1 **Anatomical characteristics and hydrologic signals in tree-rings of oaks (Quercus robur L.)**

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14 **Author Contribution Statement**

15 J.G. – wrote the paper, prepared the cross-sections and performed the wood-anatomical analysis, M.DL. –

16 developed the concept of the paper, carried out statistical analysis, wrote statistical parts of the paper and prepared

17 figures, P.H. – collected the samples, as well as hydrological and climate data, T.L. – designed the study, selected

18 the plots and trees.

19

20 **Key Message**

21 Anatomical characteristics and hydrologic signals in tree-rings of oaks from areas with regular floodings may vary,

22 even within the same forest stand, and largely depends on the micro-environmental conditions.

23

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30 **Abstract**

31 *Q. robur* decline in European floodplain forests in recent years seems to be strongly associated with the

32 deteriorating hydrological regime. We investigated the influence of the Krka River flow on tree-ring patterns of

33 *Q. robur* from the Krakovo floodplain forests (Slovenia) in order to assess the effect of micro-location conditions

34 on hydrologic signals in wood-anatomical characteristics. We selected two groups of *Q. robur* trees growing at

35 nearby locations with different hydrologic conditions, resulting in frequent autumn and spring flooding at the

36 wetter site (= W oaks) but no flooding at the other, drier site (D = oaks). We found differences between the two

37 groups in the anatomical structure of tree-rings; however, ring width proved to be the main variable determining

38 the anatomical structure of oak wood. D and W oaks responded differently to the Krka River flow in the studied

39 period. Radial growth of D oaks was negatively influenced by spring flow, but positively influenced by minimum

40 summer flow. In W oaks, ring width was positively correlated with mean summer flow. Thus, environmental

41 information stored in wood anatomical features may vary, even within the same forest stand, and largely depends

42 on the micro-environment. Reduced wood increments of D oaks suggest that growth conditions are less favourable,

43 implying a link between the health state of oaks from lowland forest and hydrologic conditions. Trees intended for

44 hydrologic reconstruction must therefore be carefully selected in order to avoid the possibility of error and potential

45 loss of information.

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Introduction

In Slovenia, oaks (*Quercus robur* L. and *Quercus sessiliflora* Salisb.) are economically very important wood species, representing about 7% of the entire wood stock (Gozdnogospodarski etc. 2006). In relation to *Q. robur*, the lowland forest area has been shrinking, due to human settlement in the past, intensive and unplanned silvicultural and agricultural exploitation of the land and conflicts of interest, so only a few lowland oak forest stands have managed to survive (Kadunc 2010). In addition, as in many European countries (e.g., Klimo and Hager 2001), a trend of decreasing vitality of *Q. robur* has been observed in most sites in recent decades (ater et al. 2001). One of the main reasons for this situation in Slovenia is ascribed to decreasing ground water levels due to changes in climatic conditions and unsuitable artificial melioration of land for agricultural purposes, for which numerous drainage ditches were excavated in the 19th century (ater et al. 2001). The most obvious response of *Q. robur* to the changing environmental (hydrologic) conditions is seen in its decreased vitality (e.g., Hager and Buchleitner 2001; Vukeli and Rauš 2001), resulting in reduced wood increment (Levani et al. 2011), which is closely related to the structure of wood and its quality (Rao et al. 1997).

In addition to major economic consequences in these areas, ecological issues associated with decreasing vitality of *Q. robur* stands cannot be neglected. The many local oak tree-ring chronologies from various sites of Slovenia (ufar and Levani 1999a, b, ufar et al. 2008) differ greatly among each other, particularly in the case of *Q. robur* from lowland sites, where tree growth is often influenced by micro-site hydrologic conditions (ater 2003; ater and Bati 2006; ater and Levani 2004; Levani 1993; Levani et al. 2011). However, tree-ring width (TRW) is only one environmental proxy, whereas others still remain to be explored. In this respect, the use of other proxies, such as wood anatomical variables, have proved to be particularly promising (e.g., Fonti et al. 2010).

Q. robur is a regular constituent of floodplain forests and is generally considered to be one of the most flood-tolerant *Quercus* species with respect to growth and survival (Prpi 2003; Schmull and Thomas 2000). However, knowledge of its growth response in such environments is scarce (e.g., Leuschner et al. 2002; Sass-Klaassen and Hanraets 2006). Due to changes in the hydrologic regime, the groundwater level and water supply might differ even in the same forest stand, which raises the question of the extent to which micro-location conditions affect tree-ring patterns of *Q. robur*. This could be an important factor for assessing the environmental sensitivity of *Q. robur* from floodplain forests in Slovenia.

To test this hypothesis, we selected two groups of adult *Q. robur* trees, growing at nearby locations with different hydrologic conditions. The wetter site (= W oaks) is characterized by frequent autumn and spring flooding,

3

81 whereas no flooding occurs at the drier site (= D oaks). In order to reduce any geographical differences in climate

82 affecting the trees under study to a minimum, the sites were chosen in the same forest stand in Krakovo forest,

83 which is in some parts often flooded by the Krka River. In particular, aims of the study were to: (1) evaluate if

84 TRW and their anatomical characteristics (including latewood) of *Q. robur* differ in flooded and unflooded areas.

85 For this purpose, we used 10 different wood-anatomical variables for the period 1970-2008; (2) to assess if selected

86 10 anatomical variables show the same pattern of temporal variation and if they contain complementary or

87 redundant information; (3) to determine if morphological characteristics of the selected variables are related to the

88 Krka River flow.

89

90 **Material and methods**

91 *Study site characteristics*

92 The research was carried out in Krakovo *Querco robori–Carpinetum* mixed forest, Slovenia (45°54'N, 15 25'E,

93 elevation 150 m), which is the largest lowland oak forest complex in Slovenia and is mainly composed of *Quercus*

94 *robur*, *Carpinus betulus* and *Alnus glutinosa* in combination with *Tilia sp., Prunus avium*, *Acer campestris*,

95 *Fraxinus angustifolia* and *Ulmus campestris* tree species.

96   The appearance of the specific forest association is mostly determined by microtopography and soil

97 properties, which, to a large degree, influence runoff, distribution and water movement into the soil. Hydromorphic

98 soils, such as pseudogley and gleysoils (amphygley), on pleistocene clays and loams with low infiltration capacity

99 prevail. The occurrence of different forms of deposits is responsible for the difference in permeability of the soil

100 surface, which in turn affects groundwater level (Accetto 1975). In rainy periods, water can temporarily stagnates

101 on the surface and slowly evaporates or absorbs into the soil. The area may remain flooded for weeks. However,

102 due to low infiltration capacity of this soil type, most of the rainwater on slightly inclined slope or a bit higher

103 elevation can runoff the surface before the soil absorbs it. This could negatively affect the hydrologic conditions

104 at such micro-locations (ater et al. 2001). Differences in the depth of the groundwater table at the same surface

105 level can be up to 90 cm within a horizontal distance of 2 m. The level of water table varies during the year, being

106 very high in the fall, winter and early spring (Žibert 2006).

