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Jan Tumajer

Quantitative vessel parameters of broadleaves as a tool for reconstruction of physical geographical processes

Kvantitativní parametry cév listnáčů jako nástroj pro rekonstrukci fyzickogeografických procesů

Doctoral thesis

Supervisor: Doc. Mgr. Václav Treml, Ph.D.

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Acknowledgements

Abstract

Trees adjust wood anatomical structure to environmental conditions, predisposing time series of quantitative wood anatomical parameters to be valuable source of palaeoenvironmental information. In this doctoral project we analysed the response of vessel parameters of i) floodplain *Quercus robur* to groundwater level fluctuation, hydroclimate variability and extreme events (droughts and floods), and of ii) *Betula pendula* to mechanical damage caused by various disturbances.

Although climatic signal as well as pointer years stored in tree-ring width chronologies of *Quercus robur* largely differ between sites, quantitative vessel parameters contain spatially-homogenous positive signal of previous year summer temperature and current year winter/early spring temperature. The only between-site difference in wood anatomical chronologies is negative effect of moisture on vessel size in floodplain, which does not occur in not-flooded lowland sites. We suggest that while tree productivity benefits from high water availability, the wood anatomical structure of *Quercus robur* is constrained by high soil water saturation in floodplain zone. In addition, the response of tree-ring widths to moisture availability is not uniform inside single stand, but subgroups of trees with completely opposite response coexist (drought limited and moisture limited individuals). The first group of trees significantly reduced their growth after decline of groundwater level, meanwhile the latter group increased productivity. Existence of subgroups with contrasting response to groundwater fluctuations was not observed in case of vessel anatomical series, where individual trees share common climatic signal.

In addition to climate and hydrological conditions, processes causing mechanical damage also alter wood anatomical structure. Vessel size observed in the first tree-ring after stem scarring was by 60 % smaller compared to value expected based on linear age trend. In the following period, vessel size continuously increased, reaching pre-event level in third tree-ring after disturbance. Considering various types of mechanical damage, scarring of bark and cambium, stem tilting and decapitation cause the strongest decrease of vessel size in *Betula pendula*, which significantly outweighs ontogenetic trends and climatic signal. Wood anatomical anomalies spread along and around entire tree stem in case of tilted and decapitated individuals; contrary, xylem compartmentalization through adjustment of vessel size takes place only nearby callus tissue in scarred trees. Root exposure and stem base burial represent disturbances with less apparent response in wood anatomical structure. In case of most serious deformations, it takes more than 3 years to recover pre-disturbance wood anatomical structure. Decline in vessel size is not adequately compensated by increase in vessel number during this period, resulting in significant drop in xylem specific hydraulic conductivity. This indicates that predicted increase in intensity and frequency of disturbances related to climate change may alter transpiration capacity of forest stands.

The results of presented studies indicate that quantitative wood anatomical parameters of broadleaves should be perceived as multi-source driven parameter integrating effects of ontogeny, climate, soil hydrology and disturbances. Vessel size contains different environmental signal than tree-ring widths. Moreover, their signal is less between-site and between-tree variable than signal stored in tree-ring widths. This makes vessel parameters valuable proxy for reconstruction of former fluctuations in hydroclimatic conditions. In addition, abrupt adjustment of vessel size may be used as a tool to date former mass-movements and other types of disturbances. However, proper approaches are required for extraction of desired part of information and filtering out the noise from time series of wood anatomical parameters.

Keywords

Abstrakt

Anatomická stavba dřeva je citlivá k vlivům prostředí, což umožňuje následné využití časových řad kvantitativních anatomických parametrů jako zdroje paleoenvironmentálních dat. V této disertační práci jsem studoval odezvu parametrů cév i) dubů letních rostoucích v údolní nivě ke změnám v hladině podzemní vody, klimatu, hydrologických podmínek a k výskytu extrémních hydrologických a meteorologických jevů (sucha, povodně) a ii) bříz bělokorých na mechanické poškození vlivem disturbancí různého typu.

Zatímco klimatický signál šířek letokruhů i letokruhové signatury vykazují velkou prostorovou variabilitu, kvantitativní parametry jejich cév mají společný prostorově homogenní signál (pozitivní vliv teploty v létě předchozího roku, v zimě a na začátku jara). Jediný stanovištní rozdíl v klimatickém signálu chronologií založených na cévách je negativní vliv vysoké vlhkosti na velikost cév, pozorovaný pouze v nivě a ne v od řeky vzdálenějších nížinných porostech. To naznačuje, že vývoj efektivních vodivých pletiv dubu je v záplavové zóně limitován vysokou saturací půdního profilu vodou, ačkoliv vysoká dostupnost vody je tam pozitivní z pohledu produktivity. Odezva šířek letokruhů ke změnám v dostupnosti vody není v případě dubů uniformní ani v rámci jednoho porostu vlivem koexistence jedinců se zcela opačným vztahem k dostupnosti vody (jedinci limitovaní suchem a jedinci limitovaní nadměrnou půdní saturací). Šířka letokruhů jedinců z první skupiny poklesla během období se sníženou hladinou podzemní vody, zatímco jedinci ze druhé skupiny ve stejném období zrychlili přírůst. Existence skupin odlišně reagujících jedinců nebyla doložena v případě časových řad anatomických parametrů cév, jejichž série pocházející z rozdílných stromů mají v rámci porostu společný klimatický signál a podobnou odezvu na extrémní události.

Kromě hydroklimatických podmínek je anatomická stavba dřeva citlivá i na mechanické poškození kmene. Průměrná velikost cév je v prvním roce po zjizvení kmene o více než 60 % menší než velikost cév očekávaná na základě lineárního věkového trendu. V následujících letokruzích se postupně zvyšuje a po třech letech dosahuje hodnot odpovídajících letokruhům před poškozením. Z rozdílných typů mechanické deformace vyvolávají nejsilnější propad velikosti cév břízy bělokoré: zjizvení kmene spojené s poškozením borky a kambia, naklonění kmene a odlomení vzrostného vrcholu a části koruny. Intenzita této odezvy výrazně převyšuje změny kvantitativních anatomických parametrů řízené ontogeneticky (věkový trend) a klimaticky. Exhumace kořenového systému a zasypání báze kmene sedimenty vyvolávají slabší odezvu v anatomické stavbě. Anatomické anomálie jsou po naklonění a dekapitaci patrné podél celého obvodu kmene i po jeho celé délce; naopak v případě zjizvení dochází k modifikaci anatomické struktury pouze v části těsně přiléhající ke kalusu (hojivé pletivo uzavírající ránu). U těchto silných forem mechanického poškození se anatomická struktura nevrátí do svého původního stavu za méně než 3 roky. Během této periody není pokles ve velikosti cév kompenzován nárůstem jejich počtu, což vede k signifikantnímu poklesu specifické hydraulické vodivosti letokruhů. To naznačuje, že očekávaná rostoucí intenzita a frekvence lesních disturbancí může ovlivnit transpirační kapacitu lesních porostů.

Výsledky předložených studií naznačují, že kvantitativní parametry anatomické stavby listnáčů by měly být chápány jako parametr ovlivňovaný několika faktory, včetně ontogenetického vývoje, klimatu, půdní vlhkosti a disturbancí. Kvantitativní anatomické časové řady obsahují jiný typ signálu než šířky letokruhů, který je navíc méně stanovištně podmíněný a neliší se mezi jednotlivými jedinci v rámci konkrétního stanoviště. To dělá z cév listnáčů cenné proxy pro rekonstrukci variability klimatu a datování hydrologických procesů v minulosti. Náhlé anomálie ve velikosti cév mohou být využity jako nástroj pro datování svahových pohybů a dalších typů disturbancí. Vzhledem k tomu, že časové řady parametrů cév jsou řízeny různými vnitřními i vnějšími vlivy, je pro získání požadované části signálu nutné použít odpovídající metodické postupy pro odfiltrování nežádoucího signálu jako šumu.

Klíčová slova

anatomie dřeva, *Betula pendula*, céva, dendrochronologie, disturbance, lužní les, *Quercus robur*, svahové pohyby

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1. Introduction

Quantitative wood anatomical parameters are a group of plant traits, which are promising source of paleoenvironmental data for reconstruction of physical geographical processes. Anatomical time series have been successfully applied for instance in fields of paleoclimatology (González and Eckstein 2003; Fonti et al. 2009; Fonti and Jansen 2012), paleohydrology (St. George 2010; Wertz et al. 2013), mass-movements dating (Hitz et al. 2008; Arbellay et al. 2010, 2012b) and fire events reconstruction (Kames et al. 2011; Arbellay et al. 2014). Great potential of quantitative wood anatomy has become increasingly used and explored since approx. 2000s; in Europe mainly in Mediterranean (Carrer et al. 2015; Pérez-de-Lis et al. 2016; Souto-Herrero et al. 2017; Castagneri et al. 2017), the Alps (Fonti et al. 2007, 2009; Eilmann et al. 2009; Arbellay et al. 2010) and Baltics (Matisons et al. 2013, 2015).

Based on metaanalysis performed in March 2015 *via* ISI Web of Science by Borghetti et al. (2016), there were 25 primary studies published since 1993 focused on climate effect on time series of wood anatomical parameters. Recently (i.e., June 2018), when searching for topics 'quantitative wood anatomy AND climate' and year '2015-2018', ISI Web of Science returns 24 additional articles, from which 19 are based on newly presented primary data (the others represent reviews and methodological articles). This indicates increasing application of quantitative wood anatomical time series in dendrochronological research. Increasing number of dendrochronological studies using wood anatomy may be related to development of standardized procedures simplifying laboratory and statistical processing (von Arx et al. 2016), as well as preference of multi-trait approaches to understand complex plant-environment interactions.

Climate change and increasing frequency of various types of disturbances including floods, windstorms and mass-movements was observed in recent decades and predicted for near future (Brázdil et al. 2009; Trnka et al. 2015; Seidl et al. 2017). It is, thus, of crucial importance to understand the mechanisms trees use to cope with both abrupt and continuous changes of environment at various levels - from the level of single cells to whole forest ecosystem. Wood anatomical structure affects hydraulic conductivity of xylem (Pallardy 2008) and, through its modification, may alter transpiration of individual trees and forest stands. Thus, patterns of wood anatomy should be considered as important driver of climatic system and possible feedback amplifying recent climate change.

The main goal of this doctoral thesis was to quantify the response of wood anatomical structure of Central European native broadleaves to climatic variability, changes in river discharge, groundwater level fluctuations and mechanical damage caused by disturbances. More specifically, we asked following questions:

- Are quantitative wood anatomical time series sensitive to climate and soil water variability?
- Is there between-site and between-tree variability in environmental sensitivity of wood anatomical parameters? If so, is it comparable or does it differ from other dendrochronological proxies?
- What is the intensity of wood anatomical anomaly caused by mechanical damage? How does the anomaly spread along and around tree stem?
- What is the contribution of individual external and internal factors (including ontogeny, disturbances and climate) to inter-annual variability in wood anatomical structure?

2. Physiological explanation of sensitivity of anatomical traits to physical geographical processes

Xylem is a complex tissue consisting of various types of cells, however, vessel elements (angiosperms) and tracheids (gymnosperms) are crucial for water transport in a plant body (Tyree and Zimmermann 2002). Evolution of conduits (vessels+tracheids) specialized for long-distance water transport probably permitted existence of plants taller than 0.3 m (Pallardy 2008). Small diameter of conduits enables existence of strong cohesion-tension forces estimated between 2-30 MPa (Tyree and Zimmermann 2002). These strong forces result in formation of continuous water column from absorbing surface at fine roots to evaporating surface in the leaves. Transport of water molecules is driven by water potential (i.e., water pressure difference between roots and canopy) existing due to the stomatal transpiration (Pallardy 2008).

The theoretical maximal transportable amount of water during conditions with specific water potential (specific hydraulic conductivity) is largely affected by the number and distribution of conduits (Sperry et al. 2006; Pallardy 2008; Hacke et al. 2017). According to Hagen-Pouseuille law, the flow rate of water along the tube increases with the fourth power of tube radius, indicating larger contribution of large vessels to water transport. However, increasing conduit size not only increases efficiency of water transport, but also reduces the ability of a tree to prevent cavitation (safety-efficiency trade-off; Sperry et al. 2006). In temperate conditions, cavitation may occur mainly during (i) extremely high water potentials (very dry conditions), when metastable water column is disrupted by air, (ii) during freeze-thaw cycles of xylem water, or (iii) as a consequence of mechanical damage to bark and cambium (Sperry et al. 2008).

Ensuring safe and efficient water transport is crucial for survival of plants in changing environmental conditions, and thus woody plants adjust their xylem anatomical structure during single year as well as inter-annually in response to contemporary water potential and stressful events. Because water potential is largely driven by climatic conditions (precipitation, evaporation) and soil water holding capacity, quantitative parameters of conduit size often correlate with climatic series and may be used as their proxy (Fonti and Jansen 2012; García-González et al. 2016). Moreover, stress response after mechanical damage to cambium (scarring), stem displacement, fires, floods, windstorms and biotic disturbances requires local conduit size adjustment to balance between safety-efficiency of xylem tissues. Abrupt adjustments of conduit size and density may later be used for dating of both biotic and abiotic disturbances (Hitz et al. 2008; Tumajer and Burda 2013; Arbellay et al. 2013; Axelson et al. 2014).

3. Internal and external factors influencing variability in xylem anatomical traits

Dimensions of individual conduits of single tree vary from year to year due to various factors. External factors are related to effects of geographical processes and include mainly climatic variability, extreme hydrological events (floods and variation in groundwater level), disturbances induced by windstorms or mass-movements, forest fires, biotic disturbances and nitrogen deposition (Fonti and Jansen 2012; García-González et al. 2016; Hacke et al. 2017). Internal factors include mainly age trend driven by increasing stem size (Olson et al. 2014). Genetic and phenotypic plasticity of wood anatomical structure was also documented (Schreiber et al. 2015).

3.1. Climate

Time series of quantitative wood anatomical parameters are sensitive to fluctuations in climatic conditions (García-González and Fonti 2008; Fonti and García-González 2008; Matisons et al. 2012). Xylem plasticity to climate was proven in two types of studies – correlative analyses based on annually resolved chronologies of quantitative wood anatomical parameters and local climatic data (Fonti and Jansen 2012; García-González et al. 2016) and/or by observation of phenotypic plasticity in wood anatomical structure of single or multiple species over large geographical gradient (Schreiber et al. 2015; Borghetti et al. 2016). As cell expansion is a turgor-driven process (Hacke et al. 2017), both types of analysis mainly observed the relationship between conduit size and precipitation (García-González and Fonti 2008; Fonti and García-González 2008), temperature (Fonti et al. 2007; Matisons et al. 2012, 2013) or their aggregate -a drought index (Eilmann et al. 2009; Fonti et al. 2009).

From the perspective of timing of climatic forcing of wood anatomical structure, three key periods include i) time of vessel formation, ii) quiescence and dormancy an iii) previous growing season (García-González et al. 2016). Direct effects of climate through modifying intensity of xylogenesis (Cuny et al. 2014) or turgor pressure (Hacke et al. 2017) are probably responsible for significant correlations of monthly climatic parameters with conduit dimensions in the growing season of tree-ring formation year. Contrary, climatic forcing from previous year might be related to indirect effects, e.g., storage of non-structural carbohydrates from year to year (Simard et al. 2013; González-González et al. 2014). Finally, temperature during winter, when cambium is dormant, alters the sensitivity of overwintering cambial derivatives by reactivation of auxin carriers (Fonti et al. 2007) and affects the amount of carbohydrates required next growing season for replacing damaged tissues (e.g., through modifying amount of snowpack and its insulation effect; Suvanto et al. 2017). Indirect effects from periods prior to tree-ring formation growing season and dormancy are typically observed in case of vessel anatomical parameters of ring-porous broadleaves (Matisons et al. 2012; González-González et

al. 2014) due to the onset of cambial activity up to one month before bud opening (Fonti et al. 2007; González-González et al. 2013; Pérez-de-Lis et al. 2016), when cambial activity is driven solely by previous year storages (Simard et al. 2013).

Specific climatic signal of quantitative wood anatomical time series geographically varies due to different dominant limiting factors of xylogenesis. For instance, vessel size of *Quercus* sp. was documented to contain positive signal of summer precipitation/moisture index in Mediterranean (González and Eckstein 2003; Alla and Camarero 2012; Castagneri et al. 2017), but negative in Alpine regions and Baltics (Fonti and García-González 2008; Matisons et al. 2015). Similarly, negative correlations of vessel size with temperature frequently occur in xeric sites (Castagneri et al. 2017) and positive in moist sites (Matisons et al. 2012). Meta-analysis (Borghetti et al. 2016) of studies extracting climatic signal from wood anatomical time series in Europe observed (i) slightly decreasing trend of conduit size with increasing precipitation and temperature, and (ii) vessel density increasing with temperature and decreasing with precipitation.

As processes limiting vessel formation differ from those controlling productivity, vessel anatomical parameters often contain climatic signal also in locations, which are 'moderate' with weak signal based on tree-ring width time series (Fonti and García-González 2008). Although specific climatic signal of quantitative wood anatomical time series depends on site conditions (see previous paragraph), it is assumed, that they are less site dependent comparing tree-ring widths (Granda et al. 2018), and thus represent promising paleoenvironmental proxy. In addition, quantitative wood anatomical parameters have low level of temporal autocorrelation, which makes the extraction of climatic signal easier (García-González et al. 2016). On the other hand, the application of quantitative wood anatomical chronologies for paleoclimate reconstructions might show some drawbacks due to variable climatic signal stored in their different frequency domains (Fonti et al. 2009).

3.2. Floods and variation in groundwater level

Floods and subsequent long lasting inundation of stems and roots significantly affects tree growth through disruption of mitochondrial respiration, onset of alcoholic fermentation with low energy yield and associated decrease of productivity (Glenz et al. 2006; Ferner et al. 2012). The intensity of flooding effect on wood anatomical structure of flooded trees is influenced by parameters including flooding character (culmination, amount of transported debris), tree tolerance to flooding (Glenz et al. 2006) and period of inundation (Copini et al. 2016). Ring-porous broadleaves affected by flooding and long-lasting inundation often build tree-rings with characteristic anomalous anatomy termed 'flood ring' (Copini et al. 2016). Typical features include reduced vessel size, increased vessel density and scattering of vessels from earlywood to latewood (St. George 2010; Wertz et al. 2013). Earlywood vessel development is stopped in submerged part after less than 4 weeks of inundation, although process of lignification probably

continues also in hypoxic conditions. The vessel size reduction compared to reference (not flooded) trees may exceed 50 % (Copini et al. 2016) resulting in significant drop in xylem theoretical conductivity. If the inundation took place during cambial activity, higher frequency of collapsed sickle shaped vessels occurs (Copini et al. 2016). Flood rings occur only in roots and submerged segments of the stem, and are absent in parts of tree which remained above the culmination water level (St. George 2010; Kames et al. 2016; Copini et al. 2016). Flood rings were successfully used to identify former flood events (Wertz et al. 2013) as well as to date paleofloods up to 350 years back (St. George 2010).

In addition, flooding often results in various types of mechanical damage to stem that trees need to cope with during current and following growing seasons through adjustment of wood anatomical structure. Most frequently occurring deformations after flooding include stem scaring, stem tilting, stem base burial and root exposure (for review see Ballesteros-Cánovas et al. 2015). Significantly reduced size (up to 77 % comparing pre-event period) and increasing frequency of vessels (475 %) and parenchyma rays (115 %) was observed in 30° wide segment of wood adjacent to flood scar in *Fraxinus excelsior* (Arbellay et al. 2010). Similar results were reported also for other broadleaved species (Ballesteros et al. 2010). The occurrence of wood anomalies restricted only to zone adjacent to scar may be interpreted as a compartmentalization of damage on tissue level - local preference of safety-strategy in close vicinity of the scar, which might be compensated by increased conductivity of xylem in more distal parts of tree-ring (Sperry et al. 2008). Significant anatomical adjustments are limited only to the year of flooding, indicating fast recovery of wood anatomical structure after flooding injury (Arbellay et al. 2010; Ballesteros et al. 2010).

Floodplain sedimentation may bury stem bases, affecting tree growth and wood anatomy through hypoxia in root layer (Copini et al. 2015). This results in modified wood anatomical structure of buried part of stem, resembling wood anatomical structure of roots - this mainly includes larger conduit dimensions, thinner conduit walls and (in case of ring-porous broadleaves) scattering of vessels over entire earlywood and latewood (Friedman et al. 2005). The sensitivity of individual trees to stem base burial probably differs between species, burial depth and sediment properties. For instance, two North American species in xeric floodplain immediately significantly responded to burials exceeding 30 cm in depth (Friedman et al. 2005); contrary, no response of wood anatomical structure of *Quercus robur* was observed after experimental burial with 50 cm of sandy soil (Copini et al. 2015). In addition, lagged response of wood anatomy for more than three years after the burial (Copini et al. 2015) represents another pith-fall for analyzing response of wood anatomical structure to stem burial. The response of flooded trees to tilting from vertical position mainly includes reduction in conduit size and reaction wood formation; decreased vessel size is often observed after root exposure due to erosion (for additional information about the effect of tilting and root exposure on wood anatomical structure see chapter **3.3**).

The effect of high groundwater level and low soil aeration is not limited only to years with large flooding events, but negative effect of moisture on vessel size was documented using correlation analysis over periods without flooding event in floodplains and wetlands with permanently high water level(Kames et al. 2016). These correlations reveal negative effect of precipitation, moisture and/or discharge on conduit size and tree-ring width (Polacek et al. 2006; Kames et al. 2016; Koprowski et al. 2018), pointing out the limitation of tree growth and xylem development through low soil aeration (Ferner et al. 2012). However, if the groundwater level is artificially reduced below some critical threshold (e.g., due to river regulation), conduit size tends to decrease and conduit density increase with increasing drought stress (Schume et al. 2004; Lageard and Drew 2008; Scharnweber et al. 2015).

3.3. Disturbances

According to 'Process-Event-Response' principle (Shroder 1980), trees respond to mechanical damage affecting their growth through adjustment of wood anatomical structure or altering speed of growth, which later may be used for dating purposes. Wood anatomical anomalies after mechanical damage represent mechanisms, which trees use to mitigate the risk of malfunction of tracheids and vessels under stress conditions (Sperry et al. 2008). Abrupt decrease in conduit size partly compensated by increasing conduit number was often observed as a consequence of mechanical damage to stem (Ballesteros et al. 2010; Arbellay et al. 2012a, 2013), which prevents cavitation of large vessels or tracheids (Hacke et al. 2017). Abrupt decline after stem scarring in conduit size may reach almost 60 % comparing pre-damage tree-rings (Ballesteros et al. 2010), however, it often occurs only in the small part of stem circumference adjacent to wound (Arbellay et al. 2012b). Formation of higher number of small conduits is probably driven by restriction of polar auxin flow from crown to roots by ethylene synthetized in wound level, which reduces the duration of enlarging phase of conduit development (Aloni 2007).

After stem tilting, trees form so-called 'reaction wood' to regain vertical orientation of stem (Groover 2016). Typical features of tension wood (reaction wood of angiosperms formed on the upper side of inclined stem) is reduced vessel size and gelatinous layer inside vessels and fibers; contrary, compression wood (reaction wood of gymnosperms formed on lower side of inclined stem) contains highly lignified thick cell-walls and high frequency of intercellular spaces (Schweingruber 2007; Groover 2016). Gravitational forcing on cambium together with redistribution of phytohormones around stem circumference are often believed to be drivers of reaction wood formation and decreased conduit dimensions (Aloni 2007; Groover 2016). Although reaction wood and conduits narrowing appear simultaneously after tilting, results of experimental studies based on both trees (Heinrich and Gärtner 2008; Tumajer and Treml 2018) and seedlings (Gartner et al. 2003) reveal, that decreasing conduit dimension is not causally linked to reaction wood formation and *vice versa*. For instance, tilting of broadleaved species to 30° from the vertical results in tension wood formation, but insignificant decrease in

vessel dimensions (Gartner et al. 2003). In addition, tilting stem to more than 45° induces tension wood formation restricted to upper part of stem, but reduction of vessel size along whole stem circumference (Heinrich and Gärtner 2008; Tumajer and Treml 2018).

Due to different function of conduits in roots (water conductivity) and stem (water conductivity + mechanical support), their anatomical structure largely differs (Gärtner 2007; Pallardy 2008; Crivellaro and Schweingruber 2015). Vessels and tracheids in roots are larger and have thinner cell walls; moreover, diffuse vessel distribution dominates in roots also of ring-porous species (Hitz et al. 2008). Abrupt change in vessel size may be used to identify the year, when the root was exposed from the soil due to geomorphological processes (e.g., mass-movement, bank erosion). In addition, abruptness of wood anatomical adjustment might be used to distinguish between gradual and abrupt (e.g., gradual soil erosion x mass-movement) processes (Gärtner 2007). Opposite process to root exhumation – stem base burial – may be also used for dating geomorphological processes (e.g., accumulation of debris-flow material nearby stem base) through analysis of wood anatomy adjustment (Friedman et al. 2005). For its description see chapter **3.2**.

3.4. Forest fires

Forest fires affect tree growth and wood anatomy through burning leaves and wooden segments of tree (Kames et al. 2011; Arbellay et al. 2014) and through excessive heating of the cambium (Bigio et al. 2010). In both cases, response of coniferous and ring-porous species usually includes reduction of conduit size and increased conduit density in order to increase hydraulic safety at the expense of reduction of hydraulic efficiency (Sperry et al. 2008; Arbellay et al. 2014). The wood anatomical response may occur in the year of forest fire or during subsequent years, depending on the timing of fire during growing season. If the fire affects tree growth during cambial activity, newly formed vessels are smaller and thyloses tend to appear inside of previously developed vessels, suggesting vessel occlusion as another safety mechanism reducing risk of cavitation (Bigio et al. 2010). The reduction in vessel size in subsequent years after forest fire may be linked to (i) lower amount of stored carbohydrates from year to year due to canopy destruction, or (ii) indirect effect of changing microclimate after large scale land-cover change due to forest fire (Kames et al. 2011). Wood anatomical anomalies persist for long time (> 8 years) in coniferous species (Arbellay et al. 2014), but are mostly limited to single tree-ring in broadleaves (Bigio et al. 2010; Kames et al. 2016).

Fire events cannot be dated using dendrochronological and wood anatomical methods with sub-annual precision due to effect of 'delayed cambial death' (Bigio et al. 2010), i.e. observed lagged termination of cambial activity and onset of callus tissue formation in heated part of stem. The lag between fire and cambial death is highly tree-dependent and probably is related to bark water content in the time of forest fire (Bigio et al. 2010). As a result, wood anatomical anomaly cannot be used as indication of forest fire precise timing.

3.5. Biotic disturbances

Biotic disturbances affect wood anatomical structure of infested trees through defoliation and associated reduction in amount of carbohydrates and phytohormones available for cambial activity. *Pseudotsuga menziensii* produces tree-rings with reduced diameter and wall thickness of latewood tracheids in periods of *Choristoneura occidentalis* outbreaks; no wood anatomical modifications occur in earlywood part of tree-rings due to specific timing of budworm phenology (Axelson et al. 2014). Periodical outbreaks of cockchafer causing significant defoliation of *Quercus* sp. are apparent as tree-rings with abrupt transition between large earlywood vessels (formed before bud opening from previous year storages) and extraordinarily small or almost lacking latewood vessels (formed in the period, when tree invested most of energy into rebuilding leaves; Schweingruber 1996). Uniform anatomical structure composed from tracheids may be distorted by traumatic resin ducts in some coniferous species after attack of stem-boring insects (McKay et al. 2003; DeRose et al. 2017); similarly, various cherry species form intercellular canals producing rubber-like material after fungal attack (Schweingruber 1996). In addition, lower specific hydraulic conductivity of xylem was observed also in case of severely browsed shrubs by herbivores (Pittermann et al. 2014).

3.6. Nitrogen fertilization

There is limited support on the effect of nitrogen deposition on long time series of quantitative wood anatomical parameters of trees. However, metaanalysis of previously published studies observed increasing conduit density but not increasing conduit size in geographical regions with high level of nitrogen deposition (Borghetti et al. 2016). This suggests that environmental stress related to nitrogen load and associated change in soil chemical composition (Hruška and Cienciala 2005) results in formation of safety-preferring small conduits, and increased water transport capacity is achieved through their increased number. Contrary, experimental studies based on exposition of juvenile seedlings to high levels of nitrogen rather suggest increasing conduit size with increasing nitrogen concentrations (Hacke et al. 2017). It is important to note, that in Central Europe both direct and indirect effects of nitrogen divergently affect tree growth (Cienciala et al. 2018) – directly, nitrogen acts as fertilizer stimulating growth (Laubhann et al. 2009), indirectly, it reduces tree vitality and growth through soil basic saturation depletion (Hruška and Cienciala 2005). Response of growth and wood anatomy to indirect effects of acid deposition tends to be delayed due to soil neutralization capacity (Kolář et al. 2015; Vejpustková et al. 2017) and thus it might not be properly captured in short term laboratory experiments.

