Tree-ring width and Variation of Wood Density in *Fraxinus excelsior* L. and *Quercus robur* L. Growing in Floodplain Forests

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Oven-dry wood density variations are reported for European ash (*Fraxinus excelsior* L.) and English oak (*Quercus robur* L.) trees growing in floodplain mixed forests in South Moravia, Czech Republic. Two sites with different water regime conditions were selected along the Dyje (site A) and the Morava (site B) Rivers. In total, 20 dominant, healthy trees were chosen to determine the tree-ring structure and the oven-dry wood density (ρ_0) along the radius of the stem cross section. The tree-ring width followed the common trend of a general decline as the trees aged. After removing the age influence, significant differences were observed in the tree-ring structure, recorded several years after water regime treatments. The European ash and the English oak ρ_0 were found to be 677.3 kg·m^{-3} and 618.2 kg·m^{-3}, respectively, significantly differing between the sites, for both species. High variability of ρ_0 was also noticed along the stem radius in both species and sites.

Keywords: European ash; English oak; Floodplain forests; Oven-dry density; Tree rings; Variability

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INTRODUCTION

Wood density (or specific gravity) variability highly depends upon environmental factors connected with hydrological processes (Martius 1992; Parolin and Worbes 2000; Csóka 2016). Kozlowski (1984) claimed that tree growth could be either increased or decreased by flooding, depending on the species and various flood traits, while Wertz *et al.* (2013) highlighted the importance of the timing, duration, and the magnitude of the flood occurrence in relation with the cambial growth. Trees growing in Amazonian areas that were flooded for longer periods were expected to have higher wood density (Martius 1992). Lawson *et al.* (2015) reported that high-density wood conveyed mechanical strength to the stems, which enabled the trees to tolerate water stress and withstand floods.

Recently, researchers have focused on the tree growth response to long-term hydrologic and climatic variability encountered in floodplain forests with altered flood regimes (Palta *et al.* 2012; Keim and Amos 2012; Gee *et al.* 2014). Astrade and Bégin (1997) related the presence of smaller and fewer vessels formed in aspen and English oak with lasting floods at the beginning of the growing season, while a previous study measured fibers with thinner cell walls and larger lumina in ash trees as a result of floods at the end of the growing season (Yanosky 1984). George *et al.* (2002) found a correlation between bur oak vessels and spring floods, while a more recent study defined that the response of the average vessel size of the English oak growing in the floodplains was negative (Tumajer and Treml 2016). Moreover, significant changes in the vessel lumen area of alder, ash, and Pyrenean oak were correlated with flash flood activity (Ballesteros *et al.* 2010). Nevertheless, the relationship still remains unclear, *i.e.*, previous studies have poorly connected wood density with mean annual rainfall, while others have correlated wood density and vessel traits with soil moisture content (Weimann and Williamson 2002; Preston *et al.* 2006; Swenson and Enquist 2007). Therefore, the fluctuations in the ground level water regulated by water regime treatments should be examined as an important driver of wood quality of the floodplain trees.

The species which are adjusted to growing in floodplain forests are the most demonstrative examples to confirm this relationship (Maddock 1976; Yin 1999). Namely, European ash (*Fraxinus excelsior* L.) and English oak (*Quercus robur* L.) commonly appear in floodplain forests, mixed broadleaved forests, moist clay-loam lowlands, or even in relatively dry calcareous sites (Dobrowolska *et al.* 2008). Both species are ring-porous hardwoods with similar oven-dry wood densities (Kollman 1951; Lexa *et al.* 1952; Jane 1956; Matovič 1984; Wagenführ 2000). The average oven-dry density of European ash and English oak wood ranges from 650 to 687 $kg{\cdot}m^{-3}$ (Kollman 1951; Matovič 1984; Wagenführ 2000) and from 650 $kg{\cdot}m^{-3}$ to 680 $kg{\cdot}m^{-3}$ (Kollman 1951; Lexa *et al.* 1952), respectively. Nevertheless, Zeidler and Borůvka (2016) reported remarkably higher values of oven-dry density (707 $kg{\cdot}m^{-3}$) referring to English oak. Other studies, focused on oak trees growing in floodplain forests, which resulted in lower values of oven-dry wood density, 584 $kg{\cdot}m^{-3}$ and 589 $kg{\cdot}m^{-3}$ (Vichrov 1954; Vavrčík and Gryc 2012, respectively).

European ash trees cover approximately 1.4% of the forested land in the Czech Republic, and oak trees cover almost 6.7% (Ministry Report 2014). Both species commonly grow within the lowland belt with areas adjacent to large lowland rivers [below 210 m above sea level (a.s.l)] which are mostly covered by floodplain forests, wetlands, inundated meadows, as well as sandy grasslands and saline habitats (Chytrý 2012).

