

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.

46

47 **Keywords**

48 hydrologic sensitivity, European oak, tree-rings, vessels, wood structure, river flow, micro-environment

49

50

51 **Introduction**

52 In Slovenia, oaks (*Quercus robur* L. and *Quercus sessiliflora* Salisb.) are economically very important wood
53 species, representing about 7% of the entire wood stock (Gozdnogospodarski etc. 2006). In relation to *Q. robur*,
54 the lowland forest area has been shrinking, due to human settlement in the past, intensive and unplanned
55 silvicultural and agricultural exploitation of the land and conflicts of interest, so only a few lowland oak forest
56 stands have managed to survive (Kadunc 2010). In addition, as in many European countries (e.g., Klimo and Hager
57 2001), a trend of decreasing vitality of *Q. robur* has been observed in most sites in recent decades (Cater et al.
58 2001). One of the main reasons for this situation in Slovenia is ascribed to decreasing ground water levels due to
59 changes in climatic conditions and unsuitable artificial melioration of land for agricultural purposes, for which
60 numerous drainage ditches were excavated in the 19th century (Cater et al. 2001). The most obvious response of
61 *Q. robur* to the changing environmental (hydrologic) conditions is seen in its decreased vitality (e.g., Hager and
62 Buchleitner 2001; Vukelić and Rauš 2001), resulting in reduced wood increment (Levanić et al. 2011), which is
63 closely related to the structure of wood and its quality (Rao et al. 1997).

64 In addition to major economic consequences in these areas, ecological issues associated with decreasing
65 vitality of *Q. robur* stands cannot be neglected. The many local oak tree-ring chronologies from various sites of
66 Slovenia (Čufar and Levanić 1999a, b, Čufar et al. 2008) differ greatly among each other, particularly in the case
67 of *Q. robur* from lowland sites, where tree growth is often influenced by micro-site hydrologic conditions (Cater
68 2003; Cater and Batić 2006; Cater and Levanić 2004; Levanić 1993; Levanić et al. 2011). However, tree-ring
69 width (TRW) is only one environmental proxy, whereas others still remain to be explored. In this respect, the use
70 of other proxies, such as wood anatomical variables, have proved to be particularly promising (e.g., Fonti et al.
71 2010).

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

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

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 *Quercus robur*-*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 campestre*,
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

111 tributaries and regularly floods, especially in spring and autumn. Data for minimal (Q_{np}), average (Q_s) and
112 maximal (Q_{vp}) 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, $T_{Jan} = -0.1^\circ\text{C}$, $-T_{Jul} = 20.1^\circ\text{C}$) 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 years old, with DBH 30-60 cm, without any visible mechanical injuries 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 slides. 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 analyzed 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

230 **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 variability 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 environmental (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 undoubtedly 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; Schnull 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 environmental/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.

368

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551

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.

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563

564 **Figure captions**

565

566 **Figure 1.** Average monthly flow of the Krka River (Q_s , Q_{vp} , Q_{np}). Q_{np} – minimal monthly rate of flow (daily
567 average) [m³/s], Q_s – average monthly rate of flow [m³/s], Q_{vp} – maximal monthly rate of flow (daily average)
568 [m³/s].

569

570 **Figure 2.** Krka River flow variables (Q_s , Q_{vp} , Q_{np}) calculated at annual scales. Q_{np} – minimal monthly rate of
571 flow (daily average) [m³/s], Q_s – average monthly rate of flow [m³/s], Q_{vp} – 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
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590 fibers in LW.

591

592 **Figure 6.** Anatomical characteristics and relations among the variables are explained by PC1 and PC3 in D oaks
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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
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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 (μm^2)
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) ($\text{n}^\circ/\text{mm}^2$)
No of ves/EW area	EW vessel density in EW (Number of EW vessels per square millimetre of EW measured area) ($\text{n}^\circ/\text{mm}^2$)
LW portion ves/Fibre	Proportion of LW vessels according to the proportion of fibers in LW (%)
LW portion	Proportion of LW (%)

