

1 **TITLE**

2 Intra-species variation in maximum moisture content, cell-wall density and porosity of hardwoods

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18 **SHORT TITLE**

19 Maximum moisture content, cell-wall density and porosity of wood

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27 **ABSTRACT**

28 Some properties of wood, such as maximum moisture content, cell-wall density and porosity, are
29 not well known, even though they affect the performance of chemical preservatives, glues and
30 coatings on wood. This knowledge gap was addressed in the present study by analysing these
31 physical properties in laurel (*Laurus nobilis* L.) wood. Laurel is a common hardwood tree in southern
32 Europe. Seventeen laurel trees were felled for the study, and 300 defect-free specimens were
33 obtained from the trees for analysis. The following mean values were obtained: wood maximum
34 moisture content, 114 %; cell-wall oven-dry density, 1198 kg m⁻³; and oven-dry wood porosity, 45 %.
35 Significant inter- and intra-tree variations in the three properties were observed. The inter-tree
36 variation was mainly attributed to the tree age, and the trend suggests that wood maximum
37 moisture content and porosity are expected to be lower in older trees than those under study. The
38 values of the three properties were slightly, but statistically significantly, lower at the highest
39 positions in the tree. Harvesting of the basal logs of young trees is therefore advisable only if more
40 porous wood is required, and commercial exploitation of the whole trunk of mature trees is
41 recommended if more compact wood is required. The variation in cell-wall density was not
42 negligible, although this variable is often assumed to be approximately constant for all wood species.
43 Maximum moisture content and wood porosity can be estimated using bulk or apparent density as a
44 predictor variable.

45 **KEYWORDS**

46 hardwood; *Laurus nobilis*; physical property; wood technology.

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59 INTRA-SPECIES VARIATION IN MAXIMUM MOISTURE CONTENT, CELL- 60 WALL DENSITY AND POROSITY OF WOOD

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62 **1. Introduction**

63 Information about wood properties is useful for wood manufacturing and is essential for optimizing
64 the use of this raw material. However, some wood properties are not well described in the literature.
65 This applies to maximum moisture content, cell-wall density and porosity, which are not usually
66 included in wood species databases (e.g. Gutiérrez Oliva and Plaza Pulgar 1967; Glass and Zelinka
67 2010; Wagenführ and Wagenführ 2022).

68 The inter- and intra-tree variation in properties should also be analysed if the aim is to provide
69 foresters with guidelines or practical rules about the type of tree or the part of the tree that is
70 harvested to supply the transformation industry with raw wood material of a particular quality. The
71 inter- and intra-tree sources of variation have generally been studied for some indicator or proxy
72 wood variables, such as apparent wood density (Lachenbruch and McCulloh 2014). Analysis of
73 variables related to porosity, such as axial conduit widening in broadleaved plants is a topic of more
74 recent interest (Anfodillo et al. 2013).

75 *1.1. Maximum moisture content*

76 In wood, water occurs as bound water, in the cell walls, of hygroscopic nature, and as free or
77 capillary water, in the void spaces of wood (Prichananda 1966). The pores are filled with air when
78 the moisture content falls below the fibre saturation point (cell-wall saturation point) (Rosner et al.
79 2010), which usually ranges between 25 and 35 % (Gutiérrez Oliva and Plaza Pulgar 1967). The cell
80 lumina begin to fill when the moisture content rises above the fibre saturation point, and the
81 maximum moisture content is reached when the cell lumina are filled with water. Theoretically, full
82 saturation of all voids in the wood can be reached (Siau 1995).

83 Estimation of the maximum possible moisture content is useful in relation to impregnation of wood
84 with preservatives, for determining the maximum quantity of preservative that can be forced into a
85 piece of wood in terms of liquid retention (weight of liquid preservative per unit volume of water
86 saturated wood) and also for determining incomplete retention of the preservative as the
87 percentage of voids filled (Siau 1995). The maximum retention of liquid preservative can be
88 computed if the maximum moisture content, wood basic density and liquid preservative density are
89 known. The main interest in estimating maximum moisture content is related to the full-cell
90 impregnation process by immersion or autoclaving, with initial vacuum and further pressure (e.g.
91 Tripathi 2012).

92 Quantifying the maximum moisture content is potentially very useful for calculating the dose of
93 liquid preservative in laurel wood that protects against biotic decay agents, because laurel wood is
94 very sensitive to fungal infections, which cause intense darkening of the material (Pulgar Lorenzo
95 and Riesco Muñoz 2018).

96 The maximum moisture content can range from about 30 % to above 200 % (Glass and Zelinka 2010)
97 and is always higher than the moisture content of wood from newly felled trees, which is 80-90 % for
98 sapwood and 70-80 % for heartwood in European hardwoods (Fernández-Golfín Seco and Conde
99 García 2007). The maximum moisture content of the sapwood of Norway spruce has been reported
100 to be 169 % (Rosner et al. 2010).

101 1.2. Cell-wall density

102 Variation in cell-wall density and the influence on the apparent density of wood (bulk density,
103 including cell-walls and voids) are important in relation to manipulating wood to supply the
104 transformation industry with a more homogenous material, in terms of apparent density and related
105 properties. Controlling the sources of variation in cell-wall density is especially useful in wood in
106 which density and quality vary widely depending on genetic factors (Zobel and Van Buijtenen 1989;
107 Riesco Muñoz and Remacha Gete 2017).

108 Cell-wall density is expressed relative to the amount of wood material excluding the voids
109 represented by the cell lumina. However, cell-wall density can also be expressed relative to the
110 wood substance excluding microvoids within the walls of the cells or relative to the material which
111 includes microvoids not filled by water because their diameter is smaller than that of water
112 molecules. Estimation of cell-wall density and porosity therefore depends on the fluid used for the
113 displacement in testing methods, as a fraction of the total porosity is due to microvoids (Siau 1995).

114 It is commonly accepted that cell-wall density in the dry state is somewhat constant in a particular
115 type of wood, with little variability between tree species (Desch and Dinwoodie 1996; Usta 2003;
116 Lachenbruch and McCulloh 2014). Indeed, it has been reported that measuring the cell-wall oven-
117 dry density of wood by water displacement yields similar results for all wood species tested, with an
118 overall average of 1,560 kg m⁻³, a lower average of 1,400 kg m⁻³ for resinous wood tissues and a
119 higher average of 1,620 kg m⁻³ for very lignified woods (Kollmann 1951). The range is 1,500-1,550 kg
120 m⁻³ for Sitka spruce (*Picea sitchensis* (Bong.) Carr.) (Weatherwax and Tarkow 1968a, b), but
121 decreases to 1,497-1,517 kg m⁻³ in some hardwood species (Kellogg and Wangaard 1969). The
122 following mean values have also been reported: 1,200 kg m⁻³ (Peraza Sánchez 2001) and 1,343 kg m⁻³
123 for European oak (*Quercus robur* L.) (Riesco Muñoz and Remacha Gete 2017), 1,500 kg m⁻³ for all
124 timbers (Hearmon and Paton 1958; Freas 1995; Desch and Dinwoodie 1996; Frihart and Hunt 2010),
125 1,530 kg m⁻³ for wood substance (Smith 1954; Lachenbruch and McCulloh 2014), 1,533 kg m⁻³ for
126 white spruce (*Picea glauca* (Moench) Voss) (Stamm and Hansen 1937) and 1,540 kg m⁻³ (Glass and
127 Zelinka 2010). As cell-wall oven-dry density exhibits low variation, the large range in apparent oven-
128 dry density (e.g. Freas 1995; Desch and Dinwoodie 1996; Glass and Zelinka 2010) can mainly be
129 attributed to variations in wood porosity related to species, tree and position in the stem.