In the medieval period, the emergence of floods in the Czech Republic (South Moravia) increased after the deforestation of sub-montane and montane areas (Ložek 2011; Chytrý 2012). Typically, rivers used to flood after snowmelt in March through April, and occasionally after heavy rainfall (mostly during summer, randomly during the year). Hence, the riparian areas of the rivers were strongly modified by floods and loamy sediment accumulation. In the last century, multiple changes of the hydrological regime occurred due to river regulations. Especially, the treatments performed in the 1930's, drastically increased the summer floods. This lasted until 1968–1972, when a new water regime treatment of the Dyje River took place, aiming at reducing the groundwater level and eliminating the floods. Similar treatments for groundwater level reduction were applied at the section of the Morava River later (1976–1977). In due course, the groundwater level decreased by around 90 cm (Dyje) and 40 cm (Morava), practically eliminating the floods. In 1984, the construction of a highway body affected certain areas of the Morava River by increasing the groundwater level again (Maděra and Úradníček 2001; Prax *et al.* 2005). Eventually, since 1992, this region has been restored by artificial and controlled spring floods (Maděra and Úradníček 2001).

Klimo *et al.* (2013) reported that the water regime treatments applied for almost 20 years (approximately 1972 to 1992) in the Dyje and the Morava Rivers have had an apparent ecological impact on the floodplain forest plants. The layer of the shrubs and young trees presented a leaf area index decrease, while the herb layer was dramatically affected, undergoing a dramatic reduction of its biomass (60 to 70%). Nevertheless, Klimo *et al*. (2013) underlined that the dominant tree species hardly responded to the alterations, from an ecological point of view. In the present work it is hypothesized that the influence of the alterations should be apparent from inspection of the wood. The objective of this study was to investigate the response of the European ash (*Fraxinus excelsior* L.) and English oak (*Quercus robur* L.) trees growing in two floodplain forest localities close to the Dyje and the Morava River by analyzing the tree-ring structure and oven-dry wood density (ρ_0).

EXPERIMENTAL

Site Characteristics

Two sites along the Dyje and the Morava River in southern Moravia, Czech Republic were selected (Fig. 1). The first site (A) was chosen to be close to the Dyje River, in Lednice (48.8072483N, 16.7947711E, 174 m a.s.l), where the groundwater level was lowered by around 90 cm during the 1970s. The second site (B) was placed in Tvrdonice (48.7146003N, 16.9901419E, 168 m a.s.l.) close to the Morava River where the water regime treatments were not effective. The most drastic alteration in this area occurred with the highway body construction which raised the ground level water again in 1984. The forests in both sites are similar *i.e.*, floodplain forest mixed stands of European ash and English oak (A: 40% and 60% and B: 30% and 70%, respectively). The mean annual temperature in both areas is 9.0 to 9.5 °C, and the annual precipitation total is 500 mm (Chytrý 2012).

Fig. 1. Sampling localities (A: Lednice; B: Tvrdonice) and method

Sampling Method

Five European ash and five English oak healthy and dominant trees were randomly selected per location (20 trees in total). The trees were over 100 years old (Table 1). Sample logs 1 m in length were obtained from trees at the breast height (1.3 m) with marked cardinal directions (from North to South). The mean diameter of the stems at the breast height ranged from 39.5 to 54.0 cm (European ash) and from 30.7 to 47.0 cm (English oak).

Transversal discs from each stem were obtained to measure the tree-ring widths (TRW). All samples were measured (at an accuracy of 0.01 mm) using a TimeTable device (SCIEM, Vienna, Austria). The obtained TRW series were processed in the

PAST4 software (Knibbe 2004) to build mean series for each species/site. The number of the tree rings refers to the breast height.

Table 1. Dendrometric Features of the Sample Logs per Site and Species (Age Measured at Breast Height; Diameter with the bark included; A: Lednice; B: Tvrdonice)

Tree	European ash				English oak			
	A		B		A		B	
	Age	Diameter (cm)	Age	Diameter (cm)	Age	Diameter (cm)	Age	Diameter (cm)
1	109	50.5	129	45.0	108	45.2	114	46.5
2	109	53.5	127	46.0	107	30.7	110	38.0
3	107	50.5	130	51.5	107	43.2	111	44.0
4	107	39.5	120	54.0	105	45.0	116	47.0
5	106	41.5	133	54.0	106	38.0	113	41.0

The TRW data were standardized before the analyses. Time-series standardization was made in R (programming environment and script) by using Library dplR (Dendrochronology Program Library in R). The authors used standardized tree-ring widths (TRWI) per species, to remove the age influence. Thereafter, sliding T-tests were compared before and after the water regime treatments to detect differences in the TRWIs. Namely, on site A, a 10-year control dataset was selected before the year 1972 (1963 to 1972) to compare gradually with the following 10-year datasets *i.e.* 1973 to 1982; 1974 to 1983; …1992–2001. On site B we compared the control dataset 1975 to 1984 with the following 10-year datasets 1985 to 1994; 1986 to 1995; … 1995 to 2004.