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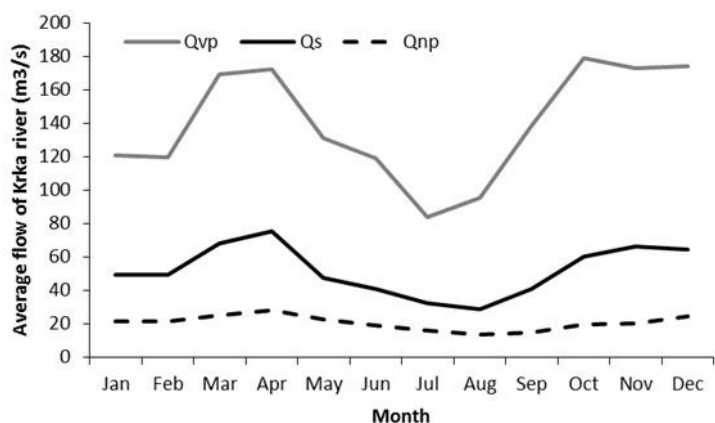
Table 2. Average values and standard deviation (SD) of measured anatomical variables in W and D oaks. TRW – tree-ring width, EW – earlywood, LW – latewood, T ave ves - Average tangential diameter of EW vessels, R ave ves - Average radial diameter of EW vessels, EW ves area - Average values of EW vessel 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.

Variable	D Oaks		W Oaks	
	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 (μm^2)	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 ($\text{n}^\circ/\text{mm}^2$)	4.092	1.778	2.242	0.833
No of ves/EW area ($\text{n}^\circ/\text{mm}^2$)	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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627 **Figures**

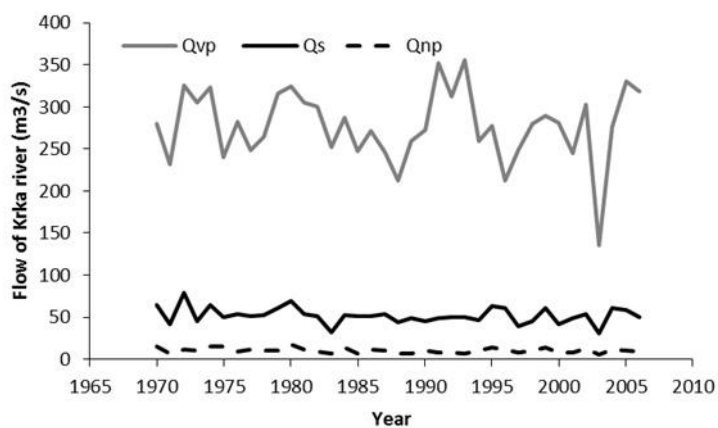
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632 [m³/s].