130 1.3. Porosity

131 Wood porosity or wood specific porosity (percentage of wood tissue occupied by pores) is an
132 anatomical variable influencing some types of industrial transformation of wood, such as
133 preservation, gluing and coating. A high degree of porosity makes wood more wettable, which can
134 facilitate impregnation of the wood by preservative or coating liquids; however, wettability can also
135 increase the probability of colonization by wood-decay fungi (Carol and Clausen 2010; Sadiku 2018).
136 In addition, porosity is decisive in gluing-related processes (wood surface sanding intensity, glue

137 dosage, bonding pressure, bonding temperature, etc.) and in the strength of the glued joints when
138 mechanical adherence is involved (Packham 1992).

139 Porosity is closely related to the surface roughness of wood, which is an important characteristic in
140 manufacturing settings in relation to e.g. sanding, finishing and adhesion (Bao et al. 2016). Surface
141 roughness strongly affects the texture, appearance and sensory perception of the wood surface,
142 with the subsequent impact on the user's experience in numerous end-use applications (furniture,
143 benches, tabletops, frames, floors, etc.) (Aydin et al. 2006; Coelho et al. 2008; Li et al. 2010).

144 Porosity is also related to the performance of the hydraulic and mechanical functions of wood
145 tissues in the tree (Lachenbruch and McCulloh 2014). Regarding the species under study, the traits
146 of the xylem influencing vulnerability to cavitation of trees belonging to the genus *Laurus* have
147 recently been studied (e.g. Rodríguez-Zaccaro et al. 2019).

148 Oven-dry wood porosity can be as low as 6 % for the heaviest woods and it can reach 93 % for the
149 lightest wood (Kollmann 1951). A value of 85 % porosity has recently been reported for *Paulownia*
150 sp., a light hardwood (Kozakiewicz et al. 2020). Differences in porosity may arise from differences in
151 the anatomy of the wood (abundance of different cell types, thickness of cell walls and size of cell
152 lumina) (Mitchell and Denne 1997; Usta 2003), which can be modified by the effect of extractives
153 (Polge 1966; Fries 1986).

154 1.4. Laurel wood

155 Information on wood maximum moisture content, cell-wall density and porosity is scarce, even
156 though these variables have important technological repercussions in wood processing. As far as
157 authors know, no information has been published on these physical variables in laurel wood, a
158 phylogenetically ancient hardwood exhibiting physical properties similar to softwoods (Pulgar
159 Lorenzo and Riesco Muñoz 2018). Laurel is a common tree species of the *Lauraceae* family that
160 grows in Spain and other Mediterranean countries, as a remnant of the subtropical evergreen
161 lauroid forests that covered the Mediterranean Region in the past, when the climate was more
162 humid (Rozas Ortiz et al. 2005). The increasing aridity of the laurel distribution area is related to the
163 high resistance of the xylem to formation of drought-induced embolisms, as a key adaptation of
164 laurel trees in response to seasonally dry environments (Maatallah et al. 2010; McAdam and
165 Cardoso 2019).

166 Laurel is an evergreen broadleaf tree that forms arboreal scrublands with forest structure (Ruiz de la
167 Torre 1979). It can reach up to 28 m in height (Rozas Ortiz et al. 2005) and has straight stems. The
168 wood has white-yellow sapwood and darker heartwood. The growth rings are visible to the naked
169 eye, and the wood tends to form semiporous rings (García Esteban and Guindeo Casasús 1989). The
170 density is moderately high and homogeneous along the stem. The wood is machinable, allowing a
171 decorative finish to be achieved. It is used to craft small marquetry objects and also for carving and
172 turnery (García Esteban and Guindeo Casasús 1990; Pulgar Lorenzo and Riesco Muñoz 2018).

173 The main objectives of the present study were to assess the maximum moisture content, cell-wall
174 oven-dry density and oven-dry wood porosity of laurel wood, as well as the inter- and intra-tree
175 variations in these variables, and also to determine the relationships between these and other
176 physical properties. The findings will help to provide values for the process variables in wood

177 manufacturing and will also aid decisions regarding how to manage this wood to reduce variations in
178 apparent density and thus produce a more homogeneous raw material in terms of density and other
179 properties related to quality.

180 **2. Material and methods**

181 Several properties related to density and dimensional stability of laurel wood in response to changes
182 in moisture content were evaluated in a previous study (Pulgar Lorenzo and Riesco Muñoz 2018).
183 The wood analysed in the earlier study consisted of a sample of 958 small, defect-free specimens
184 obtained from 17 young laurel trees (ranging from 24 to 41 years old, breast height diameter ranging
185 from 13.7 to 28.9 cm and total height ranging from 5.1 to 13.1 m), selected and felled for analysis, in
186 a stand located in Galicia (north-western Spain). Cross-sectional slices were obtained at the stem
187 base and at stem heights of 1, 2 and 3 m (when the stem diameter was large enough) in each felled
188 laurel. Slices were cut to a thickness of approximately 15 cm and were sawn to produce standard
189 prismatic specimens (Pulgar Lorenzo and Riesco Muñoz 2018). The methods used for representative
190 sampling, data acquisition and determination of physical properties, according to domestic and
191 international standards, were described in the aforementioned study. Methodological aspects
192 related to the number of sampled trees and gravimetric variable correct mensuration (Williamson
193 and Wiemann, 2010) and to sampling height in the tree (Anfodillo et al., 2013) were also considered.

194 In the present study, a subsample of 300 specimens obtained from the material analysed in the
195 previous study were immersed in water in an open tank, at laboratory temperature, for a period of
196 13 months. The temperature of the water was always 20 °C or slightly higher. The moisture content
197 of the water-saturated specimens was then determined as the difference in mass of the soaked and
198 oven-dried samples, and expressed as a percentage of the mass in the oven-dry state, according to
199 the EN 13183-1:2002 standard (CEN 2002). The value obtained was assumed to be the maximum
200 moisture content (*MM*), and full saturation of the lumens and cell-walls was assumed to have
201 occurred. The *MM* values, together with data from the previous study (density of water, volumetric
202 shrinkage of wood, apparent oven-dry density and fibre saturation point) (Pulgar Lorenzo and Riesco
203 Muñoz 2018), were used to calculate the cell-wall oven-dry density according to equation (1), in
204 which the following assumptions were made: that wet wood contains bound water dissolved or
205 adsorbed in the cell-wall and bound water therefore contributes to wood moisture content; that
206 cell-wall dimensions vary in response to changes in moisture content (cell-walls are subject to
207 shrinkage and swelling) (Siau 1995; Rosner et al. 2010); and that the density of bound water is the
208 same as the density of free water:

$$CWD = WD \frac{100 + VS}{WD \frac{100 + VS}{OD} - MM + FSP} \quad (1)$$

209

210 where

211 *CWD* is the cell-wall oven-dry density, in kilograms per cubic metre,

212 *WD* is the density of water in the voids of wood at laboratory temperature, in kilograms per cubic
213 metre,

214 *VS* is the volumetric shrinkage of wood, expressed as a percentage,

215 *OD* is the apparent oven-dry density, in kilograms per cubic metre,

216 *MM* is the maximum moisture content, expressed as a percentage,

217 *FSP* is the fibre saturation point, expressed as a percentage.