Furthermore, central boards were cut into standard specimens (20 × 20 × 30 mm) for measuring oven-dry density. The specimens were obtained respecting their position in the stem *i.e.*, radially from bark to pith (A through I). Approximately 2000 specimens were produced in total.

The specimens were dried to as much as 0% moisture content in the program oven (at 103 ± 2 °C). Each oven-dried specimen was measured in three anatomical directions and then weighed. The oven-dry wood density (ρ_0; kg·m^{-3}) of the specimens was calculated using Eq. 1,

$$\rho_0 = \frac{m_0}{V_0} \tag{1}$$

where m_0 is the oven-dry weight (kg) and V_0 is the oven-dry volume (m^3).

TRWs were measured again per specimen for the correlation analysis.

R – programming (R Development Core Team, Vienna, Austria) was also used for statistical analysis (Student's t-test, Tukey's range test) and graphic depiction.

RESULTS AND DISCUSSION

Tree-ring growth

It has been expected that the water regime alterations would be registered on the tree-ring structure of both species. The TRW was observed to have undergone a decrease along the years but without any obvious differences before and after the treatments for both species and sites (Fig. 2). Because the age directly affects the TRW (Hubbard *et al.* 1999; Day *et al.* 2001; Greenwood *et al.* 2008), as trees grow older and bigger, a general decline of TRW is observed, showing a trend that is commonly found in TRW chronologies (Esper *et al.* 2008). Hence, in our study, the decreased TRW was in line with the general trend.