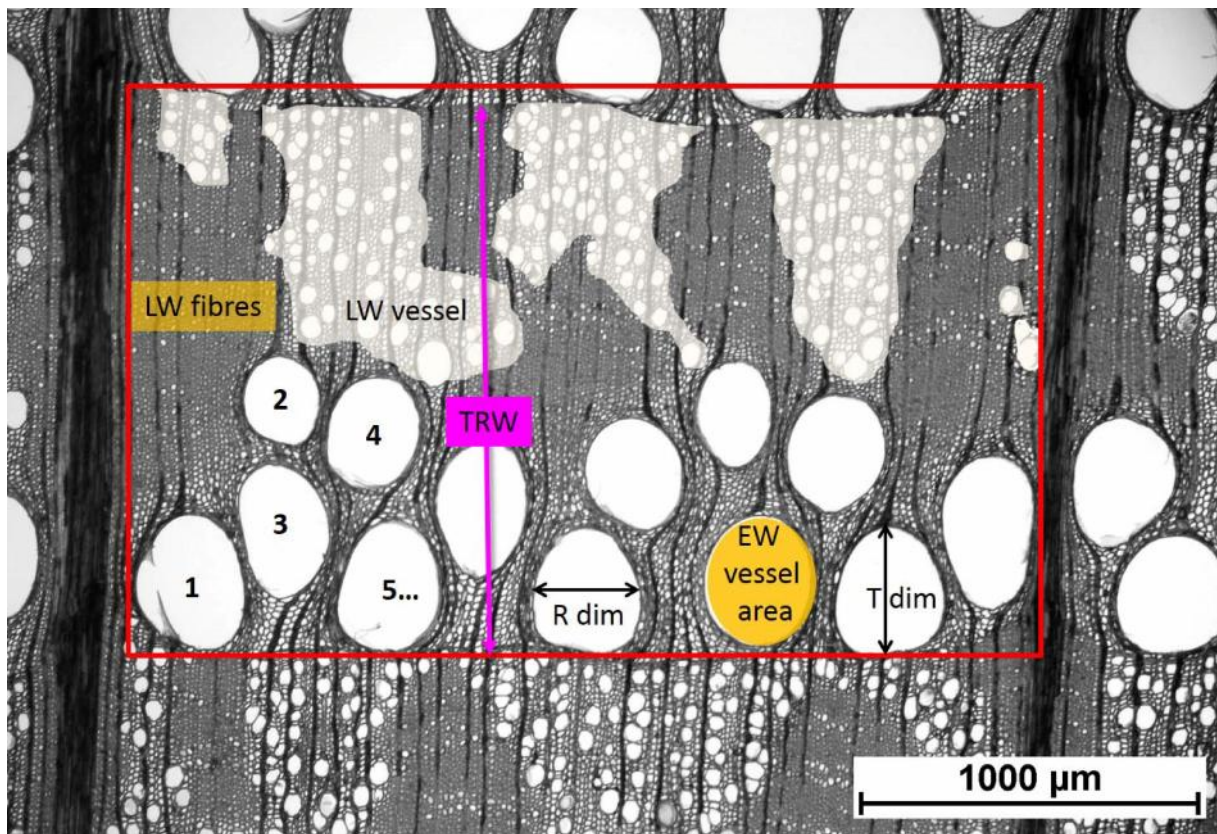
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635 **Figure 2.** Krka River flow variables (Q_s , Q_{vp} , Q_{np}) calculated at annual scales. Q_{np} – minimal monthly rate of
636 flow (daily average) [m³/s], Q_s – average monthly rate of flow [m³/s], Q_{vp} – maximal monthly rate of flow
637 (daily average) [m³/s].

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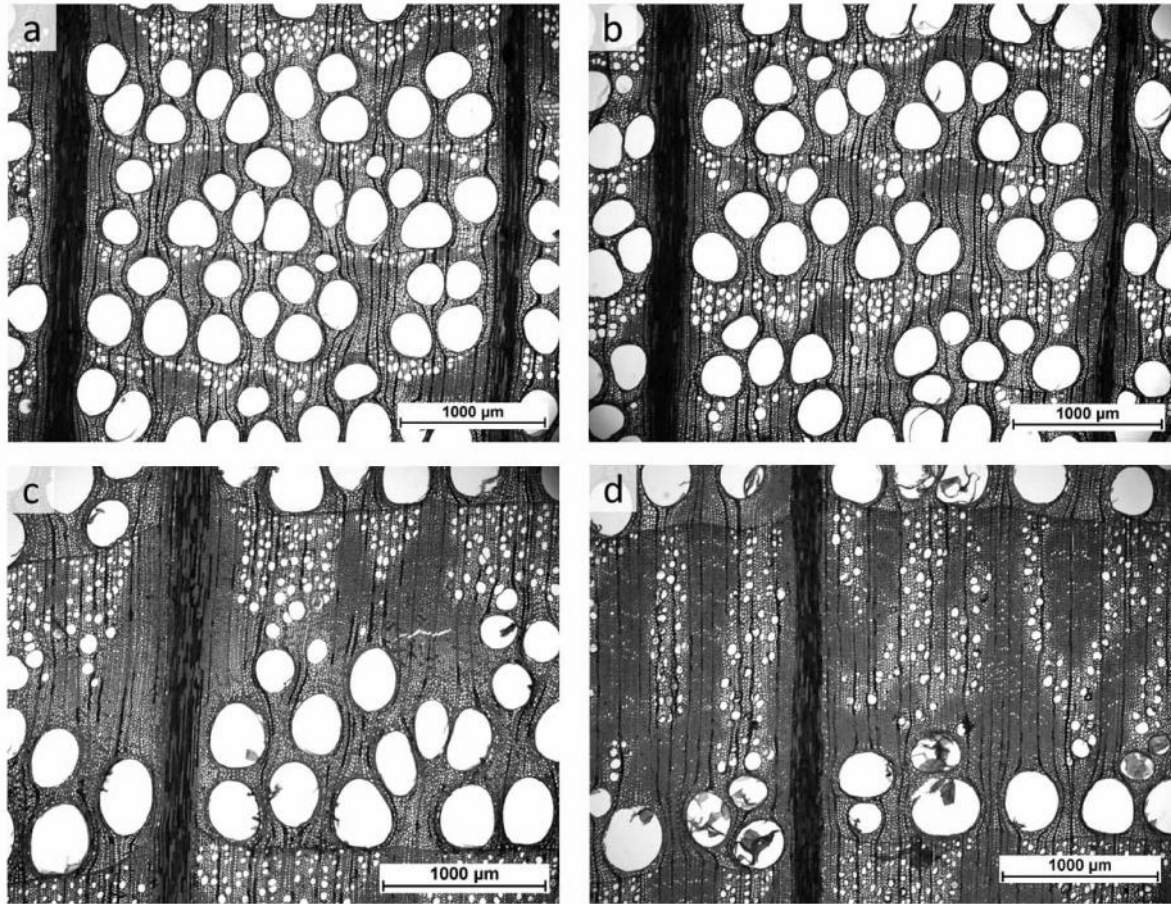


