. 5. Histograms of the tree ring response (bars) to droughts expressed by scPDSI (lines). The widths of tree rings are averaged by superposed epoch analysis and scaled. The filled bars denote significance ($p < 0.05$) of the departures from the chronology mean ring width indices

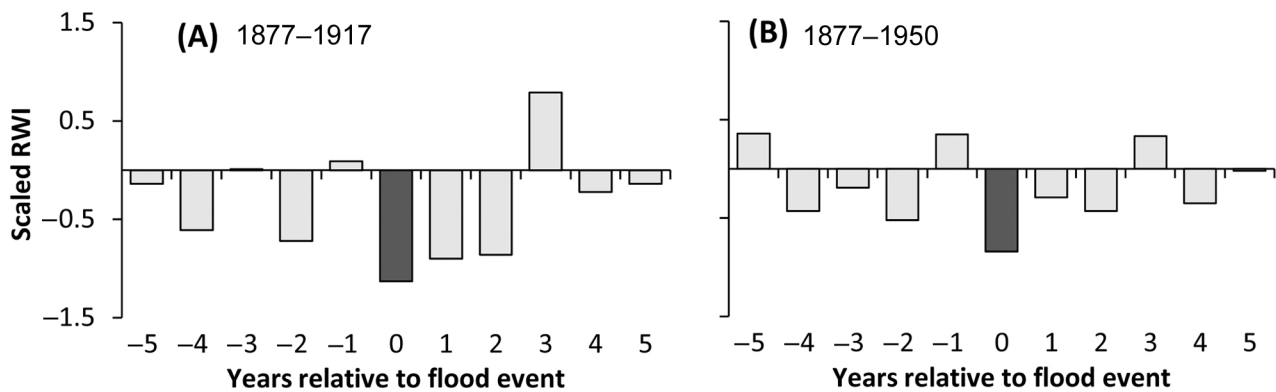


Fig. 6. Histograms of the tree ring response to flood events in the periods 1877–1917 (A) and 1877–1950 (B). The widths of tree rings are averaged by superposed epoch analysis and scaled. The dark-filled bars denote significance ($p < 0.05$) of the departures from the chronology mean ring width indices

The superposed epoch analysis allowed us to find that a decrease in the scaled tree ring width indices coincided with drought events that occurred only in May, June, and August (Fig. 5). As Figure 5 (black line) shows, the average scPDSI fell below a moderate value (-2.00 to -2.99) already one or two years before zero point, i.e. when an extreme drought event (-4) occurred, and then quickly grew. A moderate to severe (-3.00 to -3.99) May–June drought occurred a year (-1) before an extreme event provoked substantial oak radial growth slowdown in the current season, although an extreme drought (year 0) in June and August resulted in growth depression in the next growing season (year 1).

In the period covered by the raw tree ring width chronology, the largest historical floods in Kyiv that occurred in the 1877, 1908, 1917, 1931, 1970, and 1979 coincided with growth decrease in the 1877, 1908, 1917, when trees aged less than 50 years comprised more than 50 percent of the studied oaks (see Fig. 2). The superposed epoch analysis based on extreme flood events that occurred during the periods 1877–1917 and 1877–1950 showed a significant negative response for *Q. robur* tree ring width (Fig. 6), although the response was stronger in the first period.

Discussion

Oak growth-to-climate relationships

The *Q. robur* trees from the Lisnyky floodplain forest demonstrate a well-known age-related downward growth trend with mean ring width value of 2.5 mm that is inherent in trees at sites with optimal conditions throughout Europe (Friedrichs et al., 2009; Scharnweber et al., 2013; Čufar et al., 2014; Hroš & Vavrčik, 2014). The ring-width series shows a clear evidence that climate drives oak growth in the Lisnyky forest. The positive correlations with prior-August