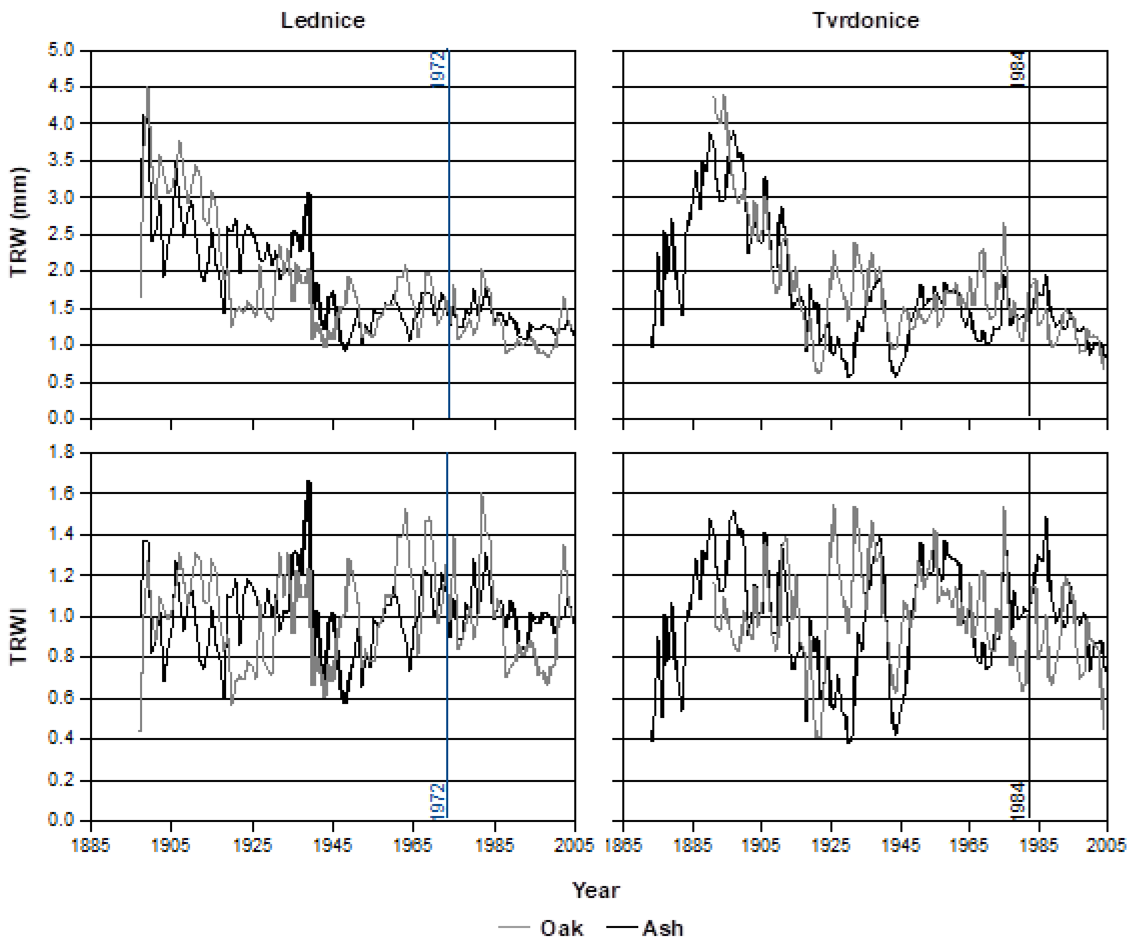

Fig. 2. The tree-ring widths (TRW) and tree-ring widths standardized analysis (TRWI) of English oak and European ash (at breast height). A: 1972 - Year of water regime treatments initiation in Lednice; B: 1984 – Year of the highway body construction in Tvrdonice

Kollman (1951) determined that European ash tree-ring width tended to be narrower (less than 5 mm) in the first 10 to 15 years, becoming proportionally wider up to 40 years of age and then continuously decreasing. In our study, this description fits better to the European ash trees growing on site B. English oak followed the same age-trend on both sites.

Nevertheless, the TRWI (free from the age influence) eventually revealed some significant differences before and after the water regime alterations in both sites. It is important to mention that the changes did not occur immediately. Both species responded to the alterations in a long-term reaction by forming narrower tree rings.

On site A, the English oak trees demonstrated a significant long-lasting decrease in the TRWIs, which started 11 years after the year of the water regime treatments (1984: p=0.012; 1985: p=0.002; 1986: p=0.001; 1987: p=0.000; 1988: p=0.000; 1989: p=0.000; 1990: p=0.000; 1985: p=0.000). On the contrary, the European ash trees showed no differences before or after the treatment. English oak, as a common species in riparian forests, can tolerate oxygen deficiency and survive several months of flooding (Blom 1999; Kreuzwieser *et al.* 2004). It tolerates a high range of soil pH (from acid to alkaline) and moist conditions, including occasionally wet soil and dry clay. It also appears to be drought-tolerant, particularly in climates with low humidity (Edward *et al.* 1994). It is known that oaks, among other floodplain tree species, have the adaptive ability to develop hypertrophied lenticels and adventitious roots, which allocate oxygen to the roots (Schmull and Thomas 2000; Parelle *et al.* 2006). English oak reacts well to drought stress by forming a deep rooting system to overcome dehydration (Abrams 1990; Epron and Dreyer 1993; Dickson and Tomlinson 1996; van Hees 1997; Schwanz and Polle 2001; Bourtsoukidis *et al.* 2014). In the present study it was noticed that on site A, where the groundwater level was decreased for more than 20 years, English oak was probably affected in a very long-term.

On site B, the exact opposite behavior was observed for the examined species. European ash had a significant decrease in the TRWIs, six years after the highway body construction (1991: p=0.034; 1992: p=0.020; 1993: p=0.016; 1994: p=0.012; 1995: p=0.002), while English oak exhibited no differentiations along the years. European ash thrives in a wide range of site types because of its high tolerance of water and nutrient conditions (Marigo *et al.* 2000; Střeštík and Šamonil 2006; Dobrowolska *et al.* 2011). The species withstands short-term floods, although stagnant water with limited oxygen supply is rather unfavorable. European ash requirements in high soil moisture have been noted in many studies, as well as its high sensitivity against root competition (Wagner 1999; Kerr and Cahalan 2004). It has been reported that the species is particularly sensitive to precipitation deficits in May and June because of budding (Wardle 1961; Braun 1977). Furthermore, the soil moisture regime contributes more decisively than the soil nutrient regime with respect to height growth (Weber-Blaschke *et al.* 2008). Many studies have insisted on the necessity of a high water supply for 30-year-old to over 100-year-old European ash stands, while Kerr and Cahalan (2004) underlined that the species grew properly when the depth of water ranged between 40 and 100 cm (Knorr 1987; Weber-Blaschke *et al.* 2008). Nevertheless, Vreugdenhil *et al.* (2006) reported intense negative effects of flooding on European ash growth. In this study, European ash formed narrower tree rings in a permanently flooded site, six years after the alteration. It still remains unclear whether this is an indirect response to the site condition or not.

Oven-dry Wood Density

The average ρ_0 (A and B) of European ash was found to be 677.3 kg·m^{-3} (Coefficient of Variance: CV = 8.7 %), in line with the literature (Kollman 1951; Matovič 1984; Wagenführ 2000), (Fig. 3a).