218 The cell-wall oven-dry density was used to compute oven-dry wood porosity (*P*), defined as the
219 percentage of void volume of oven-dry wood, according to equation (2):

220

$$P = 100 - 100 \frac{OD}{CWD} \quad (2)$$

221 The density of water was considered to be approximately 1,000 kg m⁻³ as compaction of bound
222 water is negligible (Siau 1995). Volumetric shrinkage, apparent oven-dry density and fibre saturation
223 point, which are required to compute the variables in equations (1) and (2), were obtained from the
224 previous study for each of the 300 tested specimens (Pulgar Lorenzo and Riesco Muñoz 2018). The
225 volumetric shrinkage was obtained from water saturation to dry state, as a percentage of dry
226 volume. The apparent oven-dry density was obtained as the ratio between the mass and volume of
227 the specimen in the dry state. Ring width, basic density and air-dry density (adjusted to a moisture
228 content of 12 %) were also obtained in the previous study and were included here to describe the
229 tested material in context, because of the value of density variables as tools for describing the plant
230 functionality (Williamson and Wiemann 2010), beyond the classical role of density as wood quality
231 index (e.g. Zobel and Van Buijtenen 1989; Glass and Zelinka 2010; Lachenbruch and McCulloh 2014).
232 Basic density is used as an “apparent density” estimator in this study, although it is not, *sensu stricto*,
233 a measure of wood density because its value (dry biomass in a unit volume of green wood) does not
234 represent any actual state of wood. It most closely corresponds to an ecological trait (Williamson
235 and Wiemann 2010).

236 The descriptive statistics of the physical properties were obtained after validating and refining the
237 test results. The wood properties assigned to the laurel wood were calculated as the arithmetic
238 mean values of all the valid data from the specimens obtained in the sampled trees, considering
239 specimens as sampling units, all of the same weight in the sample. Dispersion of the values the
240 properties analysed was quantified using the coefficient of variation (quotient of standard deviation
241 and mean, expressed as a percentage). The coefficient of variation represents an estimate of relative
242 dispersion and it is useful for comparing the scatter of different variables.

243 Exploratory analysis of the relationships between quantitative variables was conducted by graphical
244 inspection of the plotted pairs and examination of the Pearson’s or Spearman’s correlation
245 coefficients. The analyses were applied to the overall data and to each sub-sample of specimens
246 grouped by qualitative variables (namely tree and height in the stem). One-way analysis of variance
247 (ANOVA) was used to search for relationships between quantitative variables (namely maximum
248 moisture content, cell-wall density and oven-dry wood porosity) and qualitative variables (namely

249 tree and height in the stem). LSD post-hoc analysis was used to identify any significant differences
250 between means. The Kruskal-Wallis test, with pairwise multiple comparisons using Wilcoxon rank
251 sum test and p -value adjustment by Bonferroni's method, was applied when the assumptions for
252 ANOVA were not fulfilled.

253 Test results were considered statistically significant at $p < 0.05$ and highly significant at $p < 0.01$. All
254 statistical analyses were carried out using Microsoft Excel 2013 and IBM SPSS Statistics software
255 (version 25).

256 **3. Results and discussion**

257 *3.1. Basic descriptive statistics*

258 The main statistics of the physical properties under study are summarised in Table 1. Cell-wall oven-
259 dry density was nearly two times higher than the oven-dry density, as approximately half of wood
260 apparent volume (45 %) corresponded to pores. Cell-wall oven-dry density was lower than all of the
261 previously reported values mentioned in the Introduction. Maximum moisture content was much
262 higher than the fibre saturation point. This was expected because, in the water absorption process,
263 the saturation point of wood fibre is reached when the cell lumina are still free of water, while the
264 maximum moisture content is reached when the cell lumina are filled with water (Prichananda 1966;
265 Siau 1995).

266 **Table 1.**

267 Decay and the inherent loss of material from the vessel cell-walls and loss of parenchyma cells were
268 expected because of the long saturation time. It was therefore assumed that some of the natural
269 substances impregnating the wood were extracted and dissolved in water during the long period of
270 immersion of the specimens. The cell-wall density obtained was therefore that of partially extracted
271 wood (extraction of part of the water-soluble substances impregnating the wood). The value was
272 lower than the density of non-extracted cell walls, although removal of part of the extractive content
273 reduces the bulking effect of the low hygroscopicity of cell wall materials (Siau 1995). In addition, it
274 is possible that not all of the cell lumina were filled, despite the long immersion period. Some air
275 may remain in some of the cell voids, and therefore the moisture content determined would not be
276 the theoretical maximum. Rosner et al. (2010) concluded that "after refilling small air bubbles might
277 have been trapped in the conduits". Consequently, cell-wall density, computed by equation (1),
278 underestimates the real cell-wall density, and the wood porosity, computed by equation (2), also
279 underestimates the real value.

280 Moreover, as the specimens were oven dried in a previous test (Pulgar Lorenzo and Riesco Muñoz
281 2018), the maximum achievable moisture content of the wood would be lower due to the
282 modification of the hydrophilic behaviour of the wood surface. A study with fresh and pre-dried
283 Norway spruce sapwood revealed that only one cycle of wood dehydration, without a sequence of
284 repeated rounds of wetting-drying leading to hysteresis phenomena, increases the vulnerability of
285 hydraulic conduction and may modify the structure of the cell walls and the shrinkage behaviour
286 (Rosner et al., 2010). These possible changes influence the cell-wall density estimation with equation
287 (1), in which volumetric shrinkage is an input variable.

288 It is also possible that low molecular weight compounds were volatilized during the standardised
289 drying at 103 °C in the previous test (Pulgar Lorenzo and Riesco Muñoz 2018). Dry mass would be
290 therefore underestimated and maximum moisture content would be overestimated, partly
291 compensating for the effect described in the previous paragraph, although only a small amount of
292 mass is expected to be lost due to the drying process (Williamson and Wiemann 2010).

293 Finally, the equilibrium moisture content depends on the shape and size of the samples because the
294 moisture content is higher in thin sections than in larger specimens (Siau 1995). Underestimation of
295 maximum moisture content, cell-wall density and porosity is considered in the discussion, although
296 it did not influence analysis of the inter-tree and intra-tree variation in the variables under study.

297 As previously mentioned, the values of apparent air-dry density, basic density, volumetric shrinkage,
298 fibre saturation point and ring width were obtained for each of the specimens tested in a previous
299 study (Pulgar Lorenzo and Riesco Muñoz 2018). Regarding apparent air-dry density, the sampled
300 wood was homogeneous and moderately heavy according to the interpretation criteria in the UNE
301 56528:1978 standard (IRANOR 1978a) and the UNE 56540:1978 standard (IRANOR 1978b). The three
302 apparent density variables analysed (air-dry, oven-dry and basic density) were remarkably
303 homogeneous, as occurs in conifer wood, and less variable than is usual in hardwood species (e.g.
304 Wagenführ and Wagenführ 2022). The cell-wall density was also homogeneous, but it was expected
305 to be much more homogenous than the apparent density variables because it is not influenced by
306 the porosity as a source of variation. Wood moisture content is not a source of variation for any of
307 the four density variables under study.

308 Apparent density is calculated as the ratio between the mass (wood fibre matter and water) and the
309 volume of wood, considering the whole volume: volume of wood substance and volume of voids
310 (cell lumina and intercellular spaces), partly filled with water (Lachenbruch and McCulloh 2014). The
311 apparent density of wood therefore depends on the amounts of water, air and wood fibre matter,
312 together with the cell-wall density and the density of the water inside the wood. Analysis of oven-
313 dried wood (absence of water in cell-walls and lumina) is simpler because the apparent oven-dry
314 density only depends on the quantity of cell walls and the cell-wall oven-dry density.