3.7. Ontogenetic scaling of xylem conduits

Conduits dimensions tend to ontogenetically scale with increasing stem size due to physical constraints (Olson et al. 2014; Rosell et al. 2017) and changing polar flow of phytohormones, mainly auxins (Aloni 2007). The idea of physical constraint on conduit size is based on

assumption that resistance of water transport is increasing with increasing stem height, because of increased area of water-wall friction. However, this must be compensated in tall plants to maintain sufficient water transport through increasing conduit diameter (Rosell et al. 2017). In addition, the relative amount of auxins per number of cambial cells is lower at bottom parts of tall stems, resulting in a slow cell differentiation and long phase of lumen expansion, leading to small number of large conduits (Aloni 2007). Hence, typical age-related trend in conduit dimensions follows the trend in tree height (Carrer et al. 2015).

Ontogenetic scaling of conduit parameters represents a noise for extracting environmental signal from quantitative wood anatomical time series, which should be considered and removed using appropriate standardization approach (Carrer et al. 2015; García-González et al. 2016). Reflecting typical shape of age trend in conduit size, the most frequently applied functions for its estimation are smoothing splines (García-González and Fonti 2008; Fonti et al. 2009; Matisons et al. 2015; Castagneri et al. 2017) or positive exponential (Tumajer and Treml 2016, 2017). In case of short time wood anatomical series (<20 years), linear trend approximation (Zhao 2015) or no detrending (Arbellay et al. 2014) are acceptable as well.

4. Material and Methods

4.1. Studied geographical processes

Individual papers included in this doctoral thesis focus on the effect of climatic variability, extreme hydroclimatic events (floods and droughts) and various types of disturbances on wood anatomical structure of two native broadleaved species. We selected above listed environmental factors to represent the most important drivers of tree growth and ecosystem dynamics in lowland forests of Central Europe. For instance, climatic forcing is a dominant limiting factor of growth of trees at the edge of their species ecological amplitude (Fritts 1976) and important driver of large-scale dieback of forests in specific regions of the world (Anderegg et al. 2016). In addition, composition of floodplain forest ecosystems is adapted to periodic flooding and inundation, and thus alteration of discharge regime may affect vitality of individual trees and species composition of forest stands (Thomas et al. 2002; Janik et al. 2008). Finally, mechanical types of disturbances (including mass-movements and windstorms) are responsible for the largest damage to harvestable timber in managed forests in Europe, and due to climate change, their effect is expected to further increase (Seidl et al. 2017).

Forest ecosystems over large parts of the Czech Republic (and temperate zone in general) recently face increasing spring and summer drought stress (Allen et al. 2010; Hlásny et al. 2014; Spinoni et al. 2015; Brázdil et al. 2015; Anderegg et al. 2016; Tumajer et al. 2017). This is driven mainly by increasing trend of air temperature, which in the Czech Republic accounted 0.28 °C since 1961 (mean annual temperature) and which is the most pronounced in summer (Brázdil et al. 2009). Although insignificant trends in annual precipitation were observed in the Czech Republic during the same period, their redistribution from spring/summer to winter occurred during recent decades (Brázdil et al. 2009). This redistribution together with decreasing amount of snow in winter (Potopová et al. 2016) further amplifies growing season drought stress (Trnka et al. 2015; Jeníček et al. 2016).

In addition, discharge regimes of Central European rivers respond to climate change as well (Middelkoop et al. 2001; Stahl et al. 2010). In case of the Elbe river and its tributaries, this mainly includes increasing discharges in January and February and decreasing discharges in the period from May to July (Bormann 2010). Due to its pluvio-nival discharge regime, flooding events occur in the Elbe river floodplain mainly during spring (e.g., 1940, 1941, 1947 and 2006) or July-August (e.g., 1954, 1981 and 2002) (Brázdil et al. 2005).

Finally, the response of forest stands to mass-movement damage is of a special scientific and economical importance, because forests frequently reduce the risk of mass-movement reactivation (surface stabilization) or protect settlements from energy of mass-movements (Pánek and Hradecký 2016). Various types of slides, rockfall and flows (typology according to Varnes 1978) represent the most dangerous mechanisms of mass-movements in the Czech

Republic (Záruba and Mencl 1969; Rybář et al. 2002; Klimeš et al. 2017). Different types of mass-movements occur preferentially in different regions of the Czech Republic - for instance, rockfall occurs mainly in areas with highly weathered rocky outcrops, landslides in regions with layered geological structure (e.g., E Czech Republic), flows are characteristic for mountain regions (Záruba and Mencl 1969; Pánek and Hradecký 2016). Locally (e.g., in NW Czech Republic), the risk of mass-movements was increased by human transformation of landscape (Burda et al. 2011).

4.2. Study areas and sampling design

We used different sampling strategies and analytical approaches to address interaction between different geographical processes and wood anatomical structure of broadleaves (**Figure 1**). First, living trees were sampled to analyze the effect of climatic variability, floods and groundwater level fluctuations on wood anatomical structure of *Quercus robur*. We established robust chronologies of quantitative wood anatomical parameters. Four of them were assembled in periodically flooded floodplain segment (delimited by towns of Mělník and Roudnice nad Labem in central Czech Republic), where, recently, riparian forests also face increasing drought stress (Brázdil et al. 2005; Trnka et al. 2015). Additional two chronologies were gathered from adjacent not-flooded river terrace slope to capture differences in climatic signal of flooding-limited and drought-limited sites.

Further site chronologies of *Quercus robur* were established in Zbytka Nature Reserve and its surrounding, where forest ecosystems were previously influenced by overexploitation of artesian water aquifer in the bedrock (Čejková and Poláková 2012). There was abrupt decline of groundwater level due to water pumping in the early 1980s (for more than 5 m in 5 years), and, later, abrupt rise of groundwater level (for 3 m) due to legal restriction on the amount of pumped water in the 1990s. Both groundwater level and amount of pumped water were directly monitored using boreholes, and thus this study area represents ideal setting for analyzing response of *Quercus robur* to variation in groundwater level. Locations of site chronologies reflected depression of groundwater level and ranged from the site with most depressed level to the site with limited effect of water pumping on groundwater level oscillation.

Moreover, we analyzed wood anatomical adjustment of trees (*Betula pendula*) wounded by the rockfall nearby castle Jezeří (NW Czech Republic). Various types of mass-movements naturally occur in NW part of the Czech Republic due to geological and morphological predispositions of the Krušné hory Mts. as well as due to local slope destabilization by brown coal mining (Burda et al. 2011, 2013; Tumajer and Burda 2013). Natural forest stands composed mainly by early-successional species (e.g., *Betula pendula*, *Pinus sylvestris*) develop in abandoned parts of mines, where forest stands are frequently influenced by mass-movements. In November 2013, we sampled cross-sections and wedge cuts from overgrowing scars originating during single rockfall event in winter 2010-2011. We quantified i) the intensity of wood anatomical

adjustment nearby wound margin and in more distal parts of the tree-ring and ii) speed of recovery of wood anatomical anomaly during three subsequent growing seasons.

In addition to sampling living trees influenced by various geographical processes, we established experimental plot in NW Czech Republic, where we simulated deformations of tree stems caused by disturbances (mass-movements, floods and windstorms). Selected treatments included stem tilting, decapitation, root exposure, stem base burial with soil and stem scarring. Experimental species was *Betula pendula*. Cambial activity of treated trees was monitored for three years after the treatment. Later, trees were cut down to quantify the effect of treatments on wood anatomical structure and function. Experimental approach in the study of wood anatomical response to disturbances was motivated by high level of uncertainties (about forest stand structure and disturbance dynamics) in studies based on trees damaged by natural disturbances without knowledge about their precise dating.

4.3. Tree species

The response of wood anatomical structure to environmental conditions was studied for *Quercus robur* and *Betula pendula*. *Quercus* sp. covers 7.8 % of forest stand area in the Czech Republic (Forest Inventory CzechTerra 2015), mainly in lowlands below 400 m a.s.l. It prefers sites with deep soil horizon and is adapted to periodical short-term inundation and soil water saturation (Glenz et al. 2006). It is a slow-growing light-demanding tree and represents dominant species in final successional stages of lowland forests. *Betula pendula* covers 2.8 % of stand area in the Czech Republic (Forest Inventory CzechTerra 2015). It is light-demanding, poor-soil-tolerant, early-successional species with fast juvenile growth, early maturity and short lifespan. It often represents initial woody species colonizing abandoned post-mining or post-agricultural areas.
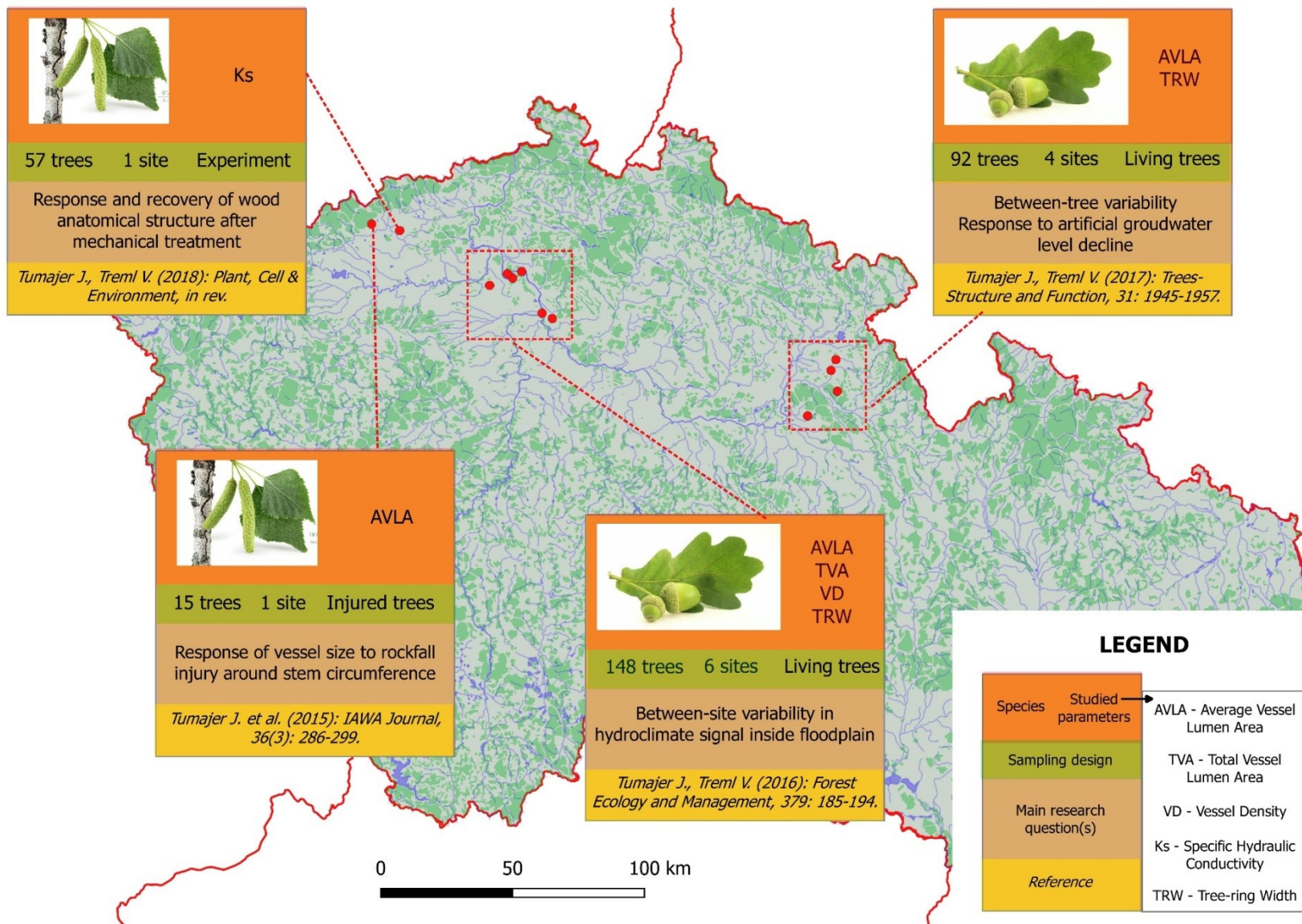
Figure 1: Overview of publications listed in this thesis with their basic description

4.4. Sample processing

All samples were processed using modern approaches used in quantitative wood anatomy (Gärtner and Schweingruber 2013; von Arx et al. 2016), with specific steps to increase vessel lumen-wall contrast, capture microimages and measure quantitative parameters of vessel structure. The procedure differed between *Betula pendula* and *Quercus robur* due to their contrasting wood anatomical structure (Crivellaro and Schweingruber 2015 and **Figure 2**). Surface area of entire core was cut using CoreMicrotome (Gärtner and Nievergelt 2010), stained with black ink and covered with white chalk powder to fill large earlywood vessels of ring-porous *Quercus robur*. Large resolution EPSON scanner was later used to scan cores at resolution of at least 1200 dpi. Contrary, small vessels of diffuse-porous *Betula pendula* are hardly visible macroscopically, and thus permanent microscopic sections had to be prepared. This included cutting thin section of wood (~20 μm) using microtome, staining using Safranin and AstraBlue solution, dehydration and fixation of the sample (Gärtner and Schweingruber 2013). Finally, microimages were captured using camera attached to microscope in 40x magnification.
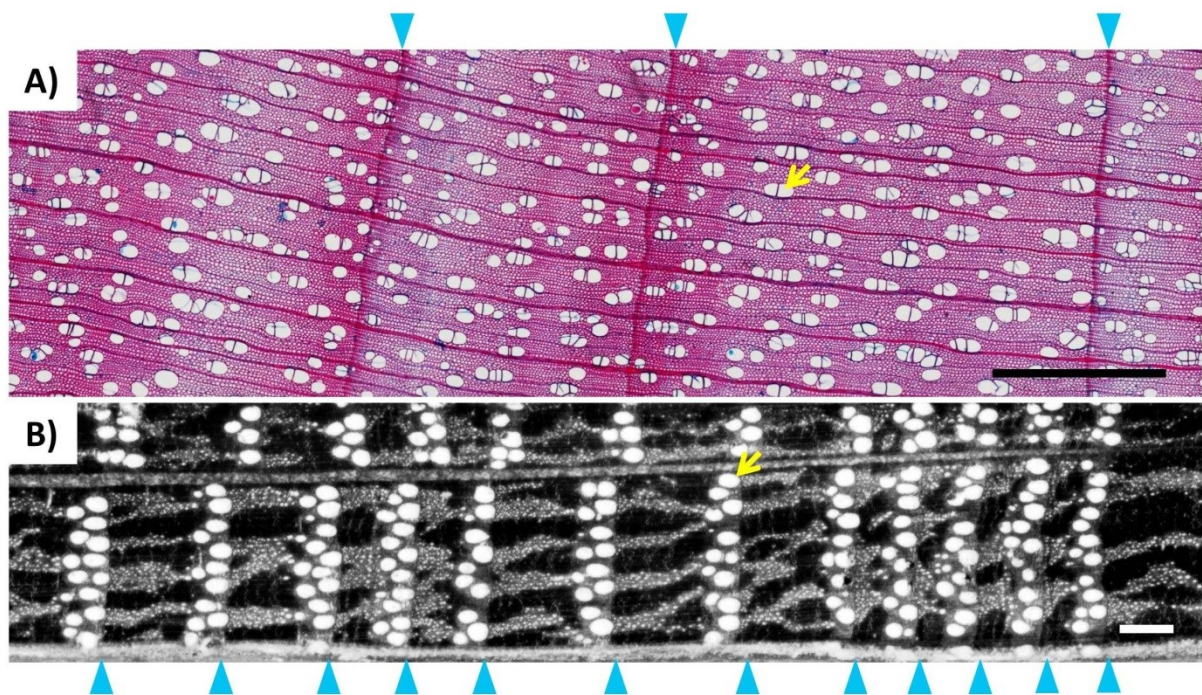
Figure 2: Wood anatomical structure of (A) *Betula pendula* and (B) *Quercus robur*
Blue triangles indicate positions of tree-ring boarders, yellow arrows point-out one vessel. Scale-bars at right bottom corner of images indicate 0.5 mm

The measurement of vessel parameters was performed using software WinCell 2011Pro (Régent Instruments Inc. 2011). Different studies included in this thesis were based on different sets of quantitative wood anatomical parameters of tree-rings (see **Figure 1**). Average vessel lumen area, total vessel lumen area and vessel density were provided as an output of WinCell

analysis; contrary, specific hydraulic conductivity was calculated according to Scholz et al. 2013. In addition, tree-ring widths were measured in case of *Quercus robur* on scanned images using WinDendro 2009b (Régent Instruments Inc. 2011).

Thorough cross-dating of all series was the first step of data processing. Because wood anatomical parameters are not reliable for cross-dating purposes (García-González et al. 2016), we based cross-dating on measured tree-ring widths. Coherence of cross-dated series was further verified using time series of vessel parameters. Because both tree-ring widths (Fritts 1976) and quantitative vessel parameters (Carrer et al. 2015) contain significant age trend, series were standardized to remove age effect from time series. In case of long time series of *Quercus robur*, negative exponential was used for standardization of tree-ring widths and positive exponential for vessel parameters. Short time series of average vessel lumen area of *Betula pendula* were standardized linearly, or their trend in specific hydraulic conductivity was approximated as linear in mixed effects-model. The quality of chronologies was quantified using commonly used coherency statistics (e.g., Rbar, EPS; Wigley et al. 1984). The existence of subsamples with contrasting long-term trends in tree-ring width and vessel anatomical time series of *Quercus robur* was verified using modified Principal Component Gradient Analysis (Buras et al. 2016).

Analysis of interaction between hydroclimatic conditions and growth or wood anatomical structure of *Quercus robur* was based on bootstrapped-correlation analysis (Zang and Biondi 2015); and the effect of extreme events (floods and droughts) was estimated using pointer-years (Schweingruber 1996). Correlation analysis was based on site chronologies or so-called 'responder chronologies' (chronology based on subsample of trees with similar trend; Buras et al. 2016). Contrary, modelling approach was used to quantify the effect of mechanical damage on wood anatomical structure of *Betula pendula*. In case of trees injured by natural rockfall, the long-term trend in average vessel lumen area was predicted in pre-event period and then extrapolated into post-event period. Subsequently, the deviance between predicted and observed values of vessel lumen area was used to quantify i) the intensity of wood anatomical anomaly in different segments of the stem and ii) the speed of anatomical recovery in following years. Between-tree and between-year variability in specific hydraulic conductivity of artificially damaged trees was decomposed into components driven by ontogeny, climate and disturbance using linear mixed-effects models (Zuur et al. 2009); and sensitivity of the model to omitting specific component was used to quantify its effect size.

5. Author's contribution statement

The presented thesis is composed of four publications related to extraction of environmental signal from time series of vessel parameters in *Betula pendula* and *Quercus robur*. Their citation and contribution statement are provided in **Table 1**.

Table 1: List of publications included in this thesis

Nr.	Reference	Journal IF	Author's contribution (%)
1	Tumajer J., Treml V. (2016): For. Ecol. Manage. 379, 185-194.	3.064	80
2	Tumajer J., Treml V. (2017): Trees-Struct. Funct. 31, 1945-1957.	1.842	80
3	Tumajer J., Burda J., Treml V. (2015): IAWA J. 36, 286-299.	0.403	70
4	Tumajer J., Treml V. (2018): Plant, Cell Environ. in rev	6.173	80

I confirm contribution of Jan Tumajer to papers listed in **Table 1**.

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Doc. Mgr. Václav Treml, Ph.D.

6.   Individual scientific papers

Chapter 6.1: Tumajer J., Treml V. (2016): Response of floodplain pedunculate oak (*Quercus robur* L.) tree-ring width and vessel anatomy to climatic trends and extreme hydroclimatic events. Forest Ecology and Management 379, 185-194.

Chapter 6.2: Tumajer J., Treml V. (2017): Influence of artificial alteration of groundwater level on vessel lumen area and tree-ring width of *Quercus robur*. Trees-Structure and Function 31, 1945-1957.

Chapter 6.3: Tumajer J., Burda J., Treml V. (2015): Dating of rockfall events using vessel lumen area in *Betula pendula*. IAWA Journal 36, 286-299.

Chapter 6.4: Tumajer J., Treml V. (2018, in rev): Disentangling the effects of disturbances, ontogeny and climate on xylem hydraulic conductivity of *Betula pendula*. Plant, Cell & Environment, in rev.

Contents lists available at ScienceDirect

Forest Ecology and Management

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

Jan Tumajer *, Václav Treml

Charles University in Prague, Faculty of Science, Department of Physical Geography and Geoecology, Albertov 6, 12843 Prague, Czech Republic

A B S T R A C T

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 (Kozlowski, 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

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 (Kozlowski, 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; Schweingruber, 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
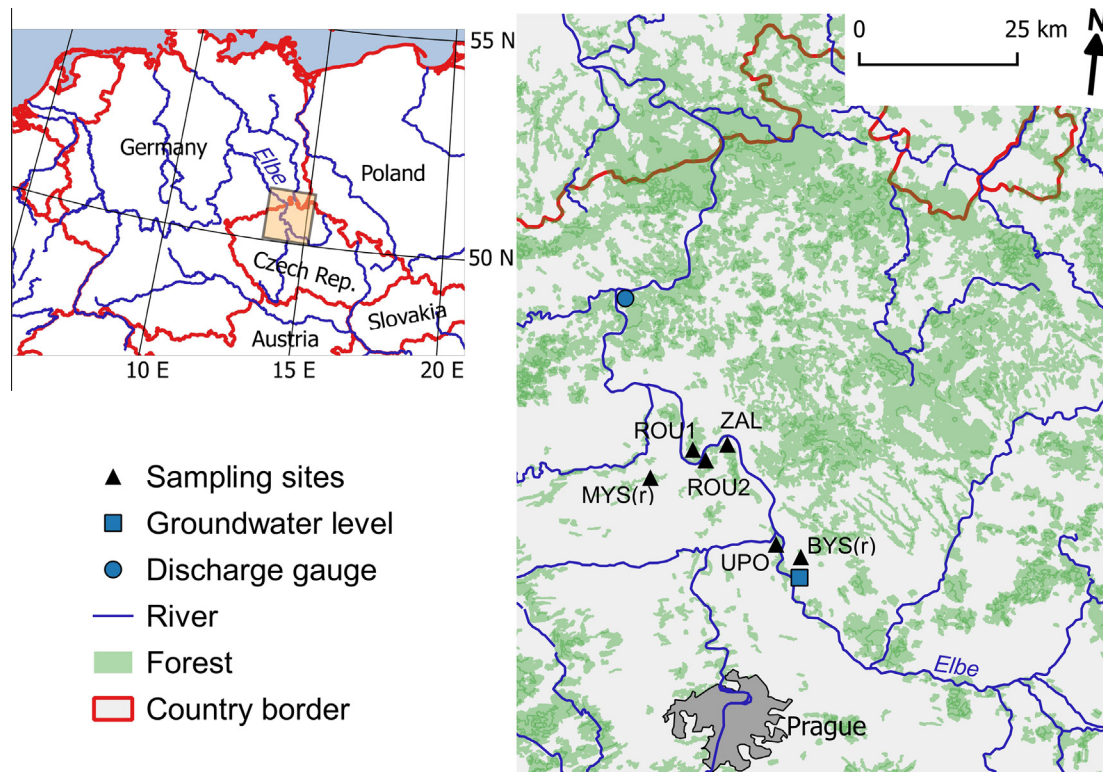
Fig. 1. Location of study sites.

(2010) reported increasing discharge in January and February and decreasing discharge from May to July.

Besides the gradual component of climate change, extreme hydroclimatic events (droughts and floods) occurred in the study area throughout the 20th century, with a significant increase in the frequency of droughts between 1990 and 2010. Brázdil et al. (2015) identified the most extreme drought events in 1953, 1959, 1976, 1992, 2000, 2003 and 2007 for the area of Czech Republic. Since 1920, floods with discharges greater than Q5 occurred in spring (March and April) in 1940, 1941, 1947 and 2006, and summer/autumn flooding events (July and August) occurred in 1954, 1981 and 2002 (Brázdil et al., 2005).

In the study area, the phase of bud break (opening) of *Q. robur* starts around 20th April, and all leaves start to develop around 7th May. Leaf yellowing starts during the second half of September, and leaf fall begins by mid-November. The in-leaf period thus lasts an average of 210 days (Hájková et al., 2012).

2.2. Fieldwork and sample processing

The fieldwork was conducted from March 2014 to October 2015. Samples were taken from 98 trees growing at four sites located on the floodplain and from 50 trees growing at two reference sites in the adjacent lowland not affected by flooding (Fig. 1, Table 1). All the sites on the floodplain were located next to the river banks. Canopy level individuals of *Q. robur* were sampled.

One core was extracted from each stem at breast height using an increment borer. The cores were stuck to wooden supports and their surfaces were cut using a core microtome (Gärtner and Nievergelt, 2010). The contrast of vessel lumina and walls was enhanced by applying black ink and white chalk on to the core surface (Gärtner and Schweingruber, 2013). The cores were scanned at the resolution of 3200 dpi and image contrast was

Table 1
Characteristics of sampled stands.

Site	Number of trees	Mean age	DBH (cm)	Height (m)	The oldest measured tree-ring
UPO	23	103	62 ± 9	30.5 ± 0.5	1856
ROU1	24	90	62 ± 6	30.0 ± 0.8	1916
ROU2	27	147	74 ± 13	29.2 ± 0.9	1823
ZAL	24	97	56 ± 7	24.0 ± 1.4	1900
MYS(r)	28	150	53 ± 11	27.7 ± 0.5	1831
BYS(r)	22	95	48 ± 4	23.5 ± 0.5	1903

DBH – breast height diameter, DBH and height are indicated as mean ± standard deviation; (r) – reference site.

enhanced using ImageJ. Measurement of tree-ring widths was performed in WinDendro 2009 (tree-ring borders were determined visually) and, subsequently, earlywood vessel anatomical parameters were measured using the software WinCell 2011 Pro (Régent Instruments, 2011). All vessels larger than 6000 μm^2 were measured and used to calculate average vessel lumen area (VLA), vessel density (VD) and total vessel lumen area (TVA) of each tree-ring of each sample. The selected threshold size of measured vessels roughly corresponds to the lower size limit of earlywood vessels in mature tree-rings of *Q. robur* (Matisons et al., 2013), and there is low systematic error in the scanning procedure for larger vessels (Fonti et al., 2009). The selected threshold is only an estimate of the minimum size limit of earlywood vessels of *Q. robur*; however, the minimum-size threshold is a commonly accepted approach to defining earlywood in ring-porous species because environmental signal of the smallest vessels is usually weak (García-González et al., 2016). The automatic detection and filtering of earlywood vessels was checked by the operator; however, manual modifications were seldom necessary, for example, due to diffuse transition between earlywood and latewood in juvenile tree-rings or due to cracks in the wood.

Average vessel lumen area as the simple quantitative anatomical parameter was measured for several reasons. It, for example, ensures comparability of our results with the findings of most other studies, provides acceptable within-tree correlation (Kniesel et al., 2015), provides a uniform and easily extractable age trend (Carrer et al., 2015), and there is a straightforward connection between variability in VLA and environmental forcing (Tyree and Sperry, 1989; Hacke et al., 2006). Total vessel area (i.e., the sum of all earlywood vessel lumen areas in the tree-ring) is usually highly correlated with earlywood width, which in most ring-porous species contains environmental signal of the previous growing season (Kniesel et al., 2015). Vessel density was defined as the total number of earlywood vessels divided by the total area of the tree-ring (Stojnic et al., 2013; Kniesel et al., 2015), thus making this parameter significantly correlated with TRW (and especially latewood width). Although we are aware that it would be more appropriate to include the total area of earlywood in the calculation, the exact determination of the earlywood-latewood boundary in ring-porous species is affected by uncertainty related to its subjective detection (García-González et al., 2016).

2.3. Data analysis

Visual cross-dating of raw series was performed for all types of proxies under investigation. However, because common signal in vessel anatomy time series is usually weaker than in TRW (García-González et al., 2016), and because trees on average had wide tree-rings (Table 2) with no missing rings or any other anomalies in tree-ring series, cross-dating based on TRW was prioritized. Since there is a significant age trend in vessel time series caused mainly by apical growth (Anfodillo et al., 2013; Carrer et al., 2015), we removed this trend from each series in a two-step process. First, we adjusted heteroscedasticity by applying an adaptive power transformation (Cook and Peters, 1997). Then, we standardized our time series by computing ratios between observed growth curves and expected growth curves (i.e. the process called "detrending"; Fritts, 1976). Detrending was performed by fitting a regression curve, the shape of which is in line with ontogenetic trends in specific types of time series (Carrer et al., 2015). In case of VLA, positive exponential was used. The regression curve was defined as:

$$VLA = A + e^{(B*Year-C)},$$

where A, B and C are parameters and Year is the calendar year. VD and TVA contained the least significant age trend, so linear detrending was preferred. A similar approach was used also in case of TRW series, which were detrended using a negative exponential function. Most of series were significantly autocorrelated (substantially more than climatic time series), the first-order autocorrelation was thus removed using autoregressive modelling (Cook and Kairiukstis, 1990).

