



Response of floodplain pedunculate oak (*Quercus robur* L.) tree-ring width and vessel anatomy to climatic trends and extreme hydroclimatic events



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ABSTRACT

Increasing temperatures and recent changes in runoff regimes observed in Central Europe might alter the growth and relative water uptake of floodplain trees. To predict responses of floodplain forests to climate change, it is necessary to determine the climatic controls over tree growth and vessel anatomy. We analysed the responses of tree-ring width and earlywood vessel anatomical parameters (average vessel lumen area, vessel density and total vessel lumen area) of pedunculate oak (*Quercus robur* L.) growing in a floodplain to hydroclimatic conditions represented by temperature, the drought index (scPDSI), river discharge, groundwater level, and occurrence of floods and drought events. Site chronologies were assembled for floodplain and reference sites and, subsequently, correlated with time series of hydroclimatic conditions. Our results show that radial growth of floodplain trees is particularly positively influenced by temperature during the growing season and during previous year's summer. By contrast, the growth of reference trees is highly drought-limited. Earlywood average vessel lumen area chronologies from both floodplain and reference sites share a positive temperature signal from January to April. However, the effect of water availability (indicated by the drought index) on vessel size is mostly negative for floodplain trees (with a maximum response to the autumn of the year preceding tree-ring formation) and positive or non-significant for reference trees. Vessel density chronologies contain the inverse environmental information as tree-ring width, however, with amplified negative correlations with current year temperatures at floodplain sites. Total vessel area is associated mostly with temperature in previous May and June. The drought index recorded exactly the same information in tree-rings as did river discharges and groundwater levels. The results of both correlation and trend analysis evidence that tree-ring width of floodplain *Q. robur* unambiguously increases with increasing temperature; on the other hand, droughts can become a serious problem affecting the productivity of reference trees growing in more distal parts of the lowland. Vessel size of *Q. robur* growing outside the floodplain recently tends to increase with increasing temperatures, making xylem more effective at water transport but also more vulnerable to cavitation.

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1. Introduction

Temperate floodplain forests are ecosystems with a high level of productivity and rapid nutrient turnover (Kozłowski, 2002; Hughes and Rood, 2003). Recently observed increasing frequency of extreme hydroclimatic events, including floods and droughts, influences ecological parameters of floodplain forests such as species composition, productivity and relative water uptake of individual trees (You et al., 2015). Shifts in run-off regimes from spring/summer to winter have been predicted (Arnell, 1998;

Schneider et al., 2013) and observed (Middelkoop et al., 2001; Bormann, 2010; Stahl et al., 2010) in the broader area of Central Europe, resulting in more frequent droughts during the growing season and winter/spring floods (Lehner et al., 2006). This regime shift, together with climatic trends, might have considerable ecological consequences, including the loss or narrowing of riparian forest bands, changes in their species composition and increasing vulnerability to hydroclimatic events (Thomas et al., 2002; Rood et al., 2008). However, there is still lack of studies dealing with the complex growth response of floodplain trees to changes in hydroclimatic variables.

Extreme floods and associated long-lasting inundation affect radial growth, apical growth and transpiration of trees through

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decreased photosynthetic activity or even defoliation (Glenz et al., 2006). Moreover, permanent soil water saturation and limited availability of oxygen to roots also limits physiological processes and tree growth (Jackson et al., 2009; Rood et al., 2010) through replacement of mitochondrial respiration by fermentative metabolism with significantly lower energy yield (Ferner et al., 2012). Glenz et al., (2006) classified factors affecting the growth response of trees to flooding into biotic (morphological and anatomical adaptations and the development stage of the plant) and environmental factors (flooding duration, depth, timing, frequency and water quality). Generally, flooding tolerance is usually higher in angiosperms than in gymnosperms, in adults compared to juveniles, in short compared to long periods of inundation and during dormancy than during the growing season (Glenz et al., 2006). Moreover, the effect of the water culmination level is also important for the extent of flood-induced anatomical anomalies (Copini et al., 2016).

Floodplain tree species, and, in general, trees with shallow roots located in the aerated zone of the soil profile, are well adapted to high groundwater levels; however, they can be limited by a lack of moisture in periods of very low river discharges during drought events (Stella et al., 2013; Singer et al., 2013). Tree-ring width in *Quercus* sp. growing in floodplain areas with artificially reduced water availability (e.g., due to the construction of levées) has indeed been reported to positively correlate with moisture (Gee et al., 2014; Čater and Levanič, 2015). The direct response of tree growth to climatic conditions is, however, often masked by responses to frequent floods, long-lasting inundation and excess water availability (Gee et al., 2014). Floods (Gee et al., 2014), droughts (Kozłowski, 2002) as well as shifts in river discharge seasonality (Rood et al., 2008) have also been observed to affect seed dispersal and seedling germination, resulting in alterations of forest species composition and the intensity of competition.