315 The value of volumetric shrinkage was high according to the interpretation criterion in the UNE
316 56540:1978 standard (IRANOR 1978b), and the fibre saturation point was intermediate according to
317 the interpretation criterion proposed by Gutiérrez Oliva and Plaza Pulgar (1967).

318 The growth ring width was much more variable (range 2-10 mm) than the other quantitative
319 properties analysed (see coefficients of variation in Table 1). This can be attributed to the diversity of
320 dimension and ages of the trees included in the sample.

321 The relative error in the estimation of the means for all the analysed variables was below 5 %, the
322 upper threshold proposed in the UNE 56528:1978 standard (IRANOR 1978a). This finding was
323 attributed to the overall homogeneity of the variables, except for ring width. The sample size was
324 therefore sufficient to obtain accurate estimators for the means given the dispersion exhibited by
325 the variables.

326 *3.2. Relationships between wood properties*

327 Maximum moisture content, cell-wall oven-dry density and oven-dry wood porosity were not
328 normally distributed or even symmetrically distributed. Spearman's correlation coefficients were
329 therefore computed in order to quantify the relationships between the wood quantitative variables
330 under study (Table 2). The lack of high correlations for ring width and other wood properties at
331 stand-level scale may be partly explained by the high variation in ring width and the low variation in
332 maximum moisture content, density variables and porosity (Table 1). However, the correlations
333 were highly significant, probably due to the large amount of data considered.

334 **Table 2.**

335 The homogeneous density observed in the laurel wood is more usual for mature conifer wood, and
336 the negative correlations between growth ring width and density (Table 2) are also typical of conifer
337 wood (e.g. Kollmann 1951).

338 Maximum moisture content and porosity were highly significant and inversely related to oven-dry,
339 air-dry and basic density. The values of the Spearman's correlation coefficients were considered
340 suitable for modelling purposes, with basic density being a good predictor of maximum moisture
341 content, and air-dry density being a good predictor of porosity. Graphical analysis of the plotted
342 pairs of maximum moisture content versus basic density and oven-dry wood porosity versus air-dry
343 density (density at 12 % moisture content) revealed that a linear or linearizable function would be
344 suitable for describing the relationships between variables (Figure 1). A small number of specimens
345 exhibited lower porosity and maximum moisture content than expected considering the density and
346 the general trends observed in the rest of the data (Figure 1). This outlier group of specimens
347 corresponded to the base of a stem with the widest rings of the sample (mean ring width 7.9 mm,
348 compared to a mean ring width of 4.8 mm for the rest of the trees). Ring width and apparent density
349 were negatively related (Table 2) and an abnormal group of specimens -in relation to ring width-
350 were therefore also expected to be outliers for apparent density, being lighter but with intermediate
351 maximum moisture content and porosity.

352 **Figure 1.**

353 Considering the subsamples from each individual tree, the correlation coefficients for maximum
354 moisture content and basic density in each tree were higher than for the whole sample only in 9 of
355 the 17 trees, probably due to the smaller sample size per tree. Similarly, the correlation coefficients
356 for porosity and air-dry density were higher than the coefficients for the whole sample only in 6 of
357 the 17 trees. Development of individual-tree models was therefore not pursued, as the findings
358 were not encouraging.

359 Cell-wall density was obviously related to the apparent density variables analysed (oven-dry, air-dry
360 and basic density), but the correlation coefficients were not high enough to enable construction of
361 predictive models of cell-wall density including apparent densities as possible predictor variables.

362 *3.3. Inter-tree variation in the wood characteristics*

363 Analysis of variance was not conducted as maximum moisture content, cell-wall oven-dry density
364 and oven-dry wood porosity were not normally distributed. The Kruskal-Wallis test was therefore
365 used, with tree as a factor. The test revealed that each physical property of the laurel wood differed
366 significantly between trees (Table 3), as also reported for *Quercus robur* (Riesco Muñoz and

367 Remacha Gete 2017). The inter-tree variation was not attributable to genetic differences, because
368 the genetic diversity was not expected to be high in sampled trees that were close to each other in
369 the same stand. There was probably a reasonable degree of relatedness among individuals growing
370 next to each other in the same plot. In addition, environmental conditions were almost constant for
371 all sampled trees as there were no remarkable differences in site quality.

372 **Table 3.**

373 The inter-tree variation in wood characteristics may therefore be attributed to tree factors such as
374 age, dimensions (breast height diameter, total height, over bark volume, slenderness) and growth
375 rate. The correlation matrix for average per tree wood properties and dendrometric tree
376 characteristics (not included here) showed that the closest relationships were those related to age.
377 The highest values of the Pearson's correlation coefficient were as follows:

- 378 - $r = -0.56^*$ for cell-wall density and tree age
- 379 - $r = -0.50^*$ for oven-dry wood porosity and tree age.

380

381 As both relationships were negative, the cell-wall density and porosity values are expected be lower
382 in trees older than those in the study. However, this is a tentative prediction as only 17 pairs of
383 values (mean wood property and tree age) were used to compute the Pearson's correlation
384 coefficient. In fact, the Spearman's correlation coefficient was not significant for any of the variables
385 tested. The possible lower porosity in older trees is an important factor to be considered regarding
386 the industrial use of laurel wood.

387 The box plots of cell-wall density and porosity distributed by tree are presented in Figure 2 and
388 Figure 3. Graphical analysis of these and the post-hoc analysis by the Wilcoxon signed-rank test for
389 paired data with the Bonferroni's correction (not included here because of the large number of
390 differences of means analysed) showed that the cell walls were lightest in trees older than 35 years,
391 except for tree number 15. In addition, trees that differed significantly from the others in terms of
392 porosity (low) were those in which ring width was smallest (trees number 9 and 16). In fact, porosity
393 and ring width were positively related, as indicated in Table 2. As laurel is a hardwood with marked,
394 usually semiporous rings (García Esteban and Guindeo Casasús 1989; Pulgar Lorenzo and Riesco
395 Muñoz 2018), a higher proportion of earlywood was expected in thin rings. Therefore, the low
396 porosity in narrow rings found in this study led us to assume that the earlywood was less porous
397 than latewood, although this contradicts the more porous nature of earlywood tissues. It must be
398 assumed that the analysed hardwood tends towards the usual pattern of diffuse distribution of
399 vessels in the ring (Figure 4) and the spring band width of the growth ring, very variable in laurel
400 wood (García Esteban and Guindeo Casasús 1989), decreases in proportion as the ring width
401 decreases, as is common in conifer wood (Kollmann 1951).

402 **Figure 2.**

403 **Figure 3.**

404 **Figure 4.**

405 Xylem tissue is under pressure to adapt to biotic and abiotic challenges (Lachenbruch and McCulloh
406 2014), and lower density values at older cambial ages are theoretically expected due to competition

407 for resources over time (Zobel and Van Buijtenen 1989). The effect of competition on density was
408 not observed in the present study, probably due to the young age of the sampled trees, in which
409 competition responses were not yet reflected in the xylem.

410 The absence of significant correlations between apparent oven-dry density and age can be explained
411 by the combined effect of a decrease in cell-wall density (lighter matter) and a decrease in porosity
412 (more matter) leading to an almost constant oven-dry density in young and older trees.