107   In addition to the groundwater level and rainwater, which may stagnate on the low permeable soil surface,

108 frequent autumn and spring floodings of the Krka River, the main river in this area, significantly affect hydrologic

109 conditions in the Krakovo forest. The Krka River belongs to the Karst Rivers. It has a rain-snow regime, with

110 runoff peaks in April and November, and minima in August and January. The Krka River has numerous small

4

111 tributaries and regularly floods, especially in spring and autumn. Data for minimal (Qnp), average (Qs) and

112 maximal (Qvp) monthly (Figure 1) and annual (Figure 2) rate of flow for the Krka River for the period 1970-2008

113 were obtained from the Environmental Agency of the Republic of Slovenia within the Ministry of the Environment

114 and Spatial Planning.

115

116 **Figure 1**

117

118 **Figure 2**

119

120   The study area is characterized by sub-pannonian continental climate. About 70 % of all precipitation

121 thus falls during the growing season (March to October) and a very small amount in winter. The mean annual

122 temperature is 10.1°C (range 8.6-12.0°C, T_{Jan} = -0.1°C, $–T_{Jul}$ = 20.1°C) and total annual precipitation 1149 mm

123 (range 827-1405 mm, P_{Jan} = 51.3 mm, P_{Aug} = 126,9 mm), as calculated from the 1970–2008 climate dataset from

124 the nearby Novo mesto climate station of the Environmental Agency of the Republic of Slovenia. The station is

125 located approximately 20 km from the forest site (45°48'N, 15°11'E; altitude 220 m).

126

127 *Tree selection, sampling and anatomical observations*

128 Penduculate oak (*Quercus ruber* L.) trees were sampled at two research plots in a Krakovo forest stand. In order

129 to reduce any geographical differences in climate affecting the trees under study to a minimum, the research plots

130 were only about 600 m apart and belong to the same forest association, but differ in the hydrologic conditions.

131 Oaks growing on the first plot were exposed to occasional flooding (= W oaks), especially in autumn and spring

132 periods, whereas in the second plot, flooding does not occur (= D oaks). The reason could be in a slightly inclined

133 surface and a bit higher elevation, which prevent the retention of the surface water.

134   Six dominant or codominant trees were selected on each plot; a total of 12 trees were thus analysed.

135 Selected trees were 80-100 yeas old, with DBH 30-60 cm, without any visible mechanical injures of stems or roots.

136 During winter 2008-2009, we took 1 cm wide cores about 1.3 m above the ground from each of the trees in order

137 to prepare microscopic slides. The material was fixed in formalin-ethanol-acetic acid solution (FEA) and

138 dehydrated in a graded series of ethanol (30 %, 50 % and 70 %) after one week. Each core was cut exactly at the

139 growth ring boundary into pieces about 5-6 cm long, so that they could be placed on microscope lides. Permanent

140 transverse sections of 25 µm in thickness were prepared on a "G.S.L. 1" Sledge microtome (©Gärtner and

141   Schweingruber; Design and production: Lucchinetti, Schenkung Dapples, Zürich, Switzerland) with disposable

142   blades. Sections were stained with safranin (Merck, Darmstadt, Germany) (0.5 % in 95 % of ethanol) and mounted

143   in Euparal and observed under an Olympus BX51 (Tokyo, Japan) light microscope and analysed with the Nikon

144   NIS-Elements Basic Research v.2.3 image analysis system (Tokyo, Japan).

145   Oak ring-porous wood is composed of several types of cells, which are specialized to accomplish their

146   function; vessels, vasicentric tracheids, libriform fibers and axial and ray parenchyma cells (Carlquist 1988). All

147   vessels are sheathed by thin-walled vasicentric tracheids and are responsible for water transport. Most of the EW

148   area is occupied by vessels that can be seen with the naked eye in the transverse plane (diameters more than 200

149   µm), whereas vessels in LW are much smaller (diameter around 50 µm). LW vessels are distributed solitarily or

150   in wide growth rings, as radially orientated groups, which alternate with groups of thick-walled libriform fibers.

151   Mechanical support is mainly provided by libriform fibers. The distribution of axial parenchyma is either diffuse

152   or in uniseriate diagonal and tangential bands. Oak has two types of rays; uniseriate and broad (up to 30 cells),

153   which are also clearly visible at macroscopic level (Figure 3).

154   We analysed the wood structure of the last 39 rings (1970-2008) in order to avoid juvenile wood, because

155   its anatomical structure and TRW significantly differ from adult wood. In each of the tree-rings, we determined

156   the measurement frame, in which we analysed various anatomical characteristics in early- (EW) and latewood

157   (LW) (Table 1). The tangential width of the frame was 4 mm and the radial width was the width of the tree-ring

158   (Figure 3); however, if multi-layered rays were present, we subtracted their area from the measured area. Visual

159   inspection revealed that the anatomical structure of tree-rings of similar width differed in W and D oaks (Figure

160   4).

161

162   **Table 1**

163

164   **Figure 3**

165

166   **Figure 4**

167

168   *Anatomical characterization of tree rings of W and D oaks*

169   Repeated measures analysis of variance (R-M ANOVA) was used to test for differences between W and D oaks

170   in all the 10 measured anatomical variables. The common period 1970-2008 was used for this analysis. Normal

171   distribution and uniformity of variance of each analysed variable was verified using the Shapiro-Wilk W test and

172   Levene test, respectively (Quinn and Keough 2002).

173

174   *Influence of river flow on tree growth and anatomical characteristics*

175   The individual measured anatomical series were standardized in the ARSTAN program (Cook and Holmes 1986)

176   by removing long-term trends using a negative exponential function followed by a cubic smoothing spline with a

177   50 % cut-off frequency and a response period of 30 years. An autocorrelation filter was applied to the detrended

178   series to remove correlations between consecutive measurements and to obtain a residual series containing only

179   high frequency variations in year-to-year series, which are expected to be mainly related to year-to-year

180   environmental variability. The indexed residual series were then averaged using a biweight robust mean to obtain,

181   both for D and W oaks, residual chronologies of each of the 10 analyzed variables.

182   The common period 1970-2008 was then also considered for multivariate analysis in order to identify

183   common modes of variability in the obtained residual chronologies. Principal component analysis (PCA) of the

184   covariance matrix of the residual chronologies was used for grouping series with similar year-to-year variations.

185   PCA was conducted using at the same time datasets of anatomical variables of W and D oaks consisting of 20

186   variables in total (10 for each group). These components were rotated orthogonally according to the VARIMAX

187   criterion to redistribute the final explained variance and to obtain more stable and robust patterns. The most

188   representative principal components were selected and the weighting components (rotated component loadings)

189   were examined to identify the pattern of association of each chronologies with each component (Kaiser 1992).

190   Correlation functions between PCA and river flow data were calculated using the DendroClim2002

191   program (Biondi and Waikul 2004), whereby the obtained significant PCA eigenvectors were the dependent

192   variables, while the independent variables were the seasonal and annual series of flow data.

193

194   **Results**

195   *Comparison of anatomical parameters in tree-rings of W and D oaks*

196   Average values and standard deviation of TRW and measured wood-anatomical variables of W and D oaks are

197   presented in Table 2, whereas the time series of their mean values and standard errors for both groups for the

198   period 1970-2008 are shown in Figure 5. R-M ANOVA confirmed that differences between the two groups exist

199   in 5 of the 10 analized variables (Figure 5).