European ash trees showed high average values on site A (689.8 kg·m^{-3}; CV = 8.9 %; range: 495.4 to 814.2 kg·m^{-3}), and lower on site B (665.1 kg·m^{-3}; CV = 8.2 %; range:

508.8 to 773.3 kg·m^{-3}). The difference between the two localities was significant (F = 1.3; p = 0.00012). The European ash trees growing on site B, were approximately 20 years older than the trees on site A. The significantly different values can be attributed to the age influence.

The average ρ_0 of the English oak trees (A and B) was found to be 618.2 kg·m^{-3} (CV = 9.9%) coinciding with previous studies (Kollman 1951; Lexa *et al.* 1952). We recorded lower average ρ_0 (584.3 kg·m^{-3}; CV = 9.5%; range: 544.7 to 652.5 kg·m^{-3}) on site A, which was different from the average ρ_0 on site B (645.4 kg·m^{-3}; CV = 7.9%; range: 632.4 to 667.4 kg·m^{-3}).

The difference between the two sites was significant (F = 8.86; p = 0.0176), which can be attributed to the site conditions, or more likely, the genetic predisposition of the individual trees. It should be noted that according to the literature, English oak trees which grow in floodplain forests generally tend to have lower densities (Vichrov 1954; Vavrčík and Gryc 2012).

The ρ_0 was examined in relation with the orientation of the samples (North and South). The marking of the cardinal directions of the samples showed no important influence on the average ρ_0 (Fig. 3b). No obvious trend was evident per species and site.

The ρ_0 values of the trees growing on site A showed a higher variability, while the respective results were rather homogenous on site B (Fig. 3c). The highest variability was recorded on the English oak trees growing on site A. Furthermore, it was observed that the two dominant ring-porous deciduous species responded differently to the alterations. After lowering the groundwater level (0.9 m) and eliminating the floods, the European ash trees on site A showed a notably higher ρ_0 than that on site B. Matovič (1984) described this negative relation between the ρ_0 of European ash trees and the level of the water during flooding. Nevertheless, English oak was inversely influenced by the reduction of the groundwater level, showing lower ρ_0.

The variation of the European ash ρ_0 along the stem radius (from bark to pith) showed no differences between the sites A and B (ANOVA: F = 0.0883; p = 0.77) (Fig. 4).

On site A, the highest average oven-dry density was 732.6 kg·m^{-3} (CV = 5%), while on site B the highest average ρ_0 was 739.3 kg·m^{-3} (CV = 1.7%). Higher wood density is expected to be found around the central part of a ring-porous tree stem (Vavrčík and Gryc 2012). On site A, the outer margins of the radial sections presented a considerably lower average ρ_0 than the central parts of the European ash stem.

In contrast to European ash, the variation of the English oak ρ_0 along the radius of the stem cross section (from bark to pith) differed significantly between the two sites (F = 9.45; p = 0.0082), (Fig. 5, Table 2).

The highest average ρ_0 was found to be 631.6 kg·m^{-3} (CV = 4.7%) and 672.5 kg·m^{-3} (CV = 5.5%) on sites A and B respectively. The outer margins of the radial sections (close to bark and pith) presented impressively lower average ρ_0 than the central parts, in line with literature (Matovič 1984).