Finally, average chronologies of all types of series were computed for each reference and floodplain site. The common signal retained in the chronologies was estimated using expressed population signal (EPS; Wigley et al., 1984) – a measure of the similarity between a given tree-ring chronology and a hypothetical chronology that had been infinitely replicated from the individual radii – and mean inter-series correlation (Rbar; Cook and Kairiukstis, 1990). The period since 1933 was further used for growth-climate analysis, where all chronologies exceed commonly used EPS threshold 0.85 for TRW and lower threshold 0.70 for vessel anatomical parameters. The lower EPS threshold for anatomical chronologies compared to TRW was applied because other studies have already emphasized naturally lower values of

Table 2
Basic statistics of individual raw site series and chronologies for the period 1933–2012.

Site	Tree-ring width					Vessel lumen area					Vessel density					Total vessel area				
	Mean (10⁻² mm)*	EPS	Rbar	Mean sens.*	AC1*	Mean (10³ μm²)*	EPS	Rbar	Mean sens.*	AC1*	Mean (mm⁻²)*	EPS	Rbar	Mean sens.*	AC1*	Mean (mm²)*	EPS	Rbar	Mean sens.*	AC1*
UPO	304	0.91	0.31	0.20	0.65	51.7	0.76	0.07	0.17	0.34	2.23	0.85	0.20	0.22	0.25	0.96	0.72	0.10	0.19	0.35
ROU1	275	0.94	0.41	0.21	0.70	51.7	0.81	0.15	0.12	0.42	2.92	0.92	0.33	0.21	0.24	0.97	0.87	0.23	0.18	0.29
ROU2	214	0.90	0.26	0.25	0.61	55.4	0.83	0.16	0.14	0.20	2.17	0.87	0.19	0.21	0.35	0.99	0.82	0.15	0.16	0.43
ZAL	280	0.90	0.29	0.25	0.66	54.6	0.79	0.10	0.18	0.30	2.21	0.82	0.17	0.21	0.23	1.09	0.76	0.12	0.19	0.22
MYS(r)	136	0.95	0.41	0.23	0.52	48.6	0.85	0.17	0.11	0.25	3.16	0.90	0.25	0.21	0.38	0.67	0.84	0.16	0.15	0.37
BYS(r)	222	0.96	0.56	0.25	0.63	48.0	0.71	0.10	0.12	0.40	2.81	0.91	0.51	0.28	0.48	0.73	0.84	0.20	0.24	0.44

EPS – expressed population signal (Wigley et al., 1984), Rbar-average correlation between individual series, Mean sensitivity – average year-to-year fluctuation of time series (Cook and Kairiukstis, 1990), AC1 – first order autocorrelation.
Statistics derived from raw series are marked by asterisks. The remaining characteristics were derived from detrended series.
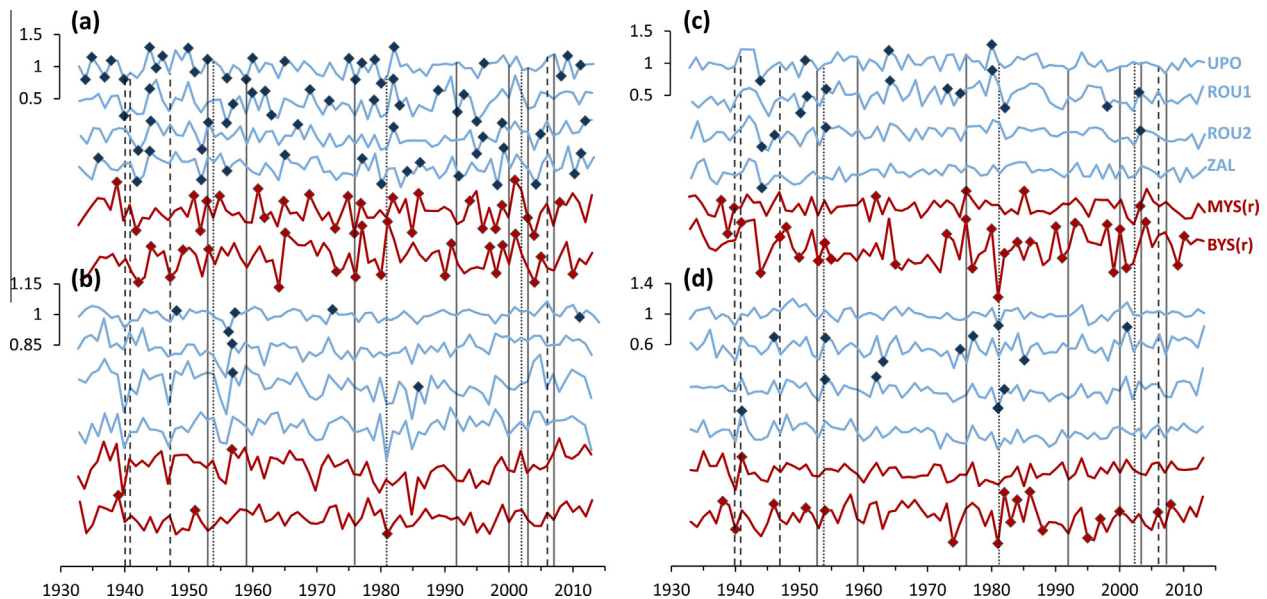
Fig. 2. Site standard chronologies of tree-ring widths (a), vessel lumen area (b), vessel density (c), and total vessel area (d). Chronologies in floodplain are blue, those in distant zones of the lowland are red. Small squares represent pointer years. Vertical lines indicate drought (solid), spring flood (dashed) and autumn flood (dotted) according to Brázdil et al. (2005, 2015). Note the different scales (variance) of different types of chronologies. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

EPS as well as Rbar in vessel time series in comparison to TRW (e.g., Fonti and García-González, 2008; Gea-Izquierdo et al., 2012; Kniesel et al., 2015; Matisons et al., 2015; García-González et al., 2016).

Similarities in medium-frequency variability were visualized using a 20-year smoothing spline, which was further used to describe general trends in chronologies of different sites. Further, breakpoints in linear trends of standard chronologies (i.e., the points where regression coefficients change) were identified using the R package 'strucchange' (Zeileis et al., 2003) with minimum segment length of 20 years.

All calculations were performed using the software ARSTAN (adaptive power transformation, detrending of series, EPS and other descriptive statistics of chronologies; Cook, 1985), MYSTAT (parametrization of VLA regression curves) and R (identification of breakpoints, R Development Core Team, 2014).

2.4. Growth-climate relationship

As climatic data, we used monthly resolved temperatures (CRU TS3.23; Jones and Harris, 2008) and the self-calibrated version of the Palmer Drought Severity Index (scPDSI) (CRU TS3.21; van der Schrier et al., 2006) with a common timespan 1901–2012. Data on discharge of the river Elbe in the Ústí nad Labem gauging station and groundwater levels from the Kly measurement station (Czech Hydrometeorological Institute) were also included in the growth-climate analysis (both as monthly average). Time series of ground-water level and river discharge were available for the year 1966 onwards. Therefore, growth-climate relationships were computed for two periods, the full period in which tree-ring and CRU data overlapped (1933–2012) and a shorter period for which all hydro-climatic data were available (1966–2012). Bootstrapped correlation coefficients over the period from the May preceding the tree-ring formation year to August of the ring formation year were used to describe the growth-climate relationship (Biondi and Waikul, 2004). Besides the quantitative detection of the effect of hydroclimatic variables on tree-rings, we also identified pointer years in all types of series and subsequently checked their synchro-

nization with the occurrence of floods and droughts in the study area (Brázdil et al., 2005, 2015). Pointer years were defined based on the algorithm of Becker et al., (1994) as years when for at least 50% of the raw series at a site the difference from the previous tree-ring exceeds a specific threshold. Because the level of year-to-year variability differed between the four types of series investigated, the threshold was set to the mean sensitivity (average year-to-year difference) of each type of raw time series.

3. Results

The oldest tree-ring measured at a floodplain site dates back to 1823, and the oldest one measured at a reference site dates back to 1831. Tree-ring width and vessel density always contained stronger common signal (expressed by EPS and Rbar) compared to vessel lumen area and total vessel area. Inter-annual variance expressed as mean sensitivity was also higher in TRW and VD than in VLA and TVA (Table 2).

Inspection of TRW and pointer years in relation to floods and droughts (Fig. 2a) revealed, that some reductions in tree-ring widths of reference trees were related to drought years (1976, 2007). In the same drought years, floodplain TRW chronologies usually record a reduction of lower intensity (or no reduction) compared to the reference chronologies. The most abrupt reduction in TRW of reference trees was observed in 1976, with significantly weaker response in floodplain sites. However, there were pointer years that were not associated with any kind of extreme hydroclimatic event. On the other hand, there were also drought or flood years with no response in both floodplain and reference chronologies (e.g., 1941, 1959). Vessel-based chronologies recorded a substantially lower number of pointer years compared to TRW. Some reductions were not of sufficient intensity in more than 50% of series to be classified as pointer years. For example, VLA chronologies displayed abrupt reductions related to spring flood events (1940, 1947, 2006) or to autumn flooding in the year preceding tree-ring formation (1954) (Fig. 2b). These events, however, usually appeared simultaneously in both reference and floodplain chronologies. Vessel density chronologies from

reference sites responded positively to the 1976 drought, and anomalies of lower intensity occurred also in 2000 (Fig. 2c). Finally, there are synchronized reductions of TVA chronologies in drought years (1953, 2000), although not confirmed by pointer years (Fig. 2d).

Correlations between TRW chronologies and monthly mean temperatures and the drought index revealed that floodplain sites contain stronger temperature signal in comparison to reference sites, where drought signal prevails (Fig. 3). A positive effect of temperature on the growth of floodplain trees is most significant for previous October, for the months preceding the beginning of

the growing season (January-March) and the months of the first half of the growing season (May-July). Moreover, tree-ring width at the UPO and ROU1 sites is also significantly negatively related to water availability during the growing season preceding the ring-formation year. Both reference sites are positively correlated with scPDSI from previous November onwards; moreover, growth is negatively linked with high temperatures during previous autumn at the BYS(r) site. The environmental signal in tree-ring widths of the ZAL floodplain site seems to be mixed, as it also contains a positive response to water abundance (albeit weaker compared to reference sites).
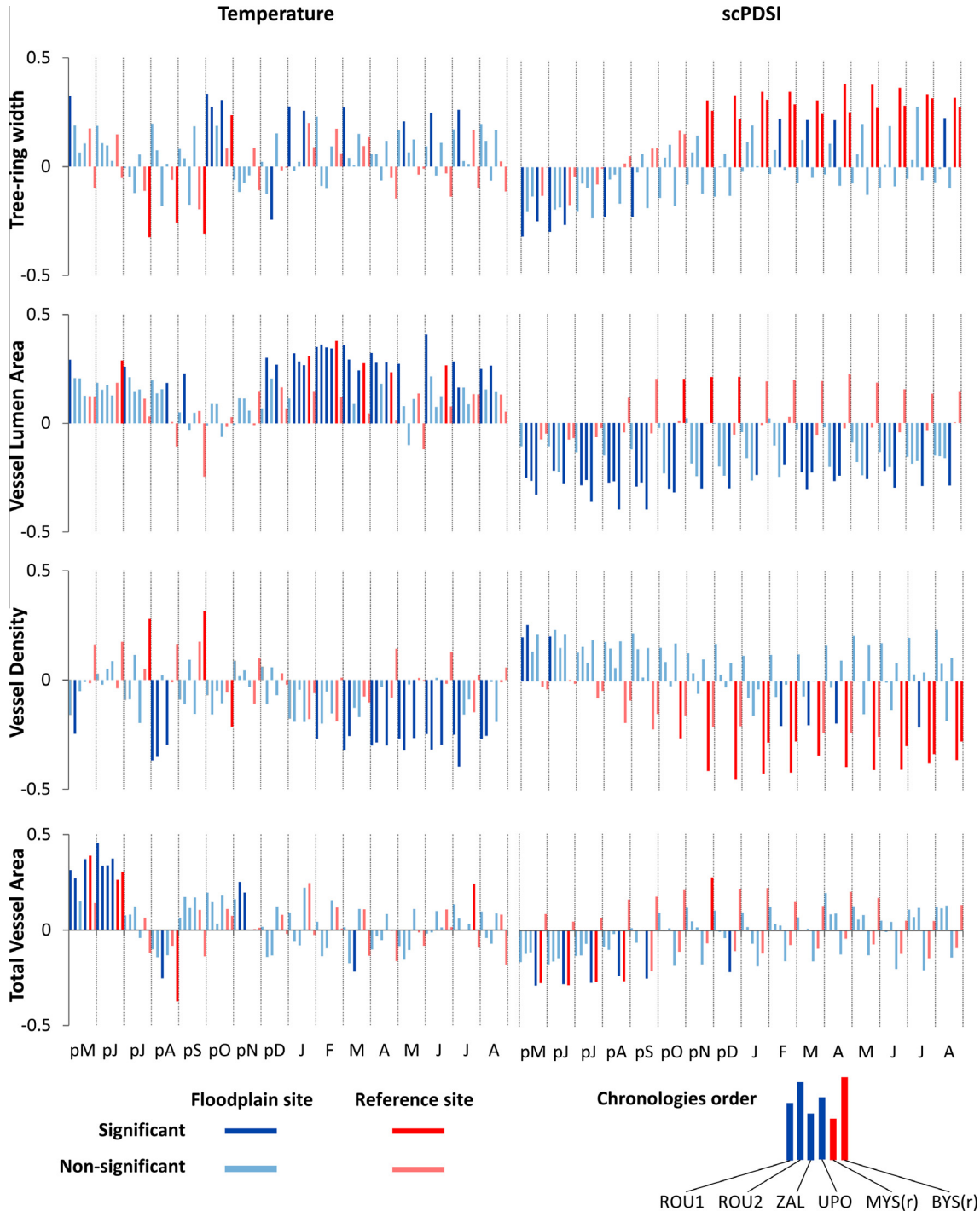

Fig. 3. Correlation coefficients between site chronologies and monthly temperatures and drought index (scPDSI) for period from May preceding to tree-ring formation year (pM) to August of the ring formation year.
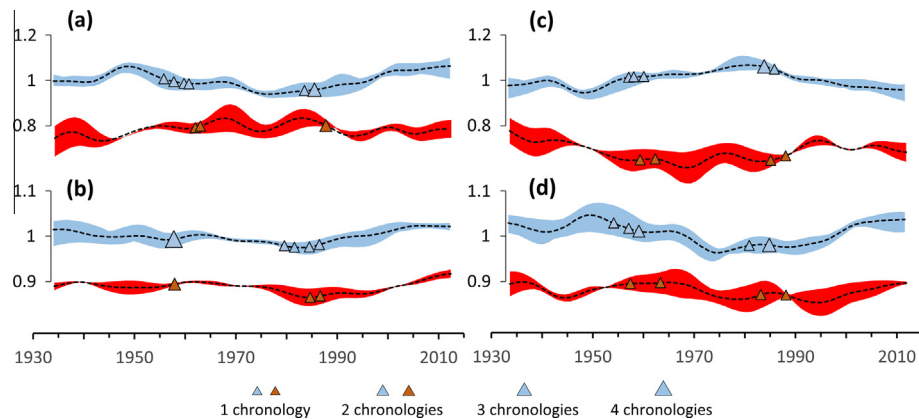
Fig. 4. Low-pass filtered tree-ring widths (a), vessel lumen area (b), vessel density (c) and total vessel area (d) chronologies of *Q. robur* of four floodplain (blue) and two reference sites (red). The buffer indicates the max-min span of chronologies with dashed line representing average. Triangles represent trend breakpoints with size of the triangle indicating synchronization of breakpoints amongst chronologies on floodplain or reference sites into the same year. Note the different scales (variance) of different types of chronologies. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Most site chronologies based on VLA of earlywood vessels are positively correlated with temperature during the January-April period of the tree-ring formation year (Fig. 3). The chronology of the ROU1 floodplain site also positively correlates with temperature during the previous growing season as well as with temperature during summer months of the tree-ring formation year. Three out of four floodplain chronologies exhibit significant negative correlations with scPDSI that are the strongest for months of the previous year and become weaker or even non-significant for the tree-ring formation year. The size of earlywood vessels in BYS(r) site is, on the other hand, stimulated by water abundance during previous year's autumn and early winter (October-December).

The pattern of correlations of VD chronologies appears to be partly reversed compared to TRW. In other words, VD at floodplain sites is negatively related to temperature in the tree-ring formation year (and partly also in the previous year), and negative significant correlations occur between scPDSI and VD of reference sites and ZAL floodplain sites (Fig. 3). However, the signal of previous year's growing conditions is shifted from October in TRW to August in VD chronologies. Furthermore, the effect of the tree-ring formation year conditions is amplified in VD (e.g., the temperature signal in the March-August period for most of the floodplain chronologies is stronger than that in TRW).

Total vessel area chronologies significantly correlate with previous year's conditions and almost lack significant correlations with current-year temperatures and scPDSI (Fig. 3). In all floodplain and reference TVA chronologies, there is a common signal of previous May and June. The correlation with previous August temperature is negative at all sites (significant for 2 of them). The UPO and MYS(r) sites share a common negative response to scPDSI during the previous growing season.

A comparison of correlation coefficients of chronologies with scPDSI and those based on river discharge or groundwater level for the period 1966–2012 (Fig. S2) confirmed that TRW of reference sites is significantly influenced by scPDSI and not by the groundwater level or river discharge (i.e., correlations with scPDSI are substantially higher than correlations with hydrological data). The same is true also for VD chronologies. For all floodplain chronologies, and for VLA and TVA chronologies of reference sites, correlations based on groundwater level and river discharges revealed almost the same kind of environmental information as scPDSI.

A comparison of smoothened TRW chronologies and trend breakpoints revealed that floodplain sites share a negative trend approximately between 1955 and 1980, followed by a positive trend since 1980 (Fig. 4a). On the other hand, the reference TRW

chronologies had limited long-term variability, with no common trend in recent decades. Trends in VLA are less obvious compared to TRW. An increasing trend is visible in floodplain VLA chronologies since 1980 to the 2000s, when it became almost constant, and in reference chronologies since 1980 to the present (Fig. 4b). Vessel density, again, copied the opposite trends of TRW, i.e., a positive trend from the 1950s to the 1980s turned to be negative in the most recent decades at floodplain sites (Fig. 4c). Total vessel area at floodplain sites had a negative trend in 1950–1975, then a stable trend until 1995 and an increasing trend thereafter. The respective chronologies for reference sites revealed an increasing trend since the 1990s, although the trends and distribution of breakpoints in TVA reference chronologies (MYS(r) and BYS(r)) apparently differed (Fig. 4d).

4. Discussion and conclusions

4.1. Influence of climate on growth and wood anatomy

The growth of floodplain *Q. robur* is stimulated mainly by temperatures during the growing season preceding the tree-ring formation year and the spring and summer of the ring formation year. Čejková and Poláková (2012) reported the same growth-climate relationships for oaks growing at waterlogged sites in the upper Elbe basin, suggesting that temperature forcing on to *Q. robur* growth is common at sites with high water availability. Latewood of *Q. robur* is produced mainly after leaf maturation and is responsible for the majority of annual variability in TRW (Saas-Klaassen et al., 2011; González-González et al., 2013). In contrast to latewood, inter-annual variability of earlywood width is smaller (García-González and Eckstein, 2003; Kern et al., 2013; Hafner et al., 2015). The effect of previous year's conditions on floodplain chronologies observed in this study can be attributed to a significant correlation between earlywood width and latewood width in the previous year in *Q. robur* (García-González and Eckstein, 2003). In contrast to floodplain stands, trees growing in the lowland outside the floodplain, and thus at sites with deeper groundwater levels, showed drought-limited radial growth. Evidence for drought-limited growth of oaks has been reported also from other areas in the broader region of Central Europe (Cedro, 2007; Friedrichs et al., 2009; Scharnweber et al., 2011; Kern et al., 2013).

While for TRW, we observed different responses to climate conditions between the floodplain and adjacent reference sites, most

earlywood VLA chronologies share a positive temperature signal of the period before and at the beginning of the growing season for both floodplain and reference localities. Other studies on ring-porous broadleaves, not specifically dealing with floodplain stands, also report late-winter and early-spring temperature signal in earlywood VLA (Fonti et al., 2007; Fonti and García-González, 2008; Eilmann et al., 2009; Matisons et al., 2015). Earlywood vessel size depends on the duration of the enlargement period before the lignification of the vessel secondary wall, which in ring-porous species is further limited mainly by the time of the onset of cambial activity (Pérez-de-Lis et al., 2016). As the onset of cambial activity is driven by temperature and the photoperiod, climatic conditions during late winter and early spring become crucial for vessel size parameters. Moreover, the onset of vessel enlargement starts in Q. robur approximately one month before bud swelling (Saas-Klaassen et al., 2011; González-González et al., 2013; Pérez-de-Lis et al., 2016). Hence, earlywood vessel development takes place mainly during the period with limited crown production of phytohormones and assimilates necessary for the regulation of xylogenesis, during which trees use previous year storage (Bréda and Granier, 1996) and phytohormones produced in situ (Aloni, 2007), resulting in the retainment of the signal of the previous growing season in VLA chronologies.

We found the difference in response of VLA to water availability between reference and floodplain sites. Excessive water amounts limit vessel size in floodplain trees (with the strongest influence during previous growing season) which can be linked with the low amount of air available to roots of floodplain trees, limiting the efficiency of photosynthesis (Ferner et al., 2012; Kniesel et al., 2015). A positive response of VLA was observed at the BYS (r) site, which is probably the driest site under investigation (e.g., growth is limited by high temperatures in the previous year), and the lack of available water results in smaller vessels with a low cavitation risk (Tyree, 1997).

The formation of ring-porous earlywood vessels mainly from previous year's storage, as described above, is in line with the prevailing previous year's signal in chronologies of TVA. Positive correlations with previous summer temperatures are common to all site chronologies, making this parameter a good candidate climate proxy that is not affected by site-specific hydrological conditions. Vessel density chronologies are proportional to TRW due to the approach applied when calculating this parameter. However, VD chronologies retain a stronger signal of current year's temperature at floodplain sites. These results suggest better performance of VD compared to TRW in growth-climate analysis, as observed in some diffuse-porous species (Oladi et al., 2014).

4.2. Recent trends in growth and vessel anatomical series

Since the 1960s, the study area has experienced a temperature increase and slightly decreasing growing season precipitation (Huth and Pokorná, 2005; Brázdil et al., 2009). While studied trees in floodplain have been increasing their growth as a result of warming, there was no distinct growth trend in reference trees, probably due to an interplay between increasing temperatures and increasing water demand and drought stress. We can thus conclude that unless the ground-water level in floodplains drops below a critical level, radial growth and productivity of floodplain Q. robur is favoured by the ongoing warming, which is not true for lowland oaks growing outside the floodplain.

Similarly to TRW, trends in chronologies of earlywood VLA and TVA also reflect growth-climate relationships and revealed a prevailing increasing trend due to gradual warming since the 1980s (VLA) or 1990s (TVA). Whereas at the reference sites, the increasing trend in both vessel area proxies remained stationary until recently, floodplain VLA and TVA trends became stable in 2000s.

Frequent small floods in the 2000s and 2010s, and the ensuing higher saturation of the soil profile, might be responsible for the detected recent stagnation of VLA and TVA chronologies in floodplain sites (Brázdil et al., 2005; Kašpárek, 2007; Daňhelka et al., 2014). In fact, frequent or long-lasting high soil saturation was observed to reduce vessel size (Astrade and Begin, 1997).

4.3. The influence of droughts and floods on tree growth and vessel anatomy

The relatively low effect of floods on conduit size observed in this study can be explained by the high flood tolerance of Q. robur, which is one of the highest among ring-porous species (Glenz et al., 2006). Q. robur is adapted to withstand high ground-water levels mainly due to a high density of intercellular spaces, an ability to form shallow adventitious roots, the presence of hypertrophied lenticels, and specific metabolic adaptations (Glenz et al., 2006). Although all spring floods considered in this study (1940, 1941, 1947 and 2006) occurred during the key period of earlywood vessel ontogenesis in Q. robur (Saas-Klaassen et al., 2011; Pérez-de-Lis et al., 2016), i.e. March-April, the duration of inundation was probably too short to be recorded in earlywood VLA. For example, the inundation during the most extreme recent flood in July/August 2002 (Qk = 100 years) lasted only 7–10 days (Bouček, 2003). Moreover, the effect of floods on tree growth and wood anatomy could be also underestimated because of taking a core in a breast height, as the strongest anatomical anomalies due to flooding are usually observed close to the stem base, i.e., in flooded parts of the stem (St. George et al., 2002; Wertz et al., 2013; Copini et al., 2016).

As regards to single drought events, there were some differences in the response of reference and floodplain TRW chronologies. In 1976, for example, there was a very strong and abrupt TRW decrease in the reference chronology yet almost no signal in floodplain chronologies, which is a common negative pointer year observed in different parts of Europe (Bridge et al., 1996; Fischer and Neuwirth, 2013; Matisons et al., 2013), especially at low elevations (Čejková and Kolář, 2009). This abrupt growth reduction was caused by extremely dry late winter/early spring followed by a hot summer, resulting in insufficient water availability during the growing season at low-elevated sites. However, our results document that the effect of this drought was marginal in floodplain stands, i.e. at sites with high groundwater level.

4.4. Conclusions

Unlike lowland stands situated far from the river, which are drought-limited, floodplain Q. robur forests unambiguously benefit from the recent warming, which increases their radial growth. Although earlywood vessel anatomy parameters (average vessel lumen area and total vessel lumen area) share a temperature signal common to floodplain and reference sites, the response of average vessel size to water availability is negative for trees growing in the floodplain and non-significant or positive for reference trees. A reduction of tree-ring widths as a consequence of extreme drought events (as in 1976) was observed in reference chronologies, but floodplain trees lack this kind of response, because of sufficient water availability. We did not observe any direct response in growth and wood anatomy to flood events, indicating that this process causes stress of a minor intensity in Q. robur growing in floodplains of pluvio-nival rivers with short water stagnation following a flood event.

Conflict of interest

The authors declare that they have no conflict of interest.

Acknowledgements

Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.foreco.2016.08.013.

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ORIGINAL ARTICLE

Influence of artificial alteration of groundwater level on vessel lumen area and tree-ring width of *Quercus robur*

Jan Tumajer[1] · Václav Treml[1]

Abstract

Key message **The response of tree-ring widths to groundwater-level decline varies among individual trees in forest stands. By contrast, vessel lumen area series contain common climatic signal of previous summer temperature.**

Abstract Drought events and the overuse of groundwater for water supply can cause significant declines of groundwater levels in naturally poorly drained forest stands. However, the documented growth reactions of trees to declines in groundwater level vary a lot and range from positive because of increased soil aeration to strongly negative because of drought stress. We analysed changes in tree-ring width and earlywood average vessel lumen area of *Quercus robur* from sites above an artesian aquifer, whose groundwater level declined in the late 1980s by about 5 m due to water pumping. Because we expected different responses of individual trees due to local microtopography and fine root distribution, we performed both site-level and tree-level analyses. Our results show that the site-level response of tree growth to groundwater-level pumping was not uniform. Individual trees were clustered into groups of drought-limited and water abundance-limited individuals. The response of trees to groundwater pumping differed between clusters—drought-sensitive trees responded negatively, whereas the growth of trees limited by water abundance remained stable or slightly increased. Inter-series correlation of drought-limited trees significantly increased in the period with the lowest groundwater level. In contrast to tree-ring widths, earlywood vessel lumen area series contained common temperature signal, with no imprint of groundwater-level alteration. Our results indicate that poorly drained forest ecosystems are characterized by a significantly individualistic response of radial growth to groundwater-level alteration. These individualistic responses could be, however, overshadowed in stand-level average tree-ring width chronologies.

Keywords Bog forest · Climate change · Growth divergence · Individualistic growth · Pedunculate oak · Responder chronology · Wood anatomy

✉ Jan Tumajer
  tumajerj@natur.cuni.cz

1 Department of Physical Geography and Geoecology, Faculty of Science, Charles University, Albertov 6, 12843 Prague, Czech Republic

Introduction

Temperate forests situated in flat, poorly drained plains adjacent to streams and rivers usually show high levels of productivity and provide various ecosystem services (Lockaby 2009). Both soil and wood biomass of these ecosystems represent a very important carbon dioxide sink and methane source (Bernal and Mitsch 2012; Mitsch et al. 2013), and alteration of the water regime of poorly drained sites might significantly impact their role in the balance of greenhouse gases (Couwenberg et al. 2011). In temperate Europe, the increasing frequency of drought events (Spinoni et al. 2015), together with increasing demand for groundwater as potable water or for irrigation, might induce a substantial decline of groundwater levels on local or regional scales (Scheidleder et al. 1999). However,

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knowledge of how tree growth responds to the alteration of groundwater levels in poorly drained temperate stands is limited.