200   Tree-rings of W oaks (average ring width = 2642.05 µm) were about 2.2-times wider than those of D oaks

201   (average ring width = 1196.31 µm) (Table 2). Average radial and tangential diameters of EW vessels and

202   consequently their cross-sectional area did not differ between the two groups. Average tangential diameter was

203   smaller than the radial one (for 15 µm in D oaks and 56 µm in W oaks, respectively) and average EW vessel area

204   was around 72000 µm^2 in both groups. The proportion of the conductive area in the EW was higher in D oaks

205   (50.09 %) than in W oaks (46.07 %), although the number of EW vessels in the EW area did not differ between

206   the two groups (Table 2). Since the proportion of LW was higher in W oaks (61.71 %) than in D oaks (42.38 %),

207   the number and total area of EW vessels per measured area was consequently lower. The proportion of vessels in

208   LW did not differ between the groups.

209

210   **Table 2**

211

212   **Figure 5**

213

214   *Common and uncommon temporal patterns in measured anatomical variables*

215   PCA analysis revealed differences in year to year dynamics among different wood-anatomical characteristics and

216   between W and D oaks. Anatomical characteristics and the relation among the measured variables can be described

217   by four components that together explained 77.2 % of the total variance. PCA analysis demonstrated that the

218   selected anatomical variables in W and D oaks significantly differed in their temporal patterns. Two components

219   of the PCA (PC1 and PC3) were mainly related to D oaks and the other two (PC2 and PC4) to W oaks (Figure 6).

220   In both oak groups, TRW and the proportion of LW were positively related (PC1 for D oaks and PC2 for

221   W oaks, respectively). These two anatomical variables were, on the other hand, negatively related to the following

222   anatomical parameters: conductive area of EW vessels and EW vessel density, and in the case of D oaks (PC1)

223   also to the share of vessels in LW (Figure 6a and b). Furthermore, in both groups were tangential and radial

224   dimensions of EW vessels positively related (PC3 for D oaks and PC4 for W oaks, respectively) and consequently

225   also average EW vessel area (Figure 6c and d). These variables were negatively related to EW vessel density, so

226   that high EW vessel density corresponds to lower EW vessel area. To summarize, we found a statistically

227   significant difference between the two groups of oaks in the following anatomical variables: TRW, conductive

228   area of EW vessels, conductive area in EW, EW vessel density and LW proportion.

229

Figure 6

231

232 *Relation between the measured anatomical variables in each of the studied oak groups and the Krka River flow*

233 Correlation between PCA components and the Krka River flow data at annual and seasonal (from previous autumn

234 to summer) time scales are presented in Figure 7. PC1 and PC3 were mainly related to D oaks whereas PC2 and

235 PC4 to W oaks. Anatomical variables of D oaks linked to PC1 were positively related to spring (mainly maximum)

236 flow and negatively to summer minimum flow, indicating that tree-rings and latewood were wider if spring flow

237 of the Krka River was lower and minimum summer flow was higher. On the contrary were conductive area of EW

238 vessels and EW vessel density higher if spring flow was higher and summer flow lower (Figure 7a). Anatomical

239 variables of W oaks linked to PC2 were negatively related to the (mean) summer flow showing its positive relation

240 with TRW and latewood widths (LWW), but negative with conductive area of EW vessels, EW vessel density and

241 the share of vessels in LW (Figure 7b).

242   We found no relation of PC3 (D oaks) and PC4 (W oaks) with the Krka River flow data, suggesting that

243 in both groups temporal variabilty patterns of the wood-anatomical variables expressed with these two PC

244 components (i.e., tangential and radial dimensions of EW vessels, average EW vessel area and EW density) were

245 not related with the Krka River flow and were probably influenced by other environmetal (climatic) factors (Figure

246 7c and d).

247

248 **Figure 7**

249

250 **Discussion**

251 *Comparison of anatomical structure in xylem of W and D oaks*

252 The properties of oak wood are closely related to TRW (e.g., Gasson 1987; Leal et al. 2007, 2008; Rao et al. 1997).

253 Studies on within-tree-variation of wood properties in a radial direction in different oak species have shown that

254 cambial age has an influence on TRW, EW vessel diameter, proportion of fibre, vessel and axial parenchyma in

255 LW and specific gravity (Gasson 1987; Lei et al. 1996). Since cambial age explains more of the variation in wood

256 density than does TRW, although TRW declines with cambial age (Lei et al. 1996; Zhang and Zhong 1991), we

257 excluded the juvenile portion of wood from our analysis.

258   Tree-rings of W oaks were significantly wider than in D oaks, with a lower proportion of EW. It is well

259 known that in ring-porous oak, LWW tends to increase with increasing TRW, whereas the width of EW (EWW)

260   remains more or less constant (Lebourgeois et al. 2004; Lei et al. 1996; Phelps and Workman 1994; Rao et al.

261   1997). More precisely, Zhang (1997) noted that with increasing TRW, LWW increases almost linearly, while

262   EWW increases a little at first, but tends to be constant (about 1 mm) when TRW is wider than 3 mm. Since the

263   anatomical structure of EW and LW is very different, their densities also vary, being for about 30 % higher in LW

264   than in EW (Guilley et al. 1999).

265   We found differences in the anatomical structure of tree-rings in W and D oaks; however, in both groups,

266   anatomical structure of the oak wood proved to be closely related to TRW. In addition to EW proportion, TRW

267   negatively influence the share of total EW conductive area and EW vessel density and, in the case of D oaks, also

268   the proportion of the conductive area in LW, which is in line with the findings of other authors (e.g., Gasson 1987;

269   Phelps and Workman 1994; Rao et al. 1997). The total conductive area in EW was slightly higher in the D oaks,

270   which can be explained by the smaller share of EW in narrow rings, which contain a lower number of vessel rows.

271   It has also been observed in other ring-porous species that in wider rings the proportion of EW vessels with smaller

272   diameters increases, thus reducing the mean EW vessel area (Eilmann et al. 2009; Fonti and García-González 2004;

273   Tardif and Conciatori 2006).

274   Most studies analysing wood anatomical features have focused primarily on the structure of EW (more

275   specifically EW vessels), while the structure of LW has only rarely been examined (e.g., Eilmann et al. 2006;

276   Phelps and Workman 1994). Our study shows that the proportion of conductive elements in LW was about 10%

277   higher in D oaks, although this difference was not statistically significant. In the case of D oaks, narrower rings

278   (less than 800 µm) contained only a small portion of LW, which was mainly composed of LW vessels and tracheids.