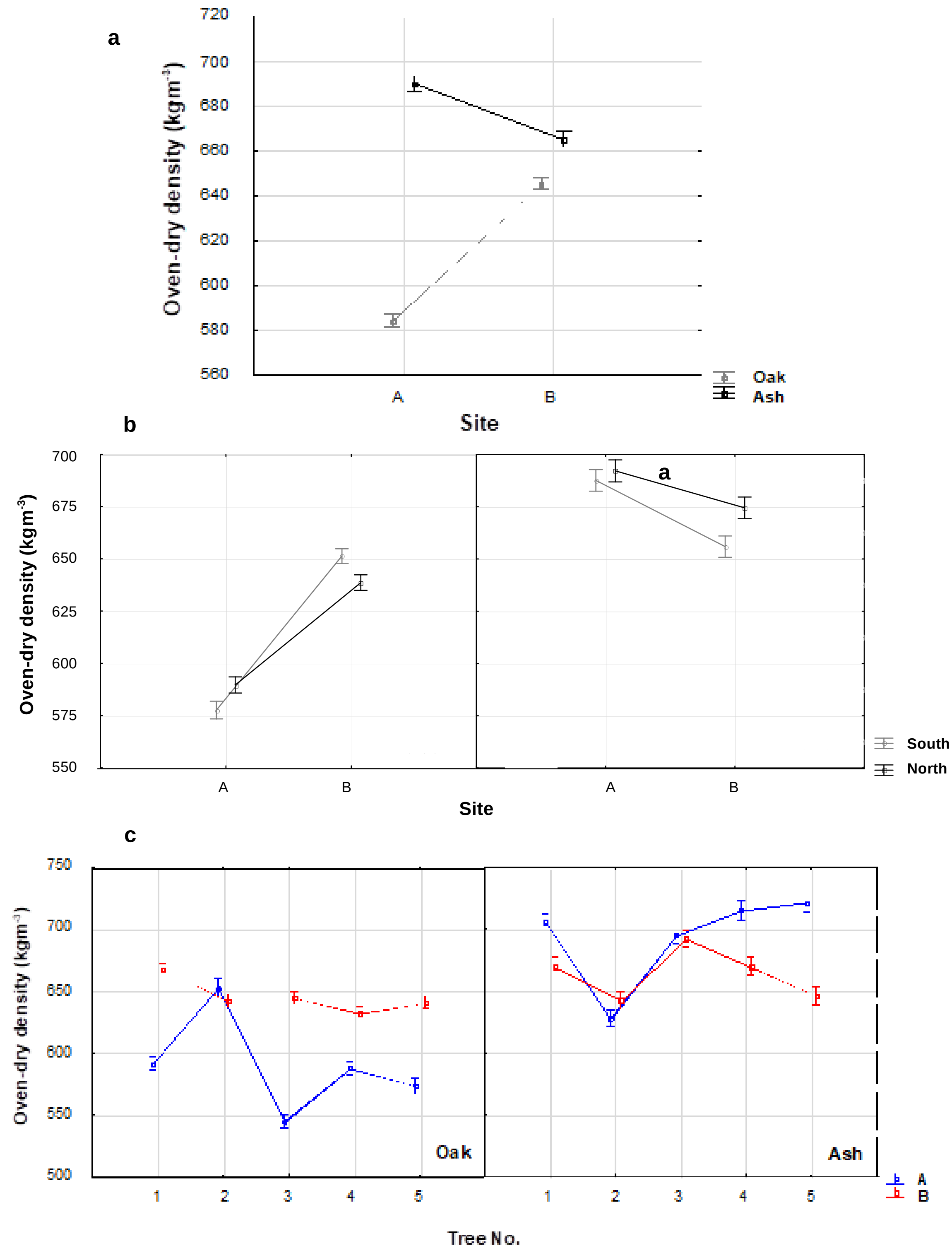

Fig. 3. The oven-dry density of both species: a) per site, b) samples obtained from two different directions (North, South) per site, c) per tree per site, (A: Lednice; B: Tvrdonice; Bars: confidence intervals).

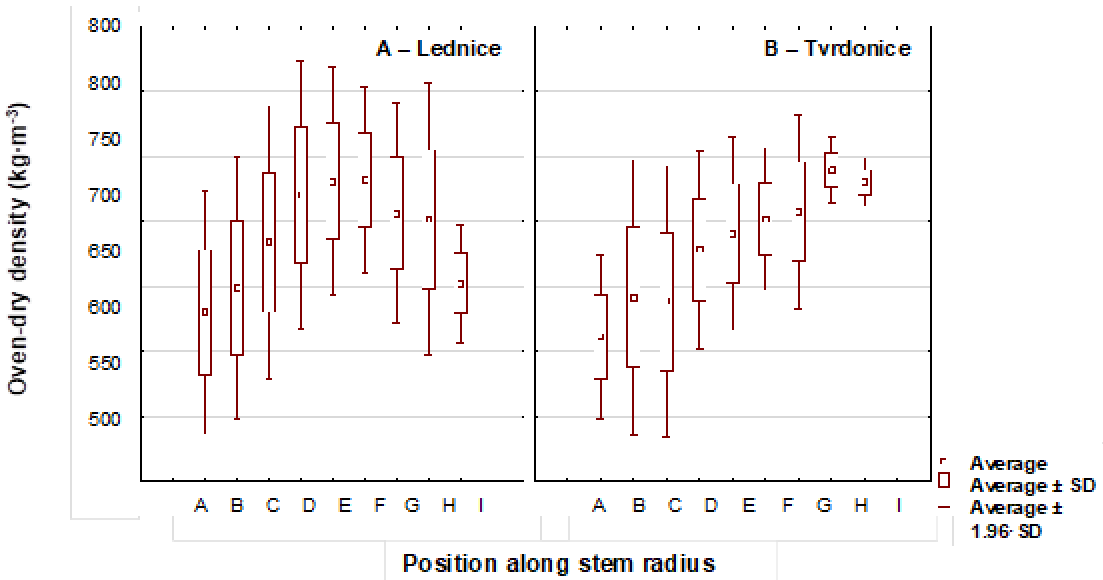

Fig. 4. European ash horizontal oven-dry wood density distribution along the radius from bark to pith (A - I) in the two studied sites. (Bars: Standard Deviation).