Former fluctuations in groundwater level can be extracted from time series of tree-ring widths and quantitative xylem anatomy using dendrochronological approaches (Cook and Kairiukstis 1990). Tree-ring width series from areas with high groundwater levels usually contain weak climatic signal, but respond sensitively to fluctuations in groundwater level (Scharnweber et al. 2015). Temperature and precipitation signal of swamp trees become amplified only if the groundwater level is artificially altered below or above some critical threshold (Cedro and Lamentowicz 2011; Peña et al. 2014). Apart from tree-ring widths, the vessel system of broadleaves is sensitive to water abundance, both directly and indirectly (Schume et al. 2004; Gričar et al. 2013). The direct response is mediated via turgor pressure during vessel ontogenesis, resulting in the formation of large vessels with high water transport efficiency in wet conditions. Conversely, a vessel size decrease may be expected in dry conditions, which also has a physiological meaning in that it reduces the risk of cavitation (Tyree and Sperry 1989; Tyree 1997). Indirectly, vessel lumen time series of ring-porous broadleaves are sensitive to water availability from previous year's summer to early spring through recharging soil water supplies or storage of carbohydrates from year to year (Bréda and Granier 1996).

The response of tree-ring width and vessel time series to fluctuations in groundwater level can be highly spatially variable depending on the microtopographical conditions of individual trees (Scharnweber et al. 2015). Decrease in the average size of vessels, increase in the vessel density and decrease in the tree-ring width are commonly observed after an abrupt depression of the groundwater level (Schume et al. 2004; Lageard and Drew 2008; Eilmann et al. 2009; Scharnweber et al. 2015). However, an abrupt decrease in vessel size is a common feature also after flooding of roots and stem bases (Copini et al. 2016), and a negative correlation between water abundance and both tree-ring width and vessel size was repeatedly observed in a floodplain zone with a steadily high level of groundwater (Polacek et al. 2005; Tumajer and Treml 2016). Differences in the lateral and vertical arrangement of fine roots of individual trees are the main cause behind the varying responses of trees to groundwater-level changes. Fine roots are the most sensitive part of the tree to drought stress (Leuschner et al. 2001) as well as flooding stress (Ferner et al. 2012) and predispose individual trees to resistance and resilience to fluctuations in groundwater level. If a substantial part of the root system is affected by drought, osmotic adjustments occur to enable roots to grow at the expense of aboveground growth (Hsiao and Xu 2000;

Thurm et al. 2016). On the other hand, low aeration of the soil in conditions of high groundwater level limits mitochondrial respiration in roots, resulting in lower energy yields from alcoholic fermentation and lower biomass productivity (Ferner et al. 2012).

The common dendrochronological approach to capturing environmental signal is averaging of tree-ring series from individual trees located in the same stand into a site (master) chronology (Cook and Kairiukstis 1990). While this approach works properly in stands with coherent growth trends among individual trees (Fritts 1976), it may mask true growth responses of stands with highly variable growth trends attributed to site microtopography or competition among trees (Wilmking et al. 2004; Zhang and Wilmking 2010; Carrer 2011; Düthorn et al. 2013; Rozas 2015). As mentioned above, poorly drained stands with microtopographic variability are good examples of ecosystems with presumably high growth variability. Assumed clusters of trees differing in environmental signal captured in tree-rings should be analysed using appropriate statistical approaches considering individualistic responses (Buras et al. 2016).

The main objective of this study is to identify the response of pedunculate oak (*Quercus robur* L.) tree-ring width and average vessel lumen area to an abrupt artificial reduction of the groundwater level at both the stand level and the individual tree level. To meet this objective, we established a transect of sites from the centre to the border of an area with an artesian aquifer in the bedrock, the groundwater level of which was significantly and abruptly reduced (up to 5 m) because of water pumping in the 1980s–1990s. For each plot, we constructed site chronologies as well as "responder" chronologies based on subgroups of trees with similar long-term trends and, subsequently, analysed their climatic signal and response to decline in groundwater level. We hypothesized that the distance of sites from the aquifer area centre would influence the strength of growth and wood anatomy response to groundwater pumping.

Materials and methods

Study area

The study is focused on the Zbytka Nature reserve and its surroundings, located in the north-eastern part of the Czech Republic (Fig. 1a, b). This area is of great environmental and economic importance due to the presence of an artesian aquifer in the bedrock, which serves as a potable water source for more than 150,000 people (Čejková and Poláková 2012). Calcareous siltstones to sandstones dominate the bedrock and, due to high water permeability
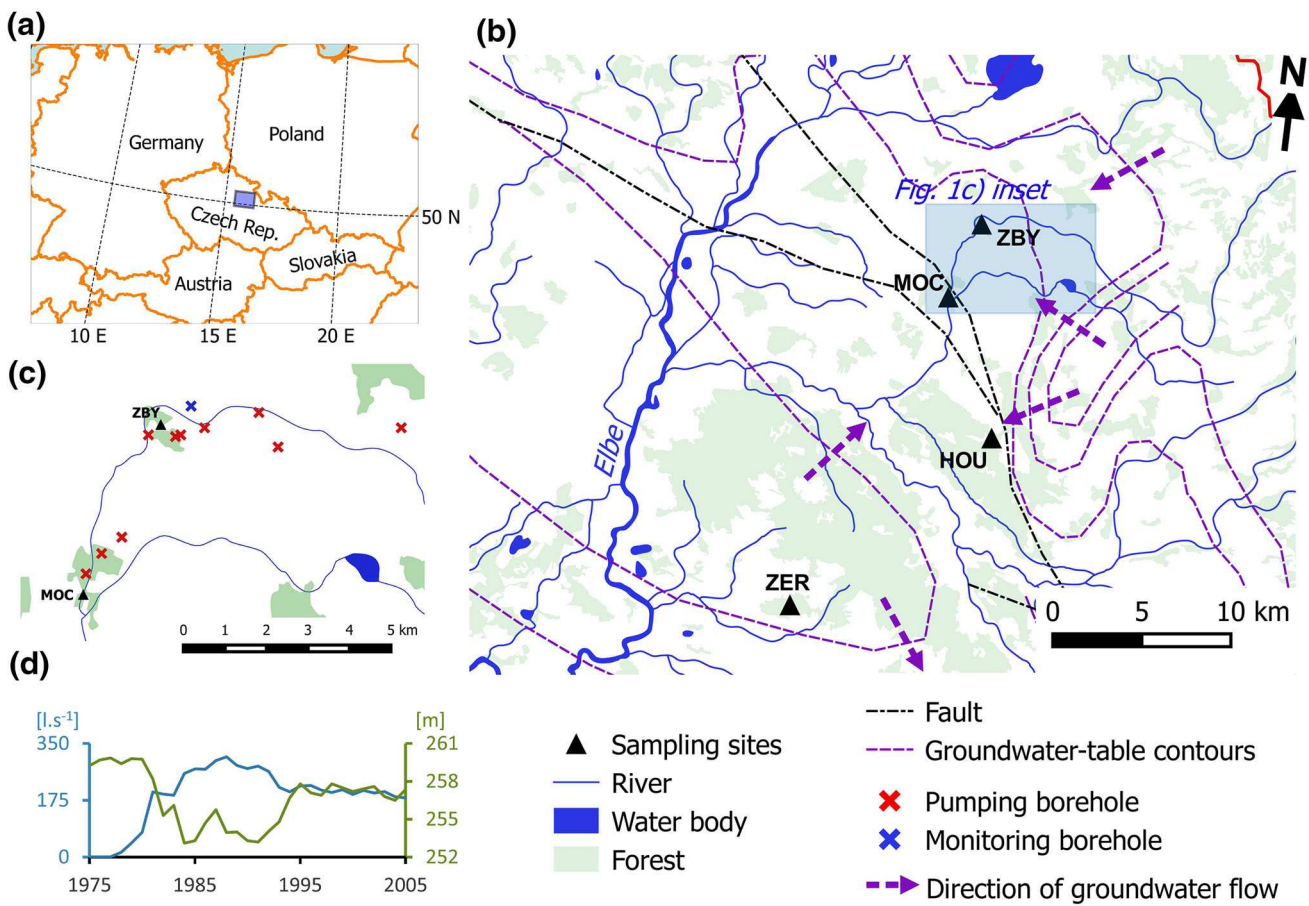
Fig. 1 Location of study sites. Position of the Czech Republic in Europe (**a**), topographical and hydrogeological setting of the study area (**b**), network of pumping and monitoring boreholes (**c**), groundwater level (*green*) and amount of pumped water (*blue*) over the period 1975–2005 in the Zbytka aquifer (**d**)

(400–500 m^2 day^{-1}), serve as an artesian water reservoir. Sedimentary rocks are present in part of the study area (approximately, 60%) covered by rocks with low permeability, causing the largest springs to be concentrated in the vicinity of faults (Lachman 2010). Fluvisols and stagnosols dominate the soil composition in the centre of the aquifer area, with an increasing proportion of cambisols and luvisols towards its margin (classification according to FAO 2006). The mean annual temperature is 8.5 °C, and the total annual precipitation equals 660 mm.

The water pumping was commenced in 1978 and reached a peak intensity between 1984 and 1992, when a network of 11 boreholes (Fig. 1c) was established with the projected maximum capacity of 710 l s^{-1}. The annual average water uptake in the whole network was almost 310 l s^{-1} in this period (with maximal monthly amount 340 l s^{-1} in April 1988), reducing the level of groundwater by more than 5 m (Fig. 1d). After the establishment of the Zbytka Nature reserve, the maximum amount of pumped water was restricted to 274 l s^{-1} in 1993 and 250 l s^{-1} in 1996. Since the second half of the 1990s, the actual amount

of pumped water fluctuates around 200 l s^{-1}; this has resulted in the stabilization of the groundwater level at approximately 2 m below the original level prior to the commencement of the water pumping (Růžička 2006; Čejková and Poláková 2012).

Fieldwork and sample processing

Four sites were sampled, the first one being in the centre of the network of pumping boreholes and the others in increasing distance from the centre of the aquifer area, the last one being located at its margin (Fig. 1b). Sites are located in an area that is hydrogeologically saturated by groundwater inflow from the east (the Orlické hory Mts) and west (the Elbe river floodplain). The elevation of sampling sites spans from 260 to 275 m.

Fieldwork was performed in two campaigns in August 2014 and April 2016. At each site, approximately 25 trees of canopy-level *Q. robur* were cored at breast height. Since there were no signs of stem eccentricities, we collected one core per tree. Moreover, sampling a single core per tree

ensured that a larger number of trees were included in site and responder chronologies (see below). In total, 92 trees were cored.

The surface of the cores was cut using a core microtome (Gärtner and Nievergelt 2010), and the contrast between vessel lumina and wood mass of tree-rings was enhanced by applying a black ink marker and white chalk (Gärtner and Schweingruber 2013). Subsequently, the cores were scanned at 1200 dpi resolution. The contrast of the images was further improved using ImageJ, and two types of dendrochronological time series—tree-ring width (TRW) and average vessel lumen area (AVLA)—were created (Table 1). The first type of series was obtained using WinDendro 2009 and the latter one using WinCell 2011Pro (Régent Instruments Inc 2011). Automatic detection of measured features (tree-ring borders and vessel lumina) was visually checked by the operator and corrected when necessary. As the environmental signal in quantitative anatomical time series of ring-porous species is amplified in the largest vessels in earlywood (García-González et al. 2016), we applied a size filter excluding all vessels smaller than 5000 μm^2.

Data analysis

Because there was high variability in tree ages both between plots and within individual plots, we excluded individuals younger than 60 years or older than 150 years (i.e. outliers) to ensure an acceptable level of age similarity across sites. This resulted in the reduction of the overall sample depth to 84 trees. The above-mentioned thresholds were identified by visual inspection of age histograms and other distribution charts, and further verified using the "common interval" algorithm implemented in the "dplR" package (Bunn 2008) in R (R Core Team 2016).

Visual cross-dating was performed to identify and correct anomalies in the tree-ring sequence (e.g. missing rings), which were, however, rare. The age trend was removed both for TRW and AVLA using the individual

standardization (detrending) approach. First, each series was corrected for heteroscedasticity using adaptive power transformation (Cook and Peters 1997) and, subsequently, a negative exponential was fitted to the TRW series and a positive exponential to the AVLA series (Tumajer and Treml 2016). The shape of the trend functions reflects the general decrease of TRW with increasing age due to continuously increasing cambium surface (Cook and Kairiukstis 1990) and hydraulic scaling of AVLA to the vertical distance between the coring position and apex (Olson et al. 2014; Carrer et al. 2015). Parameterization of regression curves was performed using the software ARSTAN (TRW; Cook 1985) and MYSTAT (AVLA). Indices were calculated as ratios between observed and expected series. Finally, site chronologies were obtained using robust averaging (Tukey's Biweight Robust Mean) of individual indexed series.

Besides site chronologies, we also averaged individual TRW and AVLA series from each plot into so-called "responder" chronologies (groups of trees with a common long-term trend; Buras et al. 2016) using principal component analysis (PCA) over the period 1955–2012 (common period of all series and climatic data; see below). The main part of the variability among the series was captured by the first principal component (common signal); however, tree-ring series vary along the second principal component (tree-specific signal)—that is why, up to three responder chronologies were defined based on significance and the sign of correlations of individual series with the second principal component (Fang et al. 2012). The responder subgroups included trees with a significant (p value <0.05) positive correlation, non-significant correlation and significant negative correlation with the second principal component, respectively (further in the text referred to as *A*, *B* and *C* responder chronologies).

As different environmental signals in TRW and AVLA chronologies of ring-porous broadleaves were documented (e.g. Fonti and García-González 2008; Matisons et al.

Table 1 Characteristics of sampled stands at individual sites

Site	Number of trees	Mean age (years)	Oldest measured tree ring	Tree-ring width			Average vessel lumen area		
				Mean ± SD (mm)	AC1	Mean sensitivity	Mean ± SD (10^3 μm^2)	AC1	Mean sensitivity
ZBY	22/19	102	1875	2.28 ± 1.23	0.58	0.25	53.2 ± 13.2	0.16	0.11
MOC	19/19	133	1877	1.60 ± 0.57	0.54	0.22	52.4 ± 10.4	0.21	0.12
HOU	22/20	81	1882	2.91 ± 1.19	0.57	0.21	50.3 ± 15.7	0.12	0.11
ZER	29/26	123	1795	1.67 ± 0.64	0.38	0.23	56.8 ± 10.6	0.16	0.10

Number of trees sampled trees/analysed trees, *AC1* first-order autocorrelation of raw series, *mean sensitivity* mean year-to-year variability of raw series

2012; García-González et al. 2016), we performed PCA separately for both kinds of series—the same tree can thus belong to different responder groups based on TRW and AVLA. The quality of individual site and responder chronologies was evaluated for the period 1955–2012 using expressed population signal (EPS; a measure of similarity between real chronology and theoretical chronology based on an infinite number of series; Wigley et al. 1984) and mean inter-series correlation (Rbar; Cook and Kairiukstis 1990). The stability of the inter-series correlation was quantified using moving Rbar (21 years long window). The proportion of total variability in individual series explained by the first two principal components was used as the quality metric of the PCA approach.

Growth–climate analysis

Mean monthly temperature (CRU TS3.23; Harris et al. 2014) and the self-calibrated Palmer Drought Severity Index (scPDSI; CRU TS3.21; van der Schrier et al. 2006) were used in growth–climate analysis. Bootstrapped correlation coefficients were calculated between monthly resolved climate data and site and responder chronologies for the period 1955–2012. Moreover, we also correlated the first two principal components of PCA with climate data. Principal components represent the main orthogonal directions of common growth variability, and their climatic signal thus captures the common signal shared by groups of trees. All bootstrapped correlations were obtained over the whole period of analysis as well as in moving windows (length = 21 years, step = 1 year) to evaluate the temporal stability of the growth–climate interaction. Correlations were calculated using monthly climatic variables from June of the year preceding the ring formation year to September of the ring formation year. Growth–climate analysis was performed using the package "treeclim" in R (Zang and Biondi 2016).

Results

Responder chronologies

The first two principal components explain a significant proportion (49–58%) of total variability in the TRW series (Table 2). Most TRW series have a uniform and significant correlation with the first principal component; however, they vary in the correlation with the second principal component (Fig. 2a). The respective proportion of explained variability is lower and does not exceed 36% for the AVLA series (Table 2). In comparison to TRW, correlations of AVLA with both principal components are

Table 2 The proportion (%) of variability in tree-ring width and average vessel lumen area standardized series explained by the first pair of principal components (first principal component/second principal component)

	ZBY	MOC	HOU	ZER
TRW	42/16	44/13	36/19	38/11
AVLA	15/12	26/10	13/11	20/9

TRW tree-ring width, *AVLA* average vessel lumen area

more variable both in terms of strength and direction (Fig. 2b).

Site and responder chronologies of TRW have considerably higher values of both EPS and Rbar than the respective chronologies based on AVLA (Table 3). While EPS tends to be higher for site chronologies (reflecting their greater sample depth) than responder chronologies, the opposite is true for Rbar. The proportion of TRW series positively/negatively correlating with the second principal component of PCA decreases/increases with increasing distance from the aquifer area centre, that is, from site ZBY to site HOU. On the other hand, the proportion of AVLA series negatively correlating with the second principal component tends to slightly decrease from the centre to the margin of the aquifer area (Fig. 2; Table 3). For all sites and both TRW and AVLA series, the mean age of the trees does not differ among responder chronologies (one-way ANOVA, p value >0.1).

Coherence of high- and medium-frequency growth variability

All TRW responder and site chronologies from the same sites show high coherency in terms of high-frequency variability. Medium-frequency (decadal) variability is similar only in the case of the ZER site (Fig. 3a). Site chronologies are generally most similar to *B* responder chronologies. Responder chronologies *A* exhibit a strong negative trend. Responder chronologies *C* either reveal no trend or increase slightly in the most recent decades. The most pronounced growth depression in TRW occurred approximately between 1995 and 1998 at sites ZBY, MOC and HOU. This suppression represents a synchronized response apparent from the majority of site chronologies as well as responder chronologies. The most apparent anomaly in temporal trends in Rbar occurred in the *A* responder chronology at site ZBY, with an abrupt increase between 1984 and 1992 (Fig. 3b). All correlations between the TRW site chronology and the respective *B* responder chronology exceed 0.92; on the other hand, low correlations (0.13–0.33) occur between the *A* and *C* responder chronologies from the same sites. Even though only two
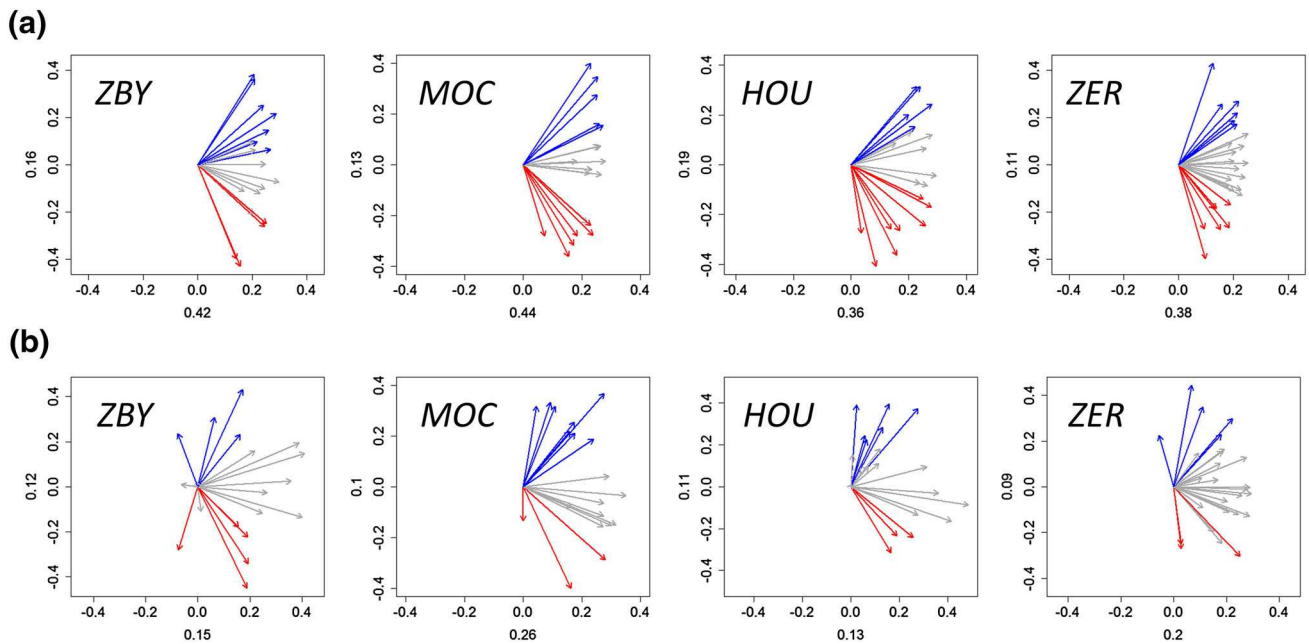
(a)

(b)

Fig. 2 PCA biplots of tree-ring width (**a**) and average vessel lumen area series (**b**). *Colours* indicate series with positive (*blue*), negative (*red*) or non-significant (*grey*) correlation with the second principal component (*p* value 0.05)

Table 3 Expressed population signal (EPS) and mean inter-series correlation (Rbar) of standardized series of tree-ring widths and average vessel lumen area calculated over the period 1955–2012

Series	Site	Site chronology			Responder chronologies								
					A			B			C		
		EPS	Rbar	N	EPS	Rbar	N	EPS	Rbar	N	EPS	Rbar	N
TRW	ZBY	0.92	0.37	19	0.91	0.60	7	0.83	0.37	8	0.89	0.66	4
TRW	MOC	0.93	0.40	19	0.90	0.64	5	0.89	0.49	8	0.83	0.45	6
TRW	HOU	0.89	0.29	20	0.87	0.58	5	0.80	0.37	7	0.85	0.41	8
TRW	ZER	0.92	0.31	26	0.74	0.29	7	0.90	0.41	13	0.82	0.44	6
AVLA	ZBY	0.64	0.09	19	0.20	0.06	4	0.64	0.15	10	0.53	0.18	5
AVLA	MOC	0.84	0.22	19	0.64	0.19	8	0.80	0.34	8	0.48	0.24	3
AVLA	HOU	0.72	0.11	20	0.62	0.22	6	0.58	0.11	11	0.26	0.10	3
AVLA	ZER	0.85	0.18	26	0.61	0.24	5	0.84	0.22	18	0.0	0.0	3

Site chronology derived from all trees sampled at the plot. *Responder chronologies* derived from subsets of trees with positive (A), non-significant (B) or negative (C) correlation with the second principal component

TRW tree-ring width, *AVLA* average vessel lumen area, *EPS* a similarity between real chronology and theoretical chronology based on an infinite number of series (Wigley et al. 1984), *Rbar* mean inter-series correlation (Cook and Kairiukstis 1990), *N* number of trees

pairs of site TRW chronologies (ZBY-MOC and ZBY-HOU) are significantly correlated, responder chronologies often correlate among sites (Table S1).

The low proportion of AVLA series correlating with the second principal component is reflected in a high degree of coherence of *B* responder chronologies and site chronologies (as the majority of the trees were included in this cluster; Fig. 4a; Table S1). There are no obvious differences in decadal trends among AVLA responder chronologies. Abrupt reductions in AVLA are mostly asynchronous between responder chronologies from the same site; however, there are synchronized short-term reductions between site chronologies. The most extreme reductions in AVLA are dated to 1985 at the ZBY, MOC and ZER sites and to 1997 and 2003 at the MOC site. Moving Rbar values of site and responder chronologies mostly share a common trend (i.e. a slight increase at the sites ZBY, MOC and ZER, and a slight decrease at the HOU site). The exception is represented by *C* responder chronologies based on a low number of trees (3) at the MOC site (abrupt increase since 1989) and the ZER site (decrease since 1977) (Fig. 4b). Similarly to TRW, there
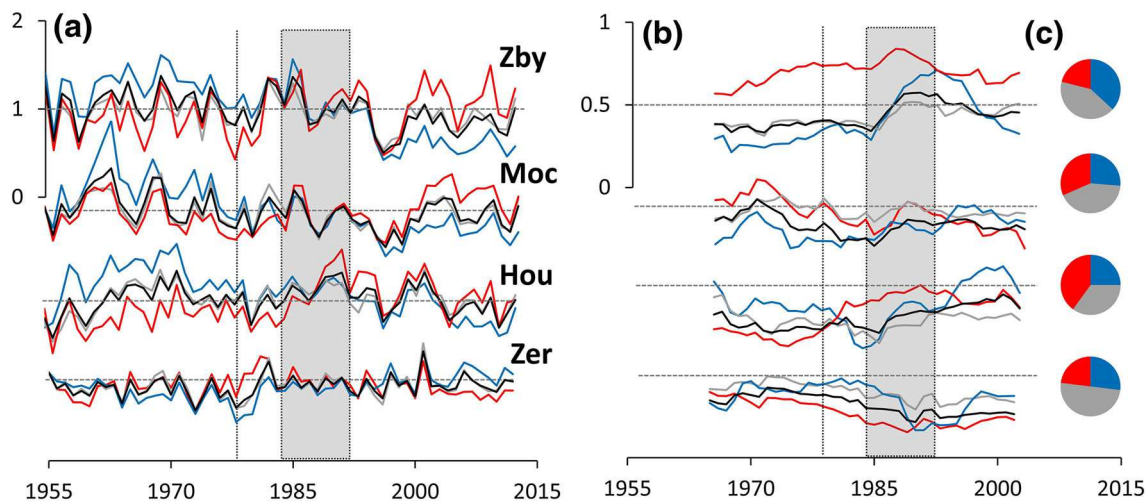
Fig. 3 Site chronologies (*black line*) and responder chronologies (*blue A* chronology, *grey B* chronology, *red C* chronology) of tree-ring width (**a**) with their respective moving 21-year Rbar (**b**) and proportions of trees included in specific responder groups (**c**). The

vertical dotted lines and *grey rectangles* indicate the commencement and peak period of water pumping, respectively (according to Čejková and Poláková 2012)
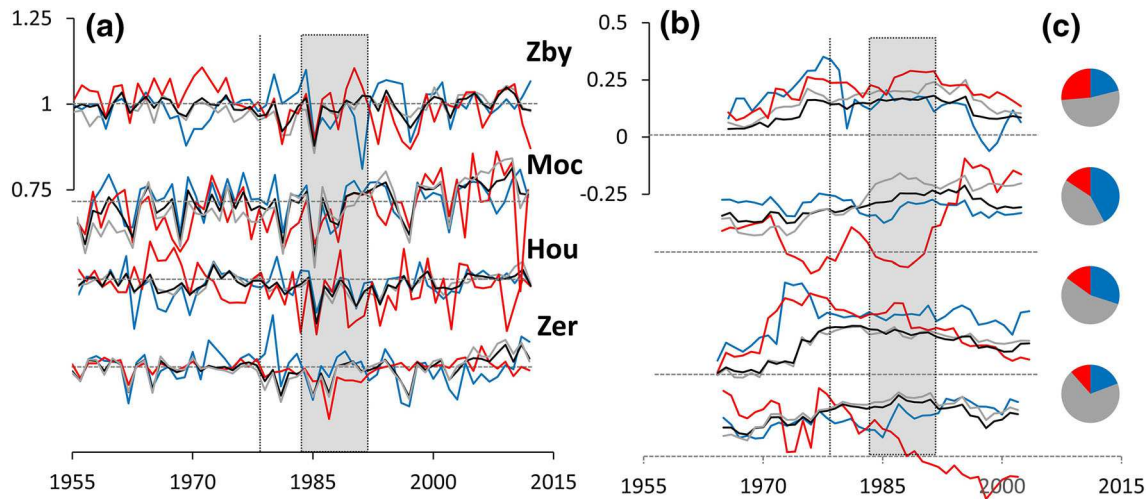

Fig. 4 Site chronologies (*black line*) and responder chronologies (*blue A* chronology, *grey B* chronology, *red C* chronology) of average vessel lumen area (**a**) with their respective moving 21-year Rbar (**b**) and proportions of trees included in specific responder groups (**c**).

The *vertical dotted lines* and *grey rectangles* indicate the commencement and peak period of water pumping, respectively (according to Čejková and Poláková 2012)

are high correlations (>0.87) between the AVLA site and *B* responder chronologies from the same site and non-significant correlations (−0.13–0.26) between *A* and *C* responder chronologies from the same site (Table S1). All site chronologies are significantly correlated with each other.