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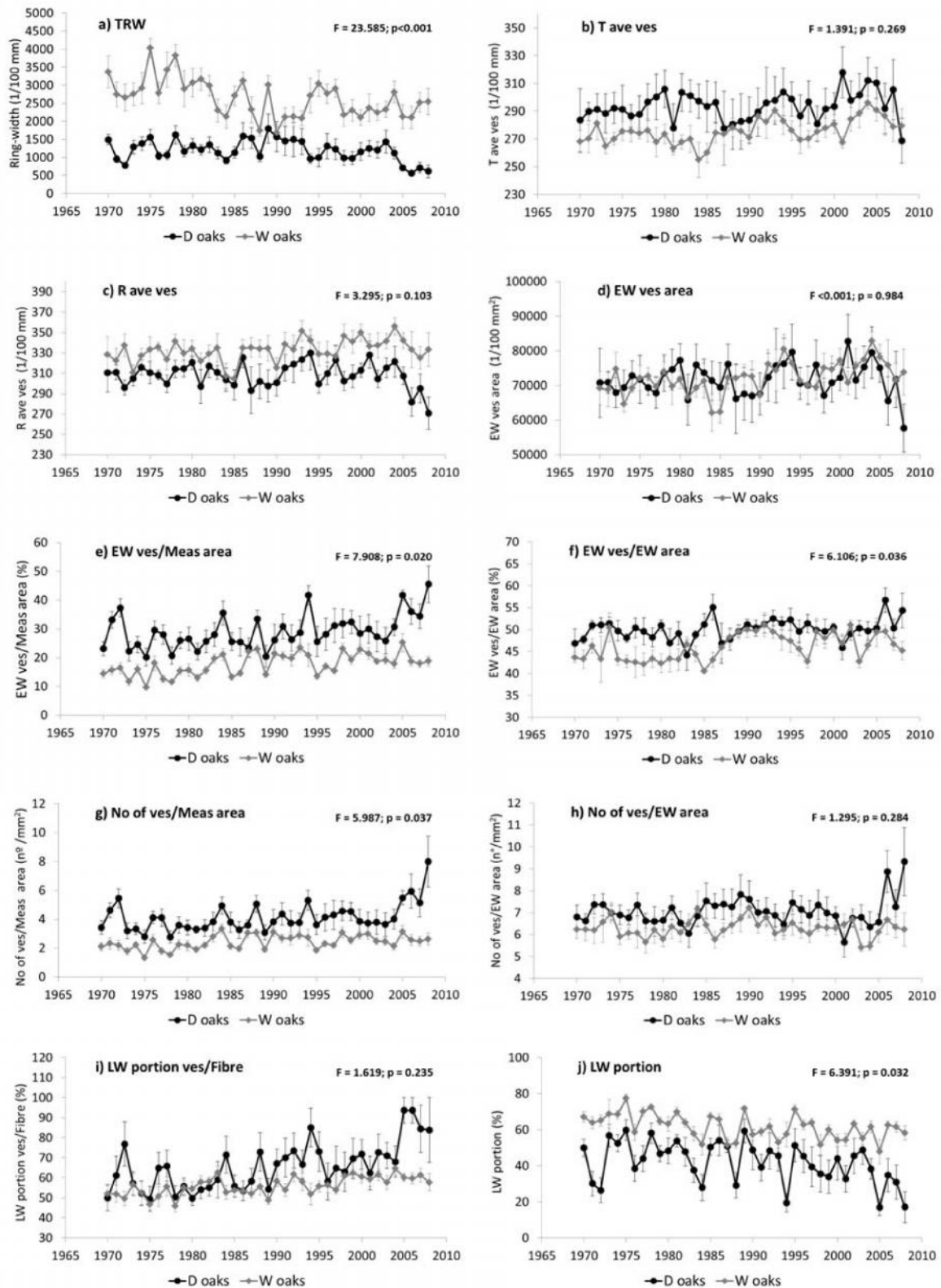
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