279   If fibers were present, they were not arranged in radial flames, as typical of oaks. LW was even absent in some

280   cases. The negative relation between the percentage of LW conductive area and TRW that was observed in D oaks

281   has also been reported by Phelps and Workman (1994). These observations suggest that the formation of LW

282   vessels has priority in LW, in comparison with fibers, indicating the precedence of the conductive function over

283   the mechanical, even though LW vessels do not contribute much to conductivity as long as there are conducting

284   EW vessels. However, as a ring-porous species, oak has strongly reduced hydraulic conductivity in early spring

285   because the large vessels in the EW from the past year become embolized either during the summer or during the

286   winter (Bréda and Granier 1996; Hinckley et al. 1979). Early spring, when a new set of EW vessels is forming, is

287   therefore an exception; at that time the ascent of sap takes place via LW vessels, which remain functional for

288   several years (Tyree and Zimmermann 2010). Vessel diameter, area and percentage of conductive area strongly

289   influence the amount of water that can be transported in the living tree, and so the higher proportion of ring

290   occupied by conductive elements, the less tissue is available for supporting, strengthening and storage. A decrease

291   in fiber proportion would then decrease the mechanical properties of LW, but the need for additional strength

292   becomes less crucial as the stem increases in diameter (Rao et al. 1997).

293   The anatomical structure of wood in *Q. robur*, which is closely related to TRW, with different proportions

294   of xylem elements and their morphological characteristics, defines the hydraulic and mechanical properties of

295   wood and hence affects the survival and efficiency of the living tree (Rao et al. 1997). In terms of wood properties,

296   an increase in the size and density of EW vessels have a negative effect on wood density (Leal et al. 2007)

297   indicating that diminished radial growth considerably negatively affects wood properties and quality of oaks.

298

299   *Relation between the measured anatomical variables in each of the studied oak groups and the Krka River flow*

300   TRW and LW density have been proven to be closely linked to environmental conditions and are therefore very

301   useful for climate reconstruction (e.g., Friedrichs et al. 2009). In this study, we have demonstrated that certain

302   wood anatomical variables of *Q. robur* have a potential also in dendrohydrological studies.

303   The two groups of oaks responded differently to the Krka River flow in the studied period (i.e. 39 years).

304   TRW and LW proportion of D oaks were affected by (mainly maximum) spring and minimum summer flow of

305   the Krka River and were wider if the flow in spring was lower but higher in summer. Since TRW (as well as LW

306   proportion) was negatively related with the conductive area of EW vessels and EW vessel density, these two

307   variables were higher if the spring flow was higher. On the other hand were anatomical variables of W oaks

308   predominantly related to the (mean) summer flow showing its positive relation with tree-ring and LW proportion,

309   but negative with conductive area of EW vessels, EW vessel density and the share of vessels in LW. Thus, in both

310   oak groups were the conductive area of EW vessels and their density undoubtely closely (inversely) related to

311   TRW. This could be explained by almost proportional relationship between TRW and LWW (Rao et al. 1997).

312   Hence, if tree-ring is wider, the proportion of LW is larger and consequently the share of EW vessels and their

313   density decreases. Wimmer (2002) considered that only a few wood-anatomical features have proved to be useful

314   for characterizing the relationship between tree growth and climate, because they are often inter-correlated with

315   more easily obtainable variables, thus providing little new environmental information. According to Tardif and

316   Conciatori (2006), EW vessel features in ring-porous species may be best used to decipher a discontinuous signal

317   related to tree growth, in particular, for understanding tree physiology. At this point, it should be stressed again

318   that, in addition to our small sample size, most dendroecological studies of *Quercus* spp. have focused on climatic

319   data and not hydrological data and have not been conducted in an area with regular flooding; it is therefore difficult

320   to compare our results with their findings. *Quercus* species are differently adapted to drought (Nardini and Tyree

321   1999). *Q. robur* is known to be a water-demanding species and is a regular constituent of floodplain forests. It is

322   generally considered to be one of the most flood-tolerant *Quercus* spp. with respect to growth and survival; it can

323   endure prolonged periods of flooding due to a better adjustment of leaf biomass production to the hydraulic

324   conductivity of the root system (Ferner 2009; Prpi 2003; Schmull and Thomas 2000). However, prolonged

325   flooding can cause a dramatic decrease in assimilation and transpiration rates (Ferner 2009).

326   Radial growth of W oaks was stimulated in the summer period (July-August) if the flow was higher. On

327   the other hand, higher flows of the Krka river did not promote the growth of D oaks although they are growing on

328   a non-flooded area. Few studies have been published on growth patterns of bog *Q. robur* and *Q. sessiliflora* , which

329   are considered to be sensitive indicators of changing ecological conditions because they grow under temporarily

330   extremely wet site conditions (Leuschner et al. 2002; Pilcher 1996; Sass-Klaassen and Hanraets 2006). Suppressed

331   growth of these oaks was probably caused by dramatic hydrological changes resulting in a shortened growth season

332   with an absence of LW (Sass-Klaassen and Hanraets 2006). Site hydrology seems to play an important role in the

333   growth and population dynamics of oaks from such areas (Leuschner et al. 2002; Sass-Klaassen and Hanraets

334   2006). Similarly, *Q. robur* decline and dieback in European floodplain forests in recent years occur particularly in

335   areas that have already been stressed by a deteriorating hydrological regime (Hager and Buchleitner 2001; Levani

336   et al. 2011; Vukeli and Rauš 2001). The lowered water table makes the rehabilitation of the forests extremely

337   difficult because the roots of the saplings in early years draw water from the soil layer, which is watered from

338   above. However, when roots grow below these layers in later years, they cannot reach the depressed water table

339   and consequently perish (Haraszthy 2001). The reduced growth of *Q. robur*, often resulting in tree death, may be

340   associated with differences in TRW, EW vessel area and carbon isotope discrimination (Levani et al. 2011).

341   Investigating xylem anatomy as a time series at the intra- and inter-annual level has already been

342   demonstrated to be a promising approach in tree biology and climate change research, particularly if complemented

343   by physiological and ecological studies (Fonti et al. 2010). Specific anatomical features, such as EW vessel size

344   and density, have been shown to be reliable ecological indicators that contain environmental information different

345   from that stored in TRW (e.g. Tardif and Conciatori 2006, Fonti et al. 2009, 2010; George et al. 2002; Sass-

346   Klaassen et al. 2011). Interestingly, we found no relation of the Krka River flow with other anatomical variables

347   (size of the EW vessels and their density in EW) of D and W oaks, suggesting that they probably depend on other

348   environmetal/climatic factors. Nevertheless, floods are often directly, but very locally, recorded in the cambium,

349 resulting in an extreme reduction in EW vessel area in *Quercus* spp. (George et al. 2002; Sass-Klaassen et al.

350 2010).

351 　　　Site-specific soil regimes often play a role in limiting moisture availability in oak forests (Charton and

352 Harmon 1973; Estes 1970). Tree-ring time series contain a lot of information about environmental conditions and

353 their impact on the growth of trees. Our study clearly shows that the hydrologic information stored in wood

354 anatomical features may vary, even within the same forest stand, and largely depends on the micro-environment.

355 Reduced wood increments of D oaks suggest that growth conditions are less favourable in the non-flooded areas

356 of Krakovo lowland forest. Decreasing growth curves are among the most obvious growth-related characteristics

357 of the diminishing vitality of trees, which is not only a species-specific but also a site-specific feature (Bigler et al.