Growth–climate relationship

Most TRW site chronologies responded negatively to temperature in the preceding July; moreover, there were significant positive correlations of the ZER site chronology with July and September temperatures, a positive

correlation of the HOU site chronology with May temperature and a negative correlation of the ZBY site chronology with the July drought index (Fig. 5a). The climatic signal in the AVLA site chronologies is common to all sites and consists of a positive correlation with temperature of the preceding growing season and early spring and summer of the ring formation year (Fig. 5b); moreover, the HOU site correlates positively with the drought index, being significant for June and July of the preceding year.

The climatic signal of the TRW *A* responder chronologies reveals significant negative correlations with summer temperature of the year preceding the ring formation year

Fig. 5 Bootstrapped correlation coefficients between monthly resolved temperature or drought index (scPDSI) and tree-ring width (**a**) and average vessel lumen area (**b**) site chronologies
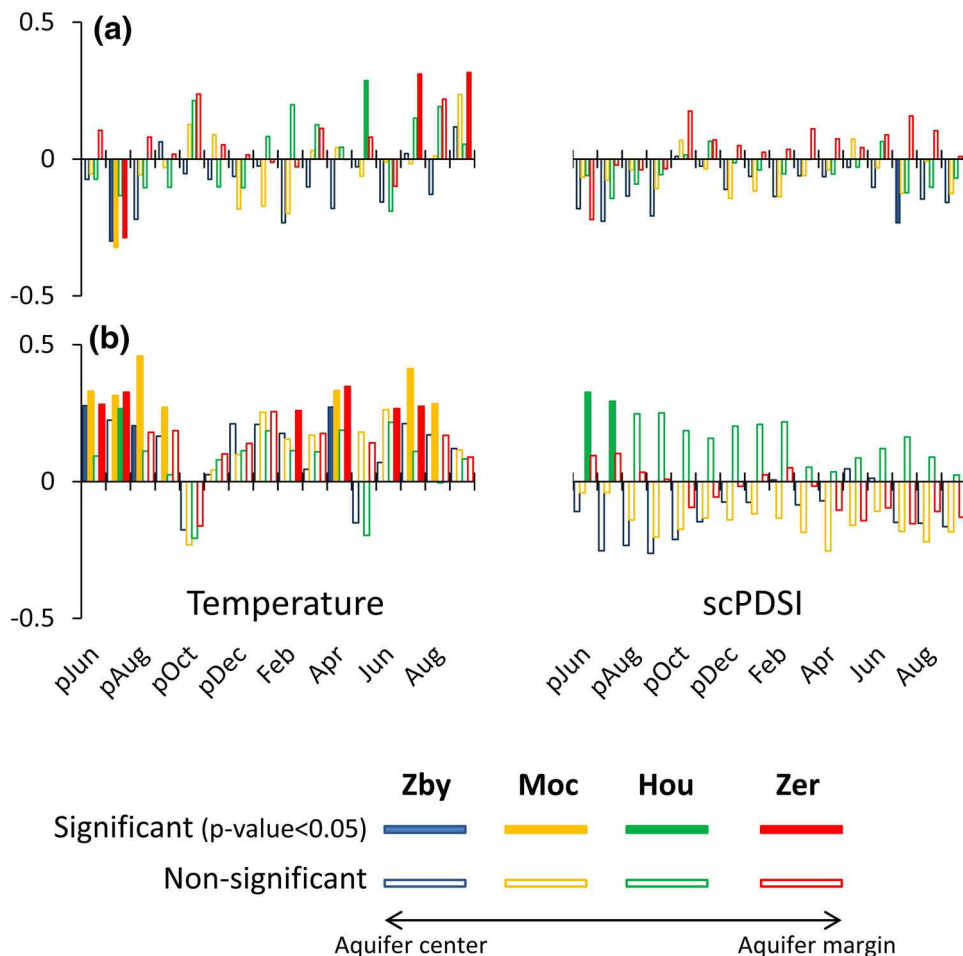
and the summer temperature of the ring formation year (Fig. 6a). This signal is the strongest in the centre of the aquifer area (ZBY, MOC) and becomes mostly non-significant at the aquifer area margins (HOU, ZER). The responder chronologies *C* correlate positively with the summer temperature of the ring formation year and negatively with the drought index in most of the analysed months. The correlations with the drought index are, however, significant only for months of the preceding year at the sites ZBY, MOC and HOU and for ring formation summer at ZBY. Responder chronologies *B* lack significant correlations with climatic data. Moving correlations indicate that all TRW site and responder chronologies from the central part of the study area (ZBY, MOC and HOU) respond negatively to the drought index in the last three decades (Figs. S1–S3). It is important to note that the strongest negative response to drought index occurred in the 1980s in *C* responder chronologies. However, the increase of negative correlations between the drought index and *A* responder chronologies appears approximately 10 years later (1990s). The duration of the period with significant negative moving correlations with the drought

index decreases from the central part of the aquifer area (ZBY) to its margin (HOU). At the last site (ZER), positive correlations with the drought index disappeared in the mid-1970s in the site and *A* responder chronology (Fig. S4).

The relationships between the AVLA *B* responder chronologies and climatic data are similar to those of AVLA site chronologies (Fig. 6b). The main climatic signal is represented by a positive correlation with temperature during the preceding summer and the period from late winter to summer of the ring formation year. The AVLA responder chronologies derived from series belonging to opposite margins of the environmental gradient (i.e. *A* and *C*) generally contain a weak climatic signal. The exceptions are *B* and *C* responder chronologies at the HOU site, which (similarly to the site chronology) lack temperature signal, but positively correlate with the drought index during the preceding year. Moving correlations of AVLA site and responder chronologies reveal mostly stable temperature signal for all sites during the period of analysis; however, negative (ZBY, MOC) or positive (HOU) significant correlations with the drought index appeared and disappeared in different periods at different sites (Figs. S5–
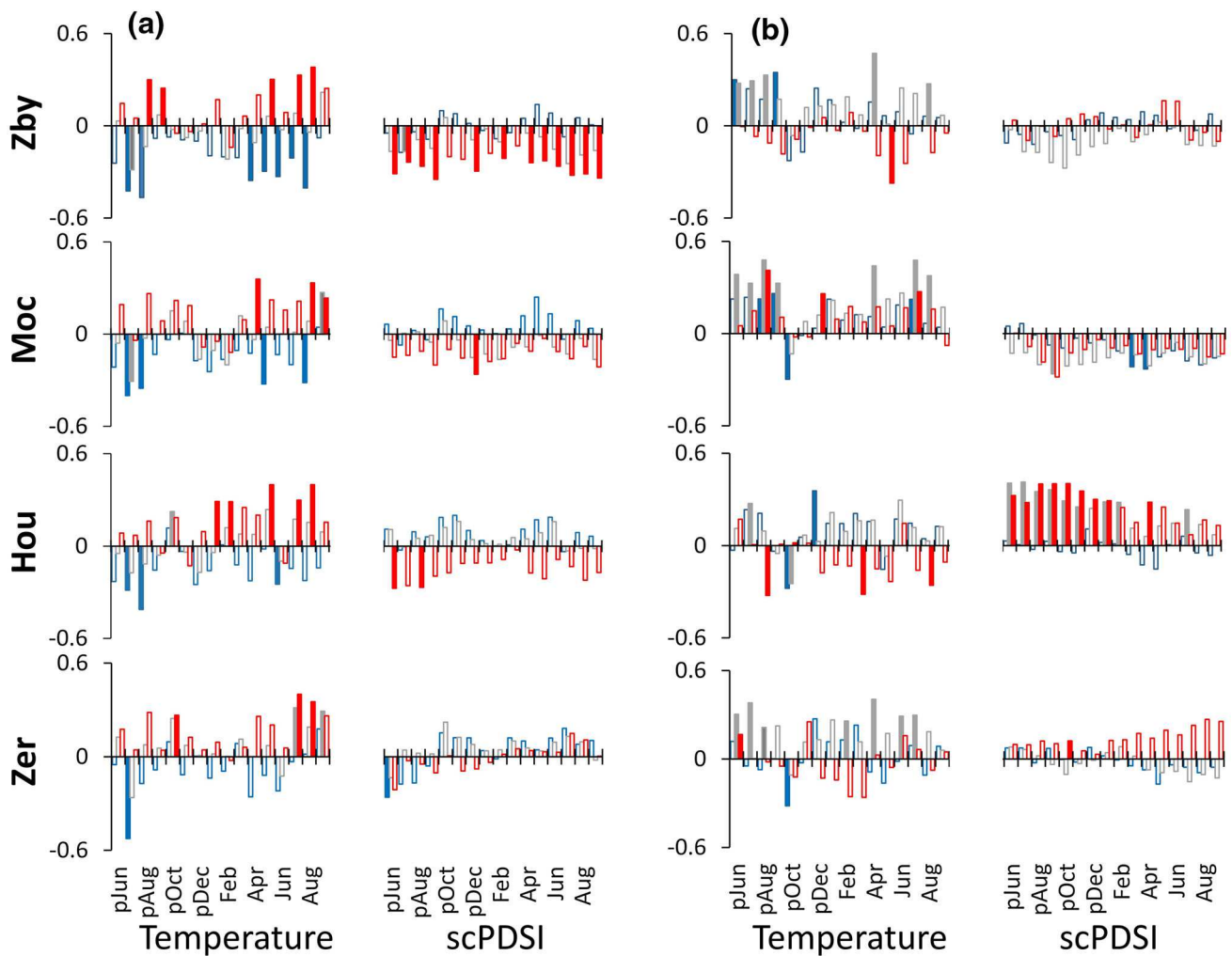
Fig. 6 Bootstrapped correlation coefficients between monthly resolved temperature or drought index (scPDSI) and tree-ring width (**a**) and average vessel lumen area (**b**) responder chronologies.

Colours refer to responder chronologies as defined in Figs. 2, 3 and 4. *Full bar* significant correlation (*p* value <0.05), *empty bar* non-significant correlation

S7). Moving correlations with the drought index are mostly non-significant at the ZER site (Fig. S8).

The correlations of the first principal components of the TRW series with the climate are weak for all sites, but the second components contain a clear signal of drought limitation. By contrast, the first principal components of AVLA have a similar set of correlations with climatic data as site chronologies; however, the second principal components have mostly non-significant correlations (Supplementary Appendix 1).

Discussion

Climatic signal in site and responder chronologies

The amount of variance explained by the first two axes of PCA together with results of correlation analysis indicates

that there is significant variability in the growth response to environmental conditions among individual TRW series from the same site. Generally, we determined two opposite climatic signals—responder chronologies *A* are drought limited (negative correlations with temperature in the previous and current growing season) and responder chronologies *C* are limited by excess water because of a high groundwater table (positive correlations with temperature and negative correlations with the drought index). This is in agreement with the expected variable response of individual trees in swamp ecosystems to fluctuating groundwater level (Scharnweber et al. 2015). Moreover, trends in assembled responder chronologies are in line with trends in their driving climatic variable—(1) drought-sensitive chronologies have a negative recent trend due to increasing drought stress during the last decades (Brázdil et al. 2015), further locally emphasized by water pumping (Čejková and Poláková 2012) and (2) chronologies limited

by excess water have a stable or slightly positive trend due to increasing evaporation (Brázdil et al. 2009) and water pumping.

In contrast to TRW, the first two axes of PCA explained a relatively low proportion of the variance in the AVLA series (less than 36%). We observed a lack of a strong common signal among individual series (as indicated by low EPS and Rbar). A weak common signal is responsible for low numbers of trees significantly correlating with the second principal component, resulting in *A* and *C* responder chronologies with mostly non-significant correlations with climate variables and unstable moving Rbar values. To check if the AVLA variability is driven by TRW, we compared the differences between groups of AVLA series clustered according to TRW (not shown). However, neither in that case did the responder chronologies significantly differ from each other. Regardless of low Rbar values, AVLA site chronologies with high sample depth have strong climate signal (García-González et al. 2016). Hence, site chronologies revealed uniformly positive correlations with temperature at the end of the previous growing season and in the current spring and summer, which is a common climatic signal observed in earlywood AVLA of ring-porous broadleaves in temperate Europe (Fonti and García-González, 2008; Matisons et al. 2012; Tumajer and Treml 2016). The strong correlation of the previous growing season can be attributed to the formation of earlywood vessels before the onset of leaf development (Fonti et al. 2007; Saas-Klaassen et al. 2011), when the xylogenesis is dependent on previous year storages (Bréda and Granier 1996).

Response of tree-ring width and vessel lumen area to groundwater-level changes

Neither TRW nor AVLA chronologies showed any abrupt anomaly as a consequence of the commencement of groundwater pumping in 1978. However, the abrupt increase in moving Rbar of the TRW drought-sensitive responder chronology from the centre of the aquifer area (ZBY) occurred at the beginning of the period of the most intense water pumping (i.e., 1984–1992), which triggered a groundwater-level decline of 5 m. This can be attributed to increased growth coherence under more limiting drought stress. Our results therefore indicate that the extreme decline in groundwater level was capable of inducing drought limitation to part of sampled trees in the centre of the aquifer area. As opposed to the ZBY site, the moving Rbar was relatively stationary in other sampling plots, indicating that the influence of water pumping and substantial reduction of groundwater level was restricted to the core of the Zbytka Nature reserve.

The most pronounced growth (TRW) depression observed in both responder and site chronologies occurred

in 1995, i.e. 2 years after the restriction on the amount of pumped water, resulting in fast recharge of its level. The intensity of this abrupt growth change was the strongest near the aquifer area centre (ZBY), less obvious at more distant sampling sites (MOC, HOU), and not apparent at the marginal site (ZER). Accordingly, Čejková and Poláková (2012) reported local dieback of oaks during the 1990s in the Zbytka Nature reserve and attributed it to the malfunctioning of old drainage channels. While trees are able to modify their root system to penetrate deeper layers of the soil during periods of low groundwater levels, this adaptation can become disadvantageous after rewatering due to hypoxia and limited respiration (Polacek et al. 2005; Cedro and Lamentowicz 2011; Ferner et al. 2012; Scharnweber et al. 2015). We did not observe any abrupt anomalies in AVLA chronologies associated with the increase in groundwater level, probably because anatomical anomalies related to inundation (flood rings) are apparent only in parts of stems or roots which are completely submerged (Copini et al. 2016).

At the ZBY site, located in the central part of the aquifer area, more than one-third of sampled trees clustered into the TRW responder group limited by drought (*A* responders), and almost one-fourth of trees clustered into the group limited by excess water (*C* responders). This finding is in line with the results of Čejková and Poláková (2012), who found their site chronology (based on a different set of trees from the ZBY site) to be responding linearly to temperature during the growing season and quadratically to groundwater level; i.e. the widest tree rings were observed during warm years with very high or very low groundwater levels. However, our results show that the positive response to both high and low levels of groundwater is probably a statistical artefact of averaging of trees with opposite growth reactions. The proportion between drought-limited and excess water-limited tree changes towards the aquifer area margins—starting with mainly drought-limited trees at the ZBY site, becoming balanced at the MOC site and with dominance of trees limited by excessive moisture at the marginal site HOU. This further supports the above described suggestion that drought stress induced by groundwater pumping was the strongest at the centre of the aquifer area due to the largest decline in groundwater level.

Moving correlations enabled an assessment of the difference between the *A* and *C* responders. They showed that since the 1950s, at locations near the aquifer's centre (ZBY, MOC), *C* responder chronologies tended to exhibit more negative correlations with the drought index (i.e. trees grew better when soil was drier) than *A* responder chronologies. Both for *A* and *C* responders, the negative relation to the drought index deepened in the period of water pumping. Later on in the 1990s, after the recovery of the groundwater level, this trend reversed or continued in

C or *A* responders, respectively. The negative response to the drought index peaked in the 1980s (i.e. during the period of the lowest groundwater level) in *C* responder chronologies, but this occurred approximately 10 years later (i.e. during an abrupt rise of the groundwater level) in site and *A* responder chronologies. We suggest that *C* responders can be interpreted as excess water-limited trees (negative relation to the scPDSI), either because they grow at waterlogged microsites or because their root system is deep. The decline of the groundwater table manifested itself in an increasing growth trend of *C* responders since the 1980s. Peak of negative correlations in the period with the lowest groundwater level can be ascribed to alterations of optimal growth conditions (low groundwater level) with unfavourable growth conditions (locally occurring water-saturated soils during seasons with high rainfall). By contrast, the growth of *A* responders declined after partial recovery of the groundwater level in the 1990s and, at the same time, their growth started to react more positively to dry conditions. Perhaps, the preceding drop of the groundwater level enabled roots to penetrate deeper into the soil, which became unfavourable after the rise of the groundwater level.

Environmental signals in tree-ring widths and wood anatomy

The main reason for building average master (site) chronologies is to amplify the common (environmental) signal and reduce endogenous noise of individual trees (Fritts 1976). However, this approach is based upon the presumption of a coherent growth response of sampled trees within individual sites. Especially in studies attempting to discern the growth response of trees to climatic change, it is desirable to consider individualistic and not mean site responses (Wilmking et al. 2004; Carrer 2011; Galván et al. 2014), because even one homogenous stand might contain both positive and negative responders. With the exception of the ZER site, the TRW series from the remaining sites shared only high-frequency variability, but differed in medium-frequency trends (decadal and longer term); so averaging them into one chronology partly decreased the common signal (Buras et al. 2016). Variability in tree-ring series can be reduced by careful inspection of microsite topography, social status and age of trees during fieldwork. However, the key factors affecting the response of individual trees to groundwater-level fluctuations include rooting depth and local hydrogeological and soil properties (Scharnweber et al. 2015), which increase the probability of individualistic growth responses at waterlogged sites.

The environmental signal of AVLA responder chronologies was not stronger than the signal of mean site chronologies. The low proportion of variability explained by the first two principal components of PCA probably indicates a complex response of AVLA to a multitude of internal and external factors. In contrast to TRW, individual AVLA series share a common absence of long-term trends, but differ in year-to-year variability, resulting in lower values of mean inter-series correlation (Fonti et al. 2007; García-González et al. 2016). Lower correlation between individual AVLA series disqualifies the PCA algorithm as a means of identifying responder chronologies, because PCA is based on eigenvalue decomposition of a correlation (or covariance) matrix. Taking more cores from a single tree to increase the common signal (García-González and Fonti 2008), increasing the number of cored trees and increasing the number of analysed principal components (Fang et al. 2012) could improve the performance of PCA when dealing with quantitative anatomical series.

PCA provides an additional interpretation of the growth–climate relationship, as the first and second principal components (containing the largest proportion of variability among series) can be correlated with climatic data. The main direction in the variability (PC1) of TRW is not unequivocally driven by the climate, so we have not identified any dominant factor driving the common growth signal in sampled oaks. The direct effects of climatic variables on TRW were the second most important (PC2), still explaining between 11 and 19% of the overall growth variance. This indicates a relatively high within-stand variability in the climate signal of floodplain oak chronologies. In addition, other studies (Hafner et al. 2015; Tumajer and Treml 2016) reported substantial regional variability in the climate signal of lowland oak TRW chronologies, which further questions the hypothesis about their homogeneity across the entire Czech Republic (Dobrovolný et al. 2016). In contrast to TRW, the main common growth signal in AVLA was obviously correlated with temperature variables. In temperate Europe, either temperatures of early spring or the temperatures of the preceding growing season influence the AVLA of oaks growing across a wide range of site conditions from waterlogged to dry (Fonti and García-González 2008; Eilmann et al. 2009; Matisons et al., 2012) and the climatic signal of AVLA is thus probably less site dependent (as well as individualistic) than the signal of TRW. This makes AVLA a promising palaeoclimatic proxy.

Conclusions

Water pumping from an extensive aquifer substantially influenced the growth of *Q. robur* only in the central part of the aquifer area, where the groundwater level declined by 5 m. However, traditional dendrochronological approaches based on average site tree-ring chronologies failed to

identify true tree-growth responses to the drop in groundwater level. One distinct subset of trees responded positively or their growth trend remained stable (trees limited by high soil moisture content), and the other responded negatively (trees limited by drought), which completely overshadowed the climatic signal in site chronologies. To overcome this problem, we clustered together trees with similar growth patterns. Responder chronologies of individual clusters showed contrasting climatic signal and clear individualistic responses to groundwater pumping. Those include (1) increasing inter-series correlation of drought-sensitive trees, (2) decreasing tree-ring widths of drought-sensitive trees and (3) stable or slightly increasing growth of trees limited by excess water. Contrarily to tree-ring widths, the mean site chronologies of average vessel lumen area contained stronger climatic signal than responder chronologies. Extraction of the common directions of variability in the vessel lumen area series is complicated due to their naturally high heterogeneity and the corresponding lower inter-series correlation. To create meaningful responder chronologies of vessel lumen areas, large sample depths are probably needed.

Future dendrochronological studies should consider individualistic growth when assessing the responses of tree stands to environmental conditions. Moreover, individualistic growth responses to environmental factors also represent a challenge for forest management, which is traditionally based on elementary management units regarded as homogeneous, neglecting their internal heterogeneity.

Author contribution statement JT performed the fieldwork, laboratory processing and statistical analysis of data. VT performed the fieldwork and statistical analysis of data. Both authors wrote the manuscript.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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DATING OF ROCKFALL EVENTS USING VESSEL LUMEN AREA IN *BETULA PENDULA*

Jan Tumajer[1,*], **Jan Burda**[2] and **Václav Treml**[1]

[1]Charles University in Prague, Faculty of Science, Department of Physical Geography and Geoecology, Albertov 6, Prague 128 43, Czech Republic
[2]Brown Coal Research Institute, Department of Geotechnology and Hydrogeology, Třída Budovatelů 2830/3, Most 434 37, Czech Republic
*Corresponding author; e-mail: tumajerj@natur.cuni.cz

ABSTRACT

Vessel lumen area is influenced by both genetic and environmental forces. Its alterations balance hydraulic water transport efficiency and safety from cavitation or embolism. We tested the hypothesis that environmental stress inflicted by rockfall injury influences average vessel lumen area in newly formed tree rings of *Betula pendula* Roth, which would make it useful for retrospective detection of rockfall events. We took samples from 11 trees injured by a rockfall that occurred in the winter of 2010–2011, specifically from the stem area adjacent to the injury, parts of the stem located perpendicular to the injury, parts located opposite to the injury, and from four undisturbed trees. We measured the mean vessel lumen area of each tree ring in every sample, comprising up to 10 pre-event tree rings and generally 3 tree rings formed after rock injury. On average, 115 vessels were measured in each tree ring. We then compared the vessel lumen area in tree rings formed after the event with that of rings formed before it as well as with values predicted by an age-trend model inferred from vessel lumen area chronologies. Our results show a strong reduction in vessel lumen area in the first tree ring formed after the event regardless of the position around the stem circumference. This reduction is strongest in wood just next to the callus tissue zone, with decreasing significance in distal parts of the stem circumference. During the three years after the rockfall, the trees mostly recovered their pre-event vessel lumen area, even right next to the place of injury. Still, this value is significantly lower than the value predicted for growth without injury. Abrupt reductions of vessel lumen area turn out to be potentially useful for identifying former rockfall events and can improve on results obtained by traditional methods of dendrogeomorphological dating.

Keywords: Dendrogeomorphology, diffuse-porosity, cambial injury, mass movement, silver birch.

INTRODUCTION

Vessels are crucial for water transport in stems of broadleaved woody species, they co-determine the physical properties and are the key to the functional adaptation and evolution of woody dicotyledons (Myburg & Sederoff 2001; Aloni 2007; Anfodillo

et al. 2013). The average transverse area of vessel lumina (VLA) is influenced both by genetic (Aloni 2007) and environmental factors (*e.g.*, Fonti *et al.* 2007, 2009; García-González & Fonti 2008; Gaertner-Roer *et al.* 2013; Arbellay *et al.* 2010, 2012a, 2013; Scholz *et al.* 2014). Based on VLA and the spatial distribution of vessels in tree rings, woody species are usually divided into two general categories: ring-porous species, with large vessels located predominantly in the earlywood, and diffuse-porous species, with considerably narrower vessels spread randomly across almost the entire area of each tree ring (Zimmermann & Jeje 1981; IAWA Committee 1989; Pallardy & Kozlowski 2008).

These differences are not the only factor affecting average VLA of wood mass. Vessel area, density and other characteristics have been proven to be sensitive to temperature and rainfall variations (García-González & Eckstein 2003; Fonti *et al.* 2007, 2009; García-González & Fonti 2008; Fonti & García-González 2008; Matisons & Dauškane 2009; Alla & Camarero 2012; Stojnic *et al.* 2013) as well as to mechanical stresses affecting tree growth caused, for example, by mass movements (Arbellay *et al.* 2010, 2012a, 2013; Gaertner-Roer *et al.* 2013), floods (St. George 2010; Tardif *et al.* 2010; Ballesteros *et al.* 2010; Arbellay *et al.* 2012b) or forest fires (Bigio *et al.* 2010; Kames *et al.* 2011). The great plasticity of vessel size is caused by phytohormonal mechanisms controlling the division of cambial cells (Aloni 2007).

Cambial division and formation of new fibres and vessels, as well as differentiation of phloem cells, is driven mainly by concentrations of phytohormones, particularly indole-3-acetic acid (IAA). Ethylene, which is produced by the callus tissue covering the scar, restricts the basipetal flow of IAA to parts of the stem below the injury (Junghans *et al.* 2004), which results in increasing concentration of IAA in areas surrounding the injury (Aloni 2007; Du & Yamamoto 2007). High IAA concentrations stimulate the division of cambial cells and greatly limit the opportunities for vessels and fibres to expand before secondary wall deposition and lignification (Aloni 2007). This is usually accompanied by increased vessel density (*i.e.*, number of vessels per ring area), partly compensating for lost hydraulic conductance. This commonly causes the formation of a large number of narrow vessels (Arbellay *et al.* 2010, 2012a,b, 2013; Alla & Camarero 2012).

Changes in VLA have important consequences for physiological strategies in establishing efficient and reliable water transport from the roots to the crown. According to the Hagen-Poiseuille rule (Tyree 1997), the efficiency of water transport increases with increasing VLA (due to a drop in the vessel lumen area/perimeter ratio, *i.e.*, a decrease in relative adhesion of water flow to the wall). This, however, also greatly increases the risk of vessel cavitation or embolism in periods of high tension of the water column or freeze-thaw cycles (Sperry & Sulliwan 1992; Myburg & Sederoff 2001; Sperry *et al.* 2008). On the other hand, when a tree is exposed to active stress, it tends to form vessels with a smaller diameter which ensures reliability of the water transport system, which is traded off by a decrease of transport efficiency (Hacke *et al.* 2006; Ballesteros *et al.* 2010; Arbellay *et al.* 2012a). Under this presumption, it should be possible to date past abiotic disturbance events, such as those mentioned above, based on the occurrence of tree rings with anomalous vessel anatomy. Dating

of such events has usually been done by comparing mean VLA values in rings formed after an event with those formed in the years preceding it (Arbellay *et al*. 2012b, 2013). However, this approach is potentially biased by the age trend in VLA as a consequence of long-term changes in tree vigour, which especially concern apical growth (Fonti *et al*. 2009). This trend is generally positive and is caused by increasing distance between the source of auxins (*i.e*., leaves) and lower parts of the stem, resulting in a decrease of the relative amount of IAA in cambial cells (Aloni 2007). In addition, little is known about how VLA responds to injury around the circumference of the stem. Arbellay *et al*. (2012b), who measured VLA in the whole area of 90° adjacent to the injury caused by flooding, pointed out that the injury signal was restricted to the 30° area from the scar margin. On the other hand, if a tree is influenced as a whole (*e.g*., by a forest fire) the reaction of VLA seems to cover the majority of the stem circumference (Bigio *et al*. 2010).