Both tree growth and xylem conductivity can be studied retrospectively using dendrochronological methods. Tree-ring widths (TRW) serve as one of proxies for estimating trunk biomass growth. By detailed analysis of tree-ring width time series, it is possible to identify the most important environmental factors that limit growth (Fritts, 1976; Schweinguber, 1996). Besides tree-ring widths, vessel anatomy also records signals of past environmental variability (Fonti et al., 2010; García-González et al., 2016). Annual fluctuations of vessel size and number are related to balancing between hydraulic efficiency of the xylem and safety from cavitation and embolism (Hacke et al., 2006; Sperry et al., 2008). The larger the vessel, the more effective it is at water transport; however, the risk of cavitation/embolism also increases with increasing vessel diameter (Tyree, 1997). Modifications to the size and number of the vessels thus serve to ensure effective and safe xylem water transport under varying external conditions and intensity of environmental stress. Fluctuations in vessel anatomical parameters (most commonly average size of earlywood vessel lumina) have proven to be sensitive to climate conditions (García-González and Eckstein, 2003; Fonti et al., 2007, 2013; Fonti and García-González, 2008; Eilmann et al., 2009; Galle et al., 2010; Abrantes et al., 2013; Gea-Izquierdo et al., 2012), floods and inundation (St. George, 2010; Tardif et al., 2010; Ballesteros et al., 2010; Wertz et al., 2013) or groundwater level changes (Schume et al., 2004). Most of the studies mentioned above focussed on ring-porous species, in which the environmental signal is maximized in time series of earlywood vessel properties (García-González et al., 2016), though vessel parameters of diffuse-porous species also contains environmental signal (e.g., Ballesteros et al., 2010; Oladi et al., 2014; Schuldt et al., 2016).

Flooding-induced anomalies in TRW and vessel anatomy most commonly observed in floodplain ring-porous species such as *Quercus* sp. and *Fraxinus* sp. are called “flood-rings” (St. George,

2010; Copini et al., 2016). Reduced average vessel lumen area, increased vessel number and slightly reduced TRW are typical features; moreover, vessels are usually spread randomly throughout the tree-ring (Wertz et al., 2013). This anomaly appears only in flooded part of the stem as a consequence of hypoxia (Wertz et al., 2013; Copini et al., 2016). Experimental study with *Quercus robur* seedlings revealed significant reduction of vessel size after two weeks of stem flooding, being most significant if occurred during bud swell or internode expansion period (Copini et al., 2016). Flood-rings occurrence was marginally influenced by the duration of inundation of seedlings (Copini et al., 2016); however, as the tolerance of trees to flooding usually increases with age (Glenz et al., 2006) this effect should be considered when analysing responses of mature trees. Moreover, “flood-rings” have been observed also in ring-porous broadleaves affected by low soil aeration due to a high groundwater level (Astrade and Begin, 1997).

In this study, we aimed to discern the response of radial growth and earlywood vessel anatomy (average vessel lumen area, vessel density and total vessel lumen area) of floodplain pedunculate oak (*Quercus robur* L.) to local hydroclimatic conditions. We hypothesized that growth of temperate floodplain trees with sufficient water saturation would record temperature signal because of the absence of drought limitation. We also evaluated recent trends in tree-ring width and wood anatomical chronologies in relation to trends in water availability and temperature.

2. Material and methods

2.1. Study area

The study area is located in the floodplain of the Czech section of the Elbe river (East-Central Europe, Fig. 1). Average annual temperature, precipitation and the river Elbe discharge are 8.5 °C, 550 mm and 256 m³ s⁻¹ (Mělník gauging station), respectively. The climate is transitional between oceanic and continental, resulting in significant inter-seasonal variability in both temperature and water availability (Fig. S1a). The river has a pluvio-nival runoff regime with the highest discharges in late winter and early spring, and minimum discharges in summer and autumn (Bormann, 2010). The floodplain sites lie on flat terrain underlain by fluvial sediments (predominantly sands and gravels) covered by fluvisols (FAO, 2006). The fluvial sediments underlying the sites reach several tens of metres in depth, and the ground water level is high (Růžičková and Zeman, 1994). Reference sites are situated outside the flood area, and their soils are represented mostly by cambisols (FAO, 2006). The elevation of individual sites ranges from 195 to 215 m a.s.l.

The study area experienced a temperature increase since the second half of the 19th century (Pišoft et al., 2004). This trend has become more pronounced since the 1980s, when the increase in temperatures became faster (Fig. S1b); for example, 13 of 20 years with the highest temperature in the period 1775–2010 occurred after 1980 (Brázdil et al., 2009). Mean annual temperatures have been increasing on average by 0.28 °C per decade since 1960, with a maximum increase in summer (0.4 °C per decade) and a minimum increase in autumn (0.07 °C per decade) (Huth and Pokorná, 2005; Brázdil et al., 2009).

In contrast to temperatures, there is no significant trend in precipitation and water availability over the last 50 years (Fig. S1c–e). However, precipitation seasonality has been changing recently – decreasing during spring/summer and increasing in winter (Brázdil et al., 2009). Due to warming, the number of days with snow cover and average snow depth has decreased significantly, especially in the lowlands and at mid-elevations, which has also resulted in seasonality shifts in the Elbe runoff regime. Bormann

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