413 The variation in apparent density is not only attributable to the balance between cell-wall density
414 and porosity, because density and other physical properties are also influenced by the relative
415 proportion of cell types. Lower wood density is explained by a smaller proportion of dense thick-
416 walled cells and a larger number of pores in diffuse porous species (Paul 1963). The presence of wide
417 vessels is more common in wetter sites and in trees relative to shrubs (Anfodillo et al. 2013). The
418 abundance of thin-walled vessels with a large lumen relative to thick-walled, small lumen fibres is
419 related to a smaller amount of cell wall material and lower density. In addition, the relative
420 abundance of parenchyma cells affects wood density because of their relatively thick walls and the
421 frequent presence of cross walls, due to the short length of this type of cell (Thomas 1991).

422 *3.4. Wood variation along the stem*

423 The intra-tree variation in the properties analysed was low but not negligible. The coefficient of
424 variation for maximum moisture content was 2 % for the most homogeneous trees and 11 % for the
425 most heterogeneous one, with the coefficients of variation of the 17 sampled trees averaging 5 %.
426 Regarding cell-wall density, the coefficient of variation was 2 % for the most homogeneous trees and
427 9 % for the most heterogeneous ones, with the coefficients of variation of the 17 sampled trees
428 averaging 4 %. Thus cell-wall density can be considered very homogeneous in the whole sample and
429 in each tree, but not almost constant, as reported in previous studies (some of which are mentioned
430 in the Introduction). Regarding the porosity, the coefficient of variation was 3 % for the most
431 homogeneous trees and 10 % for the most heterogeneous ones, with the coefficients of variation of
432 the 17 sampled trees averaging 6 %. The intra-tree coefficients of variation for both cell-wall density
433 and porosity were significantly higher in the older trees.

434 The height in the stem was the source of intra-tree variation used in this work. This was justified
435 because the expected pith-to-bark variation (Zobel and Van Buijtenen 1989; Williamson and
436 Wiemann 2010; Anfodillo et al. 2013) was a negligible source of intra-tree variation, as
437 demonstrated in a concurrent study of the authors with the same wood species (Pulgar Lorenzo and
438 Riesco Muñoz, unpublished). Variation in maximum moisture content, cell-wall density and porosity
439 along the stem was expected because the vascular network of the tree responds to the increase in
440 plant height (Anfodillo et al. 2013). Analysis of variance considering height in the stem as a factor
441 revealed that each of the physical properties of the laurel wood assessed varied significantly at
442 different positions along the stem (Table 3). This was also checked with the Kruskal-Wallis test,
443 although the variability in properties along the stem was rather small (Figure 5). In fact, the only
444 remarkable variation was that of the cell-wall density, with a decrease of 18 kg m^{-3} per m between
445 the root collar and a height of 3 m. The decrease in cell-wall density was accompanied by a decrease
446 in porosity. This acted as a compensatory mechanism to maintain the apparent density almost
447 constant along the stem: there was more matter (cell walls) per unit volume at higher positions in
448 the stem, but the matter was lighter. This is an example of the frequent mutual compensation

449 mechanism, in which the traits vary and the corresponding value of the property can remain
450 unchanged (Lachenbruch and McCulloh 2014). However, the variations in this case are of no
451 practical interest, and, from the point of view of harvesting, the wood maximum moisture content,
452 cell-wall density and porosity can be assumed to be constant along the first three metres of the
453 laurel stem. The trade-off mechanism stabilising the apparent density was the same used to explain
454 the uniformity of apparent density throughout the lifespan of the tree.

455 **Figure 5.**

456 The inter- and intra-tree variation in the properties analysed was similar to the variation in other
457 wood properties, apparently related to cambial age, although the cambial cell functionality depends
458 directly on the distance from the cambial cells to the tree apex, as highlighted by Anfodillo et al.
459 (2013). It was therefore expected that the variation in wood properties analysed in the study was
460 also apparently related to the young age of the cambial tissues.

461 **4. Conclusion**

462 Maximum moisture content, cell-wall density and porosity are expected to be lower and more
463 variable in older trees. Commercial exploitation of the complete trunk is recommended because
464 values of all three variables were only slightly lower at higher positions in the stem, although specific
465 harvesting of the basal log of young trees is advisable if more porous wood is required.

466 Porosity can be estimated by using air-dry density as a predictor variable. The variation in apparent
467 density of wood was mainly attributed to variations in porosity because cell-wall density was
468 homogeneous, although it was far from constant in the species. Further studies should examine
469 whether cell-wall density differs significantly between species.

470 From a methodological point of view, the sample size was sufficient to yield accurate estimators for
471 this type of hardwood.

472 **5. Declarations**

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675 **Figure captions**

676

677 **Figure 1** Scatter plot of oven-dry wood porosity and maximum moisture content against
678 density for the sample of laurel wood analysed. *RWm*: mean ring width.

679

680 **Figure 2** Box plot of the cell-wall oven-dry density of laurel wood in each tree. Boxes are
681 ordered by increasing age of the tree (scale not continuous). The trees are ordered by
682 increasing breast height diameter for individuals of the same age. The boxes corresponding
683 to the trees with the significantly lower cell-wall oven-dry density are highlighted.

684

685 **Figure 3** Box plot of the oven-dry wood porosity of laurel wood in each tree. Boxes are
686 ordered by increasing age of the tree (scale not continuous). The trees are ordered by
687 increasing breast height diameter for individuals of the same age. The boxes corresponding
688 to the trees with the significantly lower oven-dry wood porosity are highlighted.

689

690 **Figure 4** Planed and sanded cross-section of a laurel wood specimen (target dimensions 20 ×
691 20 mm), exhibiting the diffuse distribution of the larger vessels and axial parenchyma along
692 the radial direction of the visible rings. The end-grain surface was photographed in incident
693 light. Length of the reference bar: 25 mm. Photograph reproduced courtesy of M. Souto-
694 Herrero.

695

696 **Figure 5** Trends in the physical properties of laurel wood (cell-wall oven-dry density,
697 maximum moisture content, apparent oven-dry density and oven-dry wood porosity) at
698 different heights in the stem.

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705 **Table 1.** Descriptive statistics of assessed physical properties of laurel wood. $n = 300$ valid
 706 tests; CI = confidence interval for the mean at 95 %; CV (%) = coefficient of variation; e (%) =
 707 relative error in estimating the mean.

	mean	minimum	maximum	CI	CV (%)	e (%)
maximum moisture content (%)	114	90	146	112.6;114.8	9	0.5
cell-wall density (kg m^{-3})	1,198	942	1,360	1,189.8;1,205.5	6	0.3
oven-dry wood porosity (%)	45	33	55	44.6;45.5	8	0.5
oven-dry density (kg m^{-3})	657	542	772	651.6;662.0	7	0.4
air-dry density (kg m^{-3})	691	571	804	685.6;695.9	7	0.4
basic density (kg m^{-3})	560	470	640	555.9;563.3	6	1.9
volumetric shrinkage (%)	17.3	8.8	25.3	17.03;17.55	13	0.8
fibre saturation point (%)	33	20	53	32.2;33.1	13	0.7
ring width (mm)	5.0	1.8	9.9	4.73;5.18	40	2.3

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Table 2. Matrix of the Spearman's correlation coefficients (*r*) for the physical properties of laurel wood assessed. *n* = 300 valid tests; ** = significant at *p* > 99 %; n. s. = not significant.