   The model species chosen was silver birch (*Betula pendula* Roth), which is a diffuse-porous species. The objectives of this study were (i) to assess how dating of disturbance events is influenced by the age trend in VLA chronologies and (ii) to compare the reaction of VLA to injury around the stem circumference. To meet these objectives, VLA chronologies from different radii around the stem circumference were measured for trees injured or untouched by a rockfall event, and annual variation in VLA was evaluated by comparing modelled and measured VLA values for each tree ring. The efficiency of this approach to retrospective identification of rockfall events was compared with that of the "classical" approach based on comparing mean VLA values in tree rings formed after the event with those from preceding years (Arbellay *et al*. 2012b, 2013).
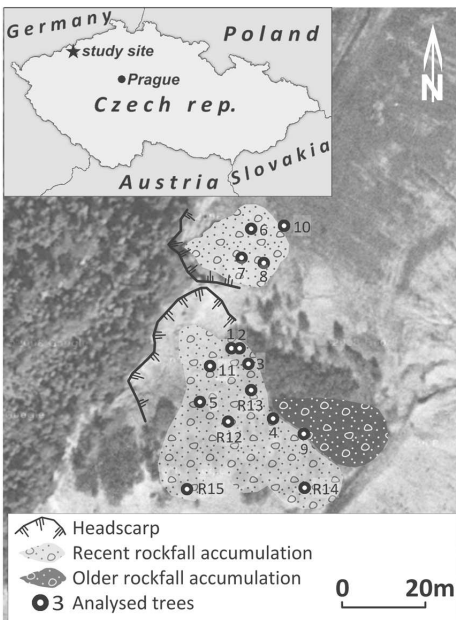
MATERIAL AND METHODS

Field sampling and sample processing

   The study was based on specimens of *Betula pendula* injured by a rockfall in the winter of 2010–2011 and a control group of undisturbed trees. The sampling site was situated below a steep rock wall in an area affected by former coal mining close to the town of Most (Czech Rep., 50° 32.8' N, 13° 30.0' E; Fig. 1). After the cessation of mining activities, vegetation dominated by *B. pendula* with *Cytisus scoparius* (L.) Link in the understorey gradually colonized the disturbed area. The mean age of trees sampled was 15.6 ± 6.1 (SD) years.
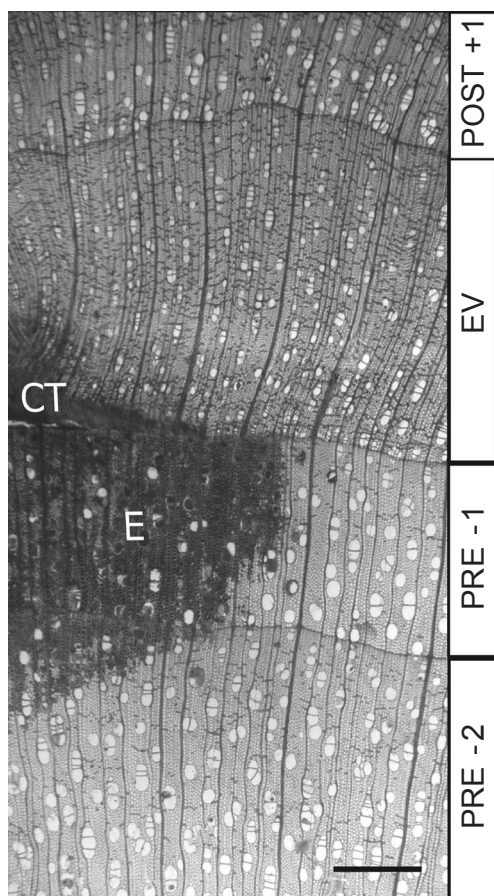

Figure 1. Location of the study site.

Figure 2. Anatomical structure of wood adjacent to callus tissue of *Betula pendula* injured by falling rocks. – CT = callus tissue; E = area of secondary metabolites deposited after vessel and fibre embolism. Scale bar = 500 μm.

In November 2013, after the end of the growing season, wedge cuts or cross sections were taken from eleven individuals of silver birch affected by the rockfall. Samples were taken from the central parts of scars, from the scar side of the stem. Further four trees growing in the same stand, but not visibly injured by the rockfall, were sampled to provide information about the growth of trees not affected by scarring. Cross sections were taken from reference trees, covering the up-slope, perpendicular and downslope parts of their circumference.

After counting tree rings on sanded sections, small cubes (approximately 1 × 1 × 4 cm) were cut from the samples (i) adjacent to the injury, and when possible also (ii) perpendicular to the injury and (iii) from the opposite part of the stem circumference. Our sampling scheme involving either sampling wedges or cross sections led to a relatively smaller number of samples from opposite and perpendicular parts of the stem in comparison to parts of the stem adjacent to injury. However, since the birch stands are deemed to stabilize terrain surface in the study area, we were not allowed to cut down all trees. A microtome (G.S.L. 1; Gaertner *et al.* 2014) was used to cut 20 μm transverse sections of wood from each sample. These sections were then stained with a solution of Astrablue and Safranin to improve the contrast between vessel walls and lumina, and dehydrated with an ethanol series and xylol (Schweingruber *et al.* 2006). Finally, permanent microsections were prepared by mounting the samples in Canada balsam.

Measurements of VLA were performed using WinCell 2011 Pro (Régent Instruments Inc. 2011). On each microsection, vessels were measured for as many rings as possible, which include up to 10 tree rings before and generally 3 tree rings formed after the rockfall event. The ring formed in 2011 was marked as EV (event ring), rings from 2012 and 2013 as POST +1 and POST +2 (post-event rings), respectively, and rings formed before 2011 as PRE −1 (pre-event rings), PRE −2, etc. (Fig. 2). The measure-

ments were performed on digital microscopic images captured under 40× magnification. Because many rings were too wide to be captured in a single image, multiple images were taken and stitched into one. When necessary, the contrast of images was enhanced using ImageJ (Ferreira & Rasband 2012).

To study vessels only and disregard generally smaller fibres, structures smaller than 100 μm^2 were automatically filtered out. Although WinCell is able to identify walls and lumina automatically, user interventions were frequently necessary, mostly to exclude erroneously detected vessels (*e.g.*, cracks). Vessels were measured in a rectangle whose width was approximately 1 mm and whose length varied according to the width of each tree ring. When measuring samples from the area adjacent to the injury, the rectangle was placed right next to the callus zone, so as not to include this tissue. Vessels were measured in the earlywood and latewood of each ring. Special care was taken to measuring at least 60 vessels in each tree ring, following Arbellay *et al*. (2012a). Very rarely did extremely narrow tree rings with not enough vessels require the width of the sampling rectangle to be expanded to encompass the minimum number of vessels.

Statistical analysis

Two basic approaches to detect disturbance events in VLA chronologies were used. First, differences in VLA were tested for between rings formed before the rockfall (aggregate value from three pre-event rings) and rings formed after it. This approach follows the studies of Arbellay *et al*. (2012b; 2013), except for the number of tree rings used as a standard (two in previous studies and three in this study). Differences between tree rings were tested using Wilcoxon's one-sample test comparing the median VLA of each tree ring with that of rings formed in the three years preceding the event. The median-based approach was taken because the distribution of vessel proportions of broadleaves typically does not fit a normal curve (see, *e.g.*, Gryc *et al*. 2008; Alla & Camarrero 2012).

The second approach considered the generally positive age trend in VLA (Adamopoulos 2006; Fonti *et al*. 2009). We modelled this trend based on rings formed before the tree was affected by any rockfall disturbance (*i.e.*, PRE tree rings) and extrapolated it to the 2011–2013 period. We fitted a linear regression line through VLA medians, as this fit best described the age trend in our chronologies based on R^2 and because it complies with the requirements of statistical tests used in further analyses. The intensity of VLA change after the rockfall event was quantified by comparing (using Wilcoxon's one-sample test) data measured for PRE, EV and POST tree rings with modelled and extrapolated median for each respective year.

In both approaches, the intensity of VLA change was quantified as the percent difference between the expected median (100 %) and the actual median of the measured data. Samples from different parts of the stem circumference were analyzed separately to evaluate differing intensities of VLA anomalies with increasing distance from the wound. Data obtained from reference trees were subjected to the same analyses. Statistical computations were performed in R (R Core Team 2014).

RESULTS

In total, 52 cross sections were prepared, of which 11 microsamples represented wood adjacent to the injury, 19 represented wood perpendicular to the injury and 8 represented wood opposite to the injury; the remaining 14 samples represented reference trees. A total of 55,582 vessels were measured, averaging 3705 vessels per tree, 1069 vessels per sample and 115 vessels per tree ring. Trees of different ages were unevenly distributed at the study site. Younger trees were generally located near the rock face (trees nos 6–8 recorded only rings formed after 2006 and 2007, respectively). By contrast, the majority of trees growing further away from the rock face was older than 15 years. The earliest tree ring measured was from 2001 (PRE – 10) in trees nos 1, 5, 9, 11 and R15. Unfortunately, two individuals (nos 5 and 6) did not form a ring in 2013 (POST +2) in the sampled part of the stem circumference (although the trees were still alive), probably due to browsing damage.

Linear fits to measured data for the pre-event period applied in the age model approach had a mean R^2 of 0.545. In all injured individuals, rings formed just after the rockfall record at least 48 % reduction of VLA (all $p < 0.001$) compared to the modelled value for the area adjacent to the injury (Fig. 3 and 4). The average reduction was by 66 %, the highest value being 82 % (Fig. 5). As for parts of the stem located perpendicular or opposite to the injury, there was also a statistically significant reduction of VLA ($p < 0.001$) in 11 samples (9 perpendicular, 2 opposite), but its intensity averaged only 32 % (Fig. 5). Seven other samples showed negative deviations in VLA, which were less significant. Increased VLA after the rockfall event was observed in one sample perpendicular and one sample opposite to the injury (Fig. 6). Statistically significant deviations between measured and modelled values of median VLA were seldom observed also in the period before the event, but their intensity was generally lower compared to the rings formed after the event. More pronounced deviations before the rockfall were found in younger trees (nos 6–8 and 10) compared to older ones. The proportion of positive and negative deviations in the pre-event period was relatively balanced, comparing proportions in event and post-event rings, where VLA smaller
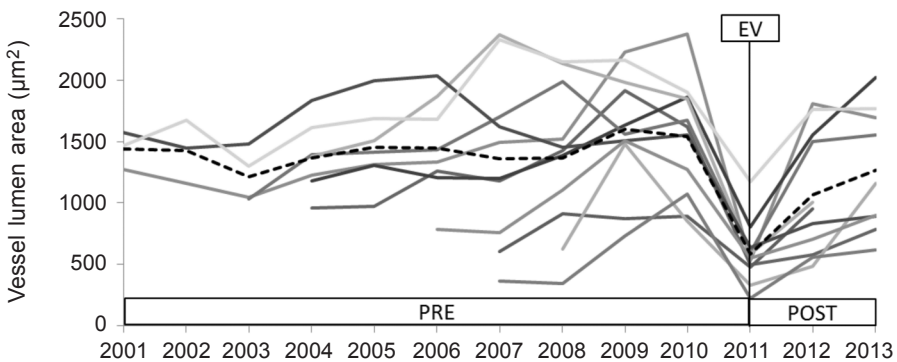

Figure 3. Average vessel lumen area in tree-ring samples taken next to scars. – Solid lines = individual trees; dashed line = mean of all samples.
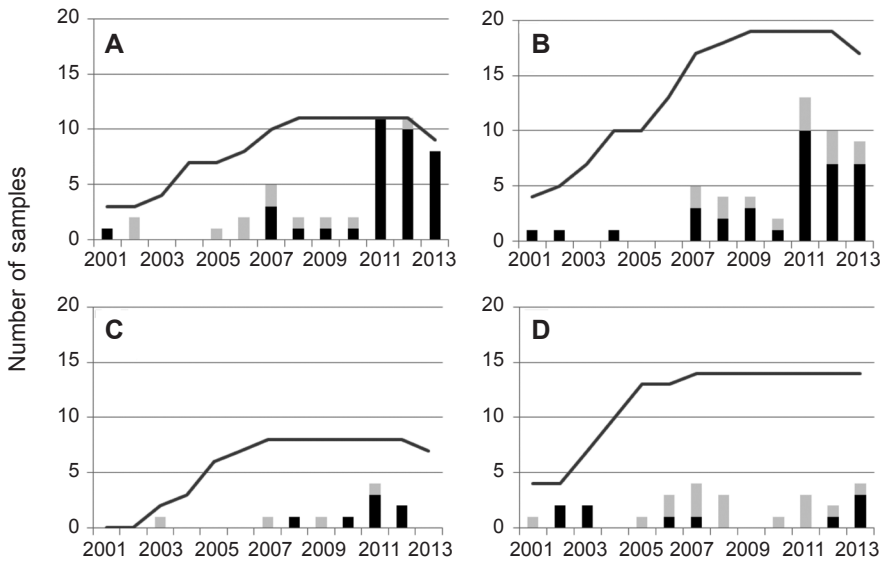
Figure 4. Number of trees recording significant (based on Wilcoxon's one-sample test) deviations of median vessel lumen area from values predicted by the age-trend model. – A: samples taken next to the injury; B: samples taken perpendicular to the injury; C: samples taken opposite to the injury; D: samples from reference trees; black bar = significant at $p < 0.001$; grey bar = significant at $p < 0.01$; line = sample depth.

than expected clearly prevails (Fig. 6). Four positive and six negative statistically significant but relatively weak deviations (not exceeding 36%) in the VLA chronologies were recorded in reference trees (Fig. 4 and 6). These anomalies do not reflect any signal considering the position of the sample around the stem circumference (see the low variability of VLA deviations of reference trees in Fig. 5).

Data processed using age-trend modelling suggest very slow recovery of VLA characteristics of wood adjacent to the injury during the three years after the rockfall event. Although the average reduction of VLA compared to the model decreased from 66% in the year of the event to 33% three years after it (Fig. 5), only one individual (no. 3) reached the modelled value. Recovery in areas perpendicular and opposite to the injury seemed to be faster; in some cases, observed values even exceeded the model projection. Deviations of measured from modelled values in perpendicularly oriented samples of post-event tree rings recorded the highest variability. Variability, moreover, increased over time – standard deviations were 25.6, 35.0 and 43.3, respectively, compared to the average standard deviation for the pre-event period of 10.7 (Fig. 5).

A comparison of values for event and post-event rings with values for pre-event rings without regard to the age trend yielded similar results concerning the year with the strongest reduction of VLA. However, the age modelling approach produced significant differences concerning the speed and intensity of recovery in the case of rings formed after the event. Deviations in the 2013 ring were on average 15% points smaller (25% points for samples taken adjacent to the injury) compared to the model-
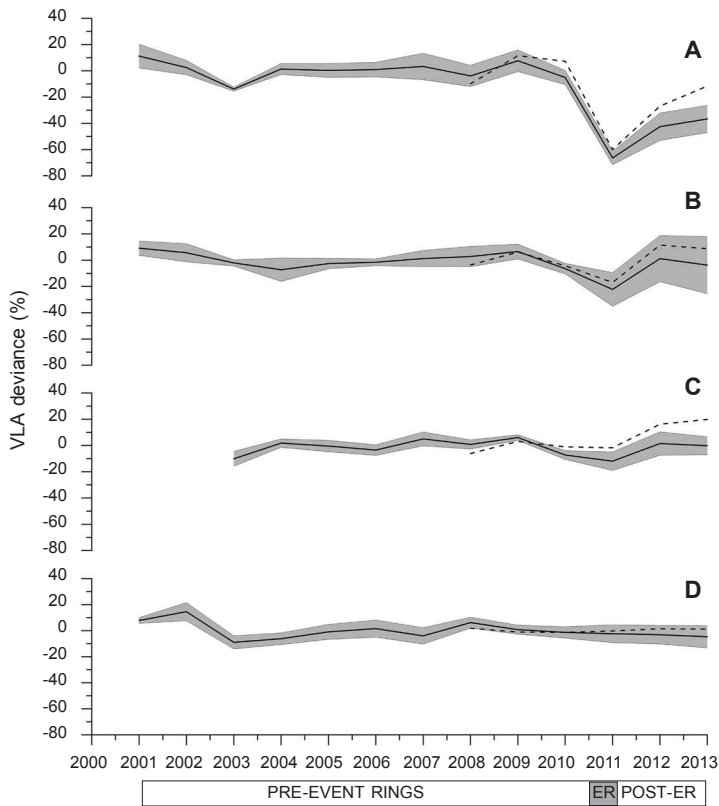
Figure 5. Mean of annual average vessel lumen area deviations from the value predicted by the age-trend model (black solid line) and the median VLA for vessels formed during three years preceding the event (black dashed line). The grey area denotes the range of ± one standard deviation from the mean. – A: samples taken next to the injury; B: samples taken perpendicular to the injury; C: samples taken opposite to the injury; D: samples from reference trees; ER = Event ring.
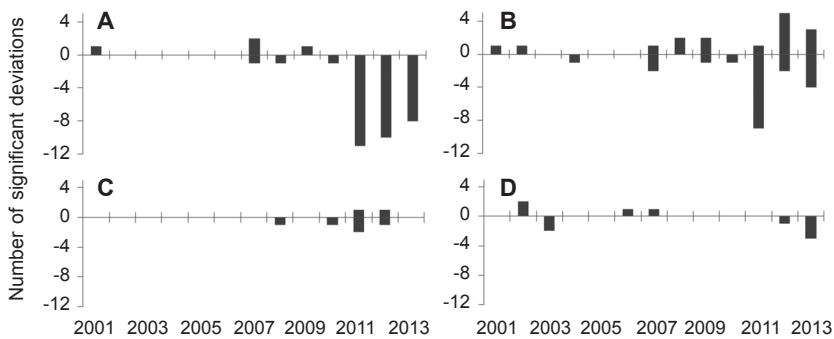

Figure 6. The proportion of positive and negative significant ($p<0.001$) deviations of median vessel lumen area from the value predicted by the age-trend model. – A: samples taken next to the injury; B: samples taken perpendicular to the injury; C: samples taken opposite to the injury; D: samples from reference trees.

based approach, which predicted apparent total recovery of trees (Fig. 5). The median VLA for the 2013 tree ring compared to the median for the pre-event period was only 11% smaller adjacent to the injury and 12% higher around the rest of the stem circumference.

DISCUSSION

Our findings indicate that VLA is sensitive to rockfall-induced stresses affecting the growth of *Betula pendula*. The most remarkable reduction of vessel lumen dimensions was recorded in wood adjacent to the injury, where the VLA in the ring formed right after the event was reduced by 60 and 66% compared to the expected dimensions. This result corroborates similar studies focusing on anatomical changes in broadleaved trees subjected to active mechanical stresses. Arbellay *et al.* (2013) and Arbellay *et al.* (2012a) documented, respectively, a 27–57% and 42–64% reduction of average VLA in individual trees of downy birch (*Betula pubescens* Ehrh.) scarred by an avalanche event. Similar research found an average reduction of 77% in VLA adjacent to the injury in tree rings of young European ashes (*Fraxinus excelsior* L.) injured by spring flooding (Arbellay *et al.* 2012b). The sensitivity of VLA chronologies to the impact of flash floods has also been documented in common alder (*Alnus glutinosa* L.; average reduction of VLA of 39%), Pyrenean oak (*Quercus pyrenaica* Willd.; 42%) and narrow-leaved ash (*Fraxinus angustifolia* Vahl; 59%; Ballesteros *et al.* 2010).

Both approaches to identifying past disturbance events – model-based and preceding VLA-based – were similarly efficient at estimating the reduction of VLA in the tree ring formed at the time of the event. However, there is an important difference when it comes to the speed of recovery in the area adjacent to the injury, where the VLA reduction is the most intensive. When comparing tree rings formed in 2013 with the median for the three years preceding the event, the two values did not greatly differ, which seems to indicate almost complete recovery of trees from the damage caused by the rockfall. As this approach does not take into account the age trend in the VLA series, this should be interpreted only as "retaining pre-event levels", not as "recovery" in the physiological sense. Comparing VLA medians of tree rings formed in 2013 with values expected based on the age-trend model revealed that vessels were on average almost 33% narrower than they probably would be if the trees were not hit by falling rocks. This finding is consistent for all eleven trees sampled in this study as well as for both subsamples of younger and older individuals.

As for wood sampled perpendicularly and opposite to the injury around the stem circumference, the responses of individual trees were not uniform. Parts of the stem located further from the injury on the transverse section generally exhibited lower deviations of median VLA from both the age-trend model and rings from the pre-event period. Some parts, however, showed positive deviations, their median VLA being higher than both the modelled VLA and the VLA in the pre-event period. Perpendicularly oriented samples also recorded the greatest variability in average VLA deviations in the ring formed immediately after the rockfall and especially in rings formed in subsequent years. This supports the conclusions of Arbellay *et al.* (2012b) who found clear and significant signals of mechanical damage in VLA series only in the 30° sector adjacent

to the injury and its weakening with increasing distance from the wound. Based on our data, 11 of 27 (*i.e.* 41%) samples representing wood located perpendicularly and opposite to the place of injury recorded a significant reduction in VLA in the event ring. This percentage also indicates the probability of successful rockfall dating based on samples from distal parts of the stem. In more detail, 47% of perpendicular samples and only 25% of opposite samples revealed a significant reduction in VLA that clearly showed a fading rockfall signal around the stem circumference.

Using both approaches to processing measured data, we recorded statistically significant variations in VLA chronologies also in the pre-event period, although their intensity was generally much weaker compared to rings formed after the event. Any attempt to explain this should primarily take into account other environmental forces affecting vessel anatomy; for example, drought stress influencing luminal extension during the primary phase of vessel ontogenesis before lignification of vessel walls (García-González & Eckstein 2003; Aloni 2007) is a precondition for VLA sensitivity to spring temperatures and precipitation (Fonti *et al.* 2007, 2009; García-González & Fonti 2008; Alla & Camarero 2012). Moreover, a linear trend is a substantial simplification of the actual age-trend in a VLA series. This is acceptable for relatively short series, but for multi-centennial chronologies, the trend rather resembles a square-root function (see *e.g.*, VLA chronologies in Fonti *et al.* 2009). In our study, the relevance of linear fit is also supported by a rather balanced proportion of positive and negative deviations of measured VLA in comparison with modelled values, which was observed both in the pre-event period in disturbed trees and in reference individuals.

Both positive and negative significant deviations in VLA were occasionally observed in young trees for the pre-event period, probably because of generally higher sensitivity of young individuals to environmental stress (Linderholm & Linderholm 2004; Stoffel 2008). The stems of small/young trees safely dissipate only a limited maximal energy of external disturbances (Dorren & Berger 2006). Higher variability of VLA in juvenile wood is also caused naturally due to abundant presence of extremely narrow microvessels in late earlywood and latewood of diffuse-porous broadleaves (Gryc *et al.* 2008). For some ring-porous species, vessels even proved to be a relevant indicator for determination of the juvenile-mature transition zone in wood. This transition zone is characterized by a reduction in VLA variability and fading of the increasing trend in VLA (Adamopoulos 2006) under the influence of gibberellin-like substances produced in roots and limiting the availability of IAA produced by the apex (Aloni 2007).

We are aware that estimating the deviations of modelled VLA and measured VLA values for all rings formed before the rockfall is, to a certain extent, problematic, as the regression model is based also on VLA of a given ring for which the comparison is conducted. To overcome this problem, we applied independent linear regression, which for ring N in the pre-event period was based on all rings formed before the rockfall, excluding N (not shown). Because both approaches yielded similar results concerning the identification of extreme changes in VLA chronologies and only slight differences in the quantification of their intensity, we, for the sake of simplicity, preferred the "dependent" regression.

Besides the effect of wounding, the development of tension wood might also affect VLA. Heinrich and Gaertner (2008) reported a significant reduction of VLA associated

with the formation of tension wood in bended diffuse-porous tree species. On the other hand, recent experimental studies (*e.g.*, see the review and results of Pramod *et al.* 2012) focusing on phytohormones (especially stress-linked ethylene) revealed development of tension wood (including the gelatinous layer) in upright stems; however, without any clear reduction in vessel dimensions. Reduction of VLA in the upper side of inclined angiosperm thus seems to be influenced rather by gravitationally stimulated tension forces affecting cambium and associated redistribution of phytohormones around the stem circumference (Schubert *et al.* 1999; Nugroho *et al.* 2013) than by formation of tension wood itself. All trees sampled in this study had vertical stems, and we observed no presence of tension wood in the pre-event period. Only occasionally did the gelatinous layer appear in fibres of event and post-event tree rings.

One important consequence of the formation of narrower vessels in response to injury is the reduction of hydraulic efficiency of vertical water transport. On the other hand, this greatly diminishes the risk of vessel embolism or cavitation (Tyree 1997; Hacke *et al.* 2006). It also helps mechanically damaged trees to stabilize their fitness in periods of the most severe stress (Arbellay *et al.* 2010, 2012a, 2013; Ballesteros *et al.* 2010; Bigio *et al.* 2010; Tardif *et al.* 2010; Gaertner-Roer *et al.* 2013). Our findings indicate that besides closing the injured area with callus tissue, VLA tends to slowly increase, which can be interpreted as a shift from a preference for safety to a strategy preferring water efficiency. The occasional occurrence of positive deviations of measured VLA in comparison to modelled VLA just after the event (event year) in perpendicular and opposite samples can be attributed to decreased competition in the forest stand (Ballesteros *et al.* 2010), as the rockfall event was severe enough to break some neighbouring trees.

The results of this study support the great potential of VLA chronologies of *Betula pendula* for retrospective dating of rockfall events and other disturbances influencing tree growth. Dating of rockfall events based on tree rings has been predominately based on dating scars caused by abrasion of bark by falling rocks (Trappmann *et al.* 2013); however, the accuracy of this approach is greatly limited by continuous overgrowing of wounds, often resulting in biased dendrochronological rockfall chronologies for most recent events (Trappmann & Stoffel 2013). When samples are collected using a Pressler borer, hitting the callus zone of an overgrown scar is possible only by chance. By contrast, when dating events based on VLA anomalies, there is no need to take samples directly from the callus zone. Although the signal diminishes around the stem circumference, rockfall scars almost exclusively occur on the upper side of the stem, which facilitates obtaining non-biased results based on wood anatomy anomalies. Because abrupt reduction of VLA in the area adjacent to the injury is caused particularly by accumulated IAA (Junghans *et al.* 2004), we can expect the opposite reaction (*i.e.* increase) in VLA in the stem portion below (Aloni 2007); however, this potential phenomenon, which might prove useful for dating purposes, requires further study.

CONCLUSIONS

Our study indicates that vessel diameter reductions are one of the key mechanisms in which trees damaged by rockfalls withstand this active stress. The tree ring formed in

the following growing season records a significant reduction (by more than 60% on average) of the vessel lumen area compared to pre-event tree rings and to the extrapolated vessel lumen area age-trend model. During subsequent years, vessel anatomy tends to slowly recover its "normal" state, reaching pre-event mean values three years after the event, albeit still significantly below the level expected based on the age trend in VLA series. When gaining broader insights into the physiology of stress recovery, it is desirable to combine both approaches to statistical data processing. Especially when analysing long VLA series, the age trend should definitely not be neglected.

The results of this study show that former rockfall events can be reconstructed based on the presence of anomalously reduced vessels in tree rings of broadleaved trees. Analysing VLA chronologies can overcome common biases in tree-ring reconstructions of former rockfall activity relying on scars, which gradually overgrow and are difficult to sample. Although the intensity of rockfall signal in VLA series diminishes from the place of injury around the stem circumference, the probability of sampling an area with significant VLA changes is still much higher than the probability of hitting injury or callus tissue. To verify the ability of vessel anomalies to indicate overgrown scars, it is strongly desirable that future studies evaluate not only variation in VLA around the stem circumference at the height of the injury, but also at different vertical distances below the position of the scar.

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1 **Disentangling the effects of disturbances, ontogeny and climate on xylem hydraulic**
2 **conductivity of *Betula pendula***

3

4 Jan Tumajer[1*], Václav Treml[1]

5

6 1- Charles University, Faculty of Science, Department of Physical Geography and Geoecology,
7 Albertov 6, 12843 Prague, Czech Republic

8 * corresponding author: tumajerj@natur.cuni.cz

9 ORCIDs: 0000-0002-7773-7081 (Jan Tumajer); 0000-0001-5067-3308 (Václav Treml)

10

11 **Abstract**

12 Increasing frequency of disturbances in temperate forests is responsible for an increasing
13 number of trees with partly damaged cambial zones or xylem conduits. Adjustment of wood
14 anatomical structure to balance between safe and efficient water conductivity is one mechanism
15 trees employ to cope with mechanical damage. The relative role of disturbances in addition to
16 ontogeny and climate in shaping xylem conduits and affecting xylem hydraulic conductivity
17 remains unknown. We performed an experiment with five different mechanical treatments
18 simulating natural disturbances of juvenile *Betula pendula* trees (stem scarring, tilting,
19 decapitation, root exposure and stem-base burial). After three years, trees were cut down,
20 conduit size was measured, and specific hydraulic conductivity of each tree ring was calculated.
21 Between-tree and between-year variability in xylem conductivity was decomposed into effects
22 of ontogeny, climate and disturbances using linear mixed-effects models. Conductivity
23 significantly dropped down after treatment in decapitated, tilted and scarred trees. The
24 response of trees with buried stems and exposed roots was generally weak. The overall effect of
25 disturbances on inter-annual variability of wood anatomical structure was greater than the
26 contribution of ontogeny and climate. Our results indicate that disturbances are important
27 drivers of xylem hydraulic conductivity.

28 **Keywords:**

29 cambial injury; disturbance experiment; mixed-effects model; quantitative wood anatomy; Silver
30 birch; tree-ring; vessel; vessel lumen area; wood

Introduction

Increasing frequency of forest disturbances has been observed during recent decades and is predicted for the near future in temperate and boreal forests (Schelhaas, Nabuurs & Schuck 2003; Thom & Seidl 2016; Seidl *et al.* 2017). Many disturbance agents (e.g., windstorms, landslides, rockfall, floods) mechanically attack tree stems, crowns or roots. To survive, trees have developed mechanisms allowing them to cope with partly damaged segments. Among others, plastic adjustment of conduit size and the proportions of conduits, parenchyma and fibers represents an efficient strategy to maintain mechanical support as well as a safe and efficient vascular system (Sperry, Meinzer & McCulloh 2008; Hacke, Spicer, Schreiber & Plavcová 2017). The imprint of past disturbances is therefore visible in conduit parameters, allowing dating of disturbance events (Heinrich & Gärtner 2008; Arbellay, Fonti & Stoffel 2012b; Copini *et al.* 2015). As conduits largely affect the capacity of xylem to transport water, disturbances might influence forest transpiration and thus feed back into climatic conditions (Matheny *et al.* 2014). However, the relative influence of disturbing events on xylem conduit traits in comparison to other factors (ontogeny, climate) is poorly understood.