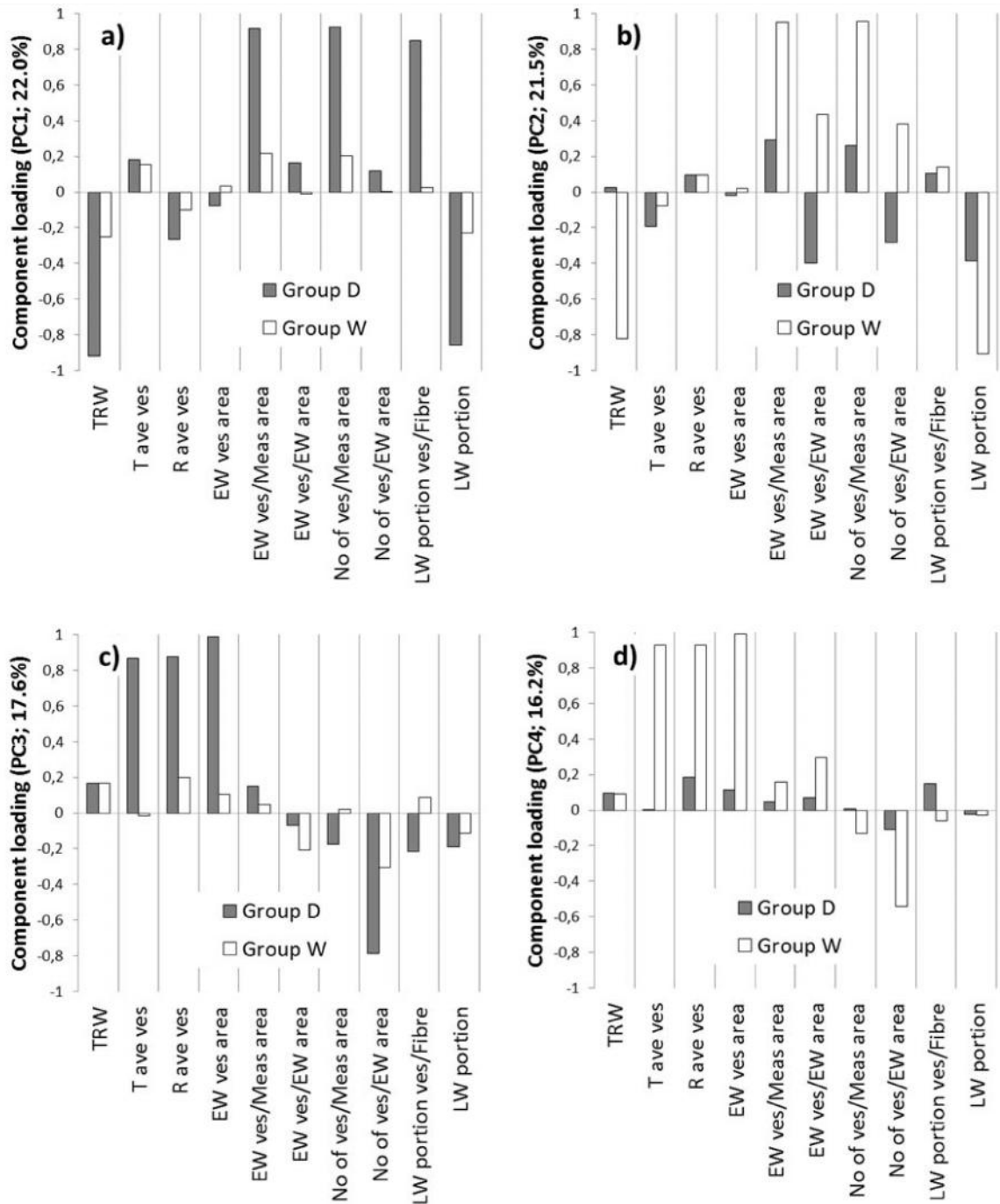
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659