358 2004). The vitality of *Q. robur* from Krakovo forest might vary, implying a link between the health state of oaks

359 from lowland forest in Slovenia and hydrological conditions. Our research suggests that oaks from the non-flooded

360 areas might experience more physiological stress and contain different hydrological information. Thus, trees

361 intended for hydrological or climatological reconstruction must be carefully selected in order to avoid the

362 possibility of error and potential loss of information in the reconstruction. However, this hypothesis is speculative

363 and for deeper investigations a larger number of sampled trees should be included from several areas in the

364 Krakovo forest. For present study, no data on groundwater were collected but these will be considered in further

365 studies in order to understand better the way *Q. robur* uses water resources and could complement the results

366 presented in this study by bringing new insight into the survival mechanisms of trees in conditions of changed

367 water availability.

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552 **Table captions**

553

554 **Table 1.** Measured anatomical variables in the tree-rings of W and D oaks. EW – earlywood, LW – latewood.

555

556 **Table 2.** Average values and standard deviation (SD) of measured anatomical variables in W and D oaks. TRW –

557 tree-ring width, EW – earlywood, LW – latewood, T ave ves - Average tangential diameter of EW vessels, R ave

558 ves - Average radial diameter of EW vessels, EW ves area - Average values of EW vessel area, EW ves/Meas area

559 - Conductive area of EW vessels, EW ves/EW area - Conductive area in EW, No of ves/Meas area - EW vessel

560 density, No of ves/EW area - EW vessel density in EW, LW portion ves/Fibre - Proportion of LW vessels according

561 to the proportion of fibers in LW.

562

563

564   **Figure captions**

565

566   **Figure 1.** Average monthly flow of the Krka River (Qs, Qvp, Qnp). Qnp – minimal monthly rate of flow (daily

567   average) [m3/s], Qs – average monthly rate of flow [m3/s], Qvp – maximal monthly rate of flow (daily average)

568   [m3/s].

569

570   **Figure 2.** Krka River flow variables (Qs, Qvp, Qnp) calculated at annual scales. Qnp – minimal monthly rate of

571   flow (daily average) [m3/s], Qs – average monthly rate of flow [m3/s], Qvp – maximal monthly rate of flow

572   (daily average) [m3/s].

573

574   **Figure 3.** Schematic illustration of the measured anatomical parameters in each tree-ring. EW – earlywood, LW

575   – latewood, T dim – tangential dimension of EW vessel, R dim – radial dimension of EW vessel.

576

577   **Figure 4.** Similar TRW (a-b and c-d) with different anatomical structure. a - Tree-ring of D oak with higher

578   proportion of EW; b - Tree-ring of D oak with higher proportion of LW; c - Tree-ring of W oak with higher

579   proportion of EW; d - Tree-ring of W oak with higher proportion of LW. EW – earlywood, LW – latewood.

580

581   **Figure 5.** Time series of of tree-ring widths and wood-anatomical characteristics of W and D oaks for the period

582   1970-2008 showing differences in some parameters (TRW, EW ves/Mean area, EW ves/EW area, No of ves/Meas

583   area and LW portion), but similarities in others (T ave ves, R ave ves, EW ves area, No of ves/ EW area and LW

584   portion ves/Fibre). Error bars indicate standard error. Repeated measures of variance (R-M ANOVA) was used to

585   test for differences between W and D oaks in all the measured anatomical variables. TRW – tree-ring width, EW

586   – earlywood, LW – latewood, T ave ves - Average tangential diameter of EW vessels, R ave ves - Average radial

587   diameter of EW vessels, EW ves area - Average values of EW vessel area, EW ves/Meas area - Conductive area

588   of EW vessels, EW ves/EW area - Conductive area in EW, No of ves/Meas area - EW vessel density, No of ves/EW

589   area - EW vessel density in EW, LW portion ves/Fibre - Proportion of LW vessels according to the proportion of

590   fibers in LW.

591

592   **Figure 6.** Anatomical characteristics and relations among the variables are explained by PC1 and PC3 in D oaks

593   (a, c) and by PC2 and PC4 in W oaks (b, d). EW – earlywood, LW – latewood, T ave ves - Average tangential

594   diameter of EW vessels, R ave ves - Average radial diameter of EW vessels, EW ves area - Average values of EW

595   vessel area, EW ves/Meas area - Conductive area of EW vessels, EW ves/EW area - Conductive area in EW, No

596   of ves/Meas area - EW vessel density, No of ves/EW area - EW vessel density in EW, LW portion ves/Fibre -

597   Proportion of LW vessels according to the proportion of fibers in LW.

598

599   **Figure 7.** Correlation between PCA scores and the Krka River flow data at annual and seasonal (from previous

600   autumn to summer) time scales. PC1 and PC3 are mainly related to D oaks (a, c) whereas PC2 and PC4 to W oaks

601   (b, d). The horizontal line indicates significance level at 95%. Qnp – minimum flow, Qs - mean flow, Qvp

602   maximum flow, AUT-1 – previous autumn, WIN – winter, SPR – spring, SUM – summer, EW – earlywood, LW

603   – latewood, T ave ves - Average tangential diameter of EW vessels, R ave ves - Average radial diameter of EW

604   vessels, EW ves area - Average values of EW vessel area, EW ves/Meas area - Conductive area of EW vessels,

605   EW ves/EW area - Conductive area in EW, No of ves/Meas area - EW vessel density, No of ves/EW area - EW

606   vessel density in EW, LW portion ves/Fibre - Proportion of LW vessels according to the proportion of fibers in

607   LW.

608

609 **Tables**

610

611 **Table 1.** Measured anatomical variables in the tree-rings of W and D oaks. EW – earlywood, LW – latewood.

612

Code of the variable	Description of the measured variable (unit)
TRW	Width of tree-ring (µm)
T ave ves	Average tangential diameter of EW vessels (µm)
R ave ves	Average radial diameter of EW vessels (µm)
EW ves area	Average values of EW vessel area (µm2)
EW ves/Meas area	Conductive area of EW vessels (Percentage of cross-sectional area occupied by EW vessels) 100* (%)
EW ves/EW area	Conductive area in EW (Percentage of EW cross-sectional area occupied by EW vessels) 100* (%)
No of ves/Meas area	EW vessel density (Number of EW vessels per square millimetre of measured area of the tree-ring) (n°/mm2)
No of ves/EW area	EW vessel density in EW (Number of EW vessels per square millimetre of EW measured area) (n°/mm2)
LW portion ves/Fibre	Proportion of LW vessels according to the proportion of fibers in LW (%)
LW portion	Proportion of LW (%)

613

614

615

616 **Table 2.** Average values and standard deviation (SD) of measured anatomical variables in W and D oaks. TRW –

617 tree-ring width, EW – earlywood, LW – latewood, T ave ves - Average tangential diameter of EW vessels, R ave

618 ves - Average radial diameter of EW vessels, EW ves area - Average values of EW vessel area, EW ves/Meas area

619 - Conductive area of EW vessels, EW ves/EW area - Conductive area in EW, No of ves/Meas area - EW vessel

620 density, No of ves/EW area - EW vessel density in EW, LW portion ves/Fibre - Proportion of LW vessels according

621 to the proportion of fibers in LW.