Conduit size ontogenetically increases with increasing height of the stem due to physical constraints (Olson *et al.* 2014; Carrer, von Arx, Castagneri & Petit 2015) and associated reduction in the polar transport of auxins (Aloni 2007; Hacke *et al.* 2017); thus, ontogeny is often believed to explain the largest proportion of variability in mean conduit size (Zhao 2015; Rosell, Olson & Anfodillo 2017). However, recent studies have reported conduit size not to be solely a function of tree size, but also to contain a significant climatic signal (Hacke *et al.* 2017), which may be used as a valuable paleoenvironmental proxy (Fonti, Treydte, Osenstetter, Frank & Esper 2009) or as a tool for determination of tree response to climatic constraints (Eilmann, Zweifel, Buchmann, Fonti & Rigling 2009; Anderegg *et al.* 2016; Castagneri, Regev, Boaretto & Carrer 2017). Indeed, climate influences cell size in all the following ways: (i) the climatically driven water potential influences the rate of cell expansion *via* cell turgor (Schreiber, Hacke & Hamann 2015); (ii) the climate during the growing season modifies the length of the expansion period (Cuny, Rathgeber, Frank, Fonti & Fournier 2014); and (iii) climate affects the amount of carbohydrates available for xylogenesis in cambial zone (Simard *et al.* 2013). Obtaining a meaningful climatic signal from a series of wood anatomical parameters often requires large sample depth and an appropriate standardization approach to filter out the effect of increasing tree size over time (Matisons, Elferts & Brumelis 2012; Carrer *et al.* 2015).

Mechanically damaged trees often abruptly adjust conduit size in response to competing demands of safety and efficiency of the stem vascular system. Disturbances mechanically damaging bark and cambium (e.g., mass-movements, floods) usually lead to decreased conduit

size in an area adjacent to damaged tissues, which might be partly compensated for by an increase in conduit number (Arbellay *et al.* 2012b; Tumajer, Burda & Treml 2015). These responses may result in a total reduction of up to 60 % of pre-disturbance conduit size, overriding both ontogenetic long-term trends and climatically-governed inter-annual variability (Tumajer *et al.* 2015). A similar decrease in conduit dimension, together with increased cell-wall thickness occurs after stem tilting due to reaction-wood formation (Heinrich & Gärtner 2008; Groover 2016). In addition, the wood structure of roots exposed due to loss of the soil in an erosion event adjusts to the lack of mechanical support by decreasing conduit size up to 50 % compared to tree-rings formed in the soil prior to exposure (Gärtner 2007; Hitz, Gärtner, Heinrich & Monbaron 2008). In contrast, after stem base burial, an abrupt increase in conduit size may occur (Friedman, Vincent & Shafroth 2005). Precise quantification of the contribution of disturbances to conduit dimensions is, however, complicated, because most of the above-mentioned studies were: (i) focused exclusively on the disturbance signal in tree-rings, while considering ontogeny and climate as noise; and (ii) based on analysis of trees without precisely knowing the timing and extent of disturbance events. Experiments in controlled conditions based on mature trees have been performed only rarely (Heinrich & Gärtner 2008; Copini *et al.* 2015).

Since forest transpiration is extremely important for forest-climate interactions, and disturbances might affect efficiency of trees in conducting water from roots to crown (Matheny *et al.* 2014), studies analyzing the contribution of ontogeny, climatic factors and disturbances to variability in conduit size are needed. We aim to fill this gap using data on inter-annual variation of xylem structure of *Betula pendula* Roth individuals that were experimentally mechanically treated three years before sampling. The specific hydraulic conductivity of tree rings was modelled using linear mixed-effects models to quantify the contributions of climate, ontogeny and disturbances to modelled values. We hypothesize that disturbance is a more important driver of specific hydraulic conductivity than ontogeny and climatic effects.

Materials and Methods

Study area and experimental design

A monospecific unmanaged forest stand of *B. pendula* located in NW part of the Czech Republic (N50° 32.041'; ° E13° 41.740', 315 m a.s.l.) was selected for this experimental study. The stand originated through natural recolonization of a former spoil heap in a post-mining (brown coal) locality. The mean (±standard deviation) tree age estimated by counting tree rings in 2015 was 14.6 (±2.0) years at sampling height. The mean diameter at breast height was 11.8 (±2.4) cm, and mean tree height was 14 (±0.7) m.

Randomly selected trees were mechanically treated in five different ways **(Figure 1)** to simulate events frequently appearing as consequences of mass-movements (including stem tilting, decapitation, stem scarring, stem aggradation by deposits, root exposure; Shroder 1980, Stoffel & Corona 2014), windstorms (stem tilting, decapitation, stem scarring; Gardiner, Berry & Moulia 2016) or floods (stem tilting, stem scarring, stem aggradation by deposits, root exposure; Ballesteros-Cánovas, Stoffel, St George & Hirschboeck 2015). The first deformation represented stem tilting to 45° from the vertical. We used 30-cm-long segments of plastic pipes to protect tree stems in places of contact with the rope used for tilting. Pressure from the rope was in this way distributed over a 30 cm long stem segment. Another group of treated trees was mechanically damaged using a hammer to abrade bark and cambium in an area of approximately 5x10 cm on one side of the stem at a height of 100 cm above the ground. In the third treatment group, we decapitated trees at a height of 6 m above the ground, but with some branches remaining below the cut. In the fourth treatment group, basal parts of stems up to a height of approx. 0.8 m were buried in local clayey soil. In the last treatment group, trees were subjected to having their roots exposed. The depth of root exposure balanced between affecting as many roots as possible and retaining sufficient root stability to hold the stem in vertical orientation. Due to the generally shallow root system of *B. pendula* at our study site, we excavated only the upper 0.5-0.8 m of soil.

To consider the effect of the timing of disturbance on wood anatomical anomalies, we performed treatments in two different periods relative to the growing season. Thus, one half of the trees were subjected to treatments performed in March 2013 (before the beginning of the growing season) and the other half were treated in May 2014 (during the growing season). The treatments were performed on different sets of trees from areas adjacent to each other within the same forest stand. Each type of treatment was represented by 9 (tilting, root exposure) to 13 (decapitation) replicates per treatment; 53 treated trees in total. Similar numbers of trees were subjected to each treatment in each of the treatment periods.

Trees remained growing *in situ* for three years after the treatment. At the end of the third growing season after the disturbance (i.e., November 2015 and 2016), we cut cross-sections from all experimentally treated trees. At least two cross-sections were cut from each stem at fixed levels above the ground **(Figure 1)**. Additionally, four control reference trees (one cross-section per reference tree) were sampled in 2016.

Laboratory processing and wood-anatomical measurements

Cross-sections were split into three or four segments regularly distributed around the circumference **(Figure 1)**, and from each segment a 1-cm-wide block spanning the bark to the pith was extracted. If the length of block exceeded 6 cm, it was split into two or three segments

to enable its mounting into a sample holder in Leica RM2125 RTS rotary microtome. The risk of wall deformation during the cutting process was reduced by boiling the sample in water and applying a non-Newtonian fluid to the sample surface (Schneider & Gärtner 2013). Transverse microsections of 25 μm thickness were cut. Each microsection was rinsed with sodium hypochlorite solution and distilled water, stained with AstraBlue and Safranin solution to enhance wall-lumen contrast, dehydrated using ethanol and Diasolve and, finally, mounted using Canada balsam (Gärtner & Schweingruber 2013).

Each microsample was scanned using a Nikon Eclipse Ni motorized microscope and NIS-Elements Ar 4.40.00 software (Nikon Corporation 2014). Images were captured at a resolution of 1.7 μm/pixel with 10 % overlap of adjacent pictures, which allowed automatic geometric stitching of the whole microimage. Subsequently, we measured various parameters of vessel lumina (area, diameter, shape index and others listed in Régent Instruments Inc. 2011) for each sample and each tree-ring using WinCell 2011Pro (Régent Instruments Inc. 2011). Measurement was performed in a rectangular area manually delimited to cover the whole tree-ring width. The width of the rectangle varied slightly among tree rings to follow recent advice on the minimum number of measured vessels per tree-ring of ring-porous species; thus, care was given to use rectangles wider than 2.5 mm (Diaconu, Hackenberg, Stangler, Kahle & Spiecker 2017) and to measure more than 60 vessels per tree ring (Arbellay, Corona, Stoffel, Fonti & Decaulne 2012a) for as many rings as possible. To focus solely on the contribution of vessels to the hydraulic structure of xylem, we excluded all objects with lumina smaller than 300 μm^2, as the majority of them probably represent fibers. No manual editing of the microimages was performed; however, vessels with broken walls, which appeared rarely, were excluded from the analysis.

In addition to measuring various parameters of each vessel lumen, we also estimated the total area of the measured segment of xylem in each tree ring. Although WinCell reports the total area of each measured rectangle, this value is strongly biased in juvenile tree rings with small radii, due to frequent overlaps of the rectangles with previous and next tree rings, such that vessels need to be manually excluded from the analysis. Thus, we estimated the precise area in each tree ring by modeling a concave hull around vessel positions using R (R Core Team 2017) and the packages 'concaveman' (Gombin, Vaidyanathan & Agafonik 2017) and 'sp' (Bivand, Pebesma & Gomez-Rubio 2013).

Specific hydraulic conductivity calculation

The lumen area of each vessel was used to calculate its theoretical hydraulic conductivity (modified from Scholz, Klepsch, Karimi & Jansen 2013 and Gebauer & Volařík 2013), with vessels assumed to be circular in cross-section, using the following equation:

$$K_{hi} = \frac{\rho \cdot A_i{}^2}{8 \cdot \eta \cdot \pi}$$

169   where K_{hi} is the theoretical hydraulic conductivity of vessel i [kg.m.s^{-1}.MPa^{-1}], ρ is water density

170   at 20 °C (998.205 kg.m^{-3}), A_i is lumen area of vessel i [m^2] and η is the viscosity of water at 20 °C

171   (1.002.10^{-9} MPa.s). Theoretical hydraulic conductivity of vessels reflects the Hagen-Poiseuille

172   law regarding higher contribution of large vessels to water transport than that of small ones

173   (Tyree & Zimmermann 2002).

174   Subsequently, K_h was converted into specific hydraulic conductivity of each tree ring

175   using the following equation:

$$K_s = \frac{\sum_{i=1}^{n} K_{hi}}{A_{xyl}}$$

176   where K_s is specific hydraulic conductivity of tree-ring xylem [kg.m^{-1}.s^{-1}.MPa^{-1}] and A_{xyl} is the

177   measured area of the respective tree ring (Tyree & Zimmermann 2002). Missing rings identified

178   by visual comparison of tree-ring width curves of sampled trees were incorporated into the

179   dataset with K_S=0.

180   *Linear mixed-effects models of specific hydraulic conductivity*

181   In the next step, inter-annual variability in K_s was modeled using linear mixed-effects models.

182   Different random and fixed effects were selected to represent parts of variability in K_s given by

183   (i) ontogeny; (ii) climate; (iii) disturbances; and (iv) between-tree variability. More specifically,

184   predictors were as follows:

185   (i)   Ontogeny is represented by *cambial age* of each tree-ring (fixed effect).

186   Approximation of ontogenetic trend in vessel dimensions by cambial age was

187   previously shown as appropriate for short (< 20-25 years) time series (Zhao 2015;

188   Anadon-Rosell *et al.* 2018)

189   (ii)   Climate is represented by *mean temperature from previous August to previous*

190   *October, temperature in current May* and *precipitation in current March* (fixed

191   effects)*.* These months and period were previously identified as the only climatic

192   variables with significant (p-value < 0.05) correlation with measured values of K_s in

193   pre-experiment period (n=4254 tree-rings). Monthly climatic data from Kopisty

194   climate station (Institute of Atmospheric Physics CAS) located in a distance of 5 km

195   from our study site in 240 m a.s.l. were used.

196   (iii)   Effect of disturbances is represented by four categorical variables (factors; random

197   effects). The first one (*phase)* indicates whether the tree-ring was formed before

198   experiment (PRE), in the year of the experiment (EY) or later (POST+1 or POST+2).

199   Three different levels were used for each of the three years after the treatment,

200   because we previously observed three years of continuous recovery of vessel size of

201   *B. pendula* after cambial injury caused by rockfall (Tumajer *et al.* 2015). Next,

202   *orientation* represents the designation for sample orientation around the stem

203   circumference (A-D). Sampling *level* indicates position along the stem (High, Low

204   /and Middle in the case of injured trees/). Finally, *timing* indicates, whether the tree

205   was damaged during the first (March 2013) or the second field season (May 2014).

206   We nested *orientation, level* and *timing* into *phase,* because we expect increasing

207   variability of specific hydraulic conductivity along (root exhumation, stem burial)

208   and around the stem (scarring, tilting) after the experiment than during the pre-

209   experimental period.

210   (iv)   The last predictor captures between-tree variability in specific hydraulic

211   conductivity and is represented by *tree* identifier used as a random effect.

212   The above described structure of the linear mixed-effects model can be summarized as follows:

$$Ks_t = \beta_0 + \beta1.CambialAge_t + \beta2.Temp(pAUG\_pOCT)_t + \beta3.Temp(MAY)_t + \beta4.Prec(MAR)_t$$
$$+ U1_t.Phase_t + U2_t.(Phase_t:Orientation) + U3_t.(Phase_t:Level)$$
$$+ U4.(Phase_t:Experiment) + U5.Tree$$

213   where t represents calendar years, β0 represents intercept, β1-4 represent coefficients of fixed

214   effects and U1-5 represent coefficients of random effects. The model was fit separately but with

215   the same structure for each type of treatment. Model structure was partly modified in the case of

216   reference trees, as all predictors related to disturbance except for orientation were not available

217   and were therefore omitted from the model. Fitting of linear mixed-effects models was

218   performed in R (R Core Team 2017) using the 'lme4' package (Bates, Mächler, Bolker & Walker

219   2015).

220   The quality of the model was quantified using marginal and conditional R^2 proposed by

221   Nakagawa & Schielzeth 2013 and, in addition, by simple pseudo-R^2 defined as a squared

222   correlation between observed and modeled values. The effect of individual predictors on

223   predictability of the model was estimated by quantifying the decrease in the above-defined

224   pseudo-R^2 due to omitting that predictor, i.e. single variable or variable groups (all climatic

225   variables, all disturbance-related variables) from the model.

226   **Results**

227   In total, more than 1.3 million vessels were measured, and K_s was calculated for 5796 tree rings

228   (i.e., on average, there were 228 vessels per tree ring). There were slightly increasing trends of

229   K_s with age regardless of treatment group, and non-significant differences in mean K_s of trees

230 treated before and during the growing season in the pre-experiment period, with the exception
231 of buried trees in the period 2007-2013 **(Figure 2)**. The strongest reductions in K_s were
232 observed after the decapitation and in tilting treatments (regardless of sample position along
233 and around the stem; **Figure S1**) as well as scarred trees (mainly in segments adjacent to the
234 scar at its level; **Figure S2**). In contrast, no abrupt response in K_s was observed for trees with
235 stem-base burial or root exposure at either sampled height level **(Figure S3)**.

236 Decapitation resulted in missing tree rings in 49 % of analyzed samples from the year of
237 the treatment, and in 99 % of tree-rings one year after the treatment. None of the decapitated
238 trees formed a tree-ring in the sampled parts of the stem two years after the treatment, although
239 trees were still living (extensive sprouting from basal segments of the stem and live branches).
240 Tilted trees exhibited missing tree rings in 7 % of the segments analyzed in the year of tilting,
241 and this value increased to 70 % two years afterwards. Other treatments did not cause increased
242 frequency of missing rings **(Figure 2)**.

243 Linear mixed-effects models successfully predicted the long-term trend in K_s during the
244 pre-experimental period as well as abrupt anomalies after the treatment. Graphic comparison of
245 modeled and measured values **(Figure 2)** reveals that their concordance tends to be better after
246 the treatment than before. Values of marginal R^2 do not exceed 0.23; however, conditional R^2
247 varies between 0.59 and 0.78 for treatment categories **(Table 1)**. The highest correlation
248 between observed and modeled values of K_s was observed in trees with decapitated crowns or
249 tilted stems and the lowest in the case of reference trees. Modeled values of K_s increase with
250 increasing cambial age (on average by 0.71 kg.m.s^{-1}.MPa^{-1} per cambial year) and March
251 precipitation (0.01 kg.m.s^{-1}.MPa^{-1} per mm) and decrease with both previous August-October
252 temperature and current May temperature (0.68 and 0.81 kg.m.s^{-1}.MPa^{-1} per °C, respectively)
253 **(Table 2)**. For three of the experimental treatments (scarring, root exposure and tilting) as well
254 as the reference category, the most important random factor was *tree*, as its coefficients showed
255 the greatest differences between minima and maxima. In the cases of stem-base buried trees and
256 decapitated trees, the coefficients of disturbance for *timing* nested in *phase* and *phase* by itself,
257 respectively, are responsible for the largest part of variability.

258 For decapitated, tilted and root exposed trees, omitting all disturbance-related
259 predictors has the strongest effect on the correlation between observed and modeled values
260 (pseudo-R^2 decreases for 37-48 %; **Figure 3**). Moderate importance of disturbance parameters
261 is also apparent for scarred trees (25 %) and stem-base-buried individuals (17 %). The
262 importance of individual disturbance predictors varies between treatments – *phase* is dominant
263 in the cases of scarred, tilted, stem-buried and decapitated trees; however, sampling *level* is
264 dominant in the case of trees with exposed roots. The effects of disturbance *timing* and sample

265 *orientation* around stem circumference seems to be marginal and do not exceed 6 % change in
266 pseudo-R^2.

267   In the cases of scarred, stem-base-buried and reference trees, the random parameter *tree*
268 has the largest influence on pseudo-R^2 **(Figure 3)**. If *tree* is not used as a predictor in the model,
269 pseudo-R^2 decreases by up to 41 % for reference trees and between 13-32 % for different
270 experimental treatments. The relative decrease in pseudo-R^2 yielded by omitting all climatic
271 factors is for all treatments lower than 17 %, always being lower than the combined effect of
272 disturbance parameters. Cambial age is the second-most important predictor of K_s in reference
273 trees (25 % decrease of pseudo-R^2 arising from its omission); however, in the case of
274 mechanically damaged individuals its importance significantly drops: moderate-to-high values
275 of importance are shown for root exposure, stem-base burial and stem scarring (27, 18 and 12
276 % decrease in pseudo-R^2, respectively), and very small importance is shown for tilting and
277 decapitation (5 and 4 % decrease in pseudo-R^2, respectively) **(Figure 3)**.

278   Histograms of residuals resemble the normal distribution, and the mean absolute value
279 of residuals is 3.5 kg.m.s^{-1}.MPa^{-1} (24 % of mean K_s). Apparently, there is an increasing trend in
280 residuals with observed values of K_s **(Figure S4)** which is driven by weaker predictive skills of
281 linear models in the case of missing tree rings (K_s=0) and tree rings with extremely low or high
282 K_s.

283 **Discussion**

284 *Disturbance effect on specific hydraulic conductivity*

285 Specific hydraulic conductivity of juvenile *B. pendula* was proven to be sensitive to both
286 ontogenetic (internal) and environmental (external) factors. For all treatments, disturbances
287 significantly influenced K_s, and leaving them out of the model yields an 17 – 48 % decrease in
288 squared correlation between modeled and observed values. In all treatment groups, the
289 combined effect of all disturbance predictors is stronger than ontogenetic scaling and also than
290 climatic forcing. Abrupt adjustment of wood anatomical structure in response to mechanical
291 damage has previously been observed in various species (Heinrich & Gärtner 2008; Arbellay *et*
292 *al.* 2012a,b) due to balancing between safety and efficiency of water transport (Sperry *et al.*
293 2008; Hacke *et al.* 2017). Stem tilting and decapitation caused the highest intensity of wood
294 anatomical adjustment due to direct mechanical impact on the stem; in contrast, stem-base
295 burial represents a rather indirect effect on wood anatomy due to soil hypoxia, causing less-
296 intensive wood anatomical anomalies. Moreover, a longer period of stem burial than three years
297 would probably be necessary to induce anatomical anomaly and, possibly, adventitious root
298 formation (Copini *et al.* 2015).

299   Considering disturbance-related predictors, correlation between observed and modelled

300 K_s was more sensitive to *phase* than to *orientation* and *level,* indicating that differences in wood

301 anatomical structure between pre-experiment and post-experiment periods are larger than

302 those along and around tree stems. Surprisingly, we observed low variability of K_s around the

303 stem circumference in the cases of tilted or scarred trees. The abrupt decrease in K_s due to stem

304 tilting was observed around the entire stem with only slightly higher intensity on the tension

305 wood side **(Figure S1)**. Similarly, a significant decrease in mean vessel dimensions was

306 observed for both the tension wood side and opposite side of the stem in two different diffuse

307 porous broadleaves after tilting to 45° (Heinrich & Gärtner 2008). This indicates, that xylem

308 conductivity after tilting is not primarily restricted by tension wood formation (influencing only

309 the upper part of an inclined stem), but rather by gravitational forcing affecting the whole

310 cambium. For instance, tilting of broadleaved seedlings of *Quercus ilex* L. to angles smaller than

311 30° successfully induced the formation of tension wood, with, however, no significant effect on

312 xylem conductivity or embolism vulnerability (Gartner, Roy & Huc 2003). In contrast, greater

313 tilting (e.g., to 80° from the vertical) could cause divergence of K_s around the stem circumference

314 by reducing both vessel size and density on the tension wood side (Heinrich & Gärtner 2008). In

315 scarred trees, the observed decrease in K_s restricted only to area adjacent to callus tissue is in

316 line with the previously observed fact that anomalies in vessel size and density occur only in a

317 sector of 30° (Arbellay *et al.* 2012b) to 90° (Tumajer *et al.* 2015) from the scar axis.

318   Our experiment simulated one disturbance event per approximately 15 years of juvenile

319 stand existence (mean tree age at sampling year). Real contribution of disturbances to variability

320 in specific hydraulic conductivity of forest ecosystems in long time series (decades to centuries)

321 is dependent on the site-specific frequency of disturbances. A 15-year rotation of disturbance

322 lies in the interval of large-scale disturbance (e.g., windstorms) recurrence estimated for highly

323 disturbed European mountain forests (Zielonka, Holeksa, Fleischer & Kapusta 2010; Svoboda *et*

324 *al.* 2014; Holeksa *et al.* 2017; Panayotov *et al.* 2017). However, the frequency of disturbances is

325 expected to increase in the future (Seidl *et al.* 2017), and thus the effect of mechanical

326 disturbances on transpiration via modifications of wood anatomical structure will increase in

327 lowland forests as well. In addition, the relative importance of disturbances versus other

328 predictors would probably be larger in adult trees compared to juveniles due to less-prominent

329 hydraulic scaling of vessel parameters (Olson *et al.* 2014).

330   The quantification of a model's sensitivity to disturbance predictors might be also

331 influenced by the number of available tree rings formed after the treatment, as experimental

332 design should include not only the period immediately following the disturbance, but also

333 several years afterwards to allow sufficient time for both adjustment and recovery. In the case of

334   our study, responses to most of the treatments (tilting, scarring, root exposure) are considered

335   immediate (Hitz *et al.* 2008; Heinrich & Gärtner 2008; Arbellay, Stoffel & Decaulne 2013;

336   Groover 2016), and the graphic representation in **Figure 2** shows that our results are in accord

337   with this. Previous studies have found varying recovery speeds of wood anatomical parameters

338   after strong mechanical events causing cambial damage (flood, rockfall, avalanche), ranging

339   from one to five years (Arbellay *et al.* 2012b, 2013; Tumajer *et al.* 2015). Based on this, our

340   experimental design included three analyzed post-treatment years. For stem-base burial, a

341   longer experiment would probably be needed to quantify its true effect on wood anatomy, as

342   wood anatomical response to this phenomenon is often delayed (Copini *et al.* 2015).

343   *Effects of ontogeny, climate and between-tree variability on specific hydraulic conductivity*

344   Ontogenetic effects are responsible for long term increase in K_s of 0.71 kg.m.s^{-1}.MPa^{-1} per

345   year on average. This trend is driven by hydraulic scaling of vessel size due to increasing height

346   of the tree (Olson *et al.* 2014; Rosell *et al.* 2017) and is a dominant continuous predictor of K_s if

347   the tree was not mechanically damaged. However, if the tree is stressed by mechanical

348   treatment, sensitivity of the model to cambial age significantly decreases to moderate values for

349   treatments influencing roots or stem base (e.g., stem-base burial) or to very low values in the

350   case of strong mechanical treatments applied to the stem. This suggests that the effect of wood

351   anatomical scaling along the stem axis is outweighed by the anatomical response to the

352   treatment (Tumajer *et al.* 2015).

353   The effect of climatic factors on predictive ability of the models was significantly weaker

354   than that of ontogeny, disturbances and between-tree variability in two types of treatments

355   affecting basal parts of the tree (root exposure and stem-base burial). Only in the case of

356   strongly damaged stems climate accounted similar importance as the ontogenetic factor (due to

357   strong disruption of the increasing trend in K_s with cambial age after the treatment), but still its

358   effect on modeled-observed concordance did not exceed 17 %. This indicates that climatic signal

359   in quantitative wood anatomical series derived from stands subjected to periodical disturbances

360   is largely masked by other effects. Additionally, ideally undisturbed stands should be used for

361   extraction of climatic signal, as their wood anatomical series would be free of disturbance effects

362   (reflecting only ontogenetic changes and climatic signal). However, it is usually not possible to

363   detect whether tree was subjected to old disturbances, so possible disturbance signal should be

364   taken into account for long chronologies. Before using quantitative wood anatomical series as a

365   paleoclimatological proxy, necessary steps to take include: (i) reducing between-tree variability

366   through sampling and analyzing sufficient sample depth to yield robust chronologies; (ii)

367   achieving a proper selection of undisturbed trees, in which climatic signal is not overshadowed

368 by disturbance effects; and (iii) appropriately removing age trends from the series (Carrer *et al.*
369 2015).

370   A significant proportion of variability in K_s is driven by between-tree differences, which
371 is in-line with studies reporting naturally lower coherency statistics (e.g., between-tree
372 correlation, expressed population signal *sensu* Wigley, Briffa & Jones 1984) for anatomical time-
373 series comparing other dendrochronological proxies (e.g., Matisons, Jansons, Katrevičs &
374 Jansons 2015; García-González, Souto-Herrero & Campelo 2016). It is important to note that
375 individual trees in present study tend to have different mean values of K_s, but to show similar
376 long-term trends and between-year variability (there is a random intercept but fixed slope of
377 continuous effects among the trees in the linear mixed-effects models). This indicates that wood
378 anatomical structure of trees with different capacity for water transport respond in a similar
379 manner to environmental influences and ontogenetic development. Drivers of observed high
380 between-tree variability are difficult to identify; however, as we were not able to reconstruct
381 series of apical growth (and thus tree height) in the past, it is possible that at least some of this
382 variability may be due to differences in tree size (Olson *et al.* 2014; Carrer *et al.* 2015). In
383 addition, microsite effect, local soil thermal conditions or genetics may influence the water-
384 conducting capacity of individual trees (Tombesi, Johnson, Day & DeJong 2010; Schreiber *et al.*
385 2015; Anadon-Rosell *et al.* 2018).

386 *Conclusion*

387   Results of this study indicate that inter-annual variability in specific hydraulic
388 conductivity must be seen as a parameter driven by multiple factors, including disturbances,
389 climate, ontogeny and tree-specific conditions. Mechanical treatment affected anatomical
390 structure of whole trees (regardless of the position of the sample along or around the stem) in
391 tilted and decapitated individuals; scarred trees adjusted their anatomical structure only in the
392 vicinity of callus tissue. In contrast, stem-base burial and root exposure induced less-
393 pronounced anomalies. Mechanical treatments represent crucial predictors of variability in
394 specific hydraulic conductivity, whose effects outweigh ontogeny and climate. This indicates that
395 future variations in disturbance frequency may alter water conductivity and transpiration of
396 forest ecosystems.

397   The described multi-source-driven character of quantitative wood anatomical time
398 series represents a challenge for their future use in environmental studies. Specific approaches
399 (e.g., standardization, reduction of between-tree variability) should be applied for extraction of
400 the desired part of time series variability for studies on past climate, geomorphological
401 processes or stand competition.