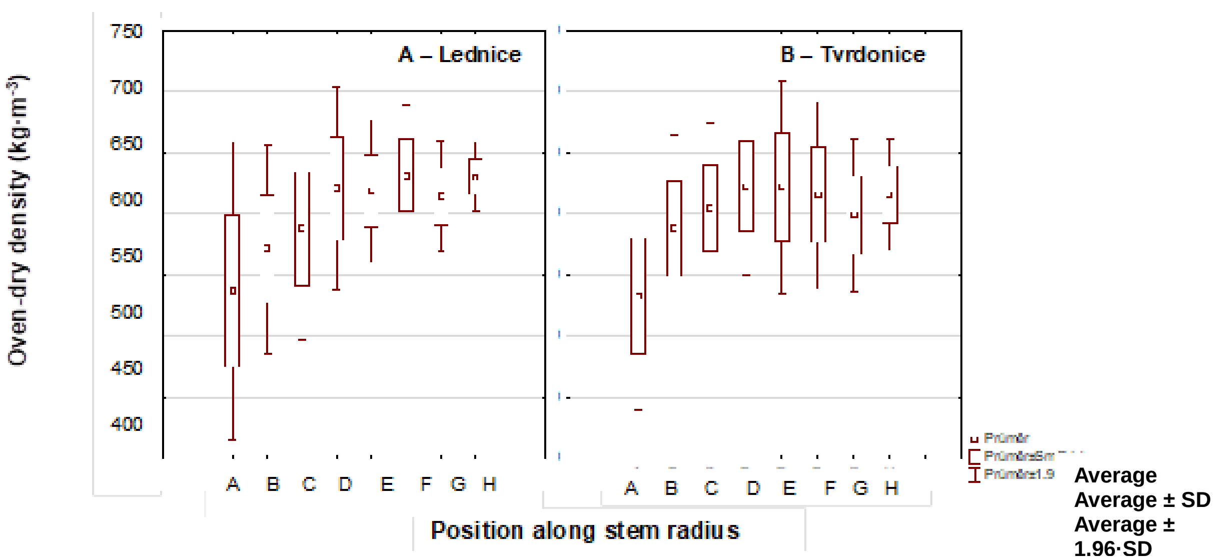

Fig. 5. English oak horizontal oven-dry wood density distribution along the radius from bark to pith (A – H) in the two studied sites (Bars: Standard Deviation).

Tukey's range test, which was performed for the ρ_0 positions along the radius of the stem cross sections per sites and species, revealed significant differences mostly close to the bark. In the case of European ash, ρ_0 was different from position to position almost along the whole stem radius whereas English oak presented similar ρ_0 only close to bark. Lower ρ_0 was observed closer to the bark in comparison with wood formed closer to the pith, most likely due to the sapwood area and narrower TRW with higher proportion of early-wood.

Table 2. Tukey's Range Test for Oven-Dry Density Position along Stem Radius in European Ash and English oak (sites A + B)

Species	European ash (A + B)								
English oak (A + B)		A	B	C	D	E	F	G	H
	A		**.000**	**.000**	**.000**	**.000**	**.000**	**.000**	**.000**
	B	**.000**		**.003**	**.000**	**.000**	**.000**	**.000**	**.000**
	C	**.000**	**.000**		**.000**	**.000**	**.000**	**.000**	**.000**
	D	**.000**	**.000**	**.000**		.130	**.000**	.843	.291
	E	**.000**	**.000**	**.000**	.999		.725	.999	.999
	F	**.000**	**.000**	**.000**	.889	.996		.581	.999
	G	**.000**	**.000**	.109	.263	.138	**.036**		.984
	H	**.000**	**.000**	.099	.999	.994	.936	.994	

Tree Rings and Oven-Dry Wood Density Relationships

European ash trees growing on site B revealed a strong correlation between ρ_0 and TRW (Fig. 6). By contrast, the relationships were weak on both sites for the English oak trees (A and B).