precipitation and prior-June temperature (Fig. 3 A) are the most prominent in the relationship between oak growth and conditions attributed to the previous growing season over entire the reference period. This pattern is probably linked to the mechanism of non-structural carbohydrates accumulation (Pérez-de-Lis et al., 2016a) contributed to cambium activity and vessel enlargement that in *Q. robur* begins before budburst, leaf expansion, and thus carbon assimilation (Sass-Klaassen et al., 2011; Pérez-de-Lis et al., 2016b). In the Lisnyky forest, the June heat significantly diminishing current tree-ring width probably leads to an overall slowdown of the xylogenesis or its cessation (Pérez-de-Lis et al., 2017). Such premature ring growth completion triggers accumulation of soluble sugars and starch providing earlywood formation with readily available energy and material during the next growing season (Barbaroux & Bréda, 2002; Pérez-de-Lis et al., 2017). The positive growth response to prior-August rainfall indicates that the Lisnyky floodplain is prone to drought in late summer and that water availability in this period may be crucial for carbon assimilation and non-structural carbohydrates storage. This pattern seems to be sustained related to natural regime of the local river that almost dries up in the mid-summer (Vishnevsky, 2007).

The moving correlation analysis revealed other significant relationships with prior growing season rainfall occurring during shorter periods and obviously related to the corresponding climatic trendlines (Fig. 1). The correlation with prior-November precipitation, for instance, exceeds the significance threshold two times – first, when a 35-yr average trendline of precipitation falls below the value of 40 mm, and second, when it exceeds the value of 45 mm. Accordingly, the initially positive correlation became negative. Over the period of the general lack of available water in the late growing season, November precipitation contributes to wood formation in the following season probably through promoted root growth (Santini

et al., 1994). The negative effect of prior-November precipitation may be related to the hypoxia in the roots induced by excess of soil-water in the dormant season (Rozas & García-González, 2012).

Another prominent feature of growth relationship with precipitation in the pre-growing period is the positive correlation with March precipitation that could only be attributed to soil saturation by water before the onset of xylogenesis. This finding has not been reported for oaks at flooded sites thus far. Given that historically the Lysnyky forest experiences flooding in early spring (Vishnevsky, 2007), the oak growth could be favored by the high amount of precipitation in March, only due to the Siverka River regulation implemented in the 1950s.

Strong positive correlation with current May–June precipitation seems to be a common response pattern of the *Q. robur* over its natural range at sites with various local conditions (Bednarz & Ptak, 1990; Rozas, 2005; García-Suárez et al., 2009; Friendrichs et al., 2009; Kern et al., 2013; Matisons et al., 2013; Čufar et al., 2014; Cedro & Nowak, 2015), as well as in floodplain forests (Čater & Levanič, 2015). This pattern suggests a direct growth response on weather conditions and indicates that the trees may need large amount of water to perform extensive physiological processes (García González & Ekstein, 2003; Fonti & García-González, 2008), i.e. evapotranspiration and wood formation, in late-spring – early summer. In contrast, a high amount of precipitation in July can reduce oak growth as figures 1 and 4 show. This feature is likely to be an attribute of flooded or waterlogged sites (Čejková & Poláková, 2012) and could be related to trends of the regional climate. Thus, the significant negative correlation with July rainfall occurs in the period of minimal temperature, but it increases following interim warming trend after the late 1930s.

The positive response of the Lisnyky oaks radial growth on May temperature is not a widespread pattern and it is common at sites near the northern edge of the species distribution range (Drobyshev et al., 2008; Matisons & Dauškane, 2009; Matisons et al., 2013; Cedro & Nowak, 2015) or at waterlogged (Čejková & Poláková, 2012) and at flooded (Tumajer & Tremml, 2016) sites in Central Europe. This fact imply that impact of regional warming in the Lisnyky forest has been mitigated probably due to the water body cooling effect coupled with canopy shading and evapotranspiration (Hesslerová et al., 2013; Elisson et al., 2017). Micro- and mesoclimate investigations in riparian ecosystems suggest that soil moisture, air humidity, air and soil temperature are different from those in surrounding territory (Brosofske et al., 1997; Danehy & Kirpes, 2000; Agafonov & Gurskaya, 2013; Capon et al., 2013; Hadaš, 2003). However, moving correlation analysis identifies the weakening

of the growth-to-May temperature association that is probably a result of both rising temperature (see Fig. 1 b for May) and the Siverka River regulation (see Fig. 3 C, D).