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539

Tables

Table 1: Quality assessment statistics of linear mixed-effects models

Treatment	Marginal R²	Conditional R²	Pseudo-R²
Scarring	0.209	0.592	0.442
Tilting	0.080	0.777	0.642
Decapitation	0.057	0.778	0.635
Root exposure	0.225	0.673	0.535
Stem-base burial	0.211	0.680	0.593
Reference	0.185	0.369	0.354

Table 2: Coefficients of fixed effects and min-max span of coefficients of random effects estimated by linear mixed-effects models

Treatment	Fixed effects					Random effects				
	(Interc.)	Cambial Age	Precip MAR	Temp pAUG-pOCT	Temp MAY	Phase	Phase: Orient.	Phase: Level	Phase: Timing	Tree
Scarring	43.267	0.498	0.004	-1.142	-1.272	-0.358 0.242	-3.060 1.663	-2.478 2.381	-3.773 1.867	-2.578 3. 161
Tilting	25.701	0.460	0.016	-0.761	-1.064	-3.826 8.463	-0.124 0.188	0 0	-3.14 2.714	-2.597 7.133
Decapitation	21.111	0.437	0.021	-0.514	-1.113	-4.648 9.468	-0.133 0.211	0 0	-4.317 4.181	-3.563 4.916
Root exposure	17.827	1.049	0.023	-0.554	-0.617	0 0	-2.260 1.312	-4.043 4.921	-1.532 1.461	-7.265 5.588
Stem-base burial	22.056	1.505	0.001	-0.880	-0.220	0 0	-1.131 1.391	-2.149 2.269	-9.553 6.561	-6.533 8.078
Reference	23.651	0.330	-0.016	-0.226	-0.593	NA	-0.297 0.616	NA	NA	-2.803 1.518

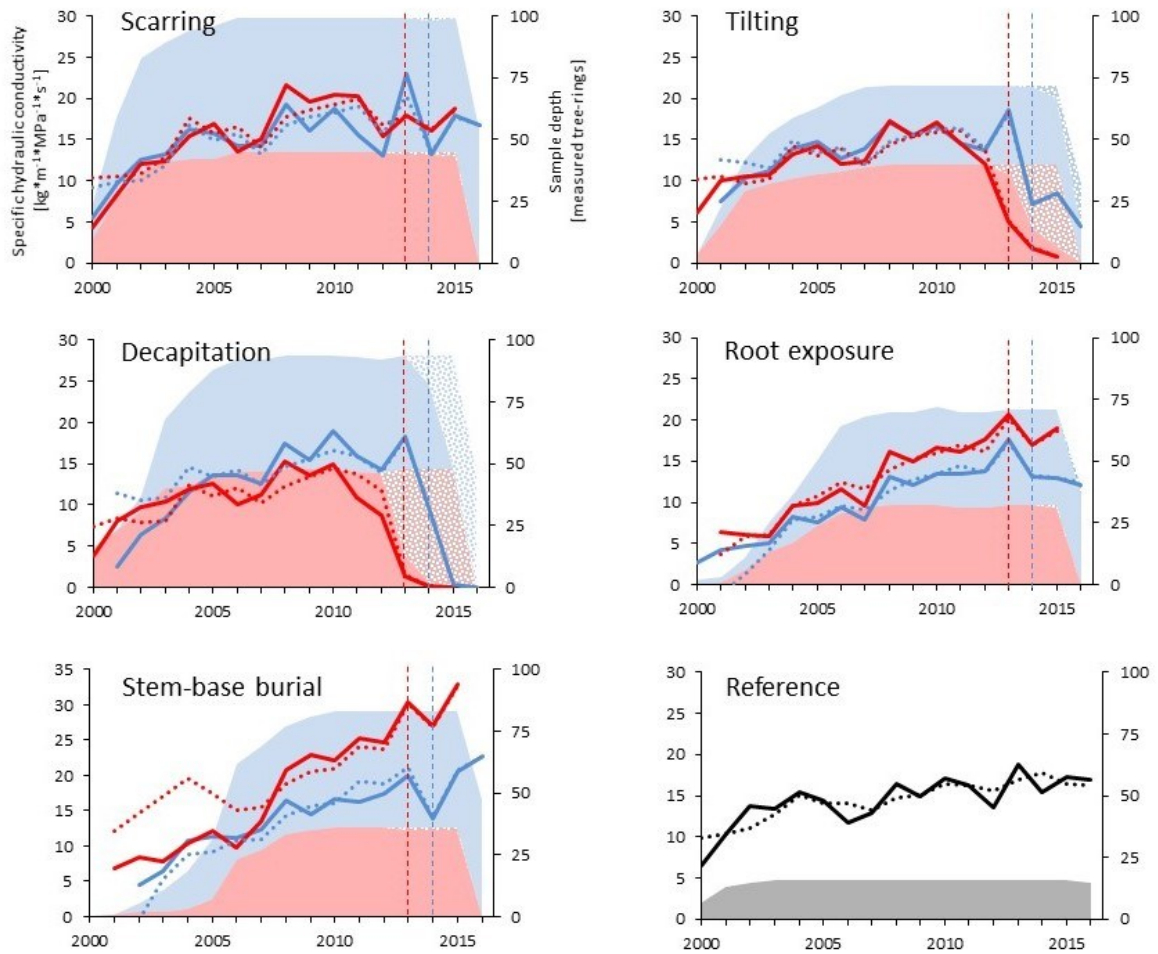## 549 **Figures**

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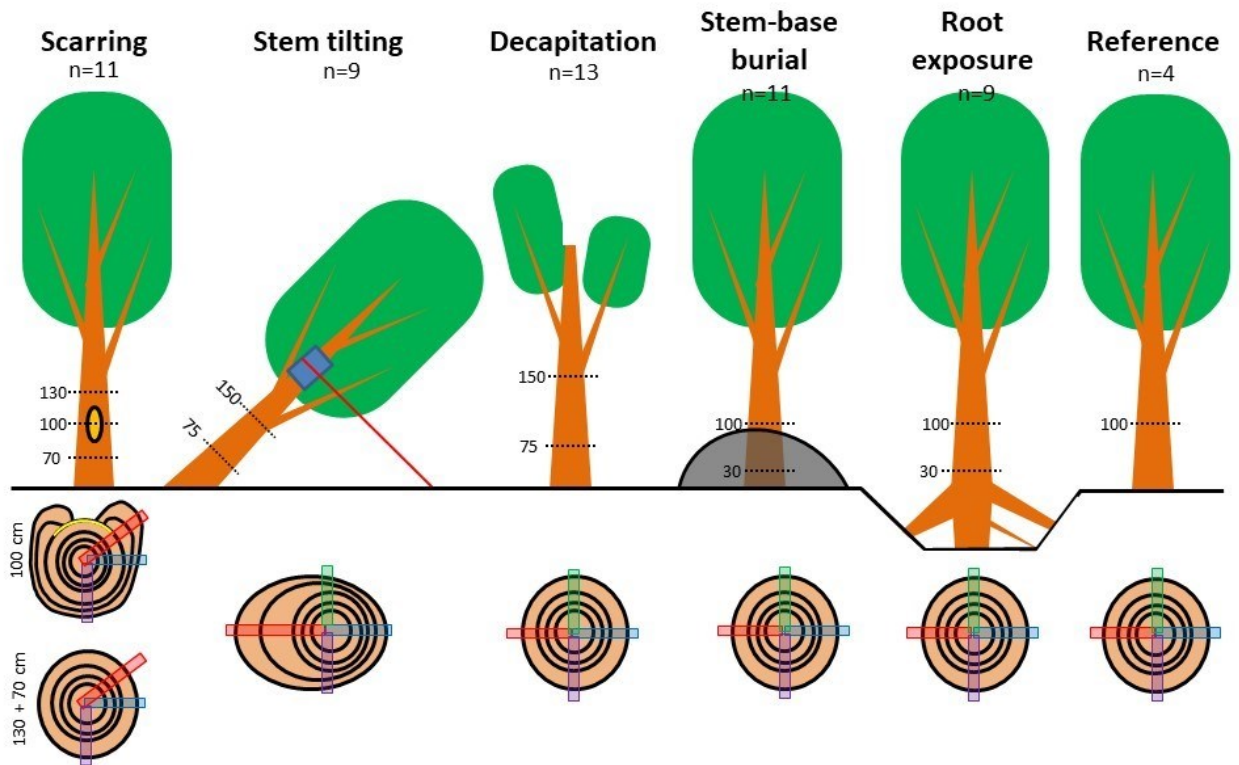
Figure 1: Schematic representation of five different experimental treatments, as well as control reference trees (n=replicates per treatment). Dotted lines indicate sampling positions (in cm above the ground). Color rectangles over cross-sections indicate positions of individual microsamples prepared from each cross-section.

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*Figure 2: Observed (solid line) and modeled (dotted line) specific hydraulic conductivity averaged for each treatment category and treatment timing (before growing season-red, during growing season-blue). Solidly shaded areas represent respective sample depths, stippled areas represent missing tree-rings with $K_s=0$. Vertical dotted lines indicate years in which the treatments were performed.*

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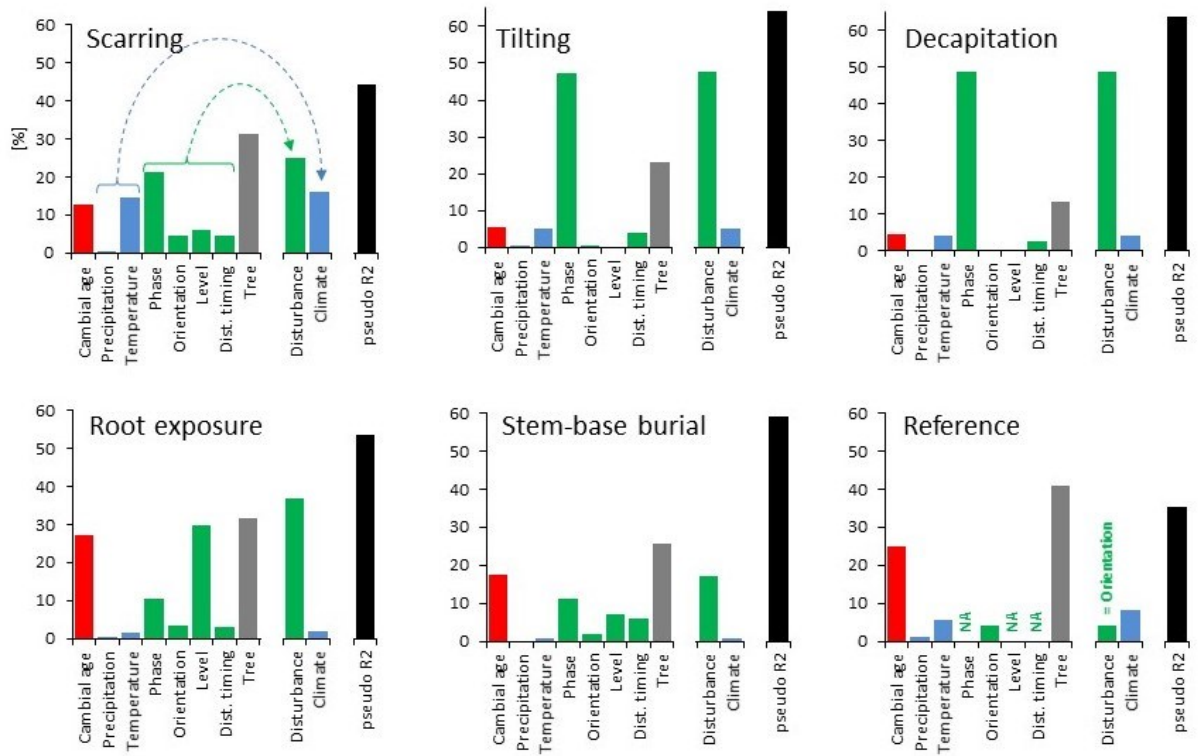
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564 *Figure 3: The effect sizes of individual predictors on correlations between modeled-observed values*
565 *of specific hydraulic conductivity*

566

567 **Disentangling the effects of disturbances, ontogeny and climate on xylem hydraulic**

568 **conductivity of *Betula pendula***

569

570 Jan Tumajer[1*], Václav Treml[1]

571

572 2- Charles University, Faculty of Science, Department of Physical Geography and Geoecology,

573 Albertov 6, 12843 Prague, Czech Republic

574 * corresponding author: tumajerj@natur.cuni.cz
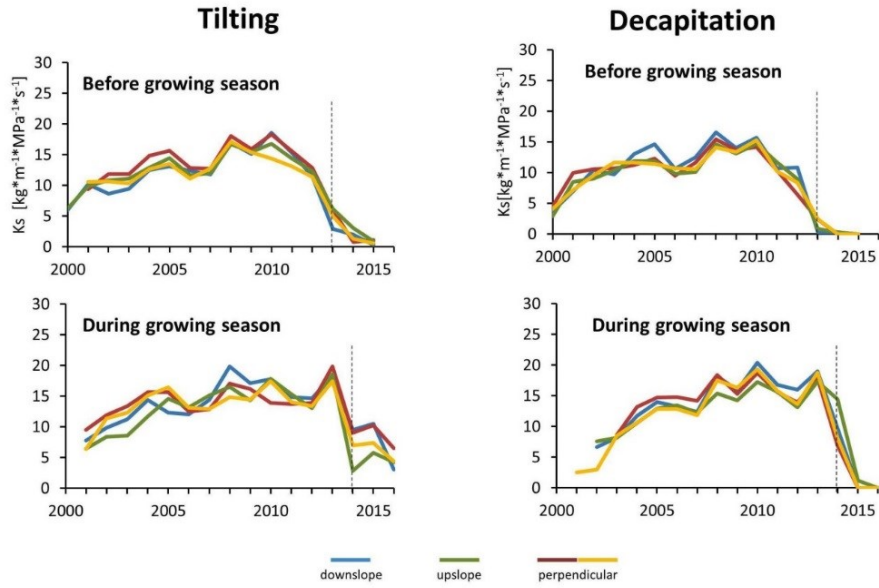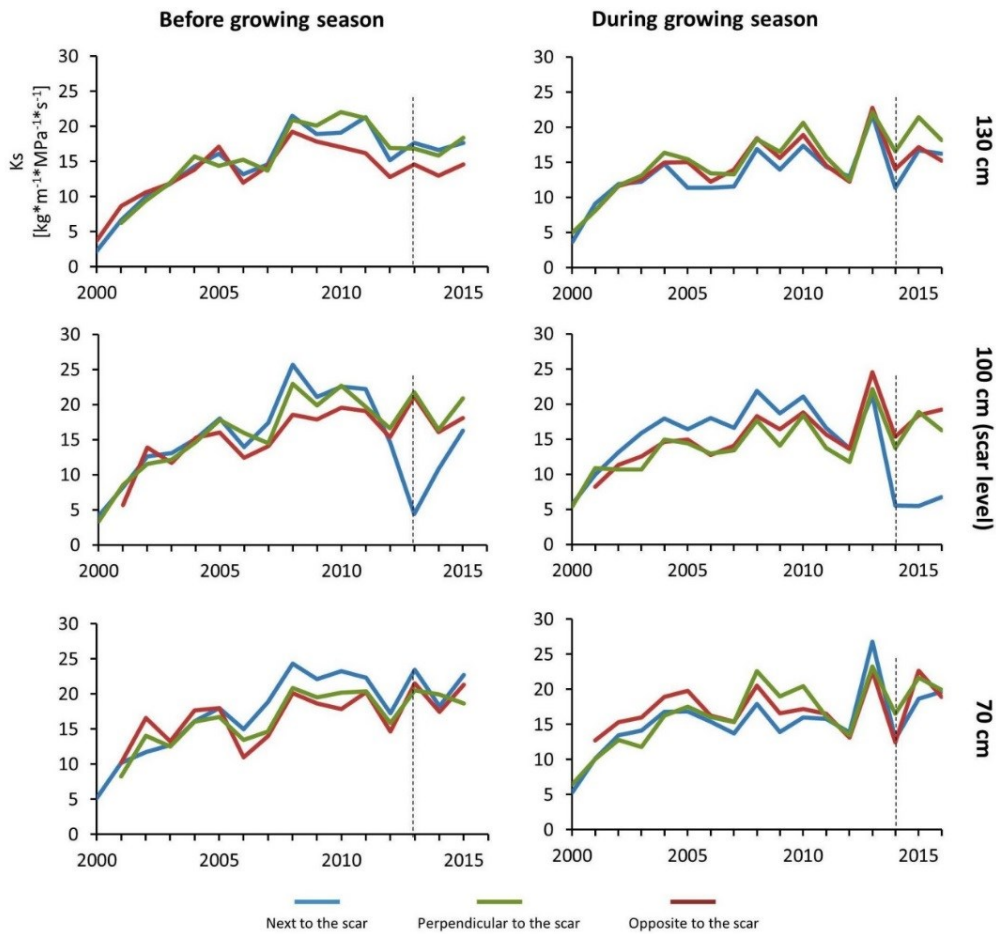
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580 # **<u>Supplementary material</u>**

581

582 *Figure S1: Observed values of specific hydraulic conductivity of tilted and decapitated trees averaged for each treatment*
583 *timing and orientation relative to stem circumference*

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585

586 *Figure S2: Observed values of specific hydraulic conductivity of injured (scarred) trees averaged for treatment timing and*
587 *position of the sample around and along the stem*
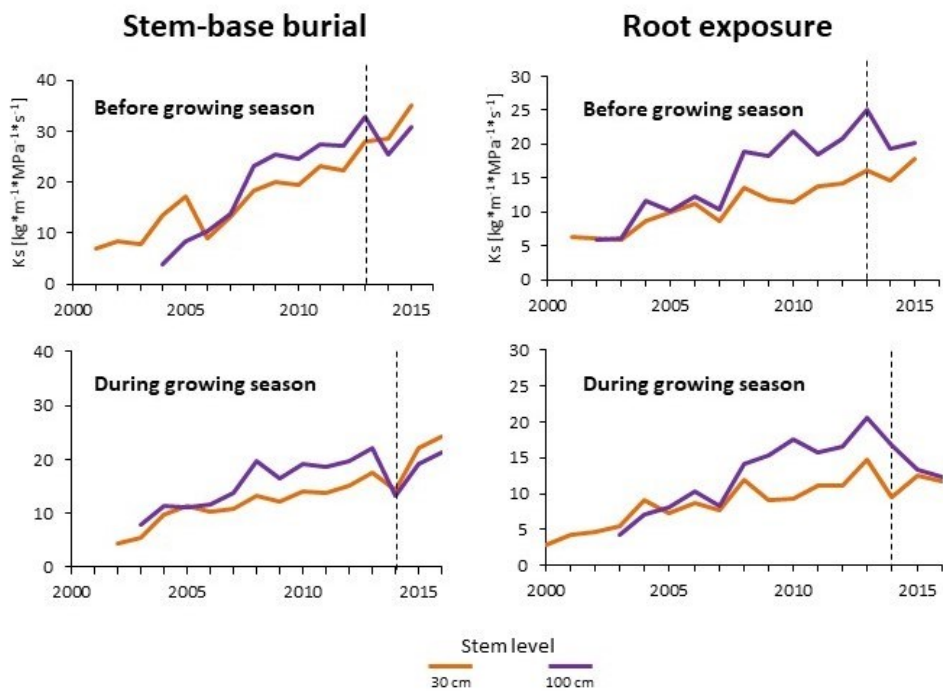
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589 *Figure S3: Observed values of specific hydraulic conductivity of trees with buried-stem base or exposed roots averaged for*
590 *each treatment timing and position of sample along the stem*

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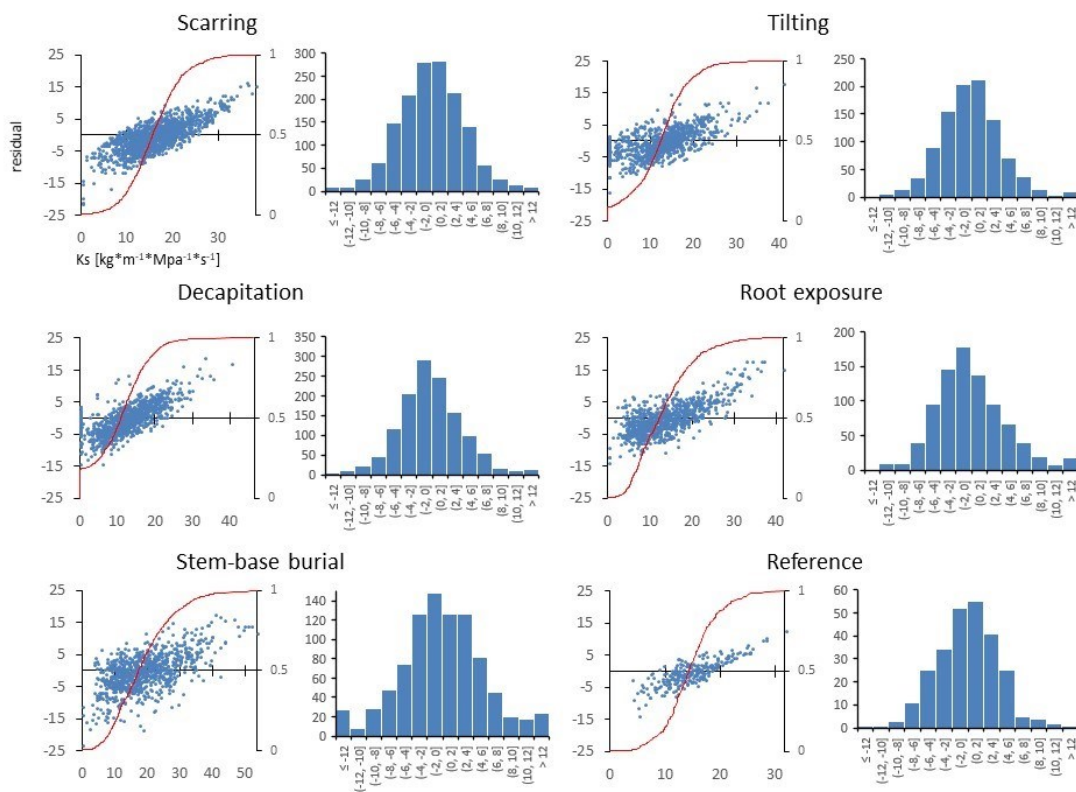
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593 *Figure S4: Charts of residuals, showing relationship between residual and observed value of specific hydraulic*
594 *conductivity (left) and histogram of residuals for individual treatments (right).*

7. Conclusions

In this doctoral thesis I exemplified that time series of quantitative vessel parameters of broadleaves are sensitive to environmental conditions and thus represent promising proxy for their reconstruction. In addition, vessel parameters are often sensitive to other environmental parameters than tree-ring widths allowing description of tree ecology in greater detail by combined use of vessels and tree-ring widths.

The main climatic signal stored in vessel size of lowland *Quercus robur* is positive effect of previous year summer temperature and current year late winter/early spring temperature. Specifically for floodplain oaks, the average vessel size is constrained by high soil moisture content. Tree-ring widths of lowland trees outside the floodplain are strongly negatively correlated with drought intensity, but weak climatic signal dominates in floodplain oaks. Our results therefore indicate that productivity of floodplain oak forests is mostly without climatic limitation, but the development of efficient conductive xylem structure is largely restricted by high level of soil water saturation. Contrary, vessel size of lowland oaks outside floodplain benefits from recent increase in temperature, but oak productivity is significantly reduced by drought stress.

Wood anatomical time series have lower mean sensitivity (i.e. average year-to-year variability) comparing tree-ring widths and they are also characterized by lower frequency of pointer years (i.e. years with extremely large or small vessels). Extremely narrow tree-rings at sites outside floodplain are mostly related to drought events (1976, 2007), however, these pointers do not occur in floodplain with well water-saturated soils. Contrary, higher frequency of tree-rings with extremely small vessels may be linked to years with spring flooding (1940, 1947, 2006) or autumn flooding during previous year (1954). This further supports our conclusion about drought-limitation of productivity outside floodplain, but excessive moisture-limitation of development of efficient vessel structure in floodplain stands. Although we documented i) negative correlation between vessel lumen area and moisture and ii) occurrence of extremely small vessels in moist years in floodplain, we did not observe typical 'flood-ring' in any of sampled *Quercus robur*. This may be a consequence of generally short periods of inundation after flooding culmination of rivers in Central Europe.

Floodplains are characterized by complex microtopography so it is reasonable to assume that there might be differences in response to hydroclimatic events among individuals within one stand. As a model we used area with artificially manipulated groundwater level. Indeed, we showed that the response of *Quercus robur* productivity to hydroclimatic variability (mostly represented by groundwater level oscillation) is not uniform inside single forest stand, but coexistence of individuals with completely opposite ecological preferences (drought-limited and moisture-limited) was illustrated. Opposite climatic signal and trends of these groups – if not

treated using appropriate statistical approaches – may shadow true trends and climatic signal of entire forest stand. This finding represents a challenge for forest management which aims to establish forests with species composition optimal for local climatic conditions. However, as we have shown, completely different climate may be optimal for individuals of single species at waterlogged sites. In contrast, average vessel size of *Quercus robur* contains similar trends and similar climatic signal among trees both inside single forest stand and among sites within a broader area.

Between-tree and between-site variability in climatic signal of tree-ring width chronologies and spatial homogeneity of climatic signal of vessel chronologies has important consequences for paleoclimatological reconstructions based on *Quercus robur*. Common response of vessel time series to environmental conditions makes them a promising proxy for reconstructions of dominant temperature signal. Contrary, high between-tree and between-site variability of climatic signal stored in tree-ring widths represents a noise in paleoclimatological reconstructions. Possible temporal variability in proportion of drought-limited and moisture-limited trees included in long chronology (combining living trees, archaeological wood and subfossil wood with unknown origin) may represent bias in paleoclimatological reconstructions.

In addition to hydroclimatic conditions, vessel parameters abruptly adjust after mechanical damage to the cambium. If tree bark and cambial zone are scarred, mean vessel size in adjacent zone significantly decreases on average for more than 60 %, distorting long-term ontogenetic increase in mean vessel size with increasing tree height. This response represents temporal shift from the preference of the efficient to safe wood anatomical structure. Scar is subsequently overgrown by callus tissue and vessel size returns to expected values, taking three years to reach pre-event level of vessel dimensions in juvenile *Betula pendula*. Tissue compartmentalization through reduction in vessel size is restricted only to an area close to callus tissue and becomes weaker in more distal parts of the stem circumference. Abrupt vessel anomalies represent a useful tool for dating former mass-movements and other types of disturbances in dendrogeomorphology.

To understand ecological significance of disturbance at tree and stand level we performed experiment with stem mechanical damage (stem tilting to 45° from the vertical, decapitation, cambial injury, stem base burial and root exposure) and observed the effect of mechanical treatment on functional trait of conductive elements – the specific hydraulic conductivity. In case of severe types of mechanical treatment (tilting, decapitation), specific hydraulic conductivity significantly drops down around and along entire stem. In both types of treatment, reduced specific hydraulic conductivity lasted for all three post-treatment tree-rings with no apparent trend for recovering the pre-event values. Because specific hydraulic conductivity represents theoretical maximum of transportable amount of water through xylem during conditions with specific water potential, decline in specific hydraulic conductivity may

alter transpiration of individual trees and forests. Changing frequency and intensity of forest disturbances thus represents important factor which may affect ecosystem-climate interaction.

Variability in time series of specific hydraulic conductivity reflects increasing tree age (tree height), climatic variability and possible effect of mechanical disturbances. Using linear mixed-effects models we were able to separate parts of variability driven by different factors and to quantify their contribution to observed values. Tree size has been often emphasized as a crucial predictor of vessel dimensions; however, our results show that it is dominant predictor only in case of vital non-damaged trees. Explanatory power of disturbances for specific hydraulic conductivity significantly outweighs both the effects of ontogenetic scaling and climatic forcing. The contribution of temperature and precipitation to predictive skills of the model is the weakest of all included predictors, especially in case of damaged trees. Therefore, in research focusing on climatic signal in vessel time series a special care should be given to i) sample undisturbed trees and to ii) standardize vessel dimensions to remove age trend.

To conclude, this doctoral thesis reported sensitivity of vessel anatomical parameters of *Betula pendula* and *Quercus robur* to various environmental conditions including climate, water availability and disturbances. Quantitative wood anatomical parameters should be perceived as proxies driven by multiple factors, and correct extraction of desired environmental information requires filtering out the other factors as a noise. Although analysis of wood anatomical time series in dendrochronology requires more laborious and time-consuming processing of samples comparing tree-ring widths, quantitative wood anatomical series contain additional environmental information useful to describe limiting conditions of tree growth and transpiration. Such information is useful for understanding feedbacks of forest ecosystems to climate, for paleoenvironmental studies and for dating of disturbance events. Vessel anatomical series are characterized by low between-site and between-tree variability in climatic signal and clear signal of mechanical damage related to disturbances – the characteristics that make them excellent tool for application in physical geography.

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