622

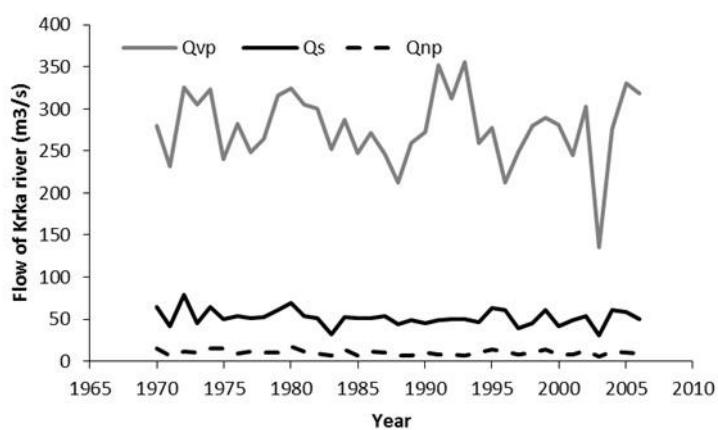|	D Oaks		W Oaks	
Variable	Average	SD	Average	SD
TRW (µm)	1196.31	593.94	2642.05	887.52
T ave ves (µm)	293.40	58.11	275.56	55.48
R ave ves (µm)	308.47	60.59	332.44	65.95
EW ves area (µm2)	71753.86	14874.27	72239.30	10252.00
EW ves/Meas area (%)	28.868	10.595	17.633	5.364
EW ves/EW area (%)	50.085	5.525	46.086	5.823
No of ves/Meas area (n°/mm2)	4.092	1.778	2.242	0.833
No of ves/EW area (n°/mm2)	7.057	1.493	6.293	1.138
LW portion ves/Fibre (%)	65.38	20.87	55.90	9.13
LW portion (%)	42.38	19.85	61.71	10.63

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Figures

Figure 1. Average monthly flow of the Krka River (Qs, Qvp, Qnp). Qnp – minimal monthly rate of flow (daily

average) [m3/s], Qs – average monthly rate of flow [m3/s], Qvp – maximal monthly rate of flow (daily average)
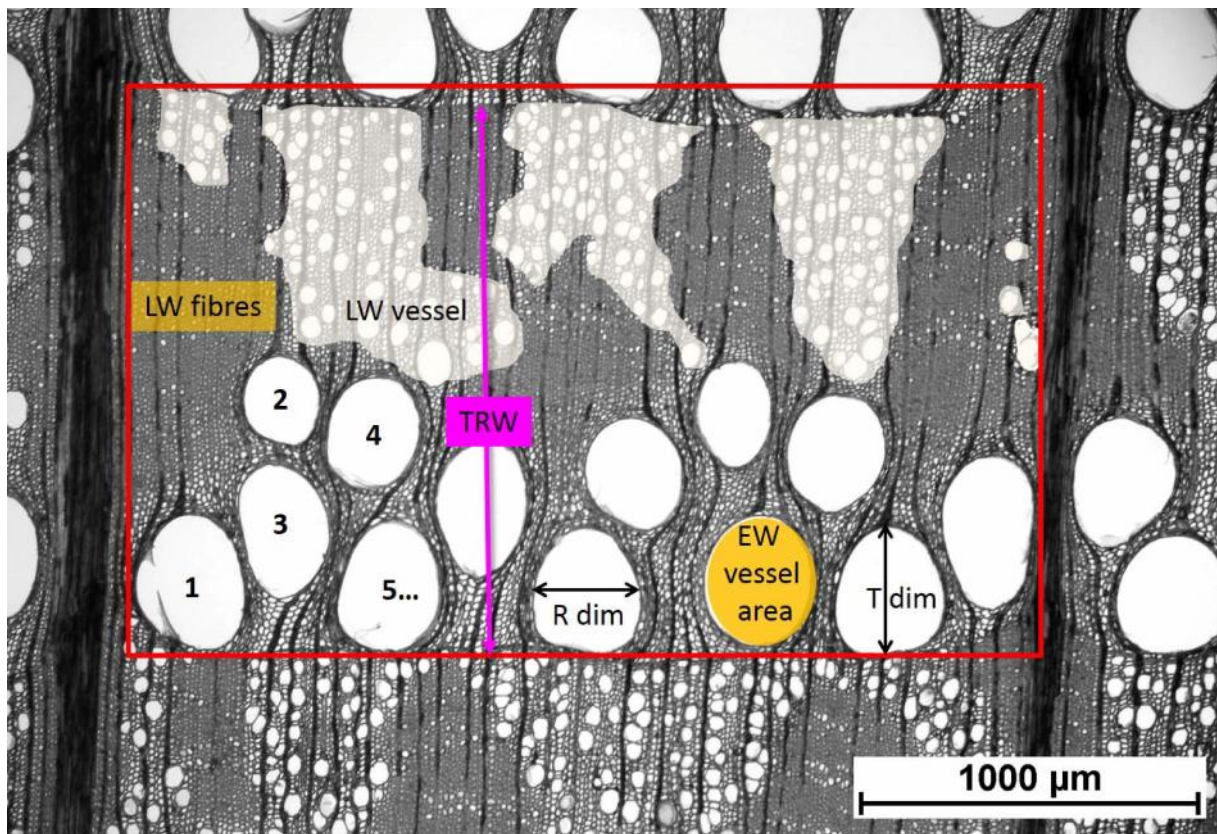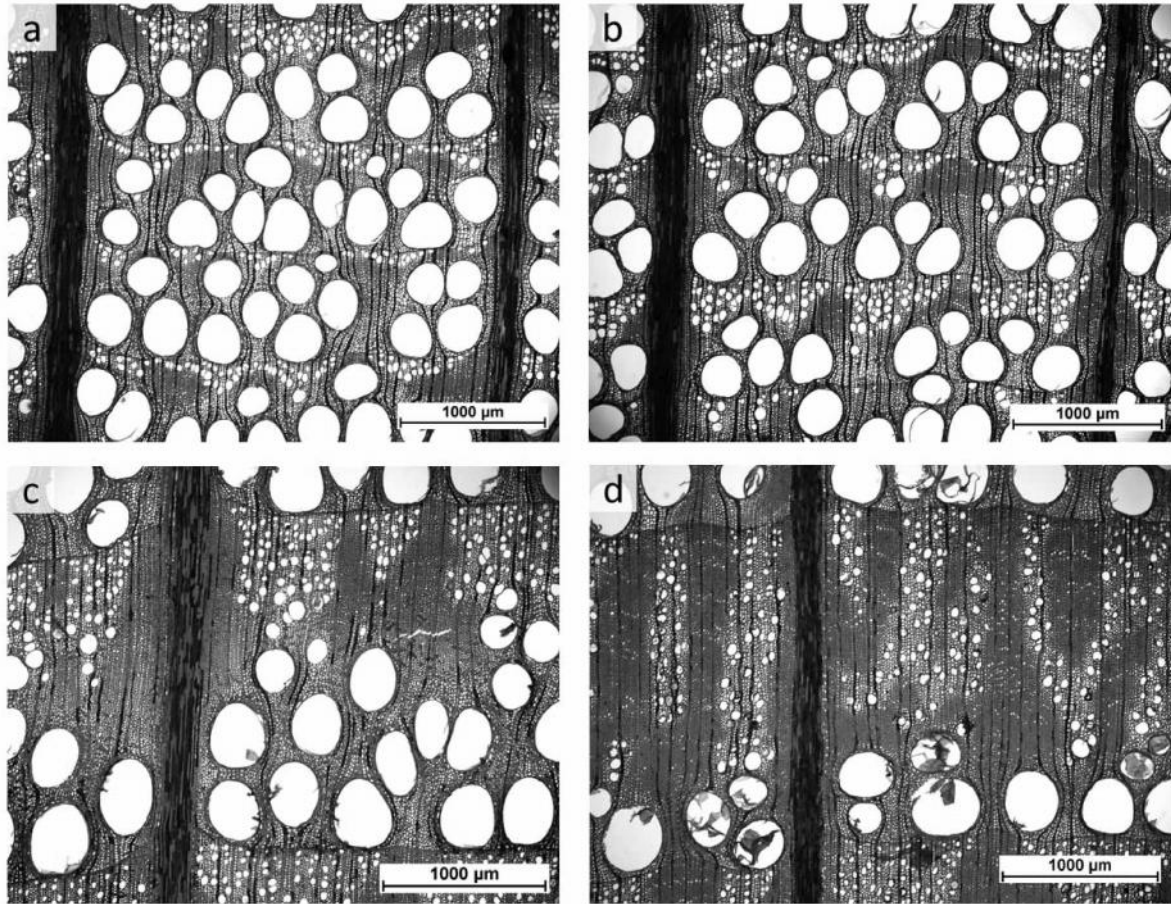
[m3/s].