The recent persistent rising trend of a 35-yr average temperature is common for all months with the only difference in its onset. For June–October months, trendlines started to grow around the late 1970s – early 1980s and obviously induced changes in the growth-climate relationship patterns revealed by the moving correlation analysis as a strengthening of the negative correlation with temperature after the 1800s. The shift to a negative growth association with January temperature is probably the most unprecedented change, which is inconsistent with results reported from Northern Poland (Pritzkow et al., 2016), but is in line with recent oak growth-climate relationship patterns in steppe zone in Ukraine (Netsvetov et al., 2017). Most of the factors tightly associated with oak growth in the Lisnyky forest, however, lost their control in the 2000s, which may be related to a climatic hiatus, i.e. the global atmospheric warming slowdown during 2001–2014 caused by a heat sink in the subsurface ocean (England et al., 2014).

The Siverka River hydrology alteration appears to have an influence on oak growth sensitivity to climate variation. The flow was channeled and several reservoirs began depleting its waters both upstream and downstream of the Lisnyky forest in the 1950s. The correlation between oak chronology and spring scPDSI increases following a channel construction and suggests a soil-water deficit during the radial growth season. The moving correlation analysis shows a weakening of correlations with scPDSI in the last 35-yr interval, which may be a consequence of the partial dismantling and the aggradation of the channel. The Superposed Epoch Analysis, however, points to a significant growth reduction in the year of moderate to extreme drought events that happen irregularly. Our observations agree with results from the Sava River floodplain in Serbia, where a low water level and rising temperature were found to depress oak growth during last 30 years (Stojanović et al., 2015a).

Ecophysiological and dendrochronological findings indicate that anatomical, morphological (Tatin-Froux et al., 2014; Copini et al., 2016), and physiological adaptations (Ferner et al., 2012) to root hypoxia allow *Q. robur* to withstand the high ground water level. Flooding mediates the earlywood vessel formation in the submerged stem part in juvenile and mature oaks (Astrade & Begin, 1997; Land, 2014; Copini et al., 2016) and leads to a reduction of the ring width in the upper stem part in juvenile trees (Copini et al., 2016). Thus, increased tolerance to root hypoxia in mature trees could explain why oaks in the Lisnyky forest lost their sensitivity to high water levels that were in close relations with floods on the Dnipro River, i.e. the

main stream. The superposed epoch analysis result (Fig. 6) infers the tree growth response on flood in the Lisnyky forest changed due to the aging processes rather than the Siverka River regulation.

Concluding remarks

We have used a combination of dendrochronological approaches and traditional statistical methods to assess the long-term dynamics of climatic response of *Quercus robur* in floodplain forest under river regulation. Previous studies utilized rather short-term tree ring chronologies and climatic series not allowing to uncover the effect of natural climate variability prior to hydrology alteration. In the present study, we show that the long-term growth-to-climate response of *Q. robur* under human-induced changes in floodplain is characterized by two distinct patterns with a crossover point corresponding to river flow regulation onset. Under natural conditions, i.e. before river regulation, extreme flooding had a negative effect on oak growth that was also governed by temperature and precipitation in the growth season. Upon river regulation, *Q. robur* trees became unexpectedly sensitive to lack of precipitation in early spring and vulnerable to extreme drought events in the radial growth season. This relationship is rather a coupled effect of the regional climate trend and river regulation, since after partial drainage failure these factors have lost their control on *Q. robur* radial growth.

The shift in the captured climatic signal demonstrates that the local alteration of the hydrologic regime may trigger unprecedented tree growth responses instigated by regional climatic trends. This study emphasizes the relevance of dendroclimatic researches from the flooded sites with altered hydrology for better understanding human impact on trees species growth-climate relationships even in regions with conditions congenial to trees growth.

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