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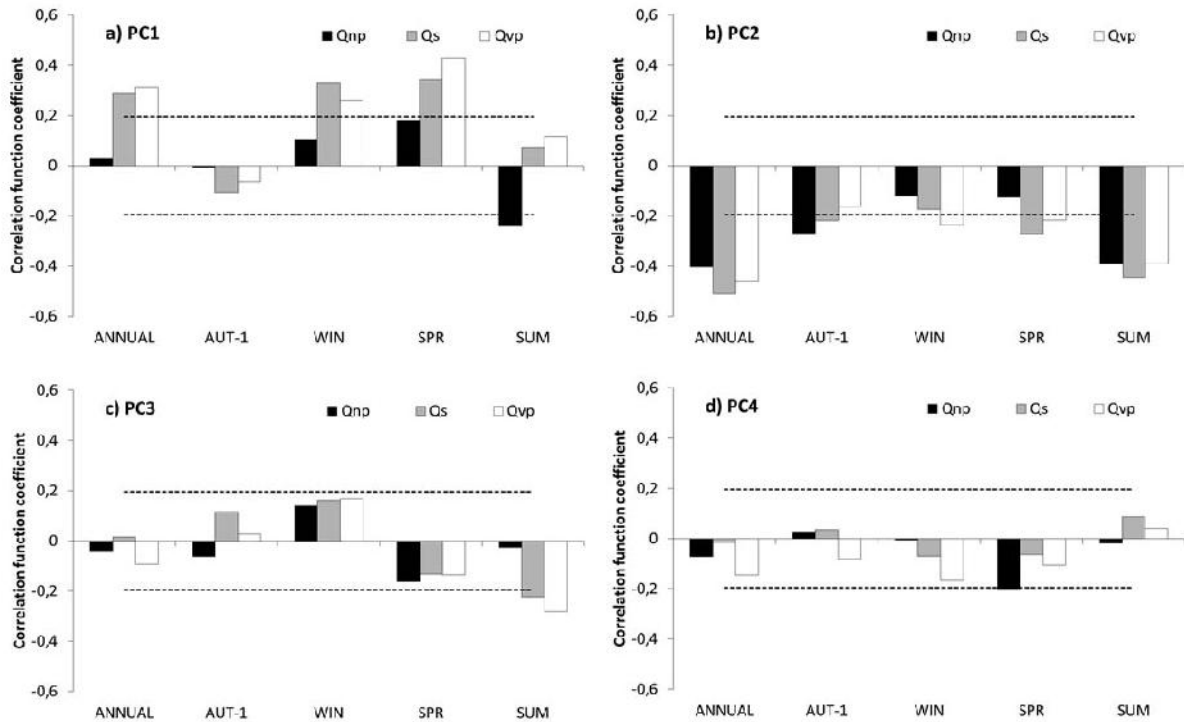
663 diameter of EW vessels, R ave ves - Average radial diameter of EW vessels, EW ves area - Average values of EW

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

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