Figure 2. Krka River flow variables (Qs, Qvp, Qnp) calculated at annual scales. Qnp – minimal monthly rate of

flow (daily average) [m3/s], Qs – average monthly rate of flow [m3/s], Qvp – maximal monthly rate of flow

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Figure 3. Schematic illustration of the measured anatomical parameters in each tree-ring. EW – earlywood, LW – latewood, T dim – tangential dimension of EW vessel, R dim – radial dimension of EW vessel.

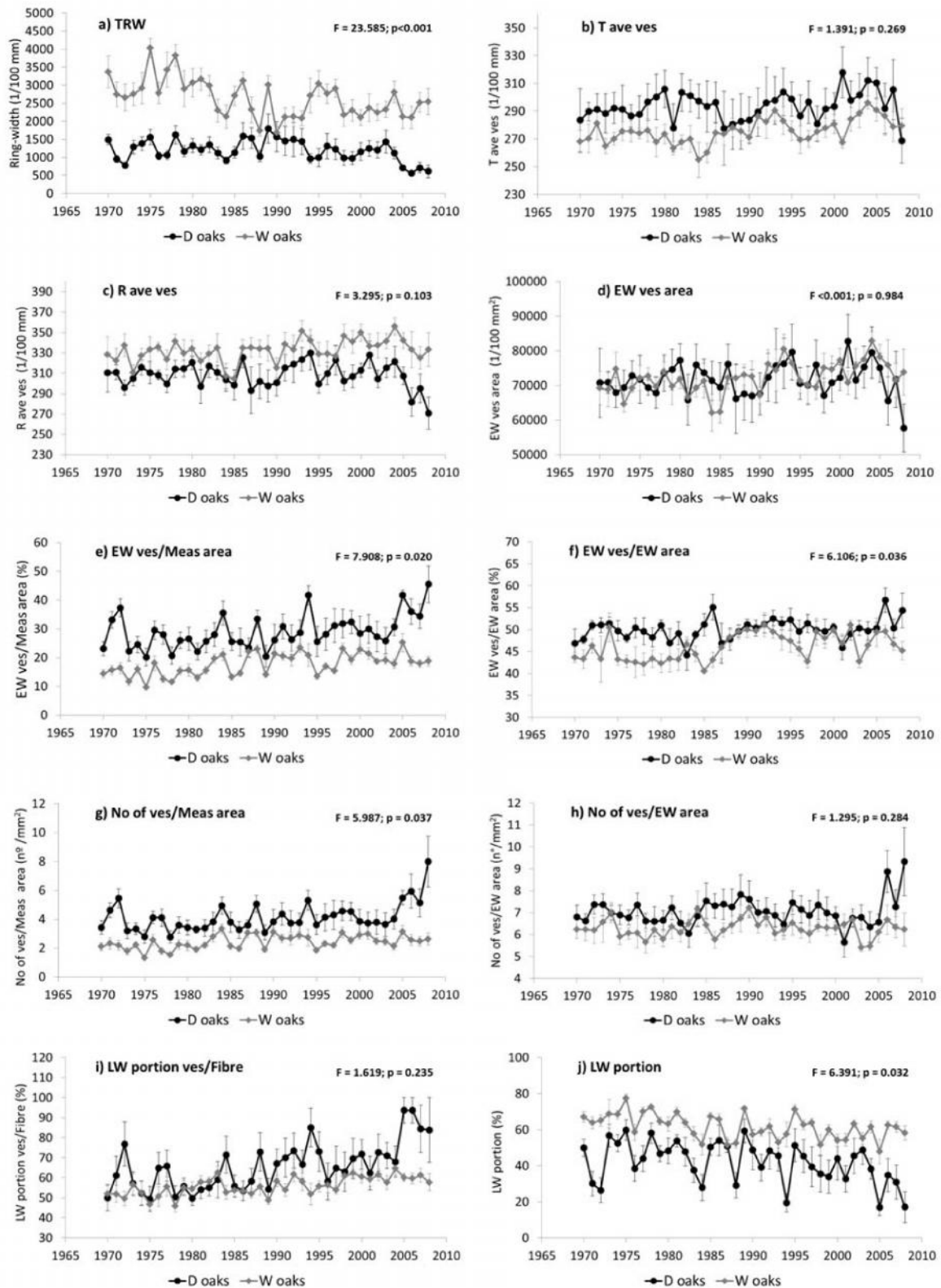**Figure 4.** Similar TRW (a-b and c-d) with different anatomical structure. a - Tree-ring of D oak with higher proportion of EW; b - Tree-ring of D oak with higher proportion of LW; c - Tree-ring of W oak with higher proportion of EW; d - Tree-ring of W oak with higher proportion of LW. EW – earlywood, LW – latewood.