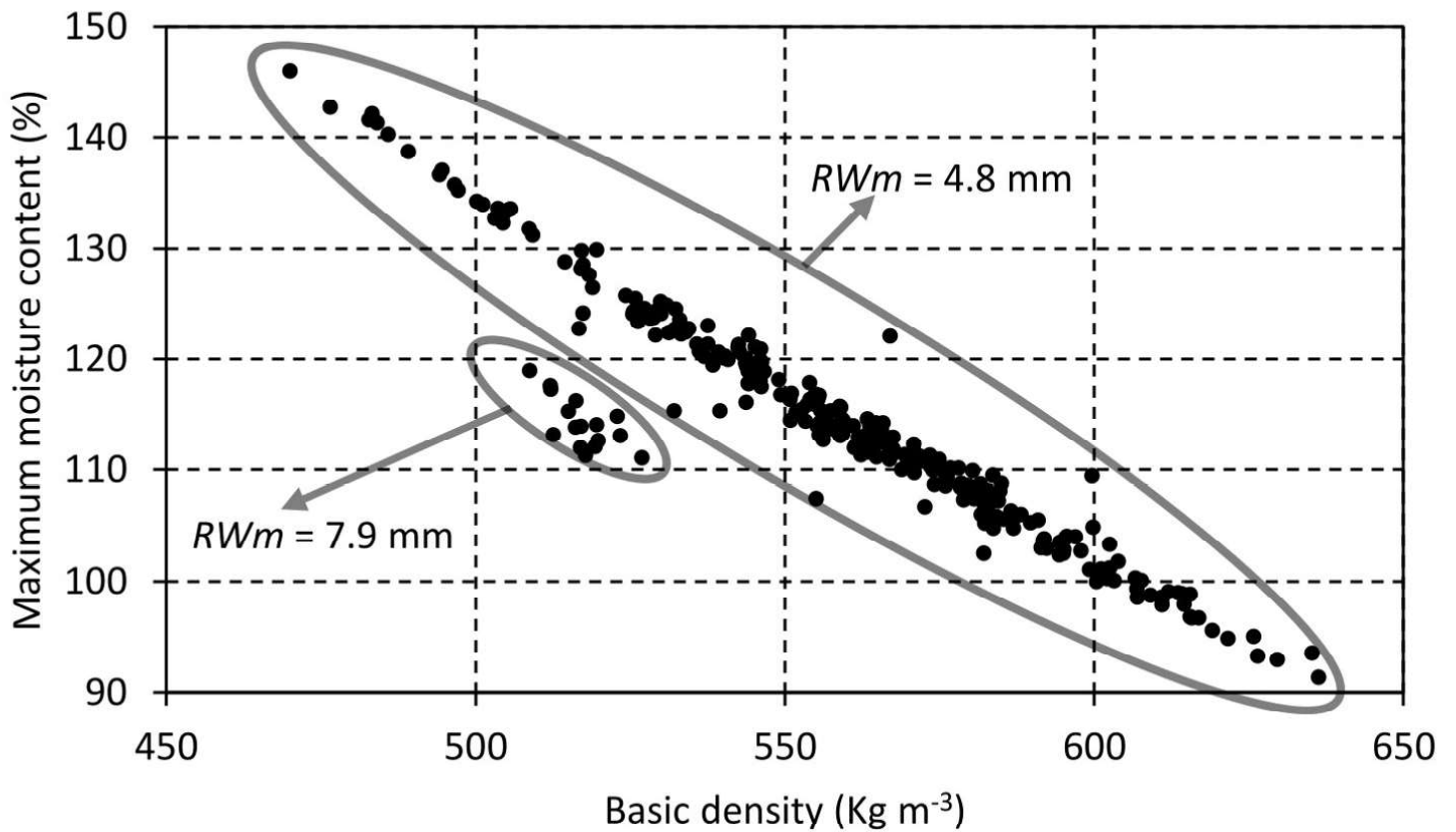
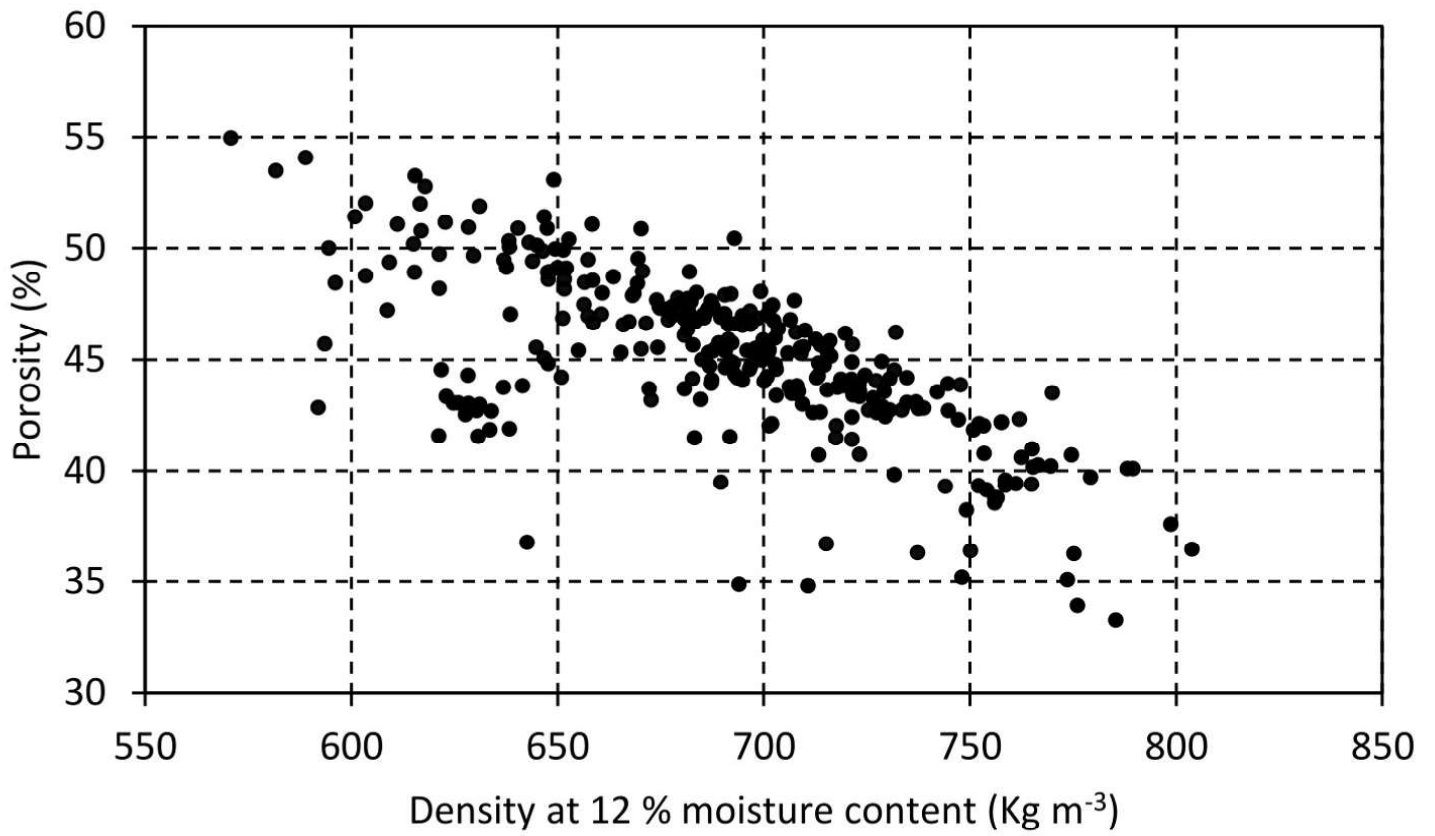
	<i>RW</i>	<i>OD</i>	<i>AD</i>	<i>BD</i>	<i>MM</i>	<i>CWD</i>	<i>P</i>
ring width (<i>RW</i>)	1.00						
oven-dry density (<i>OD</i>)	-0.30**	1.00					
air-dry density (<i>AD</i>)	-0.31**	0.99**	1.00				
basic density (<i>BD</i>)	-0.30**	0.96**	0.98**	1.00			
maximum moisture content (<i>MM</i>)	0.26**	-0.90**	-0.92**	-0.94**	1.00		
cell-wall oven-dry density (<i>CWD</i>)	n. s.	0.43**	0.33**	0.35**	-0.22**	1.00	
oven-dry wood porosity (<i>P</i>)	0.19**	-0.62**	-0.69**	-0.66**	0.78**	0.33**	1.00