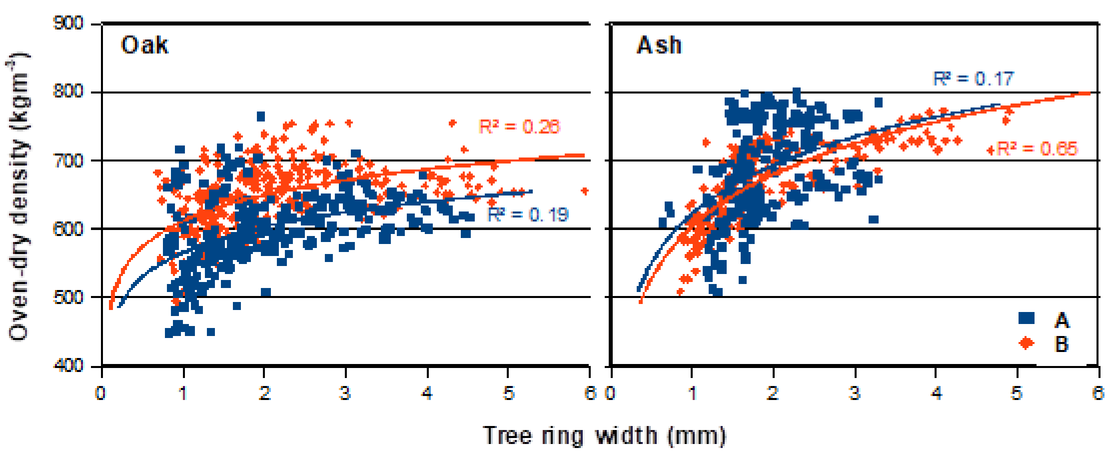

Fig. 6. Relationship between the oven-dry density and the tree ring widths per species and sites

Wood density depends on the size of the cells, the cell-wall thickness, and the interrelationship between the number and the distribution of different types of cells forming the tree-ring structure, such as the proportion of early-wood and late-wood (Panshin and de Zeeuw 1980). Because latewood cells form thicker walls and smaller lumina than early-wood cells, a higher proportion of late-wood in the growth ring yields denser wood in ring-porous wood species (Tsoumis 1991). This was confirmed by the examined European ash trees growing on both sites, which verily depicted a strong relationship between the proportion of late-wood and ρ_0 (Fig. 7).

English oak showed weak relationships on both sites, possibly due to high porosity (higher number of vessels) of the late-wood in comparison with the European ash late-wood. English oak is more tolerant and resistant to soil moisture content conditions and hence, potentially not highly affected.

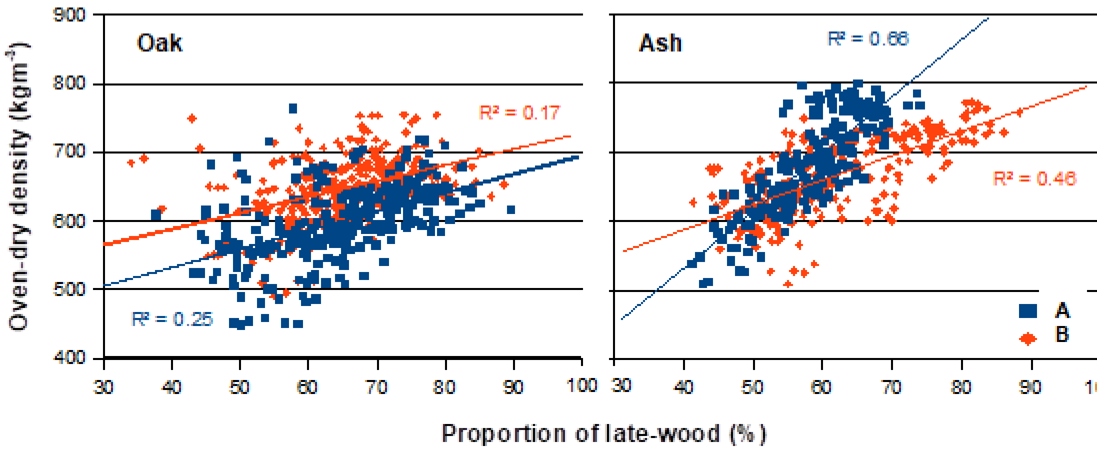

Fig. 7. Relationship between the oven-dry density and the proportion of late-wood per species and sites.

Conclusively, it was observed that both examined species followed the general age trend of the tree-ring growth. Still, there was a significant decrease in the TRWIs, which eventually occurred some years after the water regime alterations. Hence, the reaction of the trees was not immediate or directly connected to the changes. Nevertheless, the observed significant long-term differences of the TRWIs potentially provide a signal for further research. It was assumed that the water regime treatments as applied to the studied area, poorly affected the tree growth or the density of the produced wood, since eventually no solid evidence of drastic impact was recorded. The complex relationship between wood density and hydrological events (*e.g.*, rainfall/precipitation, snowmelts, and floods) needs further elucidation. An extended analysis at the cellular level (number and size of vessels, cell-wall thickness and vessel area) is needed in the future.

CONCLUSIONS

1. Tree-ring widths (TRWs) (measured at breast height) revealed no notable differences between species or sites followed the common trends of age.
2. Standardized tree-ring widths (TRWIs) showed significant long-term differences before and after the water regime treatments per site and species, but not any evident immediate reaction.
3. The average oven-dry density between the two localities was found to be significantly different for both European ash and English oak.
4. High variability of oven-dry density was recorded along the stem radius in both species and sites.

5. European ash oven-dry density was highly connected with the TRW and the proportion of the late-wood.

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