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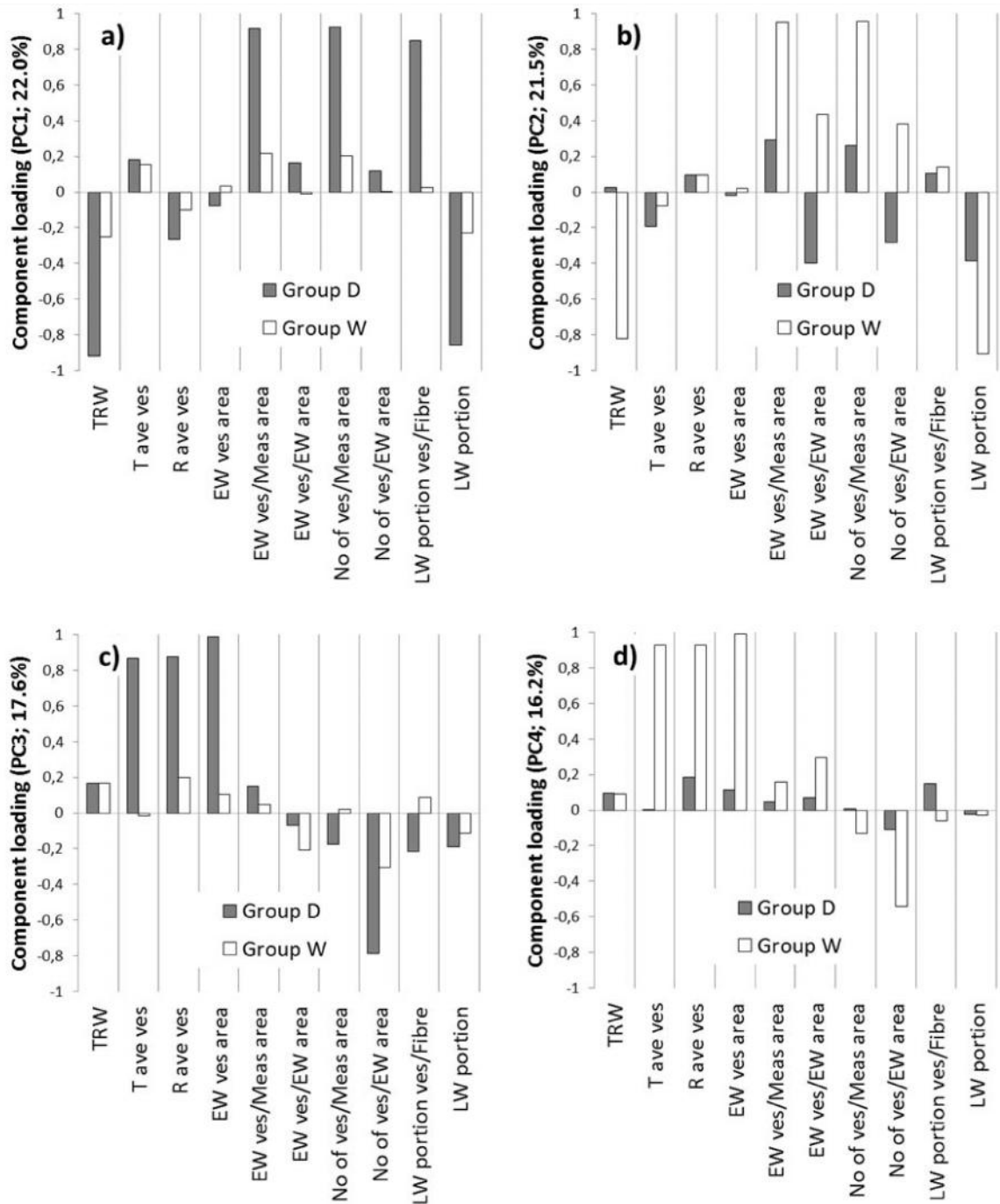
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657 area - EW vessel density in EW, LW portion ves/Fibre - Proportion of LW vessels according to the proportion of

658 fibers in LW.

659

660

Figure 6. Anatomical characteristics and relations among the variables are explained by PC1 and PC3 in D oaks

(a, c) and by PC2 and PC4 in W oaks (b, d). EW – earlywood, LW – latewood, T ave ves - Average tangential

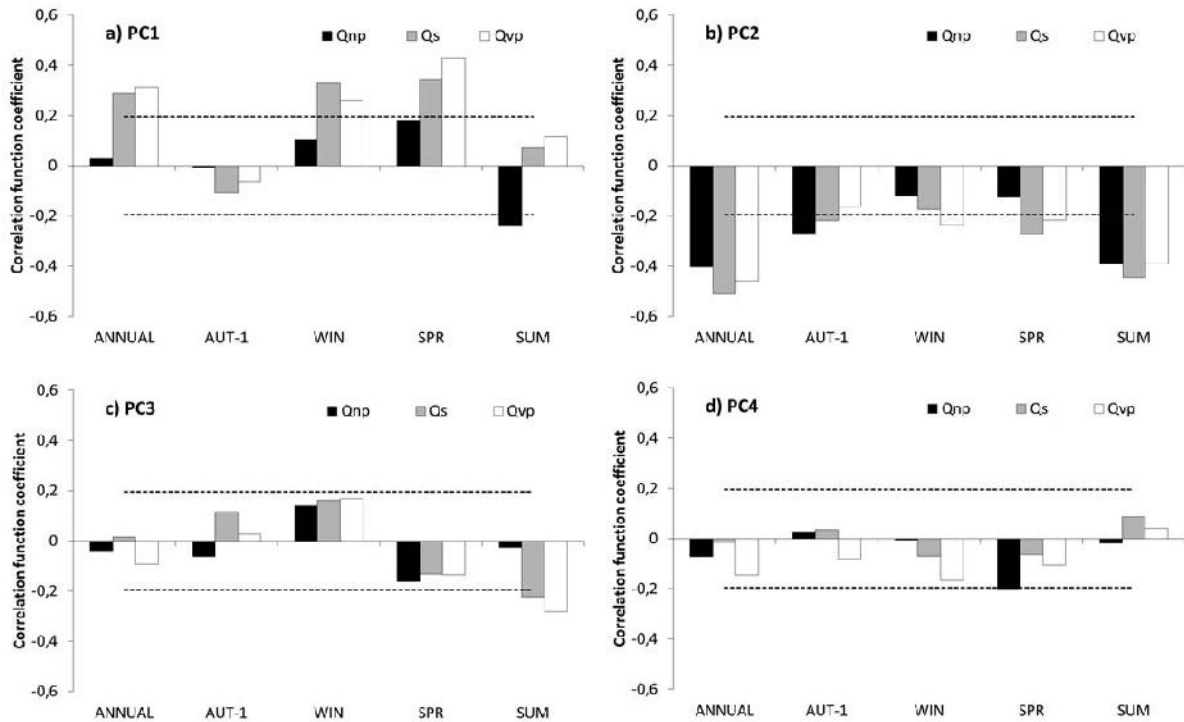diameter of EW vessels, R ave ves - Average radial diameter of EW vessels, EW ves area - Average values of EW

vessel area, EW ves/Meas area - Conductive area of EW vessels, EW ves/EW area - Conductive area in EW, No

of ves/Meas area - EW vessel density, No of ves/EW area - EW vessel density in EW, LW portion ves/Fibre -

Proportion of LW vessels according to the proportion of fibers in LW.

667

Figure 7. Correlation between PCA scores and the Krka River flow data at annual and seasonal (from previous autumn to summer) time scales. PC1 and PC3 are mainly related to D oaks (a, c) whereas PC2 and PC4 to W oaks (b, d). The horizontal line indicates significance level at 95%. Qnp – minimum flow, Qs - mean flow, Qvp maximum flow, AUT-1 – previous autumn, WIN – winter, SPR – spring, SUM – summer, EW – earlywood, LW – latewood, T ave ves - Average tangential diameter of EW vessels, R ave ves - Average radial diameter of EW vessels, EW ves area - Average values of EW vessel area, EW ves/Meas area - Conductive area of EW vessels, EW ves/EW area - Conductive area in EW, No of ves/Meas area - EW vessel density, No of ves/EW area - EW vessel density in EW, LW portion ves/Fibre - Proportion of LW vessels according to the proportion of fibers in LW.