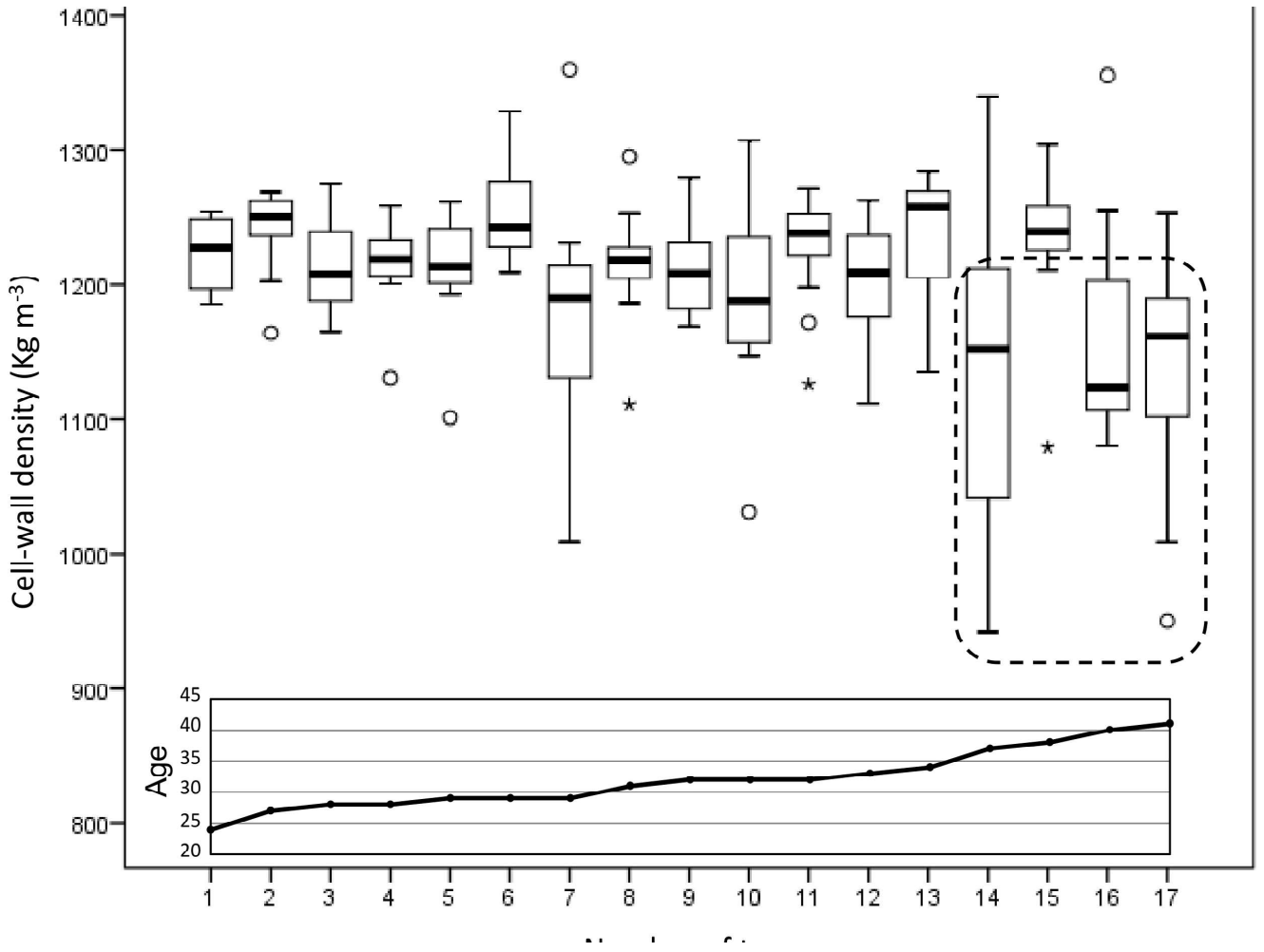
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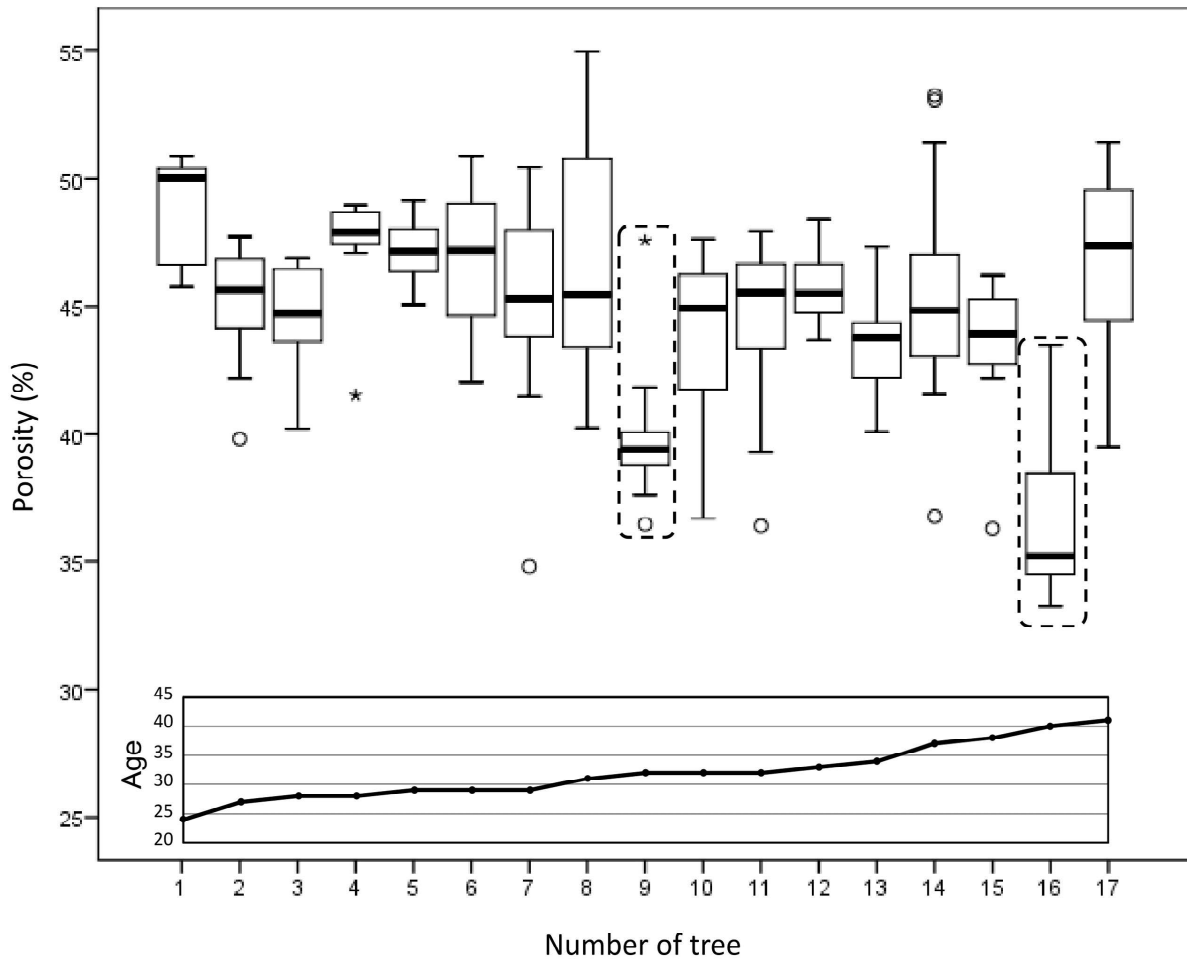
738 **Table 3.** Kruskal-Wallis Chi-squared statistic (K-W), degrees of freedom (df) and significance
 739 levels (p -values) in the Kruskal-Wallis group comparison for physical properties of laurel
 740 wood, considering the variables tree and height in the stem as factors.

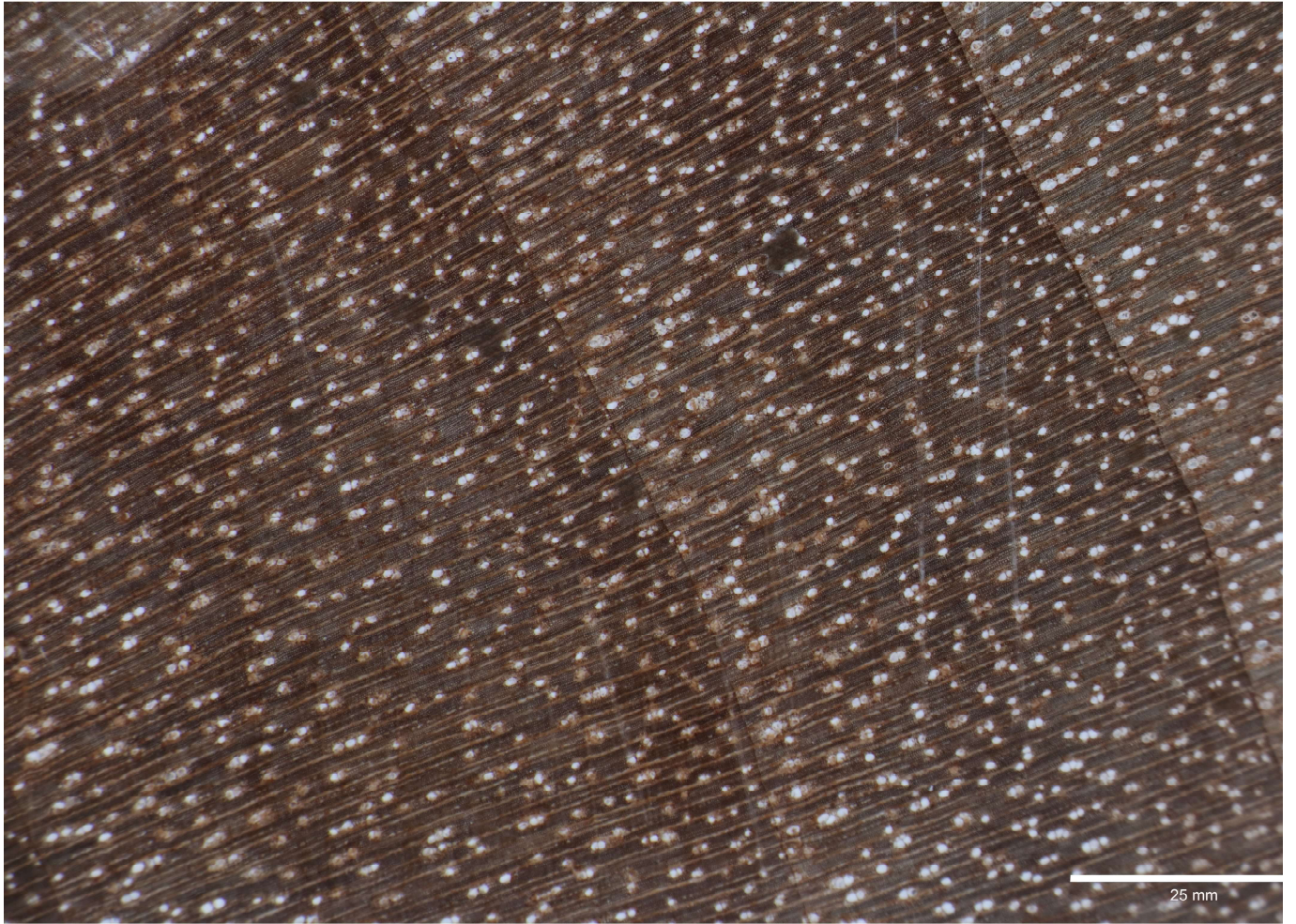
quantitative variable	tree factor			height in the stem factor		
	K-W	df	Sig.	K-W	df	Sig.
maximum moisture content (%)	151.960	16	< 0.01	28.633	3	< 0.01
cell-wall oven-dry density (kg m ⁻³)	91.683	16	< 0.01	13.583	3	< 0.01
oven-dry wood porosity (%)	88.727	16	< 0.01	40.091	3	< 0.01

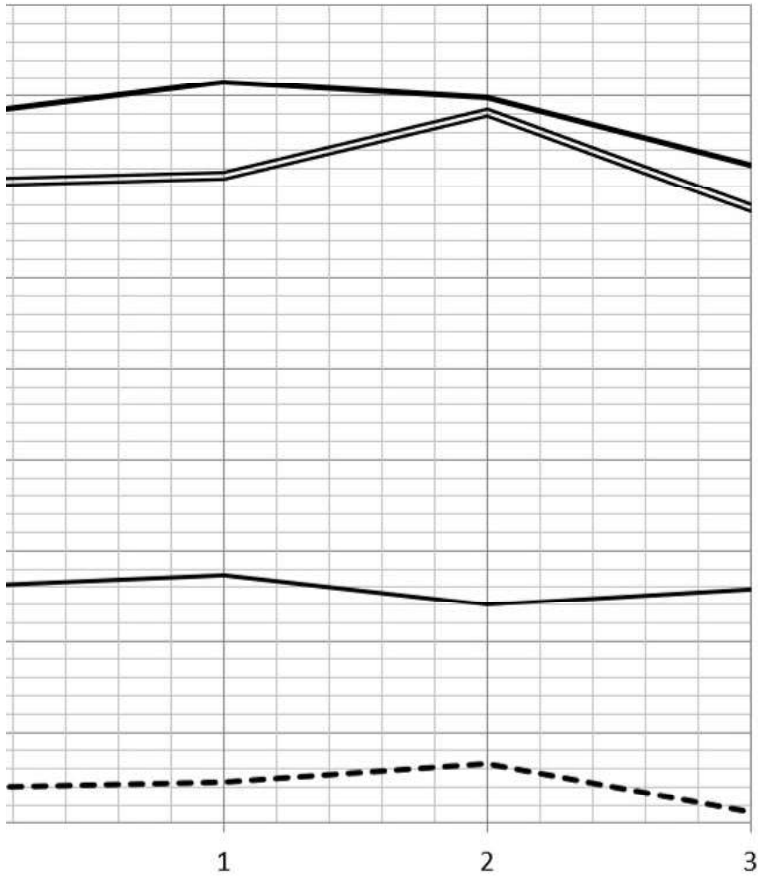
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- Mean cell-wall density (kg m⁻³)
- == Mean of maximum moisture conte
- Mean oven-dry density (kg m⁻³)
- - - Mean porosity (% x10)

Height